Modélisation du rôle du biofilm dans le fonctionnement du réseau trophique de la vasière de Brouage (Bassin de Marennes-Oléron) : influence sur les flux de carbone et conséquences sur la stabilité

Blanche Saint-Béat

THESE DE DOCTORAT DE L'UNIVERSITE DE LA ROCHELLE

Spécialité

OCEANOLOGIE BIOLOGIQUE ET ENVIRONNEMENT MARIN

Présentée par

Blanche SAINT-BEAT

Pour obtenir le grade de

DOCTEUR de l'UNIVERSITE de LA ROCHELLE

Modélisation du rôle du biofilm dans le fonctionnement du réseau trophique de la vasière de Brouage (Bassin de Marennes-Oléron) : influence sur les flux de carbone et conséquences sur la stabilité

Soutenue le 11 décembre 2012

Devant le jury composé de :

L. LEGENDRE, Professeur, Univ. de Paris VI	*Rapporteur*
J.C. MARQUES, Professeur, Univ. de Coimbra, Portugal	*Rapporteur*
N. NIQUIL, D. R. CNRS, UMR BOREA, Caen	*Directrice de Thèse*
A. VEZINA, Directeur Régional de Pêches et Océans Canada	*Co-responsable scientifique*
P. RICHARD, D. R. CNRS, UMR LIENSs, La Rochelle	*Examinateur*
C. DUPUY, Professeur, Univ. de La Rochelle	*Examinateur*
G. LACROIX, C. R. 1 CNRS, UMR BioEMCo, Paris	*Examinateur*

Thèse réalisée au sein de l'UMR 7266 Littoral, Environnement et Sociétés (LIENSs)

Université de la Rochelle-CNRS, UMR 7266, Littoral Environnement et Sociétés (LIENSs)
2 rue Olympe de Gouges
17000 La Rochelle, France

Remerciements

Je remercie tout d'abord Louis Legendre, Joao Carlos Marques, Gérard Lacroix, Christine Dupuy et Pierre Richard d'avoir accepté de participer à l'évaluation de ce travail de thèse.

J'ai vécu ces trois ans comme une aventure exceptionnelle malgré les moments difficiles. Je retiendrai d'un point de vue professionnel, l'apprentissage de la rigueur et de la communication écrite et orale, éléments indispensables pour pouvoir voler de mes propres ailes. D'un point de vue plus personnel, ces trois ans sont marqués par une belle aventure humaine. J'ai eu l'occasion de rencontrer des gens de différents horizons, qui m'ont tous beaucoup apportés et aidé à évoluer. Cette aventure est avant tout due à deux personnes ; Nathalie Niquil et Alain Vézina qui m'ont donné la chance de réaliser cette thèse. Merci de m'avoir fait confiance pour mener ce projet à bien. De plus, leur encadrement très complémentaire m'a permis de réaliser cette thèse dans le temps imparti. Merci à Alain pour ces conseils très pertinents et son œil avisé. Merci à Nathalie de m'avoir laissé réaliser mes propres choix quant à l'orientation de ce travail de thèse. Et merci à tous les deux pour les discussions scientifiques acharnées.

Merci à Sylvain Lamare et Pierre Richard directeurs successif de l'UMR LIENSs, laboratoire d'accueil pour cette thèse, ainsi que Christine Dupuy chef de l'équipe DYFEA pour leur soutien.

Au cours de cette thèse, j'ai dû discuter avec de nombreux chercheurs experts dans des domaines très variés participant à l'ANR VASIREMI, merci à eux pour leur patience et leur réponse à mes questions parfois naïves. Parmi elles un grand merci à Christine Dupuy, qui m'a guidé et soutenue en tant que chef du projet VASIREMI.

Merci à Harald et Ragnhild Asmus qui m'ont accueillie très chaleureusement à Sylt (Allemagne). La collaboration avec eux s'est avérée très instructive, agréable et bénéfique. Je les remercie également de s'être déplacés pour mon premier comité de thèse.

Merci à Alain Vézina de m'avoir accueillie durant deux mois à l'Institut d'Océanographie de Bedford, malgré son agenda très chargé. Cette expérience de deux mois au Canada a été très bénéfique pour moi que ce soit d'un point de vue professionnel, grâce aux échanges avec Alain, et d'un point de vue personnel par la découverte d'un autre laboratoire et de son

organisation. Merci également pour son déplacement en France afin d'assister à mon premier comité de thèse à Paris.

Je souhaite également remercier Cédric Bacher, Katell Guizien, Francis Orvain et Sébastien Lefebvre et Christine Dupuy pour leur participation à mes comités de thèse. Leurs conseils avisés ont été d'une grande aide. Merci pour leur écoute et leur soutien.

Un projet amorcé pendant ma thèse, qui me tient particulièrement à cœur, n'aurait pu être possible sans la collaboration de Xavier Bertin et la participation de deux stagiaires : Camille Geimer et Samuel Le Pajolec, merci beaucoup pour leur enthousiasme à participer à ce projet.

De manière générale, je tiens à remercier tous les gens du laboratoire LIENSs pour leur bonne humeur. Il a été très important pour moi de me sentir bien sur mon lieu de travail et de me faire une place au sein des chercheurs. Leur intérêt lors de la dernière ligne droite a également été essentiel pour moi puisqu'il est toujours agréable de se sentir soutenu.

J'adresse un grand merci à mes deux « mamans adoptives », Armelle Combaud et Marie Chivaille qui ont toujours été présentes et prêtes à m'aider. Grâce à Armelle j'ai eu la chance de participer à beaucoup d'événements de vulgarisation qui ont été essentiels pour moi dans l'amélioration de ma communication orale.

Merci à Géraldine d'avoir répondu à mes appels de détresse et d'avoir accepté de passer des journées entières à la relecture de certains de mes papiers.

Une pensée toute particulière va à mes colocataires du bureau 150. Tout a commencé en Octobre 2009 lorsque je suis arrivée avec quelques appréhensions au bureau 150. Pascaline, qui quelques mois plus tôt m'avait conseillé de ne pas signer mon contrat doctoral et de m'enfuir en courant, et Fred, célèbre bougon de l'URM m'y attendaient. Une fois habitués aux us et coutumes du bureau 150 je m'y suis sentie comme chez moi. J'y ai passé d'excellents moments et c'est avec beaucoup de regret et de tristesse que je les ai vus quitter le nid. Jonathan et Benoît M. accompagné de Gorgio, son vers solitaire, les ont remplacés. Malheureusement pour eux, ils ont subis mes sauts d'humeur inhérents à la dernière année de thèse. Merci à eux pour leur patience et les bouffées d'oxygène qu'ils m'ont apportés. Un merci tout particulier à Benoît M. qui m'a aidé dans la dernière ligne droite et qui a su rester stoïque face à un ordinateur possédé !

Ces trois ans de thèse n'auraient sûrement pas été vécus de la même façon sans mes compagnons d'aventure, je pense évidemment aux autres doctorants du laboratoire. Nous avons partagé d'excellents moments ensemble à rigoler et à décompresser, mais cette entente a été plus loin. Il y a une véritable entre-aide, dès qu'un d'entre nous n'est pas bien ou a des soucis, les autres sont là pour aider ou du moins pour un soutien psychologique. Travailler dans cette ambiance et savoir que quoi qu'il arrive il y aura quelqu'un pour me soutenir à été pour moi essentiel. C'est donc avec un grand plaisir que je remercie tous les doctorants : Alex, Seb, Richard, Julien, Paula, Tiphaine, Méra, Luc, Céline, les anciens : Fred, Pascaline, Gwenn, Camille P., Camille L., Thomas G., Benoît L. pour leurs conseils et les nouveaux, Alice, Aurélie et Thomas pour leur fraîcheur. Je tiens à remercier plus personnellement : Julie notre madame malchance, qui m'a toujours impressionné par sa joie de vivre et sa ténacité. Merci d'avoir contribué à ma bonne humeur par ton rire et ta « positive attitude », Joana présente depuis le début, avec qui nous avons partagé de nombreux fous-rires et de nombreuses pauses thé à refaire le monde, à fantasmer sur notre avenir. Merci pour ta joie de vivre et ton exubérance. Et enfin Florence, qui témoin de moments difficiles a su m'épauler. Merci également pour tes nombreux « sauvetage Matlab ». J'espère être à la hauteur pour toi l'année prochaine…

Merci également à Stéphanie et à Marion qui sont parties beaucoup trop tôt vers des contrées lointaines. Nos soirées filles et votre enthousiasme me manquent terriblement !

Et pour finir, cette thèse n'aurait pu être possible sans le soutien sans faille de Johann. Merci d'avoir su trouver les mots pour me rassurer et d'avoir cru en moi jusqu'au bout…

Avant-propos

Ce travail de thèse reposait sur trois parties a priori bien distinctes : une partie méthodologique, une partie sur modélisation du réseau trophique de la vasière de Brouage, et une partie sur l'étude de la théorie de la stabilité des écosystèmes. Cependant, les première et deuxième parties ne pouvaient pas être réalisées de manière indépendante puisque la modélisation du réseau trophique de la vasière de Brouage nécessite des résultats obtenus dans la première partie. La dernière partie sur la stabilité a été réalisée en parallèle des deux autres, mais la discussion sur la stabilité du réseau trophique de Brouage ne pouvait se faire qu'une fois les résultats de la modélisation obtenus. L'architecture particulière de cette thèse a engendré un effet domino inévitable : les problèmes rencontrés sur une partie ont généré des conséquences sur toutes les autres ; aucune partie de ce travail ne pouvait compenser les lacunes éventuelles d'une autre. C'est la principale raison pour laquelle mon travail de thèse ne s'est pas déroulé comme prévu initialement.

Avec le recul, les problèmes liés à la méthodologie ont été soulevés dès mon stage de Master 2 que j'ai réalisé sur le sujet. Afin d'essayer de comprendre et de cerner les problèmes rencontrés, j'ai débuté sur des modèles de réseaux trophiques réduits. Les problèmes ont persisté lors de ma première année de thèse puisque les résultats obtenus n'avaient aucun sens et étaient loin de toute réalité écologique observée sur le terrain. Lors de mon premier comité de thèse (Mars 2010), la discussion autour des problèmes méthodologiques a conclu à un problème lié à l'algorithme de la méthode lui-même. En effet, l'algorithme (développé sous MATLAB) que j'avais en ma possession était un hybride de deux méthodes. La résolution de ces problèmes nécessitait l'intervention d'Alain Vézina, auteur de l'algorithme, d'où mon séjour de deux mois (été 2010) à Halifax en Nouvelle-Ecosse (Canada). Cette collaboration a été très bénéfique : les problèmes d'algorithme ont enfin été résolus. J'ai pu alors m'attaquer à la réalisation des modèles pour la partie méthodologique. Ce travail a été long et fastidieux. Les résultats définitifs pour la partie méthodologie n'ont été obtenus qu'en juin 2012. Une soumission de ce travail a pu être réalisée les 23 Septembre 2012.

En parallèle, j'ai réalisé une large étude bibliographie sur la stabilité et la maturité des écosystèmes sous la forme d'un article de review. Bien que complexe, ce sujet m'a réellement passionnée. L'écologie théorique n'est pas facile de prime abord car la littérature qui en est

issue est très diversifiée et contradictoire. Il n'a pas toujours été évident de comprendre les concepts, les théories, de faire les liens entres eux et enfin de les synthétiser de la manière la plus simple et compréhensible possible. Pour un premier papier, les difficultés étaient multiples, et avec le recul ça n'était peut-être pas la meilleure façon de commencer cette thèse. Cet article de review était prévu à l'origine pour un numéro spécial d'Estuarine Coastal Shelf Science ; il devait constituer l'introduction générale aux notions retrouvées ultérieurement dans les articles de recherche du numéro. Malheureusement, les articles visés par la review n'ont pas pu être réalisés, celle-ci ne correspondant plus au sujet du numéro spécial, elle n'y avait plus sa place. Après un gros travail de fond, une seconde soumission à Ecology Letters, n'a pas remporté le succès espéré. Après amélioration de la forme, cette review a été soumise à Ecological Indicators.

La deuxième partie de mon travail consistait à modéliser le réseau trophique de la vasière de Brouage, il a été réalisé en dernier. Là encore je me suis heurtée à quelques contraintes. Les modèles réalisés reposent sur des données issues de l'ANR blanche « Rôle trophique des biofilms microbiens dans les vasières intertidales» (VASIREMI) qui s'est déroulée entre 2007 et 2011. Ma thèse commençant en octobre 2009, j'ai débuté au milieu du programme de recherche. Les campagnes de prélèvements/mesures sur le terrain ayant été réalisées en février et juillet 2008, peu de résultats étaient disponibles à mon arrivée. Une grande partie des données finalisées a été récoltée entre ma première et deuxième année de thèse. Ce travail de récolte, qui peut paraître anodin, a au contraire été relativement compliqué et il a nécessité beaucoup de patience, de persévérance et de diplomatie. Cette étape s'est cependant accompagnée de discussions très enrichissantes avec mes collègues sur la manière dont ils perçoivent le rôle et l'importance de leur sujet d'étude au sein du réseau trophique côtier. L'intégration des données aux modèles a ensuite nécessité une bonne connaissance des différents objets d'étude, une compréhension suffisamment fine des prélèvements/mesures/ analyses/expérimentations réalisées (incluant les modes méthodologiques) afin d'être sûre de leur bonne traduction en flux de matière et d'énergie. Il a été parfois difficile de comprendre la logique et le raisonnement scientifique qui ont mené aux résultats obtenus, surtout dans des domaines très diversifiés et hors de mon champ de compétences, que j'ai progressivement dû appréhender.

Au cours de cette thèse, j'ai eu l'occasion de travailler un mois en Allemagne afin de travailler en collaboration avec le couple Asmus. Les données utilisées dans le troisième chapitre de thèse décrivent la baie Sylt- Rømø, située dans le nord de l'Allemagne. Harald et Ragnhild Asmus étudiés cet écosystème depuis de nombreuses années et ont largement contribué à l'obtention des données utilisées pendant ma thèse. Ce travail en collaboration avec eux m'a permis de profiter de leurs connaissances du milieu et de leur expertise afin de construire le modèle de la baie de Sylt- Rømø.

En parallèle de ce travail de thèse, j'ai participé à l'élaboration de trois publications (voir les Annexes). Ma contribution à ces papiers n'a pas été du même ordre. Pour le premier, Niquil et al. 2011, j'ai réalisé la review bibliographique sur l'analyse inverse. Ma contribution au deuxième papier (Grami et al., 2011) était plus méthodologique : j'ai aidé à la mise en place du modèle du réseau trophique du lac Pavin. Enfin, dans le dernier papier (Tortajada et al., 2012) j'ai contribué à la discussion sur les indices ENA et sur l'évaluation de la stabilité qui leurs sont associée.

De manière plus personnelle, cette thèse et ses nombreux aléas m'ont permis de développer et d'acquérir des connaissances et des compétences variées et inattendues. J'ai dû faire preuve d'efficacité, de rapidité, d'adaptabilité et d'autonomie. J'ai appris à avoir une vision globale des écosystèmes, à transposer des données spécifiques à un objet d'étude, à une réalité écosystémique. J'ai dû développer mes connaissances sur les différentes espèces présentes dans l'écosystème considéré ainsi que sur les processus à travers la lecture de la littérature associée et les discussions avec des experts du domaine. Ceci à inévitablement développé mon aptitude au travail en équipe et mon intérêt pour la compréhension des organismes, des virus aux oiseaux en passant par tous les compartiments vivants et non-vivants du réseau trophique. D'un point de vue plus technique, j'ai développé mes capacités à la programmation sur MATLAB et j'ai acquis une compréhension fine de la méthode de reconstruction des réseaux trophiques. D'un point de vue théorique, j'ai compris les lois thermodynamiques régissant les écosystèmes et j'ai pu me faire ma propre opinion sur la notion de stabilité des écosystèmes par le décorticage des théories et des concepts associés.
Cependant, la plus grande leçon de cette thèse est humaine : malgré les embûches, le travail, la persévérance, l'obstination dans la recherche de la perfection, conduisent à l'aboutissement. Néanmoins, ce travail n'a ni la prétention d'être parfait, encore moins d'être une référence en

la matière. Il correspond à une synthèse de données dont l'interprétation reste personnelle. Comme pour tout modèle, des choix doivent être réalisés afin de trouver le bon équilibre entre la simplification et la réalité écologique. Ces choix se sont basés sur une approche scientifique la plus objective possible ; au moment où je les ai fait, ils me paraissaient les plus justes. J'ai cependant conscience qu'ils sont fortement dépendants de l'expérience. Mes choix et mes modèles restent donc discutables car inféodés à ma vision, mon ressenti et mon expérience.

Pour conclure, j'ai la conviction que même pour un écosystème donné, il existe autant de modèles que de modélisateurs.

Table des matières

Liste des figures

CHAPITRE 1

CHAPITRE 2

CHAPITRE 3

CHAPITRE 4

CHAPITRE 5

CHAPITRE 6

Liste des tableaux

CHAPITRE 2

CHAPITRE 3

CHAPITRE 4

CHAPITRE 5

Liste des abréviations

AMI: Average Mutual Information
APL: Average path Length
ASC: Ascendency
BCB: Benthic bacteria
BCP: Pelagic bacteria
BDC: Benthic dissolved carbon
BDF: Benthic deposit-feeders
BFI: Benthic fishes
BGE: Bacterial Growth Efficiency
BGR: Benthic grazers
BMR: Basal Metabolic Rate
BOM: Benthic omnivorous
BPC: Benthic particulate carbon
CAR: Carnivorous species
CBR: Carnivorous birds
CCI: Comprehensive Cycling Index
CIL: Ciliates
DC: Development Capacity
DC_i: Internal Development Capacity
DEP: Deposit feeders
DOC: Dissolved Organic Carbon
ENA: Ecological Network Analysis
EPS: Exopolysaccharides
FAS: Factorial metabolic scope
FCI: Finn Cycling Index
GFI: Grazing fishes
GPP: Gross Primary Production
HBR: Herbivorous birds
HNF: Heterotrophic nanoflagellates
LS: Least square
MC-LIM: Monte Carlo-Linear Inverse Modelling
MCMC-LIM: Monte Carlo Markov Chain-Linear Inverse Modelling
MCP: Macrophytes
MES: Mesozooplankton
MFB: Meiofauna
MMR: Maximal metabolic rate
MPB: Microphytobenthos
NEM: Nematodes
OMN: Omnivorous species
PDC: Pelagic dissolved carbon
PHY: Phytoplankton
POM: Matière Organique Particulaire
PPC: Pelagic particulate carbon
RMS: Root Mean Square
SEC: Sediment carbon
SMR: Standard metabolism rate
SOI: System Omnivory Index
SOM: Matière Organique du Sédiment
SUC: Suspended carbon
SUF: Facultative suspension feeders
SUS: Suspension feeders
TST: Total System Troughput
VRB: Benthic viruses
VRP: Pelagic viruses

Chapitre 1

Introduction générale

Contexte

Les écosystèmes sont soumis à des activités anthropiques croissantes (Millennium Ecosystem Assessment, 2005) qui ont un effet néfaste sur leur fonctionnement et leur durabilité. L'un des grands challenges actuels pour l'écologue est de comprendre pourquoi les écosystèmes sont plus ou moins résistants aux pressions humaines directes (exploitation accrue des ressources naturelles) comme indirectes (pollution, réchauffement climatique, etc.). Depuis plusieurs décennies, de nombreuses études sur la stabilité des écosystèmes ont vu le jour. Un écosystème est considéré comme stable lorsqu'il a la capacité de maintenir son état à travers le temps quel que soit les perturbations subies. Ces études se sont d'abord intéressées à l'impact de la diversité sur la stabilité des écosystèmes par des approches expérimentales (e.g. McNaughton, 1977; Pimm, 1991; Naeem and Li, 1997). Les résultats de ces études, souvent très contradictoires, ont prouvé l'importance de paramètres autre que la diversité pour conclure sur la stabilité des écosystèmes. Les chercheurs se sont alors tournés vers les liens entre les espèces, et notamment les liens trophiques, jusqu'à étudier les propriétés d'organisation et de fonctionnement des réseaux trophiques en lien avec la stabilité associée des écosystèmes (McCann et al., 1998; Dunne et al., 2002, 2004; Rooney et al., 2006).

Les réseaux trophiques correspondent à des schémas des flux d'énergie et de matière entre les organismes lorsqu'ils sont consommés ou consomment d'autres organismes (Pimm, 1984). Les relations trophiques entre les espèces donnent une vision holistique du système puisque les communautés s'organisent principalement en fonction de leur alimentation (Elton, 1927). Les écosystèmes, selon l'architecture de leur réseau trophique, sont plus au moins stables, certaines architectures apportant de la stabilité et d'autres pas (Link et al., 2005). Il est donc important de comprendre quelles architectures des réseaux trophiques apportent aux écosystèmes une résistance face aux perturbations anthropiques auxquelles ils peuvent être soumis.

Comme de nombreux écosystèmes littoraux, les pertuis charentais, et plus particulièrement la baie de Marennes-Oléron, sont soumis à des activités anthropiques variées. En effet, ce bassin est connu pour sa forte activité conchylicole (mytiliculture et ostréiculture). Le bassin de Marennes-Oléron est le premier bassin Ostréicole de France avec une production qui atteint

45000 à 60000 tonnes d'huitres par an (Soletchnik et al., 1999). Le bassin de Marennes-Oléron est encadré par deux estuaires (celui de la Charente au nord et celui de la Seudre au sud) et peut également être soumis à la pollution déversée par ces deux fleuves. Cette baie est également très fréquentée par les touristes tout au long de l'année avec 35 millions de nuitées comptabilisées en 2009 (1 nuitées = une nuit et une personne) et un pic en de fréquentation en Août (Conseil Général). Tous ces éléments sont susceptibles de perturber les différents écosystèmes composant le bassin de Marennes-Oléron.

La vasière de Brouage qui constitue à elle seule 30% de la zone découvrante du bassin de Marennes-Oléron (Leguerrier et al., 2004) en est un site d'étude privilégié. Ce site a fait l'objet de nombreuses études depuis le milieu des années 1990. La production primaire de la vasière de Brouage, qui est une vasière nue, est principalement assurée par un biofilm constitué de micro-algues benthiques, appelées microphytobenthos, et de procaryotes. Tout d'abord, la dominance de la communauté des diatomées au sein du microphytobenthos a été démontrée ainsi que des variations annuelles de sa biomasse (Cariou-Le Gall and Blanchard, 1995). De manière plus fine, la structure et la composition taxonomique de la population de diatomées a été analysée et a mis en avant des variations annuelles de cet assemblage qui est caractérisé par des comportements physiologiques différents (Haubois et al., 2005b). La production photosynthétique du microphytobenthos a pu être quantifiée et reliée à des facteurs environnementaux tels que la température et le cycle tidal (Blanchard et al., 1997; Guarini et al., 2000b). Des exopolysaccharides (EPS) de deux fractions différentes (les EPS dit 'bound', liés aux diatomées, et les EPS colloïdaux qui sont libres) sont plus ou moins sécrétés par les diatomées en fonction de leur production (Orvain et al., 2003a). Ces deux sortes d'EPS sont liées à des activités métabolique différentes qui restent encore à définir (Orvain et al., 2003a). Les diatomées benthiques sont de forme pennée (Round et al., 1990) et de nombreuses espèces (dites épipéliques) ont la capacité de se déplacer verticalement au sein des sédiments (Underwood and Paterson, 2003). Herlory et al.(2004) ont étudié ce phénomène sur le site de la vasière de Brouage et ont montré que la migration des diatomées est régulée par le cycle tidal et nycthéméral. Ainsi les diatomées s'accumulent à la surface du sédiment à basse mer afin de réaliser la photosynthèse, puis migrent en profondeur du sédiment lors de l'immersion et/ou la nuit (Herlory et al., 2004). Les recherches ultérieures se sont penchées sur le devenir de la production microphytobenthique à travers 1) des processus biologiques ; i.e. intégration au réseau trophique benthique, ou 2) des processus physiques ; i.e. remise en suspension dans

la colonne d'eau à marée haute. Le microphytobenthos, intègre le réseau trophique benthique via la méiofaune (Montagna et al., 1995; Rzeznik-Orignac and Fichet, 2012) et les déposivores (principalement *Hydrobia Ulvae* [1] (Haubois et al., 2005a)) qui l'ingèrent directement. La dynamique des populations de brouteurs de microphytobenthos, hydrobies (Haubois et al., 2002; Haubois et al., 2004) et nématodes (Rzeznik-Orignac et al., 2003) a été bien décrite. La pression de broutage sur le microphytobenthos a été estimée pour ces deux espèces de brouteurs (Haubois et al., 2005a; Rzeznik-Orignac and Fichet, 2012). Le broutage des hydrobies ne parait pas être influencé par la taille des diatomées mais est contrôlé par la dynamique à court-terme de la biomasse de microphytobenthos (Haubois et al., 2005a). Les nématodes broutent au minimum 13% de la production microphytobenthique (Rzeznik-Orignac and Fichet, 2012). A marée haute, une partie du biofilm est susceptible d'être remise en suspension. De manière générale, la remise en suspension du biofilm est liée à celle du sédiment (Lucas et al., 2000). L'érosion des sédiments est contrôlée tout d'abord par des processus physiques (Le Hir et al., 2000) et plus particulièrement favorisée par l'action des vagues sur la vasière de Brouage (Bassoullet et al., 2000; Gouleau et al., 2000). Le rôle des organismes benthiques dans l'érosion des sédiments et la remise en suspension du microphytobenthos a également pu être mis en avant. En effet, les invertébrés benthiques via la bioturbation favorisent la remise en suspension du microphytobenthos (Orvain et al., 2003b; Orvain et al., 2004; Orvain et al., 2006). D'autre part, un biofilm microphytobenthique bien développé et jeune stabilise les sédiments et empêche/limite l'érosion et la remise en suspension (Orvain et al., 2003a; Orvain et al., 2004). A travers le processus de remise en suspension, le biofilm constitue un élément clé de liaison trophique entre le benthos (vasière) et le pélagos (colonne d'eau). Le microphytobenthos remis en suspension est intégré au réseau trophique pélagique et peut être ingéré par les organismes suspensivores, comme démontré par la comparaison des signatures isotopiques de la source et d'un consommateur potentiel (Riera and Richard, 1996).

Ces nombreuses études ont constitué une étape essentielle qui a permis de démontrer l'importance de la production microphytobenthique sur la vasière de Brouage et son

[1] *Hydrobia Ulvae* a été renommée *Peringia ulvae*. Afin de faciliter la compréhension du texte pour les non spécialistes de la macrofaune, il a été choisi de garder le nom *Hydrobia ulvae* tout au long du manuscrit.

intégration aux réseaux trophiques benthique et pélagique via sa remise en suspension. Cependant, en 2006, de nombreuses questions restent encore en suspens notamment en ce qui concerne les procaryotes (bactéries et archées) qui constituent le biofilm microbien avec le microphytobenthos: qu'en est–il de la production procaryotique et de l'interaction procaryotes et EPS produits par les diatomées ? Quel est le devenir de la production procaryotique (i.e. quantification de la 'bactérivorie') ? Mais aussi, quel est le rôle de la lyse virale dans le contrôle de la production du biofilm microbien ? Quelle part de la production du biofilm est exportée par les oiseaux et par les poissons ? Comment quantifier plus précisément la remise en suspension du biofilm microbien ? Comment interagissent le microphytobenthos et les procaryotes remis en suspension avec le réseau trophique pélagique ? Ces diverses questions ont été abordées entre 2007 et 2011 par l'ANR blanche «Rôle trophique des biofilms microbiens dans les vasières intertidales» (VASIREMI) dont les protocoles et les résultats principaux sont présentés ci-après.

Ce travail de thèse s'intègre à ce projet de recherche par l'intégration de toutes les données de l'étude et la réalisation de modèles de réseaux trophiques. Cette approche statique est complémentaire d'un modèle dynamique qui permettra de coupler des processus biologiques et physiques. Des modèles du réseau trophique de la vasière de Brouage ont déjà été réalisés (Leguerrier et al., 2003; Leguerrier et al., 2004; Degré et al., 2006). Ces modèles ont mis en évidence certaines carences dans les données notamment au niveau du compartiment microbien. Les modèles de ce travail de thèse sont une synthèse des résultats du programme VASIREMI, comblant certaines des lacunes constatées dans les précédents modèles. Les modèles de cette thèse ont été construits sur une échelle temporelle et spatiale correspondant aux caractéristiques de l'échantillonnage du programme VASIREMI, ceci afin d'éviter une perte de qualité des données. L'ANR VASIREMI a approfondi nos connaissances sur les processus biologiques à marée basse. Ainsi dans un premier temps, seul le réseau trophique à basse mer diurne est présenté ; le but étant de partir de ce que l'on connait pour essayer de mieux appréhender ce que l'on ne connait pas/peu. Les résultats du modèle basse mer ont ensuite servi à l'élaboration de deux modèles pleine mer : un modèle qui considère la remise en suspension du biofilm microbien, et un autre où la remise en suspension n'a pas lieu. Le découplage des processus à basse mer et à pleine a aussi pour objectif de soulever de nouvelles hypothèses sur les processus ayant lieu à pleine mer qui n'auraient pas pu être visibles dans un modèle moyennant les données sur une journée. De plus, les échantillonnages

réalisés lors des deux campagnes de terrain de l'ANR VASIREMI (février et juillet) se sont concentrés sur la zone médiane de la vasière qui est caractérisée par une structure en seillons et banquette (Figure 1). Par conséquent, et afin d'éviter l'affaiblissement de la fiabilité des données VASIREMI par des extrapolations, les modèles représentent uniquement ce qui se passe sur cette zone médiane de vasière, ainsi les tables ostréicoles et le haut de l'estran ne sont pas pris en considération

La construction des réseaux trophiques est très gourmande en données puisqu'elle nécessite la connaissance des espèces du réseau trophique ainsi que les mesures des interactions entre les espèces *in situ*. Malheureusement, les limitations temporelles, techniques et financières inhérentes aux études de terrain empêchent d'obtenir toutes les informations nécessaires à la quantification des flux composants les réseaux trophiques. Ces lacunes peuvent être compensées par l'utilisation d'une méthode mathématique, appelée modélisation inverse ou analyse inverse, qui estime les valeurs manquantes des flux. Les réseaux trophiques ainsi reconstruits peuvent être soumis à une analyse de leur structure et de leur fonctionnement afin d'évaluer leur stabilité face à des perturbations naturelles ou anthropiques. L'Introduction Générale de ce travail de thèse présentera dans un premier temps le programme de recherche ANR VASIREMI et ces principaux résultats, puis la modélisation inverse, outil numérique principal de cette thèse, et enfin les objectifs de la thèse.

VASIREMI : un programme de recherche consacré à l'étude du rôle fonctionnel du biofilm microbien des vasières intertidales

L'ANR VASIREMI coordonnée par Christine Dupuy se concentre sur l'étude d'un habitat très étudié localement : la vasière de Brouage. Cette vasière nue, caractérisée par la formation d'un biofilm microbien à marée basse, a fait l'objet de nombreuses études antérieures à l'ANR VASIREMI, centrées sur le microphytobenthos et ses consommateurs directs (*Hydrobia ulvae* et nématodes) (voir le 'Contexte'). Lorsque le projet débute, des zones d'ombre restent encore à éclaircir, particulièrement en ce qui concerne les procaryotes benthiques qui auraient un rôle essentiel au sein du benthos, d'après un modèle de réseau trophique (Leguerrier et al., 2004),. D'autre part, la remise en suspension du biofilm microbien est un phénomène qui a été mis en évidence mais qui n'est pas bien quantifié. Le

devenir des micro-organismes (microphytobenthos et procaryotes) remis en suspension dans la colonne d'eau ainsi que leur interaction avec le réseau trophique pélagique sont encore mal connus. L'objectif de l'ANR VASIREMI était de compléter les connaissances déjà acquises par la compréhension du devenir du biofilm microbien au sein du réseau trophique benthique et du réseau trophique pélagique via sa remise en suspension. Un des objectifs spécifiques était d'approfondir les relations entre la production du microphytobenthos, l'excrétion des EPS et la production bactérienne. Les différentes études ont nécessité des approches *in situ* et expérimentales en laboratoire ; le couplage des deux constitue l'une des originalités de ce programme de recherche.

Cette ANR, financée de 2007 à 2011, a été divisée en 5 thèmes de recherche principaux :

1. Le réseau trophique benthique.
2. Le couplage benthos-pelagos par la remise en suspension des micro-organismes benthiques.
3. Le réseau trophique pélagique.
4. Le devenir de la production du biofilm microbien à travers l'analyse par isotopie stable.
5. L'intégration des processus par la modélisation couplée du benthos et du pelagos.

Outre différentes études réalisées en mésocosme, l'essentiel de cette ANR repose sur deux campagnes de terrain réalisées en Février (du 16 au 24) et Juillet 2008 (du 13 au 26) sur un cycle de vives-eaux/mortes-eaux. Le site d'échantillonnage se situe dans la partie haute du milieu de vasière qui est caractérisée par une structure de seillons et banquettes (voir la figure I-1). L'échantillonnage a été réalisé tous les jours lors de la basse mer.

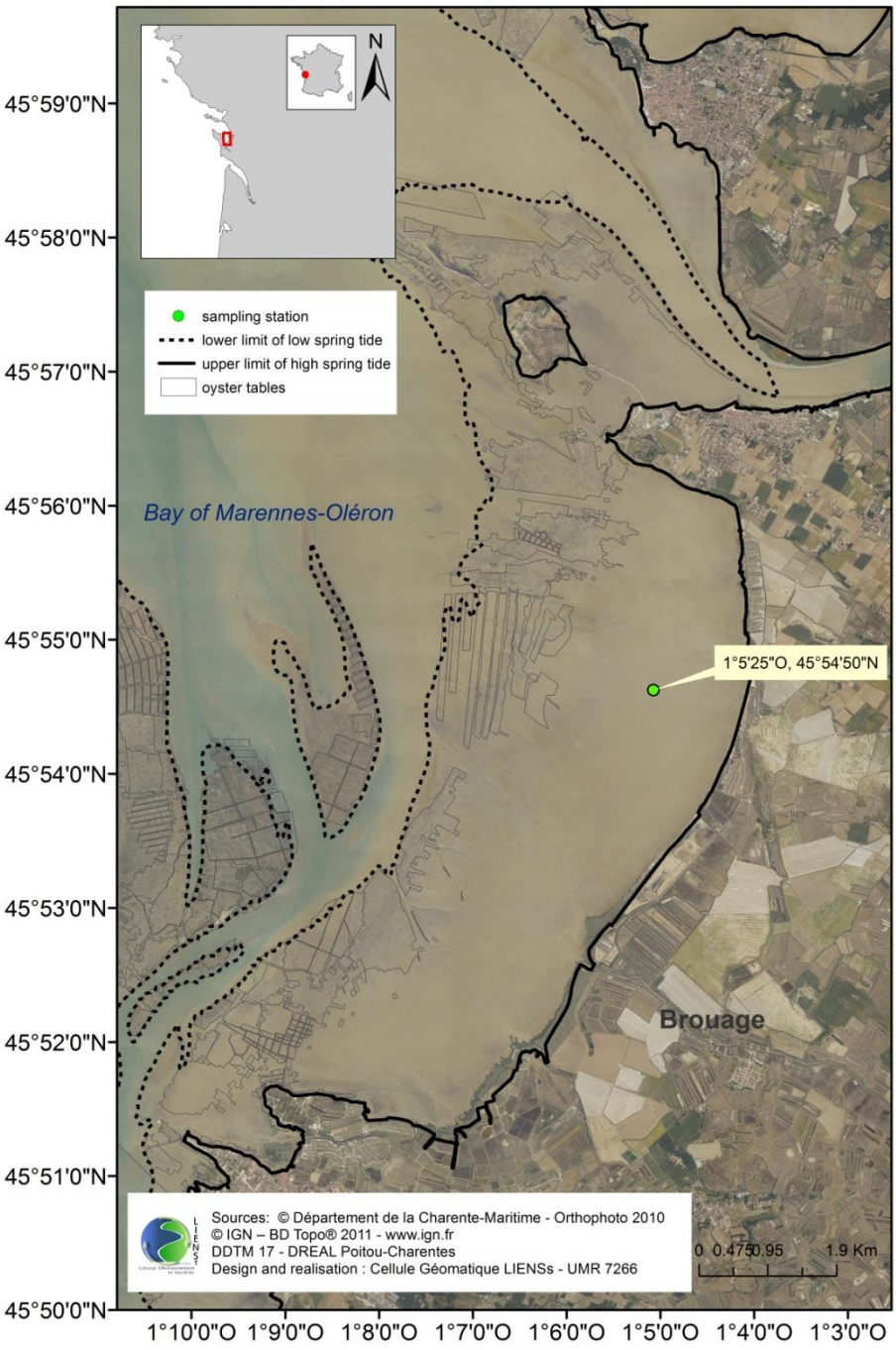


Figure I-1 : Carte de la vasière de Brouage. Le point vert représente le point d'échantillonnage VASIREMI.

1. Le réseau trophique benthique

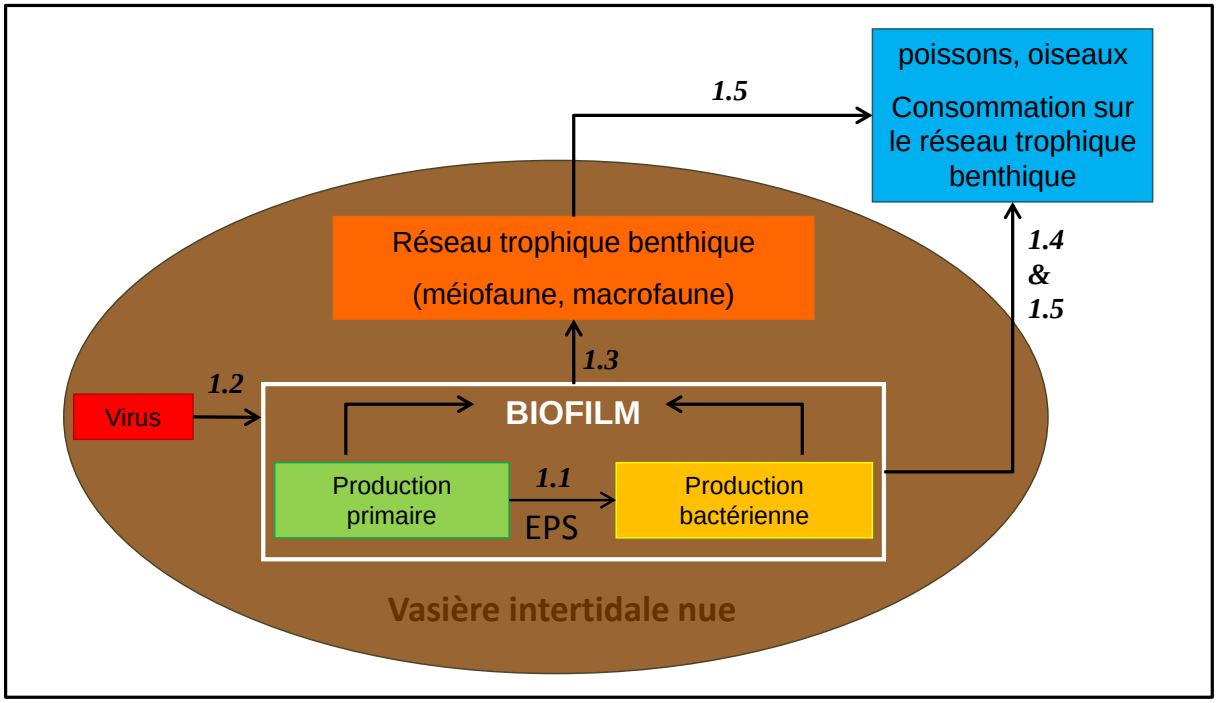


Figure I-2 : Schéma représentant les flux, les influences, et les compartiments étudiés dans le réseau trophique benthique (thème de recherche 1). Les chiffres en italiques sur les flèches indiquent les différentes sous-parties de ce thème de recherche.

Ce premier thème de recherche de l'ANR s'articule autour de plusieurs problématiques centrées sur le biofilm. Dans un premier temps, il s'agit de déterminer la production bactérienne en association avec le microphytobenthos (1.1, figure I-2). L'hypothèse de départ supposait que les EPS excrétées par les diatomées pouvaient être un substrat potentiel à la croissance bactérienne (Middelburg et al., 2000; Goto et al., 2001). La production bactérienne a donc été suivie en parallèle de la production des EPS en fonction de la période du cycle tidal et de l'âge du microphytobenthos. Suite aux travaux réalisés au cours de l'ANR, l'hypothèse de la stimulation de la production bactérienne par l'excrétion d'EPS par les diatomées a été nuancée, puisque selon les fractions d'EPS (« bound » ou colloïdaux) considérées et l'état du biofilm microbien, les conclusions ne sont pas les mêmes : les EPS colloïdaux stimulent la production bactérienne de manière systématique alors que les EPS « bound » ont tendance à l'inhiber. De manière générale, à l'échelle de la journée, les périodes de forte production bactérienne correspondent à des phases de faible activité photosynthétique. Ainsi les bactéries

ont une production plus importante pendant les phases d'immersion alors que le microphytobenthos concentre son activité en période d'émersion diurne (Agogué, comm. pers.).

A une échelle temporelle plus grande, une variabilité saisonnière de la production du microphytobenthos a été observée. En effet, la biomasse des diatomées photosynthétiquement actives est 4 fois plus faible en été qu'en hiver. En été, les diatomées sont soumises à des intensités lumineuses et des températures très fortes qui limitent la photosynthèse et donc la production associée, c'est ce qu'on appelle la photo-/thermo-inhibition (Lavaud, Lefebvre et Mouget, comm. pers.). D'autre part, un contrôle top-down des diatomées est observé sur le terrain. En effet, la forte pression de broutage, notamment par les hydrobies (*Hydrobia ulvae),* entraîne une diminution de la biomasse active de diatomées et donc de la production associée (Dupuy et Lefebvre, comm. pers.).

Antérieurement à l'ANR VASIREMI, différents organismes benthiques susceptibles d'avoir un rôle dans le devenir du biofilm (figure I-2) avaient été identifiés. Tout d'abord, les virus (1.2), abondants dans les sédiments (Hewson et al., 2001; Sime-Ngando and Colombet, 2009), semblent avoir une influence sur les bactéries sans toutefois que celle-ci n'ait été clairement quantifiée. Les expériences de suivi de mortalité bactérienne en présence de virus, réalisées au cours de l'ANR, ont démontré que les virus benthiques affectent la production bactérienne à hauteur de 11% en hiver et 40% en été (Montanié, comm. pers.).

D'autre part, la macrofaune et la méiofaune sont également des consommateurs du biofilm microbien (1.3). Les premières études sur la vasière de Brouage ont montré que la méiofaune, dominée par les nématodes, broute au moins 13% de la production du microphytobenthos (Montagna et al., 1995; Rzeznik-Orignac and Fichet, 2012). *H. ulvae*, espèce abondante sur la vasière, broute une large gamme de taille de diatomées (Haubois et al., 2005a). De plus, leur broutage est influencé par la biomasse de microphytobenthos (Haubois et al., 2005a). La bactérivorie de ces espèces benthiques était alors mal connue. Le couplage d'une approche *in situ* et d'une approche *in vitro*, au cours de l'ANR VASIREMI, a permis de mettre en évidence et de quantifier les flux reliant le microphytobenthos et les bactéries, à la macrofaune et la méiofaune. Les résultats ont montrés que la bactérivorie et l'herbivorie sont bien présentes chez les nématodes, les foraminifères et la macrofaune, mais l'herbivorie est toujours dominante (Pascal et al., 2008b; Pascal et al., 2008c; Pascal et al., 2008d; Pascal et

al., 2009). La bactérivorie dépend de la disponibilité du microphytobenthos, si le microphytobenthos est en quantité suffisante, il est préféré aux bactéries, dans le cas contraire les bactéries constituent une source alternative. Cependant, dans tous les cas considérés, moins de 6% de la production bactérienne est consommée par la méiofaune et la macrofaune (Pascal et al., 2009). De plus, les comparaisons de signatures isotopiques des différentes sources alimentaires (MPB, Matière Organique du Sédiment (SOM) et Matière Organique Particulaire de l'eau (POM)) ont montré que le MPB représente en moyenne 72% du régime alimentaire de la macrofaune en hiver et 68% en été (Richard, comm. pers.).

Les mulets (*Liza aurata* et *L. ramada*), connus pour fréquenter la vasière de Brouage, sont des espèces limnivores se nourrissant sur la matière organique à la surface des vasières. Ils peuvent également exercer une pression trophique sur le biofilm microbien (1.4). L'ANR VASIREMI s'est penchée sur cette pression de broutage exercée par les mulets en couplant une étude comportementale du nourrissage (fréquence des prélèvements et temps de prélèvement) à des analyses isotopiques du foie, du muscle et du sang des poissons prélevés sur le terrain. Il est apparu que les mulets arrivent à pleine mer le ventre vide afin de s'alimenter sur le biofilm et repartent, en fin de pleine mer, le ventre plein (Feunteun et Charpentier, comm. pers.). Ils agissent donc comme des exportateurs de carbone de la vasière vers le large. Les mulets se nourrissent principalement sur la méiofaune, puis sur le MPB et de manière plus exceptionnelle sur les bactéries (Como, comm. pers.). En été, il a été observé que le taux d'ingestion est multiplié par 5 et la fréquence d'alimentation est plus importante (Como et al., soumis). Une estimation de la fréquentation de la vasière par les mulets devait être réalisée par la méthode de capture-recapture. Malheureusement, la pêche n'ayant pas été assez fructueuse, la fréquentation n'a pu être raisonnablement estimée.

En hiver la vasière de Brouage accueille de nombreux oiseaux migrateurs, et principalement le Tadorne de Belon (*Tadorna tadorna*). Cet oiseau qui se nourrit directement sur les invertébrés benthiques peut perturber le sédiment et le biofilm microbien associé. Les résultats ont montré que le Tadorne se nourrit principalement sur les hydrobies (85%) et dans une moindre mesure sur d'autres invertébrés (Viain et al., 2011). Aucune des espèces d'oiseaux se nourrissant sur la vasière de Brouage ne semble ingérer directement du biofilm (Bocher, comm. pers.).

2. La remise en suspension des micro-organismes

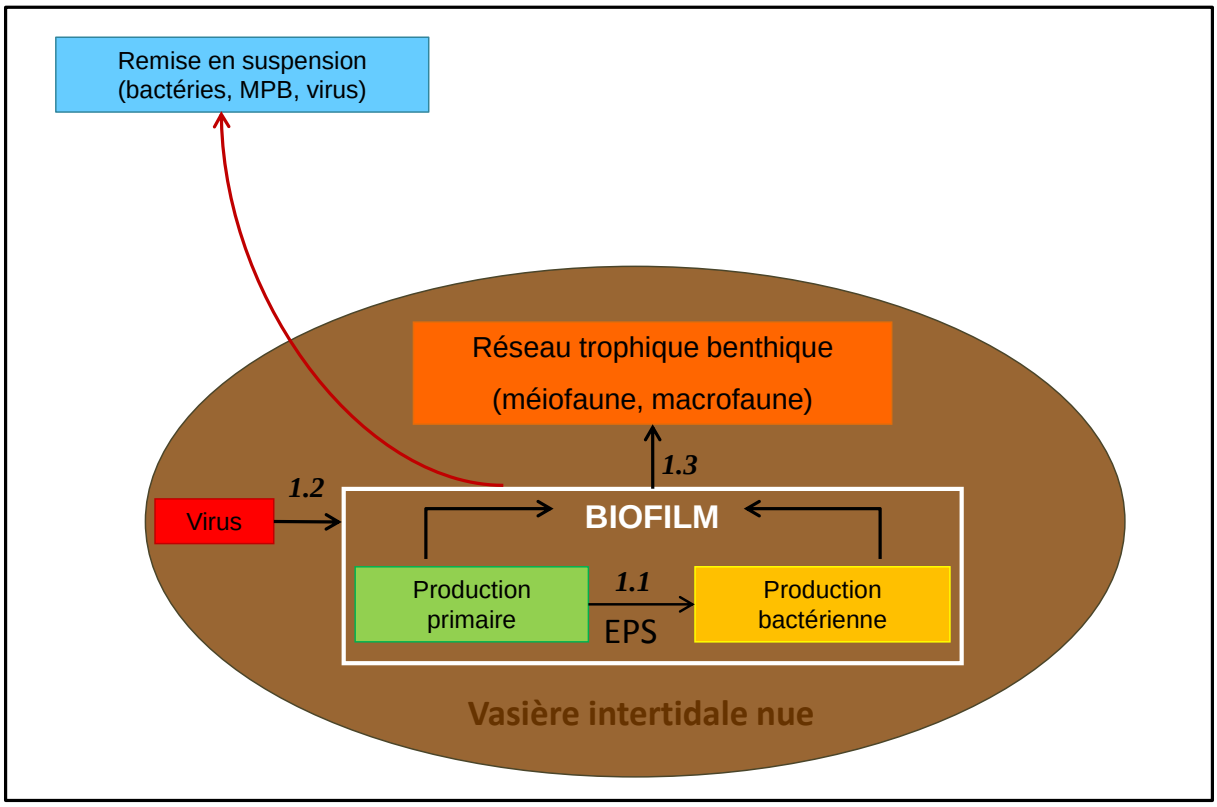


Figure I-3 : Schéma présentant le processus de remise en suspension considéré dans le thème 2 de recherche, intitulé 'remise en suspension des micro-organismes'. MPB = microphytobenthos.

L'érosion des sédiments est contrôlée par le coefficient de frottement sur le fond qui est lui-même dépendant de l'intensité du courant et du vent induisant les vagues (Le Hir et al., 2000) ainsi que de l'érodabilité du sédiment qui est définie comme la résistance du sédiment face à l'érosion (De Jonge and Van Beusekom, 1995). L'érodabilité du sédiment est extrêmement variable spatialement et temporellement puisqu'elle résulte d'une relation complexe entre les propriétés physico-chimique du sédiment, la macrofaune présente et le microphytobenthos (Herman et al., 2001b; Orvain et al., 2004). Partant de ce constat, les chercheurs de l'ANR VASIREMI se sont interrogés sur la remise en suspension des micro-organismes dans la colonne d'eau (figure I-3). Par le couplage d'une approche *in situ* et de mesures expérimentales par érodimétrie, il a été démontré que l'intensité de la remise en suspension du biofilm microbien est influencée par l'âge du biofilm et par la bioturbation exercée par la macrofaune (Orvain, comm. pers.). En été, l'activité de la macrofaune est importante, limitant

le développement du biofilm et ainsi sa remise en suspension. Les conditions hivernales sont donc plus favorables à une forte remise en suspension du biofilm vers la colonne d'eau. Les expérimentations d'érodimétrie ont montré qu'une vitesse de frottement sur le fond de 2,5 à 5 $cm.s^{-1}$ est nécessaire au transfert des diatomées et des bactéries attachées à des particules de sédiment vers la colonne d'eau. Les bactéries libres et les virus sont remis en suspension pour des frottements plus faibles. Les bactéries libres sont peu endommagées lors de la remise en suspension, elles conservent donc leur bon état physiologique et sont intégrées au réseau trophique pélagique (Agogué et Mallet, comm. pers.). Au contraire, les bactéries attachées sont endommagées et elles n'apportent au réseau trophique pélagique que de la matière organique supplémentaire. Il apparait que la remise en suspension des virus ne semble pas croître avec une augmentation du frottement sur le fond. Ceci pourrait être dû à un phénomène d'absorption-désorption sur la matière en suspension dans la colonne d'eau. Un suivi Lagrangien (i.e. suivi des masses d'eau) a confirmé ces résultats expérimentaux, c'est-à-dire un enrichissement des masses d'eau en chlorophylle *a* (proxi de la biomasse microphytobenthique), en procaryotes attachés et libres, en virus, en ciliés et en nanoflagellés. En été, la remise en suspension transfère une quantité plus importante d'organismes hétérotrophes qu'autotrophes vers la colonne d'eau. Cependant, les micro-organismes remis en suspension s'intègrent très rapidement au réseau trophique pélagique et sont donc consommés. Un suivi Eulérien (point fixe) a montré un apport d'eau du large moins chargée qui a un effet de dilution sur l'azote inorganique et sur matière inorganique particulaire, sur les diatomées et sur les bactéries (Guizien et Dupuy, comm. pers.).

3. Le réseau trophique pélagique

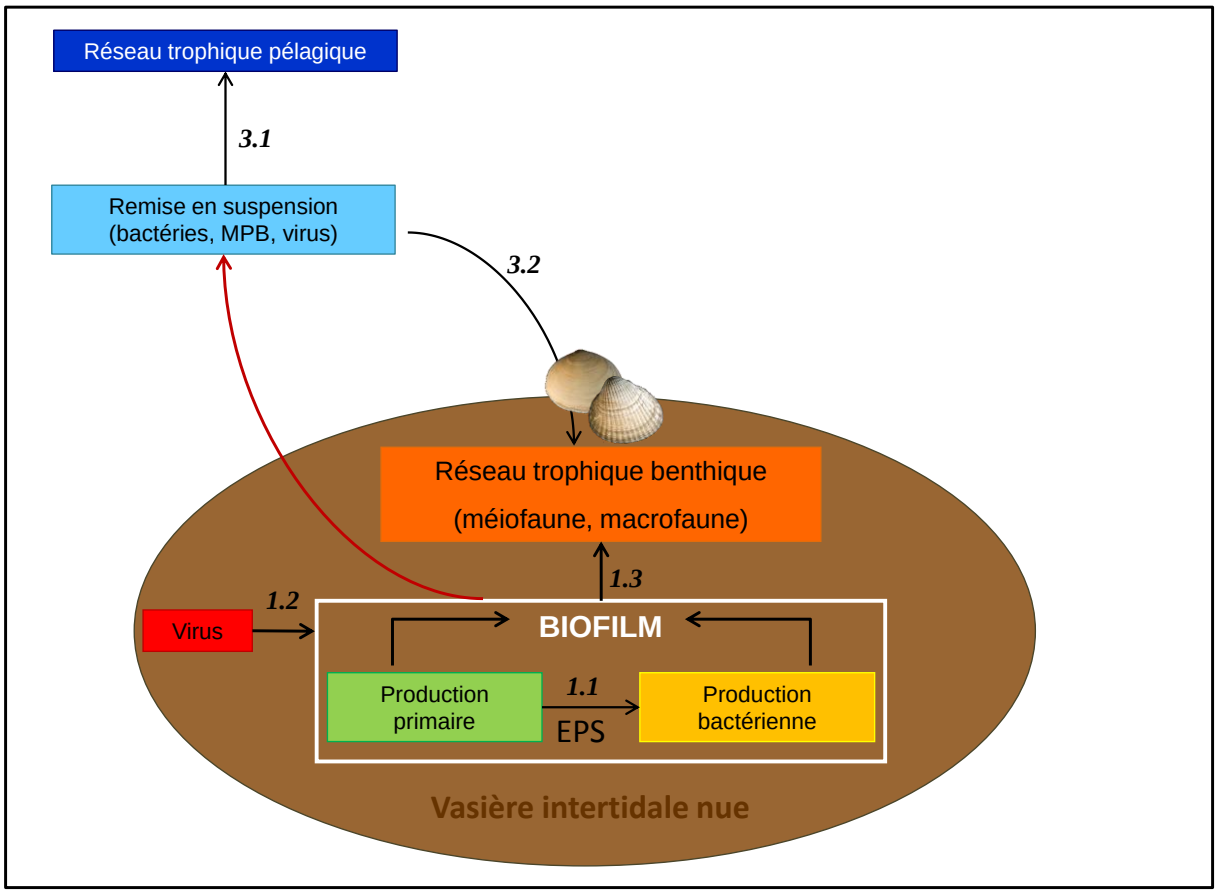


Figure I-4 : Schéma présentant le troisième axe de recherche de l'ANR VASIREMI qui comprend l'intégration des micro-organismes remis en suspension dans la colonne d'eau au réseau trophique pélagique (3.1) et la consommation du biofilm remis en suspension par les bivalves suspensivores (3.2).

Ce 3ème volet a consisté à comprendre l'influence des micro-oragnismes remis en suspension sur le réseau trophique pélagique (figure I-4). L'hypothèse de départ était que le biofilm remis en suspension pourvoit les bactériophages et les brouteurs de microalgues. Le rôle des virus pélagiques était alors inconnu. Les résultats obtenus au cours de l'ANR ont montré que, en été, une action synergique des flagellés et des virus provoque une chute de 43% de la croissance bactérienne (Ory, comm pers). La remise en suspension n'a que peu d'effet sur le potentiel de lyse virale et l'interaction bactéries-virus-nanoflagellés. Cependant, la production bactérienne est multipliée par 2 à cause de l'effet positif de la matière organique dissoute (MOD) benthique importée par la remise en suspension en été. En hiver, l'apport de MOD

benthique multiplie par 4 la croissance bactérienne qui est cependant modulée par un import de flagellés benthiques stimulant la production virale. La boucle microbienne est donc stimulée par la remise en suspension indépendamment de la saison (Ory, comm pers).

La prédation du mésozooplancton sur les nanoflagellés et le phytoplancton est inhibée lors de la remise en suspension du biofilm microbien. Les changements dans la diversité des proies et le changement de régime alimentaire du mésozooplancton impacte la production de ce compartiment. Certaines espèces voient leur production stimulée tandis que d'autres sont défavorisées et leur production diminue.

Les thèmes de recherche 4 et 5 sont basés sur des approches complémentaires et intégratrices. Les isotopes stables en carbone et en azote ont été utilisés pour décrire le devenir de la production du biofilm microbien au sein des réseaux trophiques benthique et pélagique (thème de recherche 4). Le cinquième thème de recherche a consisté à modéliser les résultats précédemment trouvés au cours des thèmes 1 à 4. Le présent travail de thèse rentre dans ce cadre en complément des modèles dynamiques développés par Katell Guizien et ses collaborateurs. Les modèles de ce travail de thèse sont des modèles statiques. Ils correspondent à un bilan des flux trophiques à un instant donné et ils prennent en compte une très grand diversité fonctionnelle, du microbien aux prédateurs supérieurs (oiseaux). Ces modèles ont pour objectif d'intégrer l'ensemble des données VASIREMI et les connaissances engendrées ultérieurement pour le même site d'étude. Ces modèles ont aussi pour but de comparer les propriétés d'organisation des réseaux trophiques par l'utilisation des indices de l'analyse des réseaux écologiques ou ENA ('Ecological Network Analysis') appliqués en sortie de la modélisation inverse, méthode présentée ci-après.

Chaque réseau trophique est caractérisé par une architecture qui lui apporte des propriétés spécifiques. Ces propriétés émergentes déterminent la stabilité des écosystèmes, c'est-à dire la pérennité de leur état en présence des perturbations environnementales subies. Le but principal de cette thèse est donc de comprendre la structure et le fonctionnement du réseau trophique de la vasière de Brouage en fonction des variations saisonnières (été-hiver) et des variations hydrodynamiques (avec ou sans remise en suspension). Ce travail de thèse a tout d'abord demandé un travail méthodologique important. En effet, la construction des réseaux trophiques est exigeante en termes de quantité et de qualité des données car dans l'idéal

chaque flux doit être quantifié. Malgré les efforts développés lors de l'ANR VASIREMI pour engranger un maximum de données sur tous les compartiments du réseau trophique, des données sur les flux restent manquantes. La construction des réseaux trophiques doit donc passer par une étape indispensable d'estimation des flux manquants, qui est réalisée par une méthode mathématique appelée analyse inverse ou modélisation inverse. Afin d'obtenir des résultats fiables et pertinents sur les architectures des réseaux trophiques considérés et les éventuelles conclusions sur leur stabilité, cette méthode a d'abord dû être optimisée.

L'analyse inverse : une méthode de reconstruction des réseaux trophiques

1. Qu'est-ce qu'un modèle ?

Un modèle est une construction simplifiée de la réalité d'un processus ou d'un système, visant à le décrire, à le comprendre et/ou à prévoir son évolution. Un même objet peut-être modélisé de multiples façons en fonction de ce que l'on veut déduire du modèle. Un modèle est donc construit pour répondre à un problème spécifique posé en amont. Si la problématique change, le modèle changera afin de répondre complètement aux nouveaux objectifs. Deux grands types de modèles se distinguent: les modèles prédictifs et les modèles descriptifs.

Un modèle prédictif a pour objectif de prévoir le comportement d'un processus ou d'un système face à des conditions variables. Ces modèles permettent par exemple de prévoir l'effet du changement climatique sur l'élévation du niveau marin, ou encore de prédire, à une échelle plus petite, le temps de découvrement de l'estran, pour une période donnée. Un modèle descriptif a une toute autre vocation puisqu'il tente de représenter la réalité observée. Les modèles utilisés dans cette thèse s'inscrivent dans cette catégorie. Ils décrivent et représentent de manière simplifiée les réseaux trophiques, c'est-à-dire les flux de matière et d'énergie reliant les espèces entre elles, sur une échelle de temps déterminée (l'émersion/immersion, le jour, la saison, l'année). Ils présentent la particularité de prendre en compte une grande diversité des flux et des compartiments fonctionnels. Les modèles de réseaux trophiques, auxquels on s'intéresse ici, correspondent à des modèles statiques, puisqu'il s'agit d'un bilan à un instant donné, sans notion d'évolution dynamique au cours du temps. Bien que ces modèles soient statiques, leur architecture et leurs propriétés

d'organisation permettent d'envisager, par le biais de la théorie écologique, des propriétés dynamiques liées à leur stabilité.

2. La modélisation inverse

Les origines de la modélisation inverse prennent racine en océanographie à la fin des années 70. L'océanographie physique, comme la recherche sur les réseaux trophiques, nécessite de nombreuses mesures sur le terrain. La quantité d'informations obtenue *in situ* est, en général, très éloignée de la quantité de paramètres nécessaires à la description de la circulation des océans (Parker, 1977). La modélisation inverse apparait comme la solution à ce problème. Elle est appelée ainsi car elle a une fonction opposée à la vocation habituelle d'un modèle. En effet, la méthode inverse estime la valeur des paramètres inconnus à partir des observations *in situ* disponibles et du modèle du système considéré (Parker, 1977). De manière générale, un modèle décrit le comportement d'une variable d'état à partir de paramètres connus et de conditions initiales (Vézina and Platt, 1988). Dans le cas de la modélisation inverse, la procédure est opposée, c'est-à-dire que l'observation des variables d'état est utilisée pour déterminer les paramètres inconnus (Vézina and Platt, 1988). Un algorithme mathématique permet, à partir du modèle et des observations faites sur le terrain, d'estimer les valeurs possibles que peuvent prendre les paramètres inconnus.

Cette méthode mathématique a été transposée de l'océanographie physique aux réseaux trophiques afin d'estimer les valeurs manquantes des flux dans un réseau trophique. Les variables d'état considérées sont alors les biomasses de chaque espèce. La première application aux réseaux trophiques fut réalisée par Klepper et Kramer (1987), puis fut reprise par Vézina et Platt (1988) pour en faire la méthode constituant la base de la modélisation inverse telle qu'elle est utilisée aujourd'hui. Différents types d'écosystèmes aquatiques ont déjà été modélisés : les premiers réseaux reconstruits par analyse inverse étaient surtout planctoniques (Vézina and Platt, 1988; Vezina and Pace, 1994; Niquil et al., 1998; Vézina and Savenkoff, 1999; Savenkoff et al., 2000), puis ils se sont élargis aux communautés benthiques.

3. Les étapes de l'analyse inverse

L'analyse inverse peut-être décomposée en 4 étapes :

1) Détermination de la topologie du réseau trophique.
2) Détermination des équilibres de masse et des équations.
3) Ajout de contraintes biologiques.
4) Calcul de la solution ou des solutions.

3.1. Détermination de la topologie du réseau trophique

Cette étape consiste à déterminer dans un premier temps les acteurs du réseau trophique autrement dit les espèces et compartiments 'non vivants' constituant l'écosystème considéré. Il est possible, par souci de simplification, de regrouper certaines espèces entre elles pour former des compartiments : on parle alors de réseaux trophiques agrégés. L'agrégation peut se faire selon plusieurs critères : par groupe taxonomique (Leguerrier et al., 2004), par régime alimentaire et mode de nutrition (Leguerrier et al., 2003), etc. Johnson et al. (2009) ont montré que ce dernier critère est celui qui altère le moins la structure du réseau trophique et qui est le plus proche de la réalité.

Une fois les compartiments vivants et non vivants déterminés il s'agit de définir quels sont les flux possibles entre ces compartiments c'est-à-dire les liens trophiques unissant les compartiments. Des questions essentielles se posent alors : Qui mange qui ? Qui ou quoi est importé ou quitte le système ? Quelle est la forme de la matière non vivante rejetée ? (Niquil et al., 2011).

Les compartiments sont toujours codés par 3 lettres (exemple : microphytobenthos = mpb). Puis les flux définis précédemment sont également codés et stockés sous forme d'un vecteur colonne nommé x. Les flux sont écrits sous la forme « C (pour carbone) espèce source TO espèce puit ». L'espèce source est l'espèce d'où part le flux (expéditeur) et l'espèce puits correspond au destinataire du flux. Si on considère le flux de broutage de microphytobenthos par les déposivores (dep), le flux est alors codé CmpbTOdep. La production primaire brute (gpp) du microphytobenthos est symbolisée par CgppTOmpb.

3.2. Détermination des équilibres de masse et des équations

Les équilibres de masse pour un compartiment donné correspondent à un bilan des flux entrant et des flux sortant. Les flux entrants sont définis comme les flux dont le destinataire est le compartiment considéré. Ils correspondent à la consommation et à l'import de ce compartiment. Au contraire les flux sortant sont déterminés comme les flux dont l'expéditeur est le compartiment considéré. Les flux sortant regroupent la respiration, l'excrétion, la prédation et l'export du compartiment considéré. La différence : somme des flux entrant moins somme des flux sortant est égale à zéro lorsque le compartiment présente une biomasse constante, ce compartiment est alors considéré à l'équilibre de masse. Dans le cas d'une différence non nulle, le compartiment est en déficit de masse si le bilan est négatif tandis qu'une différence positive signifie une accumulation de biomasse. Par défaut, l'analyse inverse considère les variations de biomasses négligeables par rapport aux flux, c'est-à-dire que la biomasse des compartiments est considérée à l'équilibre (i.e. flux entrants = flux sortants). A ces équilibres de masse viennent s'ajouter les flux dont les valeurs ont été estimées sur le terrain.

Les équilibres de masse et les flux connus (i.e. estimé sur le terrain) sont écrits sous la forme d'équations linéaires : $A * x = b$. La matrice A (m,n) (i.e. m lignes et n colonnes) est composée des coefficients des équilibres de masse et des mesures de terrain. x (n,1) correspond au vecteur de l'ensemble des flux du réseau trophique déterminé dans le 1), et b (m,1) est un vecteur ligne composé des valeurs des observations de terrain et des valeurs des équilibres de masse de chaque compartiment. La lecture de la matrice se fait de manière verticale (figure I-5).

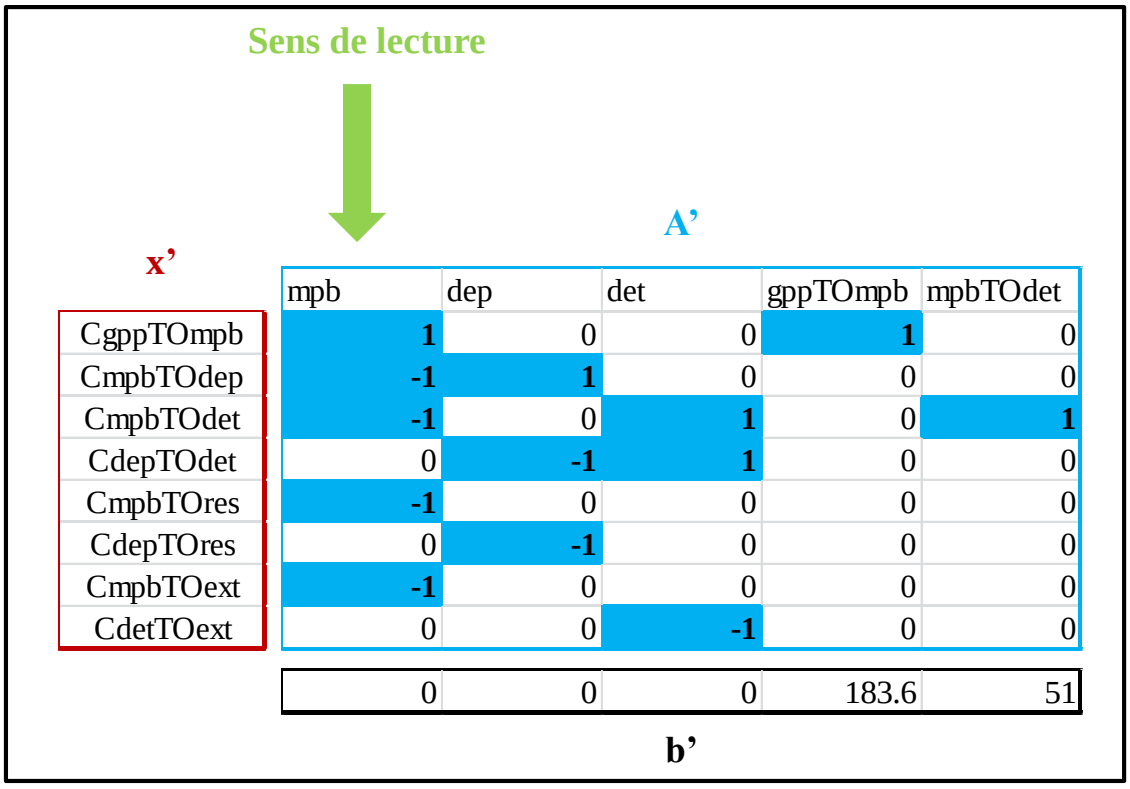


Figure I-5 : Schéma représentant les vecteurs et la matrice résultants des étapes 1 et 2. La matrice A' (n,m) correspond à la transposée de la matrice A et le vecteur b'(1,m) à la transposée du vecteur b. Prenons pour exemple la colonne 1 de la matrice A' : cette colonne correspond à l'équilibre de masse du compartiment mpb, et se lit : *1**CgppTOmpb – *1**CmpbTOdep – *1**CmpbTOdet – *1**CmpbTOres – *1**CmpbTOexp = 0. La colonne 3 correspond à la mesure sur le terrain de la production primaire du mpb et se lit *1**CgppTOmpb = 183,60.

3.3. Ajout de contraintes biologiques

Afin d'obtenir des valeurs plus réalistes pour les flux manquants, des contraintes biologiques sont ajoutées aux équilibre de masse et aux équations. Ces contraintes correspondent à des taux physiologiques (exemple : efficacité d'assimilation) ou à des données sur les flux ou les processus provenant d'un milieu/écosystème présentant des caractéristiques similaires au milieu/écosystème considéré. Ces données sont issues de la littérature et sont considérées comme des connaissances *a priori* des organismes et du type d'écosystème. Cette étape de l'analyse inverse est très importante car la précision des résultats en dépend : plus le nombre de contraintes est important et plus les bornes inférieures et supérieures de ces contraintes seront affinées, et plus les valeurs calculées pour chaque flux inconnu seront proches de la réalité et donc fiables.

Les contraintes biologiques sont écrites sous la forme : $G * x \leq h$, où x (n,1) est toujours le vecteur contenant tous les flux du réseau trophique. G (p,n) est une matrice composée des coefficients des contraintes biologiques et h (p,1) est un vecteur ligne déterminant les valeurs de contraintes biologiques. La matrice G et le vecteur h sont construits et lus de la même façon que la matrice A et le vecteur b (figure I-6).

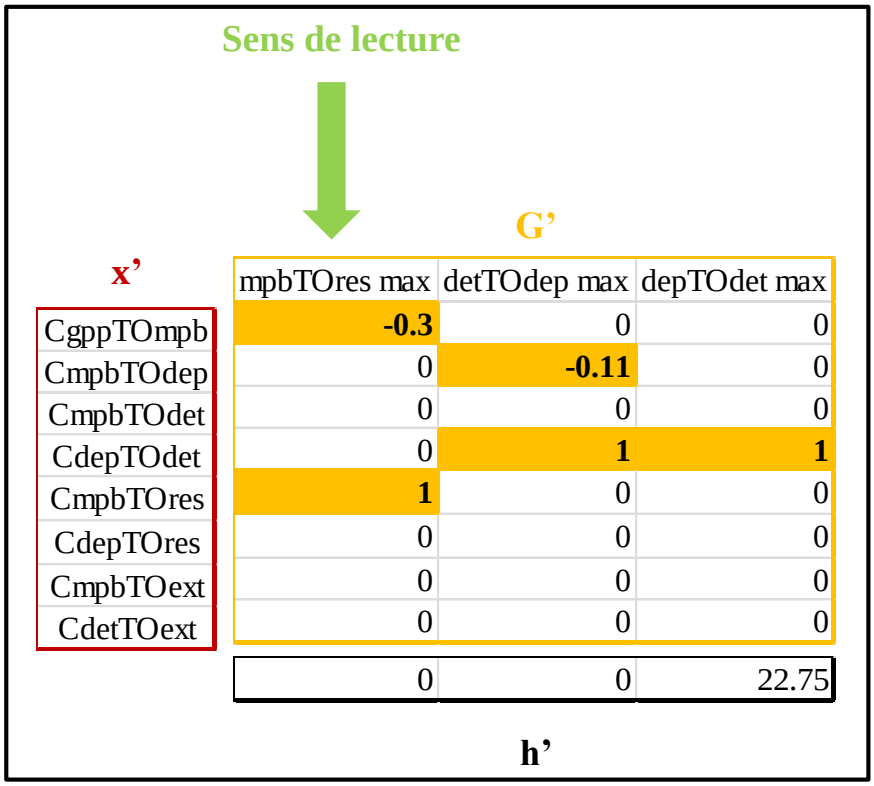


Figure I-6 : Schéma représentant la matrice des inéquations G. La matrice G'(n,p) est la transposée de la matrice G et le vecteur h'(1,p) est le transposé du vecteur h. La première colonne se lit -0.3*CgppTompb + 1*CmpbTOres ≤0.

3.4. Calcul des solutions

Grâce aux 3 étapes précédentes, un espace de solution, correspondant à un polyèdre multidimensionnel, est formé. Cet espace est limité grâce aux équilibres de masse, aux équations et aux inéquations déterminées au cours des étapes précédentes (figure I-7).

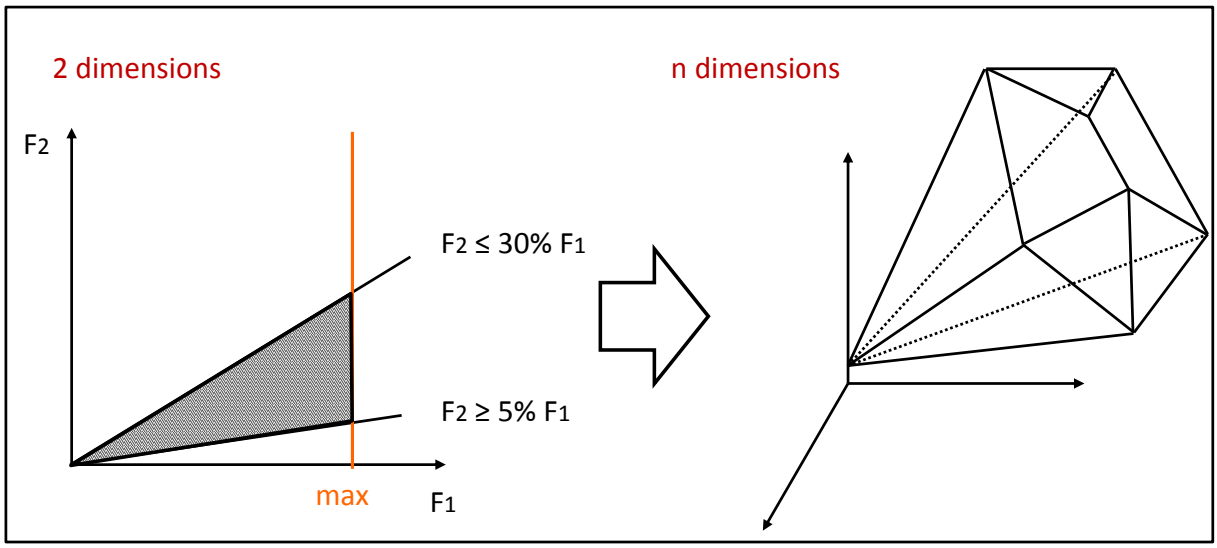


Figure I-7 : schéma représentant la formation du polyèdre de solutions. Dans le premier cas à gauche, seulement 2 dimensions (ou 2 flux) sont considérés. Le flux F_2 est compris entre 5 et 30% du flux F_1. De plus, le flux F_1 possède une valeur maximale, ainsi l'espace de solution pour le flux F_2 se réduit au triangle hachuré. Lorsque que le nombre de dimensions considérées augmente, le triangle hachuré devient la figure complexe, correspondant à un polyèdre multidimensionnel.

Après l'obtention du polyèdre, deux méthodes exploratoires peuvent être envisagées. La méthode dite déterministe (Vézina and Platt, 1988) ne propose qu'une seule solution qui remplit à la fois conditions d'équilibres de masse, d'équations et de contraintes biologique à la sortie de l'analyse inverse. Une méthode plus récente propose l'échantillonnage aléatoire de l'espace des solutions (Kones et al., 2006; Van den Meersche et al., 2009). Plusieurs solutions remplissent alors toutes les conditions pour chaque flux et sont proposées en sortie de l'analyse inverse.

4. De la méthode déterministe à l'échantillonnage aléatoire

4.1. Méthode déterministe

La méthode déterministe, comme expliqué plus haut, ne donne qu'une seule solution pour chaque flux. Cette solution, s'appuie sur un principe philosophique : le rasoir d'Occam. Ce principe repose sur la notion de parcimonie et suggère que parmi toutes les solutions possibles la plus simple est la meilleure. D'un point de vue mathématique, la solution la plus simple est celle des moindres carrés. Le vecteur solution des flux qui présente la somme minimale des carrés des flux est alors sélectionné. Cette méthode a été très souvent utilisée (e.g. Vézina et al., 2000; Savenkoff et al., 2004; Richardson et al., 2006; Forest et al., 2011) mais également très critiquée (e.g. Niquil et al., 1998; Donali et al., 1999; Johnson et al., 2009). Le choix de la solution déterministe basée sur le principe des moindres carrés a en effet des conséquences sur la structure du réseau trophique ainsi reconstruit voire même sur son fonctionnement. La minimisation de la norme quadratique des flux entraine la surestimation de certains flux et la sous-estimation d'autres flux par rapport à la valeur réelle des flux. Une étude a montré que d'une manière générale ce sont les petits flux qui sont surestimés et les grands flux sont sous-estimés (Vézina and Pahlow, 2003). Ceci a de graves conséquences sur l'ordre des flux qui est complètement bouleversé altérant ainsi la cohérence du réseau trophique. La solution des moindres carrés impacte également la description du fonctionnement des réseaux trophiques. En effet, les pertes du réseau trophique (respiration, exports) ont tendance à être surestimées (Eldridge and Jackson, 1993). De plus certain flux existant dans le milieu naturel, sont estimés comme nuls par l'analyse inverse (Kones et al., 2006), ils sont donc considérés comme inexistant dans le réseau trophique reconstruit. Ces deux dernières conséquences entrainent la sous-estimation de l'énergie circulant à travers le système et de l'énergie contenue au sein du système. Les indices écologiques ENA (Ecological Network Analysis), qui mesurent les propriétés d'organisation d'un écosystème, ont également tendance à être mésestimés par la solution des moindres carrés (Johnson et al., 2009; Kones et al., 2009). Par conséquent, la solution des moindres carrées donne aux réseaux trophiques reconstruits une structure artificielle (Stukel et al., 2012) et elle ne parvient pas à rendre compte de la complexité réelle des réseaux trophiques (Vézina and Pahlow, 2003).

Cette méthode reste cependant performante pour déterminer les états différents d'un même écosystème et réaliser des comparaisons intra-écosystémiques (Vézina and Pahlow, 2003). Par contre, dans le cas d'une comparaison inter-écosystème la méthode déterministe présente des limites. Dans l'objectif d'une méthode de reconstruction des réseaux trophiques apportant des résultats fiables aussi bien sur l'estimation des flux que sur l'interprétation écologique qui peut en être tirée, la méthode déterministe ne semble donc pas la plus adaptée.

4.2. Méthode par échantillonnage aléatoire

Contrairement à la méthode déterministe qui ne donne qu'un seul vecteur solution (une valeur par flux), cette méthode propose plusieurs solutions à partir d'un échantillonnage aléatoire de l'espace des solutions (le polyèdre). Leguerrier (2005) propose un tirage aléatoire des valeurs à l'intérieur d'un parallélépipède comprenant l'espace de solutions, l'échantillonnage aléatoire est alors basé sur la méthode de Monte Carlo (Kones et al., 2006). Cette méthode, utilisée dans des domaines très variés, comme par exemple la finance, la géométrie, la biologie, permet d'échantillonner un espace préalablement défini. Cette méthode appliquée à la reconstruction des réseaux trophiques pose quelques problèmes puisque les solutions proposées peuvent être soit à l'intérieur soit à l'extérieur du polyèdre. Les solutions en dehors du polyèdre ne sont pas acceptables et doivent être éliminées. La localisation des solutions à l'intérieur du polyèdre doit donc être testée ce qui se traduit par un long temps de calcul. Un problème supplémentaire se pose puisque l'espace des solution n'est pas totalement couvert (Wiback et al., 2004).

Van den Meersche (2009) a proposé une amélioration de l'échantillonnage aléatoire. L'échantillonnage aléatoire se fait par la méthode de Monte Carlo en chaîne de Markov (MCMC-LIM) avec un algorithme dit 'des miroirs'. L'échantillonnage et le déplacement dans l'espace se font grâce à un algorithme 'hit and run' (Smith, 1984) qui sélectionne des points de long d'un segment à l'intérieur du polyèdre. La chaîne de Markov repose sur la prédiction des éléments futurs à partir des éléments du présent ; le nouveau point est alors déduit du point précédent. La distribution de probabilité est centrée sur le point P_1, le nouveau point P_2 est séparé du point précédent par la longueur du 'jump', qui est défini comme l'écart-type de la distribution de probabilité.

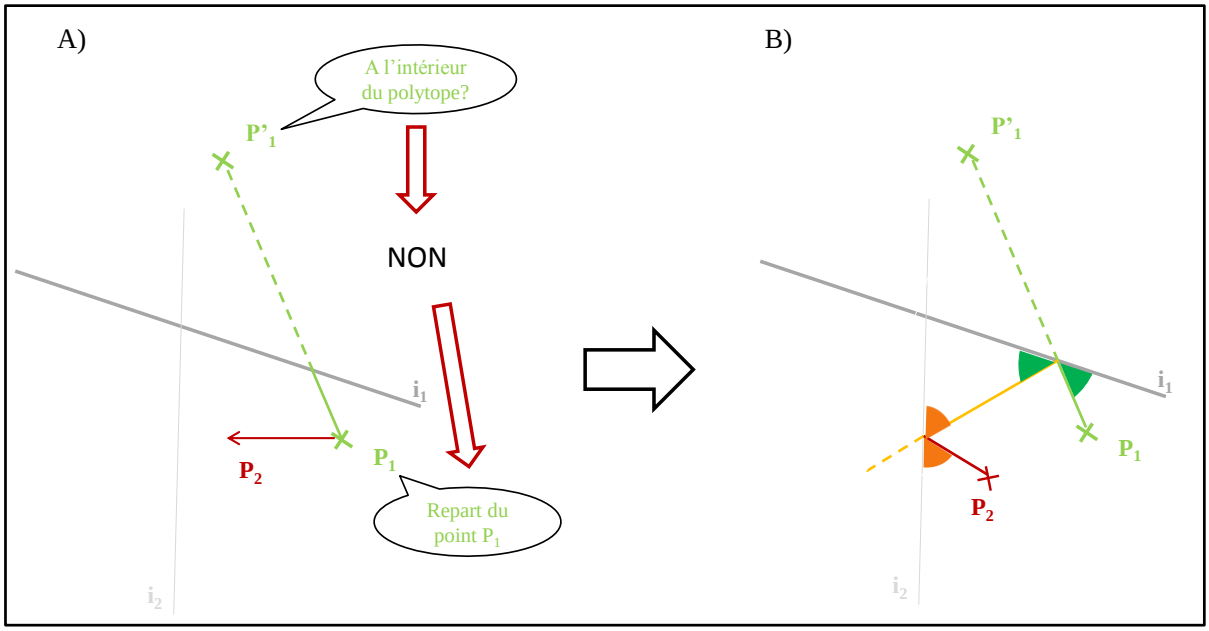


Figure I-8 : Schéma montrant la différence entre la méthode d'échantillonnage aléatoire par la méthode MCMC A) et par la méthode MCMC_ miroirs de Van den Meersche (2009) B). Dans les deux cas le point de départ est le point P_1 et le point P_2 le nouveau point échantillonné. i_1 et i_2 représentent les limites du polyèdre imposées par les contraintes biologiques (i.e. inéquations).

Dans le cas d'une méthode MCMC sans la technique des miroirs, l'échantillonnage d'un second point se fait à partir de la distribution de probabilité du premier point. Lorsqu'une solution proposée est en dehors de l'espace, une nouvelle direction est choisie à partir du point P_1 d'origine, puis les points sont échantillonnés le long de ce nouveau segment (figure I-8). L'inconvénient de cette méthode est un temps de calcul conséquent. La méthode MCMC « miroir » va générer de manière automatique un ensemble de points situés à l'intérieur du polyèdre. En effet, les parois du polyèdre vont agir comme des miroirs afin de ne proposer que des solutions à l'intérieur du polyèdre. Lorsqu'une solution s'apprête à sortir de l'espace des solutions, elle est réfléchie contre les parois du polyèdre jusqu'à ce que la solution tombe à nouveau à l'intérieur de l'espace des solutions (figure I-8). La longueur du 'jump' détermine la distance entre un point P_1 et P'_1. Si le point P'_1 se trouve hors de l'espace des solutions, un symétrique de ce point est déterminé par rapport à la surface du miroir. Si le nouveau point déterminé tombe à nouveau hors de l'espace de solutions, l'opération est répétée jusqu'à ce que le point tombe à l'intérieur du polyèdre. Chaque application de la méthode MCMC-LIM miroir est caractérisée par une valeur du 'jump' et un nombre d'itérations. Le nombre d'itérations défini le nombre de solutions échantillonnées aléatoirement au sein de l'espace

des solutions. Ces deux éléments sont essentiels et doivent être choisis de manière à couvrir l'ensemble de l'espace des solutions. Le 'jump' détermine la distance entre deux points, ainsi si un grand 'jump' est choisi alors que l'espace des solutions est réduit, le point P_2 sera souvent en dehors de l'espace de solution, ce qui se traduit par un temps long de calcul de solution. Au contraire, un 'jump' trop petit par rapport à l'espace de solution fait que cet espace est mal exploré : ses limites ne sont pas atteintes. Le 'jump' est donc choisi en fonction de l'espace de solution à couvrir et de manière à optimiser le temps de calcul de chaque itération. Le nombre d'itérations est choisi après le 'jump' et il est déterminé de façon à être sûr que l'espace de solutions soit totalement exploré. Le nombre d'itérations idéal correspond au nombre d'itérations à partir duquel la moyenne ou l'écart-type de chaque flux devient constant. De manière plus simple, si plusieurs réplicas d'une même simulation sont réalisés, pour chacun des flux, les mêmes moyennes et les mêmes écart-types doivent être trouvés si l'espace des solutions a complètement été exploré.

La méthode d'échantillonnage aléatoire présente l'avantage de proposer un intervalle de valeurs possibles pour chaque flux. Dans un contexte de comparaison inter-écosystémique, cet intervalle de solution peut être utilisé pour définir des bornes minimales maximales aux indices ENA, qui décrivent les propriétés de la structure des écosystèmes et leur fonctionnement. Des tests statistiques peuvent également être réalisés à partir de ces intervalles de valeurs.

L'analyse de la structure et du fonctionnement des réseaux nécessite parfois l'utilisation d'une valeur unique pour chaque flux. De manière intuitive, c'est la moyenne de l'ensemble des solutions proposées par la méthode MCMC-LIM qui est choisie comme solution unique (Forest et al., 2011; Grami et al., 2011). Le choix de la moyenne des solutions comme solution unique ne repose pas sur des fondements écologiques mais plus sur une évidence statistique. En effet, les solutions pour chaque flux peuvent être représentées par une distribution de probabilité : en cas de distribution normale, la solution la plus probable est la moyenne (van Oevelen et al., 2010). Finalement, on peut se demander si un choix de solution unique basé sur un fonctionnement écologique ne serait pas plus judicieux. Cette thèse se propose de vérifier cet aspect avant d'appliquer la modélisation inverse à la reconstruction du réseau trophique de la vasière de Brouage. Ce travail méthodologique nécessite la compréhension des théories associant organisation et fonctionnement des écosystèmes avec

les notions de maturité et de stabilité, afin de déterminer les fonctions écologiques à tester comme critère de sélection d'une solution unique à la sortie de la méthode MCMC-LIM.

Objectifs

Le but principal de ce travail de thèse est de comprendre, en couplant approches mathématique et écologique, comment l'organisation fonctionnelle des communautés littorales mène à une plus ou moins grande stabilité des vasières intertidales. Ce travail s'appuie sur la synthèse des principaux résultats obtenus lors de l'ANR blanche « Rôle trophique des biofilms microbiens dans les vasières intertidales » à travers la réalisation de plusieurs réseaux trophiques. Cette thèse repose sur deux grands axes :

1- Un travail méthodologique consistant optimiser la fiabilité et la performance de la modélisation inverse

Par comparaison des résultats obtenus grâce à différents critères de sélection d'une seule solution (critère initialement utilisé des moindres carrés, critères statistiques et écologiques), j'ai déterminé quel est le critère qui fournit la solution la plus fiable, c'est-à-dire la solution qui est la plus proche de la réalité et dont la qualité d'estimation est la moins variable face à la quantité d'information disponible (i.e. proportion de flux quantifiés). Cette étude demande un jeu de données complet, c'est-à-dire que tous les flux doivent être quantifiés, afin de pouvoir dégrader ce jeu de données et ré-estimer les valeurs manquantes par la modélisation inverse. Un tel jeu de données est extrêmement rare au niveau mondial. Celui utilisé dans cette étude a été déterminé pour la Baie de Sylt-Rømø en Allemagne. Les résultats de cette partie méthodologique, présentés en chapitre 3, ont fait l'objet d'une publication soumise à Ecological Modelling le 23 Septembre 2012.

Les critères écologiques testés lors de ce premier travail méthodologique ont été choisis d'après les théories de la maturité et de la stabilité des écosystèmes. Ces théories relient certains critères de maturité et de stabilité aux indices de l'analyse des réseaux écologiques (ENA). Ces indices décrivant l'état des écosystèmes, leur structure et leur fonctionnement ont été utilisés pour tout le travail de thèse soit comme critère de sélection d'une seule solution

(travail méthodologique, chapitre 3) soit pour décrire l'état du réseau trophique de la vasière de Brouage selon différentes conditions (travail de modélisation, chapitres 4 et 5). Ainsi ces deux axes de travail ont nécessité une connaissance approfondie et une vision globale du fonctionnement et de la maturation des écosystèmes. L'acquisition de ces connaissances s'est faite à travers l'élaboration d'une synthèse bibliographique soumise sous forme d'une review. La première soumission a eu lieu en Mars 2011 pour un numéro spécial d'Estuarine Coastal Shelf Science. Cette première soumission n'a pas été acceptée car elle ne correspondait plus suffisamment au focus de ce numéro spécial qui avait évolué depuis le plan initial, où les ENA avaient une place plus centrale. Après un travail sur le fond et la forme, le manuscrit a été soumis une deuxième fois à Ecology Letters en Février 2012. Malgré un intérêt pour le sujet, celle-ci a été rejetée car elle était hors du cadre de publication de ce journal. Une dernière soumission a eu lieu le 19 Juillet 2012 dans le journal Ecological Indicators. Cette review constituant la base de ce doctorat, elle précède les autres chapitres et est donc présentée dans le premier chapitre de cette thèse.

2- <u>L'étude du fonctionnement d'une vasière intertidale (vasière de Brouage) à travers la synthèse des données de l'ANR VASIREMI, par la réalisation de différents réseaux trophiques</u>

2-1- *Le réseau trophique de la vasière de Brouage en été et en hiver* : détermination de la structure et fonctionnement saisonnier de la vasière. L'hiver est caractérisé par la présence d'oiseaux migrateurs, en hivernage ou en pause migratoire, qui s'alimentent sur la vasière à marée basse. Ces prédateurs supérieurs exercent une pression trophique supplémentaire sur le biofilm et le réseau trophique benthique associé. Ces oiseaux hivernent sur la vasière et reviennent chaque année sur le site, ce qui signifie qu'ils trouvent leur nourriture en quantité suffisante. La première question qui se pose au vu de ce constat est : quelles sont les particularités de structure et de fonctionnement du réseau trophique hivernal à marée basse qui permettent de satisfaire les besoins nutritionnels des oiseaux ? Ce travail constitue le Chapitre 4 de cette thèse.

2-2- *Le réseau trophique de la vasière de Brouage selon différentes conditions hydrodynamiques* : impact de la remise en suspension du biofilm microbien sur le couplage benthos-pelagos et sa stabilité. Lors de sa remise en suspension le biofilm microbien assure

un rôle d'interaction entre les systèmes benthique et pélagique. La vasière de Brouage à pleine mer peut alors être assimilée à un méta-écosystème littoral comme défini par Loreau (2003). Un méta-écosystème est l'association de deux écosystèmes liés entre eux par un flux spatial de matière. Une structure d'écosystème considérée comme stabilisante intègre l'association de deux sous-systèmes qui montrent de fortes interactions en leur sein et qui sont connectés entre eux par des liens plus faibles (Levin, 1999). La remise en suspension du biofilm par son rôle d'interaction entre le benthos et le pélagos pourrait avoir un effet stabilisateur sur les vasières intertidales. Dans cette dernière partie, il s'agit de comprendre l'impact de la remise en suspension du biofilm microbien sur le fonctionnement du réseau trophique couplé benthos-pélagos. Les indices ENA sont alors mis en relation avec la stabilité des écosystèmes, en lien avec les théories rassemblées dans le Chapitre 2. Ce travail constitue le Chapitre 5 de cette these.

Chapitre 2

Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review

Blanche Saint-Béat[a], Dan Baird[b], Harald Asmus[c], Ragnhild Asmus[c], Cédric Bacher[d], Stephen R. Pacella[a*], Galen A. Johnson[a,c**], Valérie David[a,e], Alain F. Vézina[f] , Nathalie Niquil[a,g]

[a] Université de la Rochelle-CNRS, UMR 7266, Littoral Environnement et Sociétés (LIENSs), La Rochelle, France

[b] Department of Botany & Zoology, University of Stellenbosch, Stellenbosch, South Africa,

[c] Alfred Wegener Institut, Wattenmeerstation Sylt, List, Germany

[d] IFREMER, Plouzané, France

[e] EPOC, UMR 5805 Université Bordeaux 1 - CNRS, Arcachon, France

[f] Bedford Oceanographic Institute, Dartmouth Canada

[g] CNRS, UMR 7208 BOREA, Laboratoire BioMea (FRE 3484), Caen, France

* Present address: Environmental Sciences/Ecology Graduate Program, Corvallis, USA

** Present address: Northwest Indian Fisheries Commission, Olympia, USA

Réseaux trophiques: comment les théories relient-elles les propriétés de structure et de fonctionnement des écosystèmes avec celles relatives à la stabilité ? Synthèse

Dans le contexte actuel de pression anthropique croissante, l'intérêt croît pour la compréhension de la réaction des écosystèmes face à des pressions environnementales. La question centrale est alors de comprendre comment lier la structure et le fonctionnement d'un écosystème à sa réponse face à ces pressions en termes de persistance, de résistance ou de résilience. Les indices de l'analyse des réseaux écologiques ou « Ecological Network Analysis » en Anglais (ENA) qui caractérisent la structure et le fonctionnement des écosystèmes peuvent alors être interprétés en termes de leur potentiel lien avec la stabilité.

Comment lier structure et fonctionnement d'un écosystème (mesurés par les ENA) à sa stabilité ?

1- Les écosystèmes ne sont pas des entités figées à travers le temps. Ainsi leur structure et leur fonctionnement évoluent au cours de leur maturation. A travers la compréhension de la thermodynamique des écosystèmes, il est possible de caractériser la structure et le fonctionnement d'un écosystème mature. Les conclusions de cette partie sont principalement utilisées dans le chapitre 3, où le travail méthodologique sur la modélisation inverse se basera sur les fonctions écologiques considérées comme liées à la maturité.

2- La synthèse se penche ensuite sur l'évolution des théories sur la stabilité, présentée sous différents angles de vue (persistance, résilience ou résistance) : de la simple observation de la diversité à l'utilisation des indices ENA.

3- La dernière partie de cette synthèse met en relation les indices ENA et la stabilité des écosystèmes. Ces relations avec la stabilité sont exploitées dans le chapitre 5 en permettant d'extrapoler les descripteurs de fonctionnement du réseau trophique couplé benthos-pélagos à la stabilité des différentes situations décrites.

Principales idées dégagées :

La littérature mettant en relation la structure et le fonctionnement des écosystèmes avec leur stabilité est très vaste et parfois contradictoire. Les écosystèmes étant des entités uniques, les conclusions pour l'un ne sont pas facilement transposables à un autre, ce qui rend difficile toute généralisation

D'un point de vue thermodynamique un écosystème évolue de manière à faire circuler et à emmagasiner de plus en plus d'énergie et d'information en son sein. Ceci se traduit par une plus forte activité du système, un plus fort recyclage, une plus forte organisation (i.e. plus forte Ascendence).

D'un point de vue de sa stabilité, un écosystème doit avoir une structure et un fonctionnement laissant une possibilité de flexibilité, par exemple, en alliant faible et forte interactions, en alliant efficacité et inefficacité, en variant les types de proies (omnivorie)… Ces situations donnent à l'écosystème le moyen de tamponner une perturbation, en modifiant les relations entre les espèces.

Abstract

In the context of present global changes, interest in understanding how systems react to environmental pressures and stress has increased. Indices that characterize ecosystem health are helpful tools for the interpretation of ecosystem reactions. The central question is how to link ecosystem structure and functioning to their response to these pressures: and how to quantify their persistence, resistance or resilience. Quantification and characterization of trophic networks by Ecological Network Analysis (ENA) indices are developing rapidly, especially in the field of coastal ecology, and system structures are interpreted in terms of their potential for stability. Here we review several theories that relate ecosystem structure and function to stability. The structure and functioning of ecosystems change during the maturation of ecosystems. In a first part, the maturation of ecosystems is described using thermodynamics. The second and third parts of this paper define some concepts for analysing structure and functioning of food webs and discuss their relation to stability. The last section describes three ENA indices and their link to stability. It demonstrates that ENA provides powerful tools for describing local stability, combining quantitative and qualitative concepts. But it remains uncompleted for describing real conservation cases that combine local and global stability.

Introduction

Changes in biodiversity, such as species extinction, can lead to large consequences: alteration of the performance of ecosystems (productivity, decomposition) (Naeem et al., 1994), modification of biogeochemical cycles (Loreau et al., 2001), extinction of multiple species through cascading effects (Pimm, 1991) or cause the degradation of ecosystems (Myers et al., 2007). Modern changes in biodiversity are essentially due to impacts of human activities (e.g. habitat loss, climate change, invasive species, overexploitation, pollution) and have occurred more quickly over the past 50 years than at any other time before (Millennium Ecosystem Assessment, 2005). The conservation of species diversity and the protection of their environment are critical to maintain functioning ecosystems and ecosystem services.

Food webs are one of the major ways by which species are organized in an ecosystem (Elton, 1927). They represent the trophic interactions between species and thus describe the

communities and the ecosystem structure. Food webs integrate population dynamics, community structure, species interactions biodiversity, ecosystem productivity and community stability (Link et al., 2005). During several decades ecologists have studied the dynamics of food webs to determine the relationships between the complexity and the stability of ecosystems. Stability refers to the ability of an ecosystem to maintain its state over time, against external and internal forces that drive it away from that state. A stable food web is not a static entity. Food webs can show seasonal variability (e.g. Gironde's estuary, Chesapeake Bay) as well as variability over larger temporal scales. In spite of this variability, an ecosystem can show no modification from a given time 1 to time 2 and it is consequently regarded as stable. Two schools have been opposed in that respect. The first one considers that complex ecosystems are more stable than simplier ones based on the observation of the perennity of natural complex communities in nature (Odum, 1953; MacArthur, 1955; Elton, 1958). In contrast, May (1972, 1973), demonstrated via mathematical modelling that the complexity does not necessary beget the stability of ecosystems. This demonstration paved the path for a number of dynamical models which showed that for a given complexity, different architecture of food web exist, some of them being stable others not (Kondoh, 2005a). Consequently, it appears crucial to determine which kind of architecture provides stability to the ecosystems.

Two kinds of stability can be distinguished: local and global stability. The local stability corresponds to the maintenance of the original state after small perturbations (Pimm, 1991), or small changes away from its equilibrium state (Chen and Cohen, 2001). It does not give information on how the ecosystem might react to stronger perturbations. When environmental perturbations occur, an ecosystems can switch from one state to another one (May, 1977; Scheffer et al., 2001). The threshold refers to the maximum perturbation an ecosystem can undergo without shifting to another state and corresponds to the basin of global attraction (Scheffer et al., 2001). Alternative states are observed in the case of coral reef damage (Bellwood et al., 2004; Hughes et al., 2010), lake and estuary eutrophication (Baird et al., 2004b).

Food webs can be described by qualitative (diversity, number of flows) or by quantitative (magnitude of flows) features. Indices derived from Ecological Network Analysis (ENA), which combines the qualitative and the quantitative aspects of ecosystem dynamics, can be

considered as emergent system properties (Ulanowicz 1986). ENA is defined as "a systems-oriented methodology to analyze within system interactions used to identify holistic properties that are otherwise not evident from the direct observations" (Fath et al., 2007). The rapid development of the use of ENA, especially in coastal ecology (Christian et al., 2005), has led to interpretations of these food web properties in terms of their potential for local stability. Highlighting holistic properties of food webs, ENA indices appear to be a potentially powerful tool to assess ecosystem stability, with possible applications in management.

The aim of this review is to synthesize current theories which link food web structure and functioning to stability properties of ecosystems. We focused on local stability and analyzed more specifically ecosystem response to one important type of perturbation: changes in species richness through extinction or through colonization by invasive species. The first part explores the application of thermodynamics to ecosystem studies and describes the maturation of an ecosystem from an energetic point of view, because two ecosystems at different stages of maturation will probably have two different responses to perturbations (Pérez-España and Arreguín-Sánchez, 2001; Brando et al., 2004; Coll et al., 2008). The second part explores the theoretical debates concerning the role of diversity. The third part analyses the food webs context of this debate from binary to flow-weighted networks. The last part presents the theories linking three ENA indices, characterizing different levels of organization through ecosystem maturation (omnivory, cycling and Ascendency) to community of system stability.

Thermodynamic analysis of ecosystem maturation

Classical thermodynamics is the study of the energetic behavior of non-living systems, where systems are closed and isolated. Two fundamental laws of thermodynamics were described in the XIXth century. The first introduced the ideas of mass and energy conservation: in an isolated or closed system, the quantity of energy is constant; it only changes from one state to another. The second law, states that physical processes are irreversible and associated with the notion of entropy, measuring the disorder in a system. Entropy increases in closed systems until they reach the thermodynamic equilibrium. This corresponds to the equality between the entropy of a system and that of its surrounding.

Entropy and exergy are the two magnitudes which determine the state of a system. Biological systems are open and exchange energy and matter with their environment (Meysman and Bruers, 2010). These exchanges give special thermodynamic properties to biological systems relative to closed systems. Part of the incoming energy is used to order ecosystems and maintain a low entropy relative to the external environment (Jørgensen, 1992; Jørgensen and Fath, 2004). Exergy is expressed in terms of the work that the incoming energy in the ecosystem is able to do.

1. Ecosystems are unique

Ecosystems are not isolated, (Marques and Jørgensen, 2002), but open and not in thermodynamic equilibrium because of fluxes and flows of energy and material across the borders of the system, and within it (Fath and Patten, 1999). Ecosystems strive to maintain a state of low entropy relative to their surroundings (Jørgensen and Fath, 2004).

In nature, all ecosystem processes are irreversible (Jørgensen and Fath, 2004). At each process energy is lost in the form of heat that contributes to entropy production (Morowitz, 1968) implying that processes involving energy flux are associated with disorder (Ulanowicz and Hannon, 1987). There are two primary types of incoming energy : 1) solar energy that enters the ecosystem via photosynthesis (figure II-1), 2) the energy bound in chemical components which flows through the boundaries of ecosystems via inorganic or organic nutrients pools (Nielsen and Ulanowicz, 2000). Incoming energy is used to move the ecosystem far from the thermodynamic equilibrium and thus decrease the disorder in the ecosystem. Part of the incoming solar, or proper, energy is transformed into heat (Marques and Jørgensen, 2002) and permanently lost from the ecosystem. This metabolic conversion, also called exergy dissipation, corresponds to the organism's respiration. The excess quantity of incoming energy is stored by biomass building (Marques and Jørgensen, 2002). The difference between incoming energy and dissipative energy equals stored energy (Nielsen and Ulanowicz, 2000). The energy bound in chemical components is not dissipated from the system but it is ejected via advective fluxes. The energy exported this way is lost for the considered ecosystem, but can be used by any other ecosystems (Nielsen and Ulanowicz, 2000).

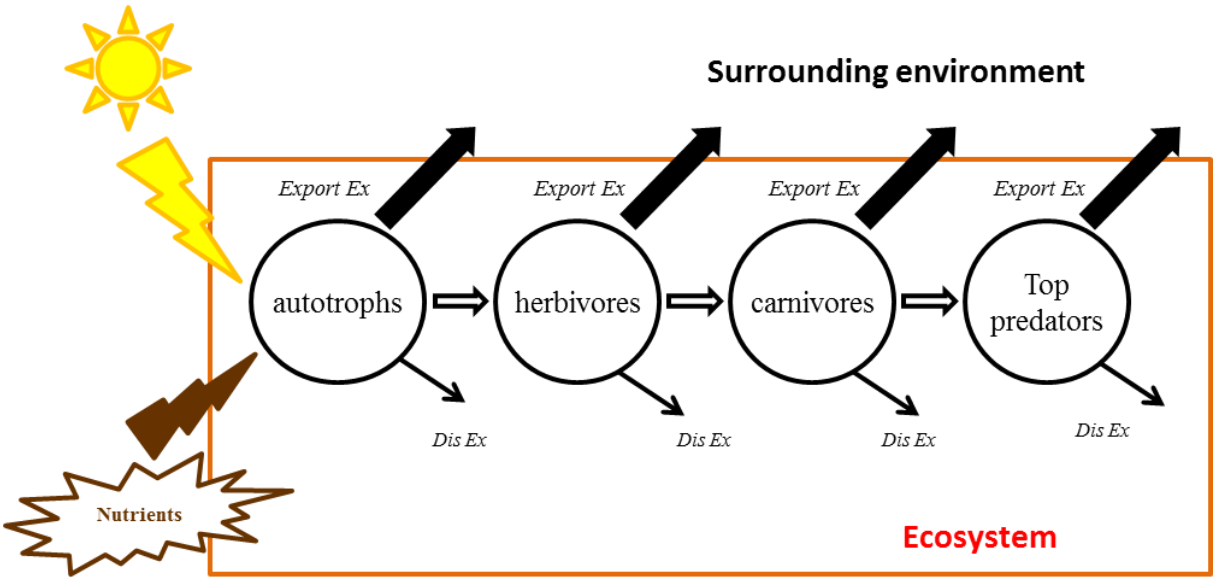


Figure II-1: Diagram of exergy within a food web. Dis Ex: dissipation of exergy and Export Ex: export of exergy. Modified from Nielsen and Ulanowicz, 2000

2. Ecosystem maturation (growth and development)

As with all living systems and organisms an ecosystem is a structure which comes into existence, evolves and matures through increasing complexity (Frontier et al., 2004). Ecosystem growth is considered to be an increase of measurable quantities, such as biomass (Marques and Jørgensen, 2002) or flows (Ulanowicz, 1986). Growth can be characterized by the number of compartments, the biomass of each compartment, and the Total System Throughput (TST). TST is defined as the sum of all flows in an ecosystem and is a measure of the total activity of the ecosystem. The development of an ecosystem is an increase in ecosystem information and in the organization of ecosystem structure (Ulanowicz, 1986; Jørgensen, 2000; Marques and Jørgensen, 2002). Ecosystems have the capacity for self-organization. The concept of self-organization in ecosystems has its roots in the thermodynamic theory of dissipative structures (Prigogine 1945, 1947) and in Bronowski's (1973) concept of stratified stability. Four steps are described for the growth and development of ecosystems (Ulanowicz, 1997; Jørgensen and Fath, 2004):

1. Biomass or energy with low entropy enters into the ecosystem
2. The physical quantity of biomass increases within the ecosystem by increasing

the number or the mass of the components (e.g. species) in the ecosystem

3. Network growth increases the number of trophic connections, and leads to an increase in the number of matter and energy cycles and an increase of energy flux in and through the ecosystem.

4. System information increases corresponding to a more efficient organization of the ecosystem (i.e. that accumulates energy).

2.1. Entropy production

According to the min-max entropy production principle (Aoki, 2008), two or three levels of entropy exist in aquatic systems. At earlier development, the entropy is low and progressively increases to reach the highest level at maturity. Entropy then decreases until a minimum level (i.e. return to thermodynamics equilibrium) during senescence. This tendency is observed in other biological systems, such as the human body. The dissipation of energy follows the same tendency: an increase during the growth, to obtain a maximal level of dissipation at maturity, followed by a decrease with the natural degradation (i.e. ageing) of the ecosystem (Jørgensen et al., 2000).

Meysman and Bruers (2010) considered a few 'entropy production' hypotheses on food web models that have been proposed before. They first confirmed that the entropy production rate in a biological system is always higher than in non-living systems (Ulanowicz and Hannon, 1987). The second hypothesis is called the state selection principle: if a system can attain multiple steady states, the stable state is the one which presents the highest entropy production rate. The second hypothesis is not validated: the stable state is not inevitably the state where the entropy is maximal (Meysman and Bruers, 2010). Thus the entropy is not really maximized in an ecosystem.

2.2. Exergy

Exergy corresponds to the measure of potential to do work for a given quantity of energy (Ulanowicz et al., 2006). The calculation of exergy (Ex) is:

$Ex = T_0 * (S_0 - S)$ (2)

with S, the entropy of the ecosystem, S_0, the entropy of the ecosystem's environment, and T_0, the environmental temperature. If Ex = 0 the ecosystem is in equilibrium with the surrounding environment (Jørgensen, 1992).

Ecosystems evolve toward a state with the highest possible exergy. During development ecosystems are subjected to pressures at two different levels: the individual level and the community level. At the individual component scale, the level of exergy could be improved by an increase of energy imported from outside and by the optimisation of transfer efficiency (i.e minimum dissipation) (Nielsen and Ulanowicz, 2000). According to the availability of resources and an organism's needs, an organism can partition its biomass differently (Odum, 2002). For example, a plant can develop large leaves if the light is low and roots could be developed in the case of low nutrient soil content (Odum, 2002). At the community scale, the addition of internal flows and cycling optimize exergy (Nielsen and Ulanowicz, 2000). Both of these strategies lead to an increase of exergy transfer between compartments and exergy storage (Jørgensen and Fath, 2006), measured by an increase of global activity (TST).

3. Maturation and species succession

During the first step of ecological succession, an ecosystem optimizes the utilization of exergy available in its environment. This increase in energy leads to an increase of biomass and flows (as described in the previous paragraph). At this stage, organisms present in an ecosystem waste a lot of energy, thrive in conditions where resources are abundant but the environment is variable, with high reproduction and turnover rates and low stocks of stored energy (Ulanowicz and Hannon, 1987). As ecosystems continue to develop, the number of flows increases and cycling stores exergy; the network grows (Ulanowicz, 1997; Jørgensen and Fath, 2004). The last step of ecological succession is the increase of organization and information (Ulanowicz, 1997; Jørgensen and Fath, 2004), and in turn the ecosystem increases entropy production (Jørgensen et al., 2000). By a particular positive feedback, called autocatalysis, one element in a loop influences the consecutive elements (Ulanowicz, 2009). The autocatalysis exerts a selection pressure on organisms to obtain more and more efficient autocatalysis. The pioneer organisms are progressively replaced by more efficient

counterparts. If two organisms receive the same amount of energy at the same entropy, the organism which extracts more work is considered to be the most efficient from energetic point of view (Ulanowicz and Hannon, 1987). These new organisms develop with limited resources and in competitive environments. At maturity, the total dissipation and entropy production are higher than at the first step of succession (Kleidon et al., 2010). The highest activity of the most efficient organisms (i.e. more work for a same quantity of energy) implies a greater dissipation that leads to a greater entropy (Ulanowicz and Hannon, 1987). However the dissipation/TST ratio decreases due to an increase of TST, so the exergy content within the ecosystem is the highest possible.

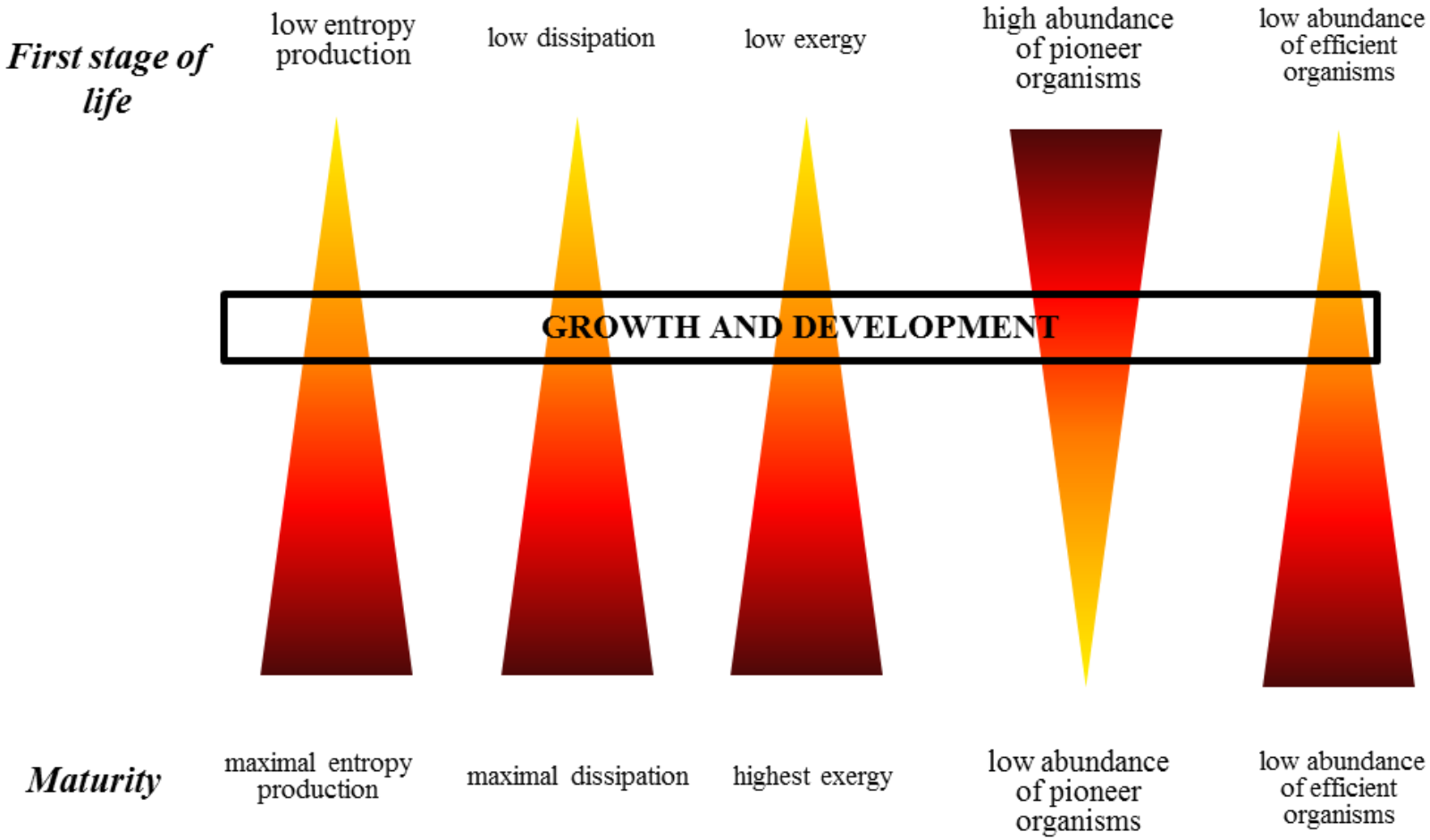


Figure II-2: Summary diagram of the growth and development of ecosystems.

During the process of maturation of an ecosystem, this review once again points out that the diversity as well as the trophic organization undergo changes. The two following parts analyse how diversity and flow organization can influence ecosystem stability, apprehended along the concepts of resilience, persistence, resistance and robustness (box 1).

Box 1: Some concepts of stability

In ecology, every authors have not the same definition of the stability and thus 163 different definitions for 70 concepts of stability have been listed (Grimm and Wissel, 1997). The fact that the same terms are often used for different things hampers understanding and distorts conclusions. Furthermore, the diversity-stability relationship can change according to the definition chosen for a given mechanism (Ives and Carpenter, 2007). In this paper, we focus on four concepts of stability and use one definition for each concept:

- Resilience is the speed with which a system returns to the equilibrium state after a perturbation (De Angelis, 1980; Pimm, 1991). A long return time corresponds to a low resilience. The resilience of a community depends on the least resilient species (the slowest to go back to equilibrium).
- Persistence is the time that a variable stays in the same state before changing to another (Pimm, 1991). Persistence corresponds to a measure of the ability of a system to maintain itself through time (Loreau et al., 2002)
- Resistance is defined as the ability of an ecosystem to maintain its original state in the context of external perturbation (Harrison, 1979). A high resistance corresponds to only small changes (in number and intensity) within an ecosystem.
- Robustness refers to the durability of ecosystem integrity which is responsible for stability. Robustness corresponds to a measure of the quantity of perturbation that an ecosystem can withstand before changing to another state (Loreau et al., 2002). The higher the robustness, the more stable the food web is.

Role of species diversity in ecosystem structure and functioning

1. Species richness increases the resistance of ecosystems

McNaughton (1977) suggested that in general high biodiversity acts to minimize the risk of large changes in an ecosystem in response to environmental perturbations. High richness of species provides a higher stability to the properties of the communities (Cardinale et al., 2012) such as the regulation of the variability of populations (Cottingham et al., 2001) and the stability of the primary production through time (Hector et al., 2010). Experiments about the invasion of species in grassland plots show that local biodiversity reduces the establishment of a variety of invaders, as well as the success of invading plants (Kennedy et al., 2002). Manipulation of diversity in grassland suggests that a high diversity increases inter-specific competition and thus reduces the risk of invasion (Naeem et al., 2000; Hector et al., 2001). Besides, in the context of species extinction, a great number of species with the same function in a community leads to a higher probability that ecosystem properties can be maintained (Chapin III et al., 2000). This hypothesis was tested by experiments and mathematical models with varying numbers of species per functional group (Naeem and Li, 1997). After the extinction of one species, secondary extinction is less likely if the number of species per functional group increases and the number of links remains the same (Naeem and Li, 1997; Borrvall et al., 2000). The presence of a species assures that its role is fulfilled within an ecosystem. If this species disappears, its functional role does not exist anymore unless another species can assume its role.

Food web resistance to species extinction changes depending upon the trophic position of the removed species (figure II-3) (Pimm, 1991; Borrvall et al., 2000). The risk of secondary extinction is higher if autotrophic species are lost than when a member at a higher trophic level is removed. The loss of autotrophic, or basal, species modifies fundamental ecosystem processes and impact severely on ecosystem functioning (Knops et al., 1999). An experimental reduction of plant richness showed that a lower plant diversity leads to a lower diversity of herbivorous insects, of predators and of insect parasites (Knops et al., 1999). Thus autotrophic species impact on higher trophic levels through bottom-up control. However, an analysis on time series data (Myers et al., 2007) and a review by (Baum and Worm, 2009)

showed that the extinction of predators have a degrading effect on oceanic ecosystems. Moreover, the presence of consumers can prevent competitive exclusion. In absence of consumers, a dominant species excludes others plants and thus decreases the diversity of the community (Gough and Grace, 1998). Existence of herbivores in a community leads to the coexistence of the producers (Brose, 2008). In a simple producer community the producer which has the greatest nutrient consumption efficiency dominates and increases its biomass until it out-competes other producers. If herbivorous species are added to this ecosystem, then they feed on the dominant producers and so regulate their biomass. Consequently, for the same amount of nutrients, more species could coexist. The top-down control allows an increase in the diversity of species that can feed on the same resource.

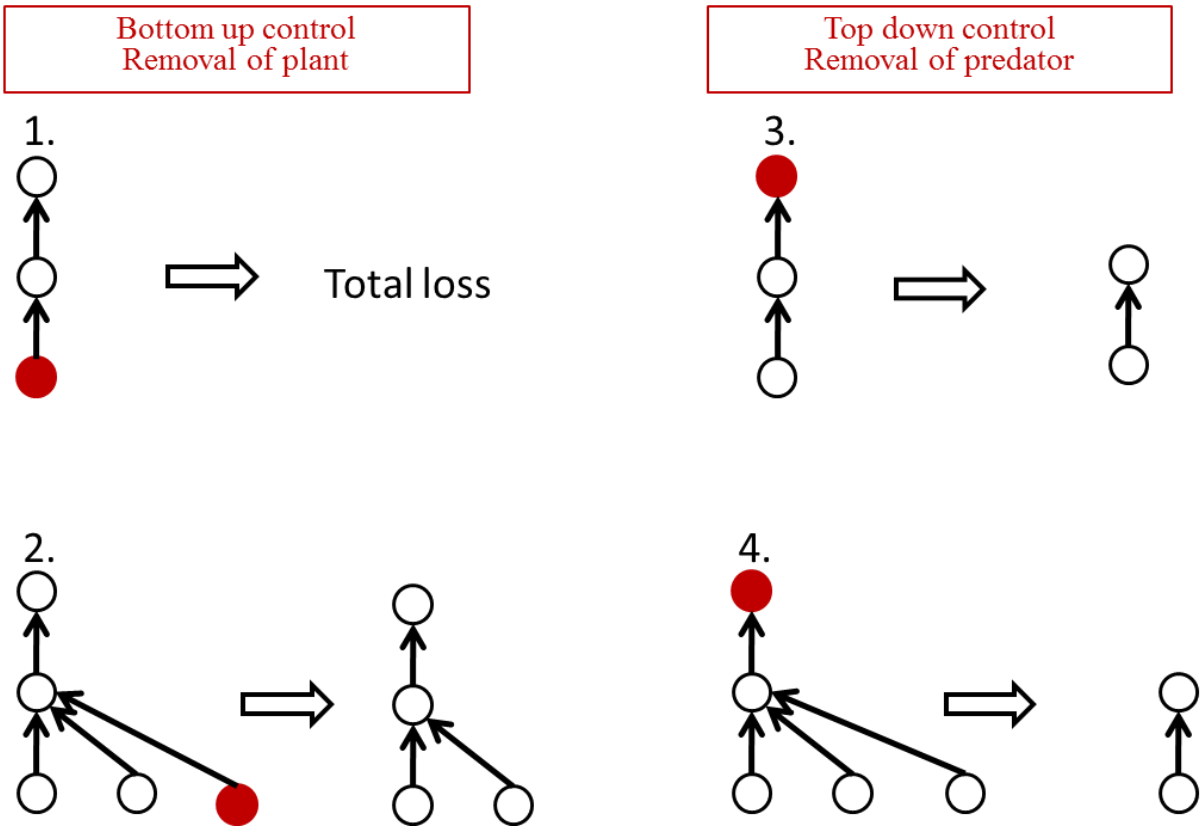


Figure II-3: Diagram representing the variation of food web reaction according to the species removed. Red ring are the removed species. Modified from Pimm, 1991. 1. The autotroph is essential for the chain. 2. The diversity of autotroph species in the consumer diet buffers the extinction of one of them. 3. The extinction of the top predator species leads to a shortening of the chain. 4. The top predator removal leads to an increased pressure of primary consumer, leading eventually to the extinction of some autotrophs.

2. Influence of resources

The community resistance to species invasion is controlled by others factors than diversity. *In situ* experiments showed that diversity explains only 25 percent of the variation of the community resistance to invasion (Levine, 2000). Resources availability plays a central role in the relationship between diversity and the success of species invasion (Stachowicz et al., 2002). Beisner et al. (2006) concluded that resource availability and species richness are important in resistance to invasive species and thus in the establishment of new invasive species in established communities. Diversity has a negative effect, while resource availability has a positive effect on the probability of establishment of invasive species. These results are confirmed by a microcosm study involving microbial communities, which showed that the interaction between diversity and resources supply leads to a positive relationship between diversity and invasions (Jiang and Morin, 2004).

Davis et al. (2000) proposed a fluctuating resources theory to explain the process of invasion. An environment which has a great variability of available and relevant resources is more likely to be invaded than an ecosystem with stable resources (Rejmanek, 1989). The success of species invasion is higher when a perturbation causes an increase in available resources (Davis et al., 2000). Irrespective of environmental conditions, the total use of available resources is crucial to avoid invasive species. The complete use of resources can be facilitated by diversity due to three mechanisms: complementarity or niche partitioning, facilitation and sampling effect (Fridley, 2001). Complementarity avoids the competitive exclusion of plant species, for example in the use of different types of resources, or different use of space or time for the same resource. Facilitation occurs when "a species modifies its environment in a way favourable to a co-occurring species" (Fridley, 2001). The sampling effect is a term used to describe the higher probability to have more productive or more resistant species in a species-rich community. In general, diversity has a buffering effect : i.e. it reduces temporal variation in productivity (Yachi and Loreau, 1999) and has a performance enhancing effect (Yachi and Loreau, 1999; Tilman et al., 2001). Additionally, the temporally averaged mean productivity is higher. Diversity promotes a sustained and high productivity through a sustained and complete use of available resources.

3. Influence of species identity

Each species has a particular trophic behavior, metabolism, etc., that directly influences its physical surrounding and directly and indirectly other species in its ecosystem. Some studies have tried to separate the impact of species identity from that of species diversity on ecosystem processes, especially on productivity (Hooper and Vitousek, 1997; Tilman et al., 1997; Emmerson et al., 2001; Downing and Leibold, 2002). Laboratory experiments on the changes in macrofauna composition showed the significant effect of species identity on ecosystem processes via bioturbation (Solan et al., 2004; Ieno et al., 2006). Field experiments in an intertidal system, (O'Connor and Crowe, 2005) draws the same conclusion. Other studies on manipulation of functional groups showed the importance of species function in the resilience (resistance) of ecosystems (Sankaran and McNaughton, 1999; Wardle et al., 2000). Due to the effect of species identity, the species diversity does not guarantee the resistance of ecosystems to a perturbation. However, a greater probability of resistance is found in more diversified communities because of the sampling effect.

Number of trophic links and interaction strength

Apart from the effects of species numbers and identity, theoretical and field investigations have highlighted the impact of patterns of interactions on the relationship between diversity and stability. The following section brings out some of the salient results from this work.

1. Connectance

1.1. Definition

The topology of a network can be described by several indices (Jordán and Scheuring, 2004), one of which is the connectance, which measures the amount of trophic connections within a food web. The connectance (C) is defined “as the fraction of the total trophic connections that are actually observed in nature” (Paine, 1988) and is characterized by two parameters

$C = t_L / (S (S - 1) / 2)$ (1)

Where S = the number of species, S (S-1)/2= the maximum number of possible binary connections linking species of a community and $t_{L=}$ the number of trophic links within the food web.

1.2. Increased connectance minimizes the risk of change

An increase in the number of connections dissipates the effect of fluctuations of distributed species (MacArthur, 1955) and enhances stability. MacArthur's hypothesis could be explained with the principle of "do not put all of your eggs in the same basket". It is the same principle within food webs: a species should have several connections with different species so that if a prey species disappears, the energetic need of the predator species would shift to another prey species and secondary extinction would be less likely (see omnivory section). In general, extinctions of random species or of the least tolerant species do not have the same consequences (Ives and Cardinale, 2004) and depends on the food web structure that creates compensation. In the case of random removal, compensatory effects decrease the change in species abundance. Successive extinctions of species diminish the resistance of the whole ecosystem due to the decrease in the compensation potential. In the case of extinction of the least tolerant species, the surviving species have a greater average resistance to the stress. A higher connectance increases ecosystem resistance as well as resilience (De Angelis, 1975). Connectance appears to be a good indicator of the food web robustness and indirectly of ecosystem stability (Gilbert, 2009). The robustness of a food web is reduced when the removed species is the most connected (Dunne et al., 2002). Thus the most connected species assures a higher connectance and robustness, from which follows that stability increases with (Dunne *et al.* 2002, Solé & Montoya 2001).

The effect of connectance on the ecosystem stability depends on the pattern of the connections. In the case of random removal, a food web with a high level of clustering (i.e. species are more connected to some species than others) have a higher resistance to the secondary extinction (Montoya and Solé, 2002). On the contrary, a random food web with the same number of species, the same number of links and the same links density is more sensitive to the random removal of species (Solé and Montoya, 2001). Another method

(dominator trees) concluded that a species which plays a central role in energy delivery (the most connected species) more likely causes the extinction of other species if it is removed (Allesina and Bodini, 2004). However, the most connected species do not necessarily have the highest impact on the ecosystem. Indeed, a more detailed study on the hubs (i.e. the most connected species) dividing trophic connections into two kinds of links: functional and redundant (Allesina et al., 2009). Redundant links have no impact on robustness when they are removed. Thus hubs species, which could carry many redundant connections are not necessarily the most important species in the food web.

2. Interaction strengths

More recent studies have also indicated that interaction strengths, and patterns formed by interactions, are important for ecosystem stability. The word "interaction strength" is not used consistently within ecology. The different kinds of interaction strength can be divided into two groups: those that refer to the effect of an individual of one species on an individual (*per capita* effect) or on the whole population of another species near equilibrium (Laska and Wootton, 1998), and those that refer to the impact of changes in properties of one link or a set of links on the dynamics of other species or the functioning of the whole system (Berlow et al., 2004). The first category only refers to the characteristics of a direct link between species. The second one considers the direct and indirect links between species. In this discussion, weak interaction strengths refer to species that have a limited direct effect on another species.

2.1. Importance of weak interactions

Oscillations between a consumer and its resource are lessened if there is a weak interaction for each strong interaction (McCann et al., 1998). This pattern tends to prevent species extinction, thus the resistance of ecosystem is higher. Neutel et al. (2002) supported McCann's (1998) study by showing that weak and strong interaction strengths are organized in trophic loops that give ecosystem stability. A trophic loop is defined as "a pathway of interactions from a certain species through the web back to the same species without visiting other species more than once, hence a loop is a closed chain of trophic link" (Neutel et al.,

2002). The existence of both kinds of interactions is necessary for the stability of ecosystems. For a given number of species, suppression of weak interactions destabilizes the system (Borrvall et al., 2000; Pinnegar et al., 2005). Moreover, if diversity increases, the food web would be stable if and only if prey-predator interaction strengths are mixed with weak interactions (McCann, 2000). Thus, weak interactions act as a stabilizing force in food webs due to their capacity to fluctuate or change within ecosystems.

2.2. Mixing weak and strong interactions provides a higher resistance

A structure with both weak and strong interactions gives an ecosystem a higher resistance to environmental perturbations. The heterogeneity of interactions modifies the dynamics of an ecosystem and gives stability to food webs (Rooney et al., 2006). Through a theoretical analysis, illustrated by examples of food web models, Rooney et al. (2006) characterized pathways by their turnover rate and showed that a consumer integrates fast pathways and slow pathways. The turnover rate (production/biomass ratio) of a consumer is linked to the interaction strengths with its prey items. A fast flow (short turnover) is dependent on many strong interaction strengths as opposed to as a slow flow. Rooney's model (2006) showed that the asymmetry of flow (fast and slow flows) brings stability to the model. A consumer with weak and strong interactions intensely feeds on the abundant species, regulating its abundance, and only occasionally feeds on other species, whose populations can increase without competition with other species. For example, a great asymmetry is observed in the Gironde estuary (Lobry et al., 2008). Two types of energy pathways were identified one from detritus, the other from primary producers. Through seasons, the same species shift their food resources. In summer consumption relies on primary producers and in winter on organic matter input. The asymmetrical structure leads to an optimal use of resources and guarantees annual stability. Furthermore, some strong flows and several weak interactions for the same consumer bring an adaptive trophic behavior to this consumer in response to quantitative or qualitative changes in resources. Mathematical models suggest that this consumer adaptive food choice gives persistence to an ecosystem (Kondoh, 2003; Loeuille, 2010). Utilizing different food web models, (i.e topology, population dynamics), it was shown that adaptive foraging behavior leads to a great stability (Uchida and Drossel, 2007). Due to its strong and weak interactions, a species can modulate its predation pressure on other species. The

predator adapts its trophic behavior to the available resources. Moreover, the stability (in terms of resistance) depends on the speed in which a predator adapts to his predation pressure (Rooney et al., 2006). The more quickly adaptation takes place, the smaller are the changes within the ecosystem. Thus, an ecosystem can keep all its functions and resist perturbations. McCann and Rooney (2009) by their synthesis of empirical and theoretical papers demonstrated that food webs are composed of adaptable apex consumers (McCann et al., 2005; McCann and Rooney, 2009) with slow and fast pathway influencing the dynamics and the stability of food webs. Most of these ideas are summed up in Table II-1.

Authors	**Tested concept**	**Stability**	**Method**
Influence of structure complexity			
1. diverdity of species			
Kennedy et al., 2002	diversity species	resistance increases	experimental
Brose et al., 2008	diversity species	resistance increases	experimental
Beisner at al., 2006	diversity species +low production	resistance increases	experimental
Naeem and li, 1997	diversity species	resistance increases	experimental
Borrvall et al., 2000	diversity species	resistance increases	model
2. Connectance			
Dunne et al., 2002	connectance	robustness increases	experimental
Solé and Montoya, 2001	connectance	robustness increases	model
Mac Arthur, 1955	connectance	resistance increases	theory
De Angelis, 1975	connectance	resilience increases	model
Influence of the functionning of ecosystem			
Pinnegar et al., 2005	weak interraction	resistance increases	model
McCann et al., 1998	weak interraction	resistance increases	model
Rooney et al., 2006	mixing strong and weak interactions	resistance increases	model
Kondoh et al., 2003	mixing strong and weak interactions	persistence increases	model
Uchida and Drossel, 2007	mixing strong and weak interactions	resistance increases	model

Table II-1: Summary table linking published results, tested concepts and methods to stability. Warnings: the relationship between species diversity and stability depends on the removal species (Pimm, 1991; Borrvall et al., 2000) and the relationships between connectance and diversity depends on the type of species extinction (Ives and Cardinale, 2004). The redundant links have not impact on the robustness of ecosystems (Allesina et al., 2009).

Linking Ecological Network Analysis indices to stability

The quantitative and qualitative concepts described above, and associated tools, are combined within the ENA methodology (e.g. Ulanowicz, 1986, 1997; Ulanowicz, 2004). The following paragraph reviews the state of the art on theories combining emergent properties characterized by ENA indices to the stability properties of resilience and resistance. They mainly imply 3 emergent properties.

1. Cycling

A cycle represents a series of transfers between components in an ecosystem beginning and ending in the same compartment without going through the same compartment twice. From an energetic point of view, Higashi et al. (1993) defined cycling as a transformation of used, non-dissipative energy within an ecosystem.

1.1. Cycling indices

The Finn Cycling Index Finn (1976) gives the proportion of the total flow in a system that is recycled . It corresponds to the ratio between the sum of flows involved in cycling and the Total System Throughflow. The Total system Throughflow corresponds to the total flow into or out of each compartment (Fath et al., in press). However in the literature the FCI is often calculated by Tc/TST where Tc is the amount of system activity devoted to cycling and the TST corresponds to the input and output for each compartment. This difference in the calculation underestimates the value of the FCI (Fath et al., in press), the some precautions must be taken in ecosystem comparison. It was extended by Patten and Higashi (1984) to take into account the storage (i.e. delayed flows) in compartments, due to its great importance in the generation of network properties (Patten and Higashi, 1984). Cycling and storage change the properties of ecosystems, especially the ratio of indirect flows to direct flows and thus the availability of energy for all trophic level (Patten et al., 1990). The Finn Cycling Index was corrected a second time because it did not take into account every flow implicated and generated by cycling (Allesina and Ulanowicz, 2004). Thus Allesina and Ulanowicz proposed

a new index called Comprehensive Cycling Index (CCI), which gives the real importance of cycling. Flows involved in cycling are estimated as the difference between the sum of flows and all simple paths (i.e path without repeated compartment).

Detritus is an essential compartment to consider in a study of cycling. Flows from or to the detritus pool contribute strongly to the total cycling of ecosystems (Fath and Halnes, 2007). Detritus is a source of energy and nutrients for living organisms in almost all food webs (Moore et al., 2004). Cycling allows the use of elements that would otherwise be lost from the system. Due to this capacity it can modify the physical-chemical characteristics of ecosystems and in an indirect way impact species. The greater the amount of cycling in an ecosystem, the more important the indirect effects (Fath and Halnes, 2007). Thus, at the time of food web construction, it is important to consider detritic compartments. These compartments must be well described and detailed (i.e. they must not be aggregated). Studies show the importance of detritus in food web dynamics (Allesina et al., 2005), and in the calculation of system indices (Allesina et al., 2005).

1.2. Cycling and stability

Cycling seems to increase the resistance of ecosystems. Cycling gives ecosystems a way to optimize exploitation of their environment. Cycling allows a better use of energy and matter introduced into the system (Higashi et al., 1993), by transforming energy bound to matter from non-living states into a form, which can pass through compartments again. When perturbations occur, cycling reduces impacts on the ecosystem by acting as a buffer against large changes and can increase the ability of the ecosystem to resist changes. However, the effect of a perturbation that disrupts the cycling process can be questioned. For instance, if nitrification is reduced by a perturbation, the cycling of nitrogen is disturbed with severe consequences on the ecosystem.

Cycling modifies the resilience of the ecosystems. Some studies have shown an increase in the resilience while others suggested a decrease in resilience at high cycling levels. The resilience of ecosystems increases with cycling in the case of a modification of nutrient concentration within ecosystems (Loreau, 1994). Moreover, a sensitivity analysis on a pelagic

food web model showed that cycling increases the resilience of ecosystem (Hosack and Eldridge, 2009). Vasconcellos et al (1997) applied a dynamic model (Ecosim) on 18 previously constructed marine mass balance (Ecopath) models to study the effect of an increase in fish mortality on the ecosystem stability. Results suggested that higher cycling (a high FCI) decreases the return time to the initial state after a perturbation (Vasconcellos et al., 1997). However, according to food-web model mathematical analysis, resilience falls with an increase in number of cycles within the system (De Angelis, 1980). From his perspective, the behaviour of resilience time appears to be linked to the time energy or matter stays within the system (De Angelis, 1980). Cycling increases the residence time of nutrients within the system (Herendeen, 1989). Longer the residence time is, less resilient the system is (De Angelis 1980). Marleau et al. (2010) moderated previous studies, showing that the resilience depends on the type of recycled elements. The cycling, of detritus issued from consumers favours resilience, whereas cycling issued from autotrophs decreases resilience (Marleau et al., 2010).

The relationship between cycling and stability is not always simple. Indeed, Pomeroy (1970) and Jordan (1972) showed that the recovery time of a system with high cycling is slower due to the limited import of nutrients. Baird et al. (2008, 2011) have clearly shown that the behaviour of energy (or carbon) differs substantially from that of biogeochemical networks in which currencies such as nitrogen and phosphorus are used. The high redundancy values calculated for N and P models could buffer perturbations. Considering these studies, cycling indices alone are not sufficient to determine the resilience of a system. Models with different levels of limiting nutrients show that the relationship between cycling and stability depends on nutrient enrichment. At a high nutrient level, resilience is higher with cycling, whereas it is the opposite at low nutrient levels (Marleau et al., 2010).

2. Omnivory

An omnivore is a species which feeds at more than one trophic level (Pimm and Lawton, 1978). For example, an omnivorous predator feeds on both autotrophs and a variety of heterotrophs (figure 4). Omnivory is often associated with the notion of redundant

connections (Williams and Martinez, 2004). Redundant connections correspond to parallel pathways between two compartments (figure II-4).

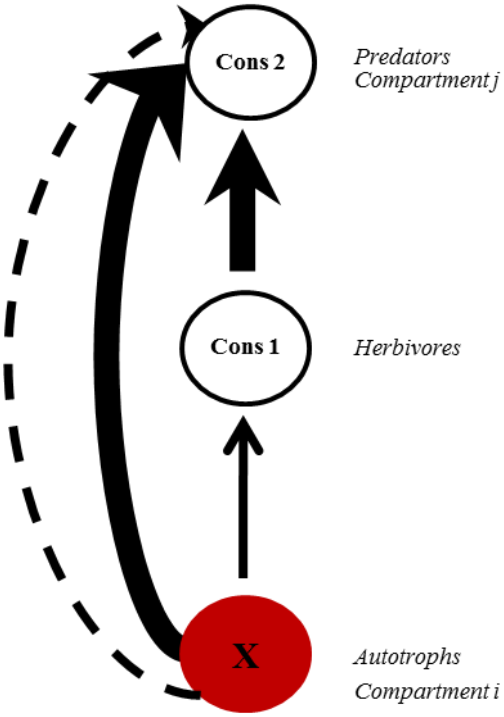


Figure II-4: Diagram showing how omnivory is defined and leads to direct as well as indirect pathways. The rounded solid arrow refers to the direct pathway between the compartments and dotted arrows correspond to the indirect pathway. The largest rounded solid arrow corresponds to omnivorous links. The *cons 2* is an omnivorous species, it feeds on two trophic levels: *cons 1* and *X* linking directly *cons 2* and *cons 1* and *cons 2* and *X*. The *cons 2* is indirectly linked with *X* through *cons 1*.

2.1. Advantages of omnivory

Omnivory gives trophic flexibility to an ecosystem. After an extinction of a species, polyphagous species (including omnivores) could feed on other resources. This ability reduces the risk of extinction of these species (MacArthur, 1955). Moreover, changes in trophic interactions allow a better exploitation of ecosystem resources (Michalski and Arditi, 1999). Omnivorous predators can adapt their predation pressure to the abundance of their prey. Omnivorous species can change their impact on species; specialized predators do not

have this ability. Trophic specificity (monophagy) leads to a stronger prey-predator interaction (Montoya et al., 2006). Consequently, when the prey of a monophagous predator goes extinct, it feeds intensively on one or some alternative species. The indirect effects of this change are also strong and the initial effect of the perturbation (extinction) of the community is increased (Fagan, 1997).

Omnivory gives the ecosystem a better control of changes in the event of environmental perturbations. Being linked to different trophic levels, omnivorous species allow a faster response of ecosystems to a perturbation (Fagan, 1997). Omnivores are usually at the third or higher trophic levels (i.e. correspond to predator levels). If a perturbation affects low trophic levels, omnivorous species, which are directly connected to this level, can react quickly. A specific predator must wait till the perturbation reaches it, thus the response time could be longer. On the other hand, omnivory increases the resistance of ecosystems due to its ability to buffer oscillations in ecosystems. Mathematical models and experiments demonstrate that omnivory changes the pattern of trophic level abundances in response to enrichment (Diehl and Feißel, 2000). Omnivorous species regulate the abundance of other components of ecosystems and allow the coexistence of all components.

2.2. Omnivory and stability

Most recent studies conclude that omnivory has a stabilizing role. The addition of omnivory to a simple food chain (three species food chain) locally stabilizes the food web (McCann and Hastings, 1997). These authors suggested that an unstable equilibrium becomes a stable equilibrium with the addition of omnivory. A food web model with three trophic groups (primary producers, primary consumers and secondary consumers) suggests that omnivory stabilizes the food web in the context of loss of species (Borrvall et al., 2000). Indeed, omnivory avoids secondary extinctions and it also increases ecosystem resistance. Furthermore, omnivory increases the resilience of ecosystems in the context of manipulation of species density (Fagan, 1997). Emmerson and Yearsley (2004) tested ten food webs with a Lotka-Volterra system, and their results showed that weak interactions enhanced ecosystem resilience only when omnivory is present. Based on this work, omnivory decreases the return time to equilibrium state after a perturbation.

Nevertheless, there is no simple conclusion on the role of omnivory in ecosystem dynamics.

The effect of omnivory, as either a stabilizing or a destabilizing factor, depends on the system from which it derives (Vandermeer, 2006). Three different forms as parent systems were tested: tritrophic chain, competition (a same resource for two predators) and polyphagy (two resources for the same predator) (Vandermeer, 2006). Omnivory does not have the same effect on stability in each of these systems. Furthermore, omnivory that is built within the same food chain (redundancy like figure 4) does not contribute to the stability of food webs (Allesina et al., 2009). Omnivory, which corresponds to redundant connections, can be removed in this case without consequence on the ecosystem robustness to secondary extinction.

3. Ascendency

The notion of Ascendency was formulated by Ulanowicz (Ulanowicz, 1980), who aimed to derive from information theory a metric that takes into account both growth and development of ecosystems. The calculation of Ascendency considers two system metrics, namely the Total System Throughput (TST) and the Average Mutual Information (AMI). The TST describes the size of the system as the total sum of values of flows that pass through the system, whilst the AMI corresponds to the degree of specialization in a flow network (Ulanowicz, 2004). Ascendency is considered as a measure of activity and organization within the system (Ulanowicz, 2000). It is sensitive to environmental changes and ecological successions (Mageau et al., 1998). For example, oligotrophic lakes show a higher Ascendency, due to a higher AMI value, than eutrophic lakes (Salomonsen, 1992). However, eutrophication causes an increase of Ascendency in ecosystems due to a rise of TST compensating for a fall of the AMI value (Ulanowicz, 1997). During maturation, ecosystems develop in order to increase their activity (i.e. the TST) and the storage of energy (Jørgensen and Fath, 2006), while their structure also evolves towards an increase in Ascendency (Ulanowicz et al., 2006).

3.1. Relative Ascendency

A complementary notion to Ascendency is the relative Ascendency, which corresponds to the ratio between Ascendency and Development Capacity (DC). The Development Capacity describes the maximal possible value of Ascendency that the specific ecosystem could reach. The relative Ascendency excludes the effects of the TST, thus it measures the degree of system order (Ulanowicz, 2009) and allows comparison between ecosystems (Heymans et al., 2002). The difference (1- relative Ascendency) allows estimating the reserves in an ecosystem and is called overhead (φ). To secure sustainability, organized and non-organized parts of ecosystems should be in equilibrium (Ulanowicz et al., 2009). Indeed, an ecosystem's reserve and its capacity to change determine the ability to outlast and resist new perturbations. Ascendency evaluates the organised part of ecosystems, which is considered as the efficient part of the ecosystem. On the contrary, overheads represent the fraction of the development capacity that does not appear as organized structure (Bodini and Bondavalli, 2002) and quantifies how the system is inefficient (Baird et al., 2008). They represent system inputs, outputs, dissipation, and functional redundancy (Baird and Ulanowicz, 1989). Systems with a relative Ascendency value equal to zero or one are systems at thermodynamic equilibrium. Thus ecosystems present a value of relative Ascendency between zero and one (Ulanowicz, 2009). Ranking ecosystems on the basis of their maturity states, Christensen (1995) showed that overheads tend to increase during the maturation of ecosystem and the relative Ascendancy decreases with maturity, which is in conflict with hypothesis of Ulanowicz (1986) suggesting that relative Ascendancy increases with maturity. Overheads take into account dissipation that is expected to increase during maturation of ecosystems and can explain the strong positive correlation between overheads and maturity. To eliminate dissipation effect on the relation maturation and relative Ascendency, the internal Ascendency is considered (A_i). Internal Ascendency and internal development capacity (DC_i) refer internal flows alone and exclude transfers across the boundaries of the ecosystem. Thus, the difference between DC_i and A_i is equal to the functional Redundancy (R, as defined in paragraph 4.2.) of the ecosystem. An A_i/DC_i ratio which does not much differ from A/DC ratio demonstrates the low dependence on external connections (i.e. connections between an ecosystem with its environment) (Baird et al., 1991; Baird et al., 2011). For example, a comparative study of four tidal estuaries measures an A_i/DC_i ratio which did not much differ from A/DC ratio, demonstrated the low dependence on external connections of these four tidal estuaries (Baird

and Ulanowicz, 1993). Contrary to this example, the food web of the Gironde estuary that is based on detritus coming from riverine and terrestrial inputs (Lobry et al., 2008), shows a great difference between A/DC ratio (48%) and A_i/DC_i (17%).

3.2. Ascendency and stability

It is important to distinguish two types of stability to understand the role of Ascendency (Ulanowicz, 2003). A system with a high internal stability corresponds to a system with sufficient internal constraints to allow a highly organised structure. These systems are characterized by a high Ascendency due to high mutual information (AMI). The internal constraints protect the system structure against changes arising within the ecosystem, but leave the ecosystem vulnerable to external perturbations. Extremely constrained ecosystems are senescent and can collapse when they have to confront new perturbations (Ulanowicz et al., 2009). In the case of external perturbations, higher overhead helps to counterbalance the effects of perturbations. Thus these ecosystems show a low Ascendency, or a strong redundancy (many parallel connections) and high overhead in general. Moreover an increase of Ascendency decreases ecosystem resilience, as the return time is longer (Virgo et al., 2006). Analyses of empirical data confirm this conclusion (Heymans et al., 2002; Heymans et al., 2007). To summarize, a stable system needs a sufficient amount of both system organization and overhead (Ulanowicz, 2003). The reserves of an ecosystem are critical for the sustainability of ecosystems (Ulanowicz et al., 2009). They lead to possible adaptive ecosystem behaviours. Due to overheads, especially redundancy, the ecosystem structure can evolve to counter the effects of external perturbations. The balance between Ascendancy and overhead seems to give resistance and resilience to ecosystems. Section 5 is summarized in table II-2.

	Maturity	*Resistance*	*Resilience*
Cycling	increases	increases	increases
Omnivory	increases	increases	increases
Ascendency	increases	increases the resistance of internal perturbations	decreases

Table II-2: Summary table showing the most commun link between Cycling, Ascendency or Omnivory and resilience or resistance, depending on the context and considered models.

Conclusions

The focus of the last decades on stability concepts and theories has been on various patterns of ecosystems: from the organization of species diversity in trophic networks, through the characterization of the topology of binary trophic networks, to flow-weighted food-webs properties. The diversity-stability debate has not resulted in any generalization, as variations in species composition and resources availability can change the conclusions based on food web structure alone. Increased connectance or the association of strong and weak interaction strength are generally considered as increasing system resistance. Similarly, ENA indices have been subjected to debate. The literature gives contradictory conclusions about the connections between stability properties and indices such as omnivory, cycling and Ascendency. However, some general features can be identified (table II-2). For a young ecosystem, organization is low, and vulnerability to perturbations is high. However, its resilience is high, due to quick development of trophic plasticity. During maturation of ecosystems, omnivory, Ascendency and cycling increase, bringing ecosystems to better resistance. Balance between these three structural features can lead to a better resistance and resilience of ecosystem due to the introduction of reserves and fast compensation.

ENA indices are powerful tools to identify different ecosystems states (Baird, 2011) and to differentiate ecosystem structure under different conditions (Dame and Christian, 2007), but the generalization of a link between emergent ecosystem properties and stability remains tenuous. The first task to be done is a modification of these indices to complete this generalization and fully document how ENA indices inform local stability. Moreover, in a context of ENA application to environmental management, the local stability study in not fully adapted and long-term press perturbations should also be addressed, with a special

attention to alternative stable states. Such long-term stability studies are crucial in the case of species conservation. One way of assessing the relationship between ecosystem change (for the better or worse) is to compare selected ecosystem properties derived from ENA (such as the Average Mutual Information, Flow Diversity, The Ascendency/Development capacity ratio) over temporal scales measurable declines in these would indicate a regression in system development, function and perhaps health. An increase, on the other hand, would indicate an improvement in ecosystem function and development. The challenge is to link ENA indices to the impact of press perturbations. Experiments are necessary to explore how the emergent ecosystem properties are linked to the existence of alternative states. Understanding the acute mechanisms of shift, how to avoid this shift and how to reverse this process is one of the big challenges of management (Hughes et al., 2010).

ACKNOWLEDGEMENTS

The authors thank Robert E. Ulanowicz for critical reading and improvement of the manuscript, Elisa Thébault for her helpful comments, and Delphine Leguerrier and Alain Franc for initial discussions on stability. Blanche Saint-Béat Ph.D. work is financed by the CNRS and Région Poitou-Charentes. This work is a contribution to the COMPECO project (Comparison of food web properties of semi-enclosed soft-bottom littoral ecosystems: identification of human and environment forcing variables, consequences for stability, in order to define ecosystem health indicators) financed by the programme PNEC/EC2CO, to the ANR-blanche VASIREMI (Trophic significance of microbial biofilms in tidal flats), and to the Procope Hubert Curien programme.

Chapitre 3

The mean function provides robustness to linear inverse modelling flow estimation in food webs: a comparison of functions derived from statistics and ecological theories.

Blanche Saint-Béat[1], Alain Vézina[2], Raghnild Asmus[3], Harald Asmus[3], Nathalie Niquil[1,4]

[1] Université de la Rochelle-CNRS, UMR 7266, Littoral Environnement et Sociétés (LIENSs), La Rochelle, France

[2] Bedford Oceanographic Institute, Dartmouth, Canada

[3] Alfred Wegener Institute, Wattenmeerstation Sylt, List, Germany

[4] CNRS, UMR 7208 BOREA, Laboratoire BioMea (FRE 3484), Caen, France

La fonction moyenne apporte de la robustesse à l'estimation des flux trophiques par la modélisation inverse linéaire : comparaison des fonctions dérivées des statistiques et des théories écologiques.

La modélisation inverse est un outil très performant et précis pour estimer la valeur des flux manquants dans les réseaux trophiques. Des avancées méthodologiques récentes ont perfectionné la méthode par l'utilisation d'un algorithme de Monte Carlo en chaîne de Markov (Van den Meersche, 2009) permettant l'échantillonnage aléatoire de l'espace des solutions. A la sortie, une distribution de probabilité est obtenue pour chaque flux. Dans un contexte de comparaison d'écosystèmes, cette méthode permet de développer des tests statistiques pour comparer le fonctionnement des écosystèmes via le calcul d'indices écologiques de réseaux (ENA) sur l'ensemble des solutions obtenues. Cependant pour certaines analyses plus précises (e.g. mise en place des chaines de Lindeman) une seule solution par flux est nécessaire. Par défaut, la moyenne de l'ensemble des solutions pour chaque flux est utilisée comme solution. Cet article a pour objectif de déterminer si la moyenne est réellement la meilleure fonction à utiliser lorsqu'une seule solution pour chaque flux doit être considérée, et compare une série de fonctions statistiques et écologiques. Ces dernières étant choisies en fonction des théories reliant les indices ENA à la maturité des réseaux trophiques (chapitre 2).

Quelle est la fonction, écologique ou statistique, la plus pertinente pour sélectionner un unique jeu de valeurs pour les flux d'un réseau trophique ?

Par une stratégie de dégradation /reconstruction d'un jeu de données caractérisant les réseaux trophiques des différents habitats d'un écosystème très bien décrit : la baie de Sylt- Rømø, différentes fonction sont testées pour choisir une unique solution pour chaque flux.

Les fonctions écologiques sont issues des conclusions du chapitre précédent, étudiant la stabilité des écosystèmes en lien avec leur maturité par l'intermédiaire des indices ENA.

Les résultats confirment que nous recommandons d'éviter l'utilisation des fonctions basées sur la médiane et la minimisation des moindres-carrés des flux. Si certaines fonctions écologiques donnent de bons résultats (la meilleure étant l'omnivorie), la fonction de la moyenne apparait comme celle qui estime le mieux les flux manquants du réseau trophique quelle que soit la quantité d'information considérée pour la construction du modèle.

Ce sont donc les résultats obtenus par application de la fonction de la moyenne qui seront utilisés pour présenter les flux estimés et des indices ENA, lorsque ces derniers ne peuvent pas être appliqués à l'ensemble des solutions estimées (plusieurs centaines de milliers pour chaque modèle), dans les articles sur la vasière de Brouage (chapitres 4 et 5).

Un travail complémentaire, bâti sur les mêmes simulations, sur l'effet du type de flux pris en compte pour la construction des modèles est en cours et donnera lieu à des recommandations sur les flux à estimer en priorité, lorsqu'on souhaite construire un modèle de réseau trophique (voir Discussion générale).

Abstract

Quantitative estimates of carbon flows within food webs are increasingly viewed as essential to progress on a number of questions in basic and applied ecosystem science. Inverse modelling has been used for more than 20 years to estimate flow values for incomplete data sets. Monte Carlo Markov Chain linear inverse modelling calculates a probability density function for each flow. Among this distribution of possible values for each flow, the mean is generally chosen when a single solution is needed. The objective of the present study is to compare the robustness of the result when using the mean function, compared with 2 other statistical functions and 7 ecological functions derived from ecological theories on ecosystem maturity. The performance of the various functions was tested by comparing their accuracy in reconstructing a complete data set, the marine food web of Sylt-Rømø Bight, with known flows systematically removed. This was carried out on seven habitats and for 4 levels of degradation of the information. The robustness of each function was measured by comparing the estimated values of flows from inverse modelling after degradation with values from the original, complete data set. The analysis of results shows that the error of the estimated flows increases with the degradation of information, independent of the considered function. Two functions, the mean and the System Omnivory Index, provide more precise results than the others independent of the level of degradation of the information considered. The mean had the least impact on the reconstruction of food web flow values and on their organisation described by ecological network analysis indices.

Introduction

For several decades researchers have been studying the evolution of ecosystems, their structure and their functioning (e.g.Odum, 1969; Ulanowicz, 1980; Dunne et al., 2002). In the current context of the growing impact of human activities on the environment, this field of research has become increasingly important. Indeed, it is essential to understand what type of structure and organization support the sustainability of ecosystems. This issue is not only theoretical but is societal as well, and it is gaining interest from politicians and managers. For instance, the Marine Strategy Framework Directive (MSFD) has been commanded by the

European Commission to define what is meant by a healthy ecosystem as an essential step towards sustainable environmental management.

Ecosystems are complex entities that combine biological, chemical and physical processes. Food webs are models representing transfers of energy and matter in an ecosystem between organisms when they are eaten or feed on others organisms (Pimm, 1982). Because biological communities mainly are structured according to their trophic links (Elton, 1927), food webs encompass the interactions and the processes structuring ecosystems (e.g. Leguerrier et al., 2004; Fath et al., 2007; Gascuel et al., 2008).Food web models help to describe the functioning and emergent properties of ecosystems. Hence, food webs are key to understanding how ecosystems work and provide a powerful tool to analyse them.

Food webs have been studied qualitatively using the binary network method, i.e. the presence or the absence of flows between organisms (e.g.Pimm, 1991). Many important insights have been gained by this approach; however, many important properties of ecosystems, such as recycling and dynamic behaviour, remain out of reach of these techniques. It has been suggested, for example, that quantitative analysis of flows is essential to elucidate the global stability properties of ecosystems (Kondoh, 2005b; Link et al., 2005). Such quantitative descriptions require estimates of the flows of matter or energy among the nodes of the food web at the highest level of detail possible. However, such complete *in situ* data sets are rarely available. Usually, only some of the flows and species are known, and it is common that the data concerning low trophic levels are missing (van Oevelen et al., 2010). In practice, the ratio of unknown to measured flows is around 4:1 (Vézina and Pahlow, 2003). One of the challenges of methodological research on food webs is therefore to find a universal and systematic method that would allow reconstructing the unknown flows with the least sensitivity to information gaps.

Inverse modelling, based on matrix calculation of linear equations (van Oevelen et al., 2010), reconstructs flows that are not measured *in situ* (Vézina et al., 2004). Inverse modelling originated in physical oceanography and was first applied to such under-determined (i.e. more unknowns than available data) biological systems by Klepper and Kamer (1987). Later, Vézina & Platt (1988) proposed the least-squares inverse modelling method on which present

methods rely. Typically in inverse modelling, measured flows are expressed as equalities and the constraints as inequalities that bound a multidimensional space in which all solutions for the unknown flows are assumed to lie. The number of unknown flows being higher than the number of equalities (including measured flows), the number of solutions that fulfils the equalities and biological constraints is infinite. Least-squares inverse modelling (Vézina and Platt, 1988) selects the solution with the minimal sum of squared flows from this solution space.

The minimization of the quadratic norm (i.e. the least square solution) is based on the parsimony principle derived from Occam's razor (Vézina and Platt, 1988). It suggests that among a set of solutions the simplest one is always the best. This approach was used in many aquatic ecosystems including pelagic (e.g.Vézina and Platt, 1988; Niquil et al., 1998; Marquis et al., 2007; Grami et al., 2008; Forest et al., 2011) and benthic communities (e.g. Eldridge and Jackson, 1993; van Oevelen et al., 2006b; Garcia et al., 2011). Nevertheless, the minimization of the quadratic norm was often criticized due to its consequences on the reconstruction of the networks and on ecological interpretation (e.g.Eldridge and Jackson, 1993; Niquil et al., 1998; Donali et al., 1999; Kones et al., 2006). Recent studies have quantified the biases induced by the Least Square criterion on the estimation of several Ecological Network Analysis (ENA) indices (Johnson et al., 2009; Kones et al., 2009).

Kones (2006) improved food web inverse modelling by a random sampling approach. This new method, Monte Carlo Linear Inverse Modelling (MC-LIM), instead of calculating a single best solution, attempts to decipher the solution space in its entirety by randomly selecting the solutions that fall within that space (also called a polytope). The MC-LIM algorithm is extremely inefficient in that it typically requires many tries before finding a solution within the bounds of the polytope (Kones et al., 2006). Van den Meersche et al. (2009) resolved this problem by developing a simple technique to reflect proposed solutions inside the walls of the polytope until one was found that fell within all the bounds. This method, called Monte Carlo Markov Chain Linear Inverse Modelling (MCMC-LIM), is the most common method used now to reconstruct food webs by determining the likelihood distributions of the flows rather than unique estimates.

These likelihood distributions can be used to assess the precision of the reconstructions and allow statistical comparisons across ecosystems or ecosystem states (Grami et al., 2011). Nevertheless, it remains useful also to be able to summarize each flow by one estimate that we believe is representative of its likelihood distribution and then derive a complete flow network with the unique estimates for each flow. The most obvious estimator is the mean and is generally used to summarize the multiple solutions which are proposed by the MCMC-LIM method (Kones et al., 2006; Gontikaki et al., 2011; Grami et al., 2011). However, other functions, either from statistics or ecology, could be used to select a single solution from each flow likelihood distribution calculated by the MCMC-LIM method. Some ecological indices have been proposed to reflect states that ecosystems tend towards; therefore, it is not inconceivable that a solution derived from a global ecological index could better represent the structure of the ecosystem than a simple statistical construct like the mean or minimum norm. We predict that reconstructions of unique flow networks based on different estimators or indices will behave differently when the level of information available to constrain the reconstruction changes, that is, when we progressively remove data from an initial best informed state. We would expect further that a more representative estimator of unique ecosystem structures will be more robust to such changes in available information, that is, its estimates of the flows will remain closest to the estimates derived with the most available data as data are progressively removed. In this study, we investigate how different methods to extract unique flow networks from MCMC-generated likelihood distributions behave as the available data are degraded from the most fully informed state.

For this study, we took advantage of the availability of a fully determined food web model (one in which all flows were known) and randomly replaced known flows with inequalities at four levels of information (known: unknown ratios). This allowed tests of the performance of the least square solution (Vézina and Platt, 1988) and a variety of goal functions for selecting a unique solution from the MCMC-LIM distribution. We estimated the robustness of each function by comparing the initial values of the flows with the estimates of the flows generated by each goal function as the information is degraded. The criteria used to determine the quality of estimation of flows by each function were (1) respect of mass balance, (2) percent of error, (3) root mean square (RMS) error, which lessens the effect of small flows, (4) Spearman correlation to verify the organisation of flows, and (5) ENA indices, to determine the impact of the goal functions on the structure of reconstructed food web. Statistical tests

were used to test the hypotheses that degradation of information did not influence the distribution of percent error and that RMS error was independent of the goal function.

Material and methods

1. Study area

The Sylt- Rømø Bight, located at the border between Germany and Denmark (54°52' to 55°10'N, 8°20' to 8°40' E) (Baird et al., 2004a), is a part of the Wadden Sea. The bay is separated from the North Sea by the islands Rømø and Sylt to the west, and is bounded by the mainland of Denmark and Germany in the east and by both a rail way dam and a street dam connecting both islands with the mainland to the South and North, respectively. Water exchange with the North Sea occurs only through the small opening (2.8 km) between the two islands. The bay covers a surface area of 404km² and has a. mean depth of 4.2 meters. Salinity varies from 28psu to 32psu and temperatures from -1°C in winter to 20°C in summer (Baird et al., 2004a). The water is renewed every 19 to 29 days (Baird et al., 2004a).

2. Description of data used

The data set used in this study comes from Baird et al. (2007) and describes the food webs of the 8 habitats of the Sylt- Rømø Bight: *Arenicola* flats, Muddy sands, Mudflat, Sandy shoals, Sandy beaches, Mussel beds and Sparse and Dense *Zostera noltii* beds . These food webs are composed of 56 living compartments and 3 non-living compartments. Baird et al. (2007) described the community composition and quantified the biomass, production, respiration, consumption, diet composition and egestion for each species or species group of the Bight. The biomasses were measured *in situ* for each compartment and given in $mgC.m^{-2}$. The data set of Baird et al. (2007) is a mix between field measurements and values estimated by empirical formulae based on local biomass and adapted to the local species for the production, respiration, consumption and excretion-egestion, expressed in $mgC.m^{-2}.d^{-1}$. The production and respiration of autotrophs were measured in the field. Production of other compartments

was estimated from P/B ratios adapted to the local species using their local biomass (Baird et al., 2004a). Respiration of other compartments was estimated by *in vitro* measurements for macrofauna, by allometric relationships for fishes (Baird et al., 2004a) and birds (Aschoff and Pohl, 1970; Kersten and Piersma, 1987; in Scheiffarth and Nehls, 1997) and from P/R for meiofauna (Witte and Zijlstra, 1984). Excretion of macrofauna was estimated by experiments and the excretion-egestion rates for other compartments were determined by rates in the literature or by the difference between consumption and assimilation. The consumption of heterotrophic organisms was defined as the sum of production, excretion and respiration (Baird et al., 2004a), except consumptions of fishes (Mann, 1965) and birds (Scheiffarth and Nehls, 1997)which were estimated by empirical formula .

3. Model construction

To convert the complete data set into a basis for testing the different goal functions for selection of a unique solution from MCMC-LIM, we first determined the topology of the food web to be tested and then created different experimental units with different levels of uncertainty. The first step for inverse modelling is the determination of the topology of the food web, i.e. the compartments and the flows that constitute the food web. In order to facilitate the manipulation of the food web models, the number of compartments was reduced by aggregation. Aggregation is a process of grouping some compartments together into a single one according to a specific criterion. Here, species with the same diet and the same method of predation were grouped together. Baird et al. (2004), following this criterion, reduced the food web model from 59 compartments to 18 compartments which are listed in Table III-1. This type of aggregation by nutrition mode is the one that least affects the structural and functional properties of food webs (Johnson et al., 2009). Because species composition varies between habitats in the Sylt- Rømø Bight, the seven models (the mussel bed habitat was not considered) do not contain the same number of compartments. The sandy beaches and sandy shoals models contain 11, the *Arenicola* flats, Muddy sand and Mudflats have 13 compartments and the Dense and Sparse *Zostera noltii* beds have 16 compartments.

Compartments	Abbreviations
Phytoplankton	PHY
Microphytobenthos	MPB
Macrophytes	MCP
Free living bacteria	FLB
Benthis grazers	BGR
Benthic deposit feeders	BDF
Suspension feeders	SUS
Benthic omnivorous	BOM
Benthic fishes	BFI
Carnivorous birds	CBR
Herbivorous birds	HBR
Sediment bacteria	SEB
Meiofauna	MFB
Suspended carbon	SUC
Sediment carbon	SEC
Dissolved organic carbon	DOC

Table III-1: Table listing the name of the compartments and their abbreviation included in the Sylt-Rømø Bight food webs.

For inverse modelling, once the topology of a food web model is determined the known values are organized as linear equalities and unknown values are constrained, when possible, using linear inequalities. The linear equalities were constructed by first imposing mass balance conditions on the flows through each compartment, corresponding to the difference between the sum of the inputs (e.g. ingestion) and the sum of the output (e.g. respiration, egestion). For the compartments which are at steady-state, the mass balance is equal to 0. Next, the quantitative information, which corresponds to observations or field measurements (Baird et al., 2007), is added to the model as equalities. The mass balance and the quantitative information are expressed as linear equations $A * x = b$. The matrix A expresses the mass balance and the field observation as a combination of coefficients of the carbon flows, x represents the flows of the food web, and b is a numerical vector containing the values of the known flows (Vézina, 1989).

4. Inequalities

To obtain more realistic values for unknown flows, biological constraints are added in linear inequalities of the form $G * x \leq h,$ .where the matrix G contains the coefficients of the biological constraints (Vézina, 1989), x represents the flows of the food web, and h is a

numerical vector containing the value of the biological constraints respectively. The inequalities are additional information corresponding to the efficiencies or the rates of the biological processes extracted from the literature and they represent the *a priori* knowledge of the network (Vézina and Platt, 1988). Because each flow in the model would be removed in the tests of goal functions, each flow was limited by biological constraints. As explained above (i.e. description of data used), some flows were measured *in situ* and others were estimated by empirical formula or by biological constraints. In order to maintain consistency with the Baird model (Baird et al., 2007), the constraints were developed from the same formulae when possible. The inequalities (listed in Table III-2) concern respiration, consumption and egestion, for all living compartments. Moreover, production was estimated for the macrofauna and the sediment inhabiting bacteria, and export for fishes and for the carnivorous and herbivorous birds. Except for autotrophs and bacteria, inequalities were scaled to the biomass estimates for each compartment.

4.1. Respiration

The limits of the respiration for autotrophs and bacteria were determined from the production. For other compartments, allometric relationships provided the minimal and maximal values of respiration.

The respiration and the egestion of the benthic bacteria are limited by the bacterial growth efficiency (BGE) determined for a coastal bay (delGiorgio and Cole, 1998). The meiofauna respiration was estimated by an allometric relation using the body-mass range of the meiofauna as defined for the Wadden Sea (Witte and Zijlstra, 1984). The limits of the macrofauna respiration were calculated based on the model and the virtual handbook of Thomas Brey (2001; 2010). The minimum fish respiration value was evaluated from the standard metabolism rate (SMR) determined for benthic fishes (Killen et al., 2010). The minimal oxygen consumption by fish was adapted to the body mass of Sylt- Rømø fishes with the formula proposed by Schurmann and Steffensen (1997). The maximal respiration rate was estimated from a factorial metabolic scope (FAS) corresponding to the ratio between the maximal metabolic rate (MMR) and the SMR. The FAS used here was the one previously determined for salmon (Brett, 1965). Salmon are athletic fish which swim long distances. In contrast, the fishes in the Sylt- Rømø Bight are benthic fishes with limited movement; their

MMR is thus inferior to the salmon's MMR. The minimal respiration (basal metabolic rate: BMR) of birds was estimated by an allometric relation (Aschoff and Pohl, 1970; Kersten and Piersma, 1987; inScheiffarth and Nehls, 1997) and a separate formula is used for the herbivorous birds (Jacobs et al., 1981).

4.2. Production

The maximum bacterial production is limited by the annual average of P/B (bacterial production/ bacterial biomass) from the Brouage mudflat (Pascal et al., 2009). Since the Sylt-Rømø Bight is less productive than the Brouage mudflat, the annual P/B average is considered as a maximum value for the Sylt- Rømø Bight. The values of the maximal macrofauna production for each trophic compartment were estimated from a maximum P/B ratio.

4.3. Consumption

A maximal efficiency of production of 0.87 (Brey, 2001) was applied to the production, previously determined in order to estimate the maximum consumption for the macrofauna. Consumption by carnivorous birds, which was produced from the daily energetic expenditure (Scheiffarth and Nehls, 1997; Le Mao et al., 2006) and calculated from the BMR, was expressed in kilojoules (KJ). The conversion factor 1mgC = 45.7 Joules (Salonen et al., 1976) allowed us to convert the kilojoules to milligrams of Carbon. For the herbivorous birds, the principle of calculation was similar but the formula was different and the consumption was expressed in Kcal (1 Kcal=4.187 $kJ.d^{-1}$ (Nienhuis and Groenendijk, 1986)).

4.4. Egestion-Excretion

The maximal excretion of macrofauna was calculated from the maximal consumption with a minimal assimilation efficiency of 0.21 (Brey, 2001). Maximal ratios of assimilation and maximal ratios of the net growth efficiency for macrofauna and meiofauna were added. For carnivorous and herbivorous birds, the assimilation efficiency rates were applied to the range of consumption in order to obtain the minimal and maximal value of egestion.

4.5. Export

The maximal export of the fishes and the birds was considered as the difference between the maximal consumption of this compartment and the sum of the minimal respiration and excretion. The export of particulate carbon in the sediment was considered as lower than the difference between inputs and the minimal consumption of consumers.

Processes	Compartments	Lower limit	Upper limit	Sources
Respiration	Microphytobenthos	0.05*gpp	0.5*gpp	(Vézina, 1989)
	Macrophytes	0.14*gpp	-	(Ouisse et al., 2010)
	Benthic bacteria	BGE=0.11	BGE=0.61	(delGiogio and Cole, 1998)
	Meiofauna	-	NGE=0.50	(van oevelen, 2006)
	Macrofauna	-	NGE=0.70	(van oevelen, 2006)
	Fish	BMR	MMR=16*BMR	(Brett, 1965)
	Birds	BMR	MMR=14*BMR	(McKechnie and Swanson, 2010)
Consumption	Meiofauna	8.8 ngC.ind^{-1}.d^{-1}	875 ngC.ind^{-1}.d^{-1}	(Schiemer, 1987)
	Macrofauna	-	P/C=0.87	(Brey, 2001)
	Fish	C=1.25*(P+2R)		(Mann, 1965)
		R=SMR	R=MMR	
	Carnivorous birds	C=N*3*MR*(1/AE)		(Scheiffarth ans Nehls, 1997)
		MR=BMR	MR=MMR	
	Herbivorous birds	C=N*3*MR*1.67		(Jacobs et al., 1981)
		MR=BMR	MR=MMR	(Nienhuis and Groenendijk, 1986)
Egestion	Microphytobenthos	0.05*gpp	0.73*gpp	(Vézina & Platt, 1988) (Goto et al., 1999)
	Macrophytes	0.05*gpp	0.5*gpp	(Vézina & Platt, 1988)
	Meiofauna	AE=0.57	AE=0.77	(van Oevelen, 2006)
	Macrofauna	AE=0.21	AE=0.75	(Brey, 2001) (van Oevelen, 2006)
	Fish	AE=0.5	AE=0.9	(Leguerrier et al., 2004)
	Carnivorous Birds	AE=0.80		(Scheiffarth ans Nehls, 1997)
		C=Cmin	C=Cmax	
	Herbivorous Birds	AE=0.43		(Madsen, 1989 *in* Tinkler et al., 2009)
		C=Cmin	C=Cmax	
Production	Benthic bacteria	-	P/B=0.94	(Pascal et al., 2009)
	Macrofauna	-	P/B=0.05	(van oevelen, 2006)

Table III-2: List of inequalities used in this study. B=biomass, C=consumption, P=production, N=number of individuals, Gpp=Gross primary production, BGE=Bacterial growth production, NGE=Net Growth Efficiency, A/E= Assimilation Efficiency, MR=Metabolic Rate, BMR=Basal metabolic Rate, SMR=Standard Metabolic Rate, MMR=Maximal Metabolic Rate.

5. Strategy of the study

The original model is determined by a number of equalities equal to the number of the flows of each habitat. Only one flow value is unknown and it is directly estimated by the corresponding mass balance equation. Thus the original model was even- determined. To come up with a set of models to use to test our hypotheses, we progressively removed information (removed equalities, leaving the associated inequalities) until we exceeded the standard 1:4 ratio of known flows to unknown flows (Vézina and Pahlow, 2003). For each level of information degradation (3:4, 1:2, 1:4, 0:4) equations were removed randomly. Twenty-five percent of the equalities were removed for the first level of degradation, another 25% (50% total) for the second level of degradation, until the final level where only inequalities remain. At each step of degradation eight different treatments were applied. A treatment corresponded to a set of randomly chosen equations (i.e. a quarter of information) for the same food web model, which were removed. For each step, the classical inverse modelling (Vézina and Platt, 1988) and the MCMC-LIM (Van den Meersche et al., 2009) were run to estimate the values of the unknown flows. For the MCMC-LIM, 100 000 solutions were sampled randomly with a jump length of 20. The jump length, which defines the distance covered within the polytope for one iteration (Van den Meersche et al., 2009), and the number of iterations were chosen in order to cover the whole solution space. The convergence of the mean and standard deviation values towards a stable value were used as indicators of the coverage of the solution space. All simulations were made with Matlab 2009a.

6. Tested functions

Different functions were used to select a unique solution from the 100 000 results from MCMC-LIM for each flow. The tested functions fall into two groups: statistical and ecological indices that embody hypotheses about the structure of ecosystem. Solutions calculated by the MCMC-LIM can be represented by a likelihood distribution for each flow (van Oevelen et al., 2010). The mean of the solutions for each flow is always a valid solution (van Oevelen et al., 2010). However, many of the likelihood distributions are skewed, which leads us to consider another measure of central position like the median. We also tested seven

ecological functions (listed in Table III-3) from Ecological Network Analysis (ENA) indices and based on the emergent properties of the ecosystems. These properties, which are derived from thermodynamics rules, describe the maturity, the structure and the functioning of the ecosystem. Network ecologists have proposed that mature ecosystems have maximum values of certain ecological indices, such as Ascendency (ASC) (Ulanowicz, 1986), Total System Throughput (TST), and Finn's Cycling Index (FCI) (Odum, 1969). It is thus reasonable that using these ecological indices as goal functions for the selection of a unique MCMC-LIM solution may produce results that are close to reference flow values and network indices. Consequently, the maximization of some ENA indices was tested for the selection of a single solution at the end of the MCMC-LIM. Two of them, the Total System Throughput (TST) and the Finn's cycling index (FCI), represent the growth of the ecosystem by estimating the energy flowing through and retaining inside the ecosystem. The others describe the development of the ecosystem by estimating the organization of flows of the ecosystem: the Ascendency, the relative Ascendency, the overheads and the system omnivory index.

Functions	Measure of what?	Calculation	Reference	Theory on maturity	Reference
Statistical					
Mean	central position of the likelihood distribution		van Oevelen et al., 2010	-	
Median					
Ecological					
Total System Throughput (TST)	global activity of the ecosystem	sum of flows	Ulanowicz, 1986	maximization	Odum & Pinkerton, 1955
Finn Cycling Index (FCI)	cycling	ratio cycle/ total number of flows	Finn, 1976	maximization	Odum, 1969
Average Mutual Information (AMI)	specialisation of flows	$\text{AMI} = \sum_{i=1,j=1}^{n} f_{ij} Q_i log(\frac{f_{ij}}{\sum_{k=1} f_{kj} Q_k})$	Hirata & Ulanowicz, 1984	maximization	Ulanowicz, 1986
Ascendency (ASC)	organisation of the network	AMI*TST	Ulanowicz, 1986	maximization	Ulanowicz, 1986
Relative Ascendency (relASC)	Oganized part of the network	ASC/C	Ulanowicz, 1986	maximization	Ulanowicz, 1986
Overheads	Unorganized part of the network (=reserves)	=C-ASC	Ulanowicz, 1986	maximization	Christensen, 1995
System omnivory Index (SOI)	Omnivory	SOI=mean(OI/log(C_i))	Christensen & Pauly, 1992	maximization	Christensen, 1995
		$\text{OI}_i = \sum_{j=1}^{n} (TLj - (TL_i - 1))^2 . \text{DCij}$	Christensen & Pauly, 1992		

Table III-3: Functions tested in this study. For the AMI fij is the fraction of the total flow from j which passes through i. Qi corresponds to the probability that unit of energy passes through i. fkj and Qk represent the total flow from j and the probability that a unit of energy passes through others compartment. C corresponds to the Development Capacity, which describes the maximal possible Ascendency for a considered ecosystem. OI corresponds to the Omnivory Index of a particular compartment of the food webs. TL_i is the trophic level of the prey, TL_j is the trophic level of the predator and DC_{ij} is the diet contribution of a prey to the diet of its predator.

7. Evaluation of the quality of the proposed solution

A single solution was chosen from the 100 000 flow solutions estimated by the MCMC-LIM method for each treatment by calculating the appropriate statistic (mean or median), or selecting the flow solution that maximized each ENA index. The maximum value of each function was determined to obtain a set of single solutions for each flow. The solutions of the even-determined model ($x = A/b$) were used as a reference for comparison with the solutions selected by each goal function. We used several measures of deviations from reference to investigate the behaviour of the functions with level of information degradation. First, the distance from the mass balance estimated from the reference was calculated. The mass balances were calculated from the estimated values for each compartment. The distance from the mass balance was computed by the absolute value of the difference between the mass balance of the reference and the mass balance of estimated values. Next, the percentage of the relative error (i.e. difference between the reference and the estimated values divided by the reference) was calculated for each flow. The relative errors were grouped into ranges of percentage in order to obtain a distribution of percent errors. The hypothesis H_0, which supposed a distribution of percent of error independent of the level of degradation of the information considered was tested by the Friedman test in Matlab 2009a. The Friedman test is a non-parametric test, similar to two-way ANOVA, which we chose as the data do not follow a normal distribution..Third, Spearman coefficients of correlation were estimated to verify for each level of degradation the conformity of the set of estimated values of flows with the set of reference values of flows. Finally, the RMS was estimated for each tested function. The RMS corresponds to the square root of the mean of the square difference between the reference and the estimated values. If the RMS is low, the set of solutions is close to the reference and thus the function is robust. The Kruskal-Wallis test was used to test hypothesis H_0 which suggests a RMS independent of the function considered. This nonparametric version of the ANOVA one-way was performed with Matlab 2009a. It was followed by a multiple comparison test (Tukey test) to determine what functions significantly differ from others. We also looked at how the choice of the function affected the estimation of ecological indices, used here not anymore as an optimizing function for choosing the best flow value but as a descriptor of the functioning properties of the obtained food web. Specifically, we explored the impact of some functions (Total System Throughput (i.e. TST), Ascendency (i.e. ASC), Overheads, Least Square, mean, relative Ascendency and System Omnivory Index (i.e. SOI)) on four ecological

indices: the internal relative Ascendency, the AMI, the Relative Ascendency and the FCI. The relative Ascendency and the AMI estimate the organisation in the ecosystems and the trophic specialisation, respectively. The internal relative Ascendency (A_i/DC_i) that estimates the internal organization of the ecosystem refers to internal flows alone and excludes the exchanges across the boundaries of the ecosystem. The A_i/DC_i and the FCI were chosen because they are considered as a powerful index in the comparison of ecosystems (Baird et al., 1991).

Results

The mean, the least square and the ecological functions resulted in flows with a distance from the original mass balance close to 0 (0.64) and constant for every level of degradation of the information (Figure III-1). Using the median to select among possible flows resulted in a distance from the mass balance that progressively increased as the level of information decreased (Fig III-1). The variation of the error on the mass balance of food webs, measured by its standard deviation, increased as the information decreased.

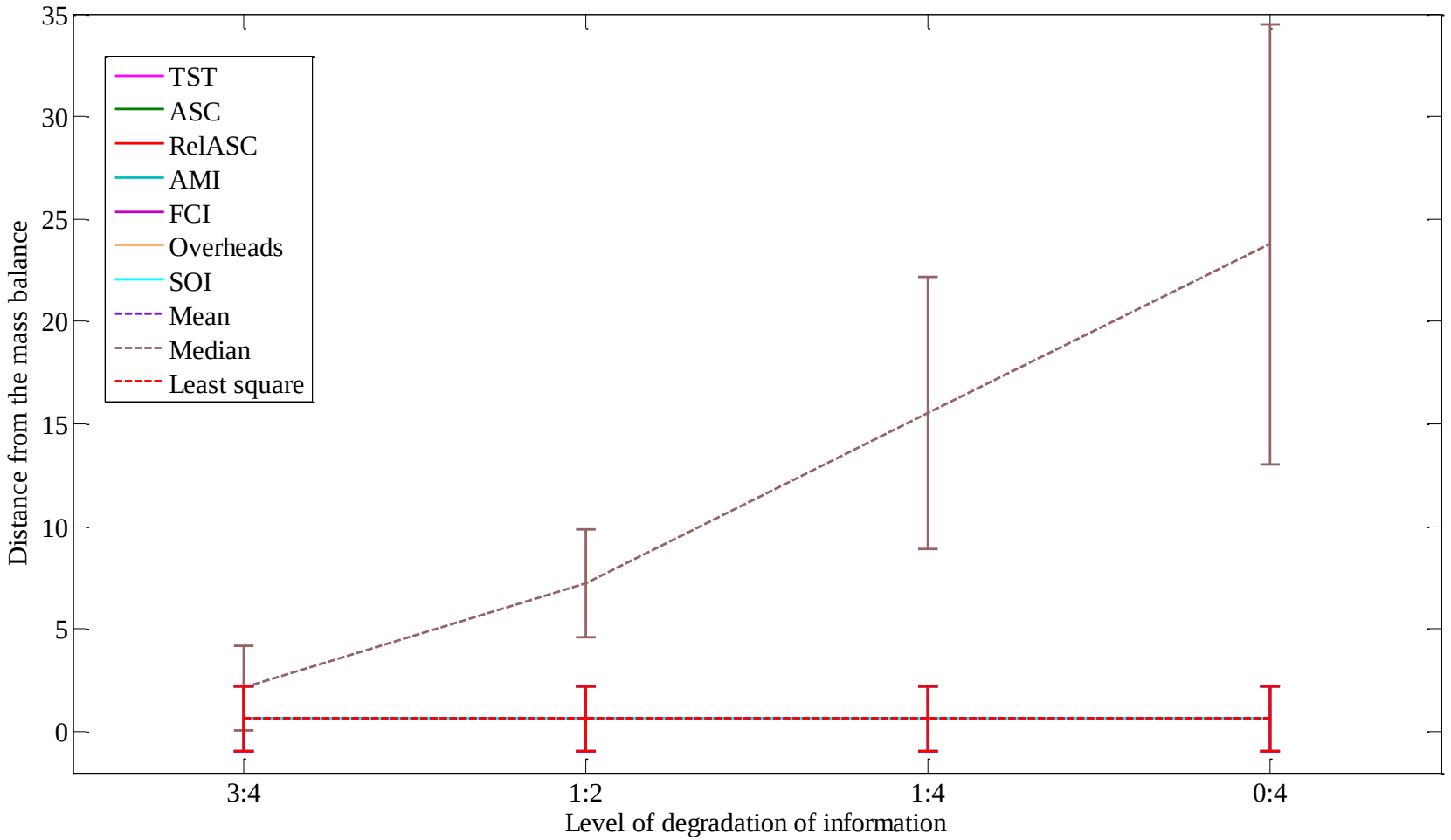


Figure III-1: Plot showing the distance between the mass balance, calculated with reference values and the mass balance estimated from the estimated values of flows. The base line represents nine functions (TST, ASC, RelAsc, AMI, FCI, Overheads, SOI, Mean and Least square). The error bars represent the standard deviation of results due to the treatment applied to each food webs model.

The MCMC-LIM appeared to be sensitive to the degradation of information irrespective of the function considered (Fig III-2). Indeed, the frequency of large errors consistently increased as the information contained in the model fell. For the first level of degradation (3:4), a majority of flows were estimated with less than 1 % error and the frequency of high percent errors was low. At each level of degradation of information, the frequency of the high percentage of error progressively increased. For the last level of degradation, a majority of flows were estimated with an error superior to 100%. The hypothesis H_0, that the distribution of flow for each range of percent error remains similar irrespective of the level of degradation, was tested by the Friedman statistical test. H_0 was rejected ($p<0.05$), thus the frequency distribution was significantly influenced by the degradation of information. Variation due to the treatment applied to the MCMC-LIM, the habitat considered and the random sets of equation removed was highest for the treatment in which half the information was removed (error bars in Figure III-2).

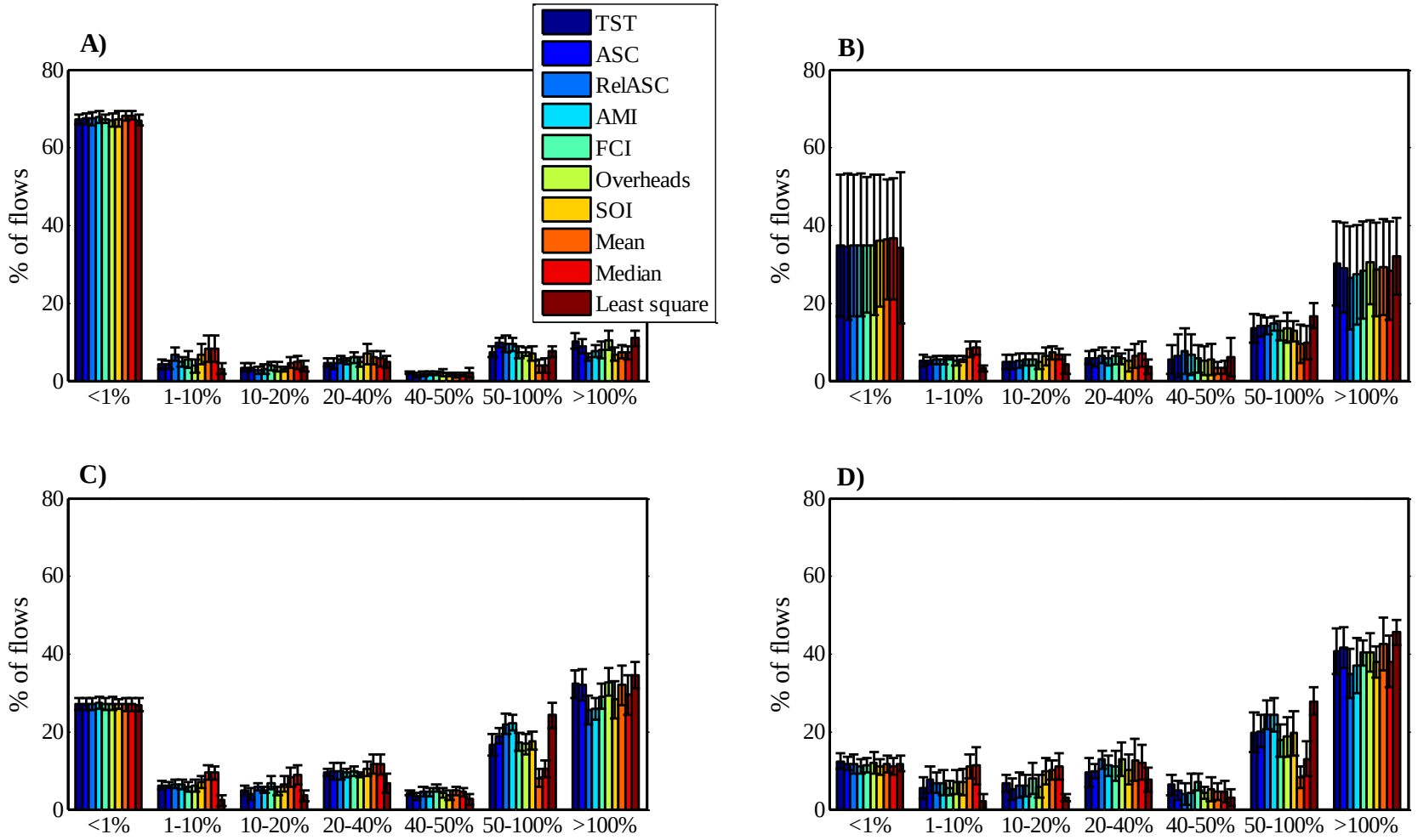


Figure III-2: Frequency distribution of the different ranges of the percentage of error. Each histogram represents a level of degradation of information. A) corresponds to the first level of degradation of the information (3:4), B) represents the level 1:2, C) is the third level of degradation (1:4) and D) 0:4 all information is removed.

The estimated values and the reference values of each flow presented high Spearman correlation coefficients independent of the level of degradation of the information considered (Table 4). The correlation coefficient decreased with the decrease in quantity of information contained in the model. Even at the extreme level of degradation the estimated values of flows remained correlated to the reference. The statistical functions presented the highest Spearman correlation coefficients, while the LS solution showed the lowest Spearman correlation coefficients. The slope of the regression between reference and estimated value remained close to 1 independent of the level of degradation considered. Some functions, such as LS, TST, ASC and Overheads, were more likely to have slopes greater than 1.

	Level of degradation of the information			
Function	**3:4**	**1:2**	**1:4**	**0:4**
Mean	0.972 ± 0.017 (0.984)	0.948 ± 0.017 (0.964)	0.927 ± 0.020 (0.969)	0.894 ± 0.025 (0.971)
Median	0.973 ± 0.017 (0.984)	0.949 ± 0.017 (0.964)	0.930 ± 0.018 (0.969)	0.893 ± 0.025 (0.974)
LS	0.954 ± 0.021 (0.943)	0.927 ± 0.024 **(1.047)**	0.876 ± 0.050 **(1.152)**	0.720 ± 0.091 **(1.228)**
TST	0.960 ± 0.018 (0.988)	0.933 ± 0.020 **(1.028)**	0.909 ± 0.029 **(1.090)**	0.822 ± 0.059 **(1.126)**
ASC	0.954 ± 0.023 (0.998)	0.922 ± 0.029 **(1.019)**	0.894 ± 0.030 **(1.074)**	0.808 ± 0.051 **(1.073)**
FCI	0.971 ± 0.019 **(1.013)**	0.950 ± 0.017 (0.995)	0.908 ± 0.024 **(1.015)**	0.827 ± 0.028 **(1.017)**
ASCrel	0.968 ± 0.016 **(1.013)**	0.933 ± 0.024 (0.997)	0.896 ± 0.026 (0.995)	0.774 ± 0.061 (0.989)
AMI	0.956 ± 0.016 (0.992)	0.925 ± 0.027 (0.973)	0.884 ± 0.024 (0.974)	0.749 ± 0.077 (0.950)
Overheads	0.957 ± 0.018 (0.985)	0.930 ± 0.025 **(1.013)**	0.9056 ± 0.031 **(1.076)**	0.829 ± 0.054 **(1.104)**
SOI	0.969 ± 0.016 (0.989)	0.936 ± 0.019 (0.967)	0.903 ± 0.023 (0.996)	0.826 ± 0.051 **(1.021)**

Table III-4: Showing the Spearman correlation coefficients between the different levels of degradation of information and the reference. Values in parentheses correspond to the value of the slopes of the regression between the estimated values and the reference values. Values in bold correspond to the value of slop superior to 1. All levels of degradation are correlated with the reference (p-value<0.05)

The differences observed above were confirmed by the values of the RMS (Fig III-3 and III-4). The relative order of medians of RMS for the different functions remained the same irrespective of the level of degradation. The mean and the median had the lowest RMS for every level of information except the level of greatest information degradation. They were followed by the SOI and the relASC. The TST, ASC, Overheads and LS always had the highest RMS (Fig III-3). The same trend was observed with the mean of the RMS (fig III-4). The mean and the median presented the lowest root mean square, while the LS presented the highest RMS. The ecological functions fell between these extremes. The SOI, relASC, AMI and FCI lines were close to the mean–median line. TST, Overheads and ASC were close to the tendency of LS.

The ranges of the RMS values varied according to the goal function and the level of degradation considered. They determined the variability due to the habitat and the set of equations removed. The ranges of RMS were doubled between the first and second level and slowly increased between others levels of degradation. The ranges of RMS values were larger for TST, ASC, Overh. and LS (Fig III-3).

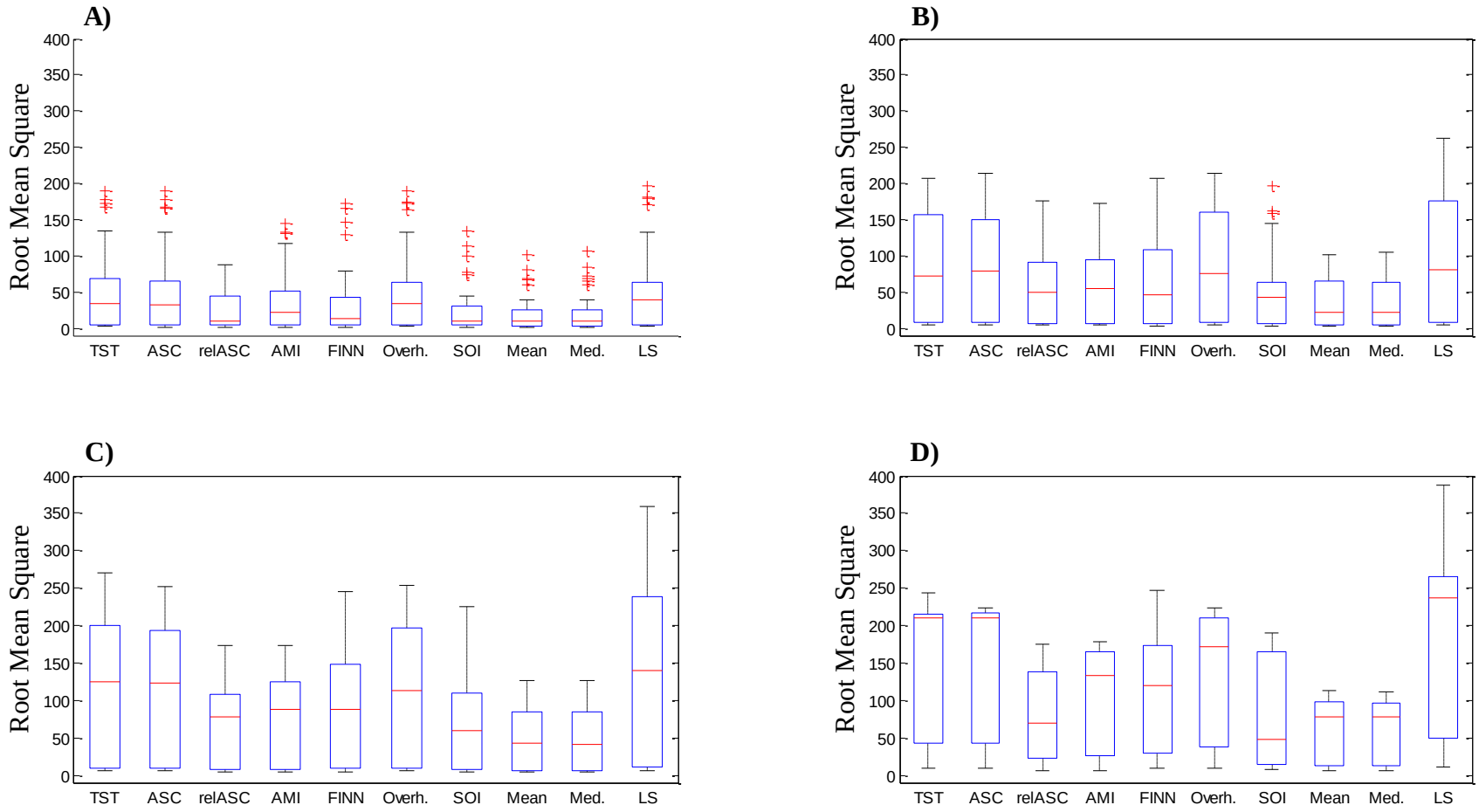


Figure III-3: Boxplot representing the RMS of each tested functions for every level of information degradation. For the three first, graphs were made with 56 values (8 treatments per habitats) and for the last one only seven (one replicate per habitat). A) represents the first level of degradation (3:4), B) is the level (1:2), C) corresponds to the third level of degradation (1:4) and D is the last level of degradation (0:4).

Every function showed a linear increase of the RMS with increasing degradation, except the AMI and the relASC, which presented a break of tendency for the second and for the third level of information degradation (Fig III-4). The slope for each function was not the same leading to an increase of the distance between functions as the level of information decreases. A Kruskal-Wallis test was performed on the data (n=175 for each function) to determine if there was a significant difference between functions. H_0, which suggested that every function present a similar RMS, was rejected (p-*value*<0.05) and the functions are thus significantly different. A test of multiple comparison showed that the mean, the median, the SOI and the relASC were significantly different from the TST, ASC, Overheads and LS. The FCI and AMI functions significantly differed from the mean and the median.

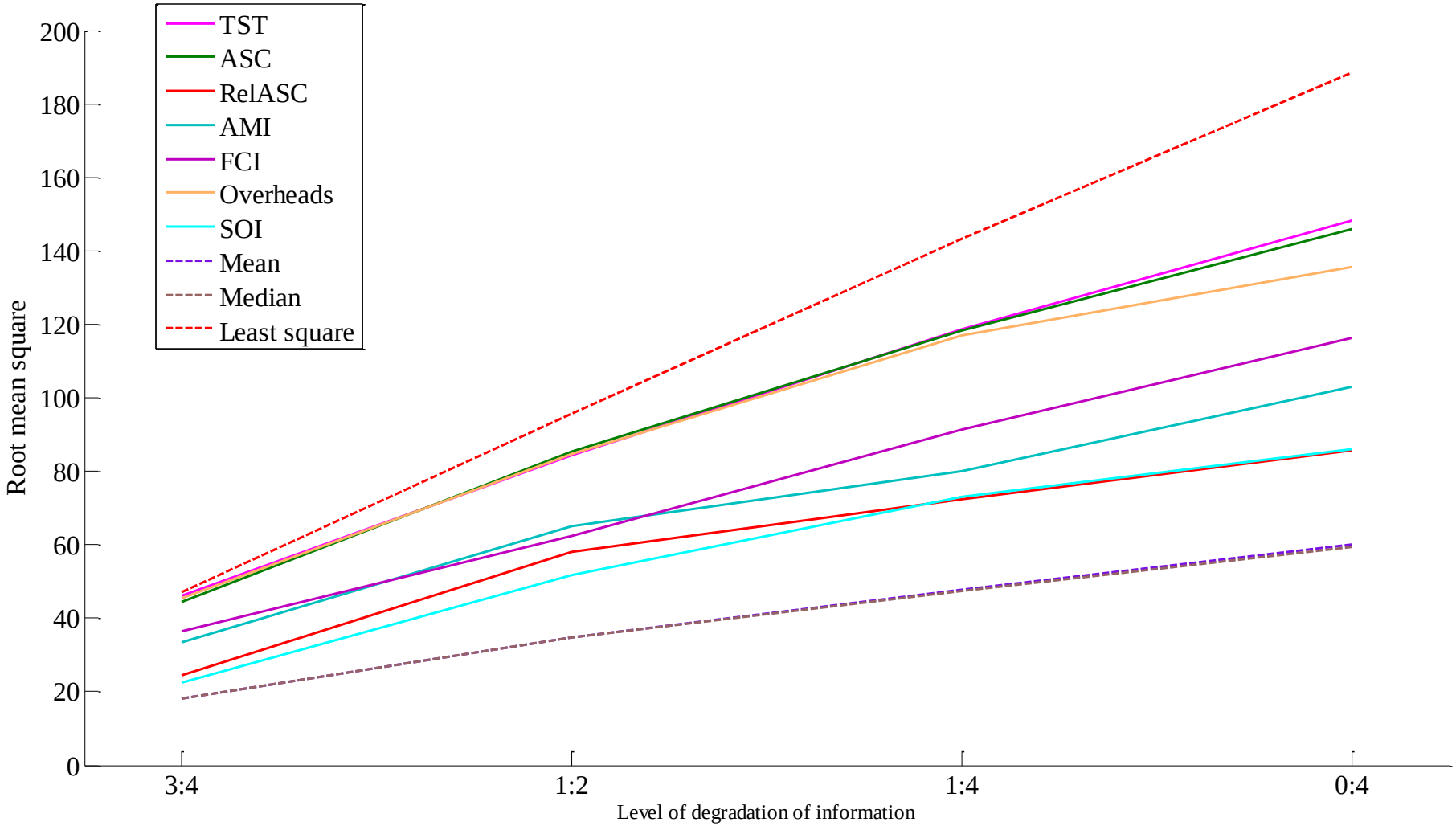


Figure III-4: Plot showing the mean root mean square of all habitats for each function according to the level of degradation of information (3:4, 1:2, 1:4, 0:4).

The network indices calculated from the estimated value of flows did not differ much from the indices calculated from the reference value of flows (Fig III-5), although some differences between functions was observed. The impacts of goal functions on the relative Ascendency and the AMI indices appeared to be similar. For these two indices the highest over-estimation was observed for the relative Ascendency and the Ascendency functions, while the mean and the overheads under-estimated these two indices. The SOI and the TST functions were the closest to the reference value of the indices. Only the relative Ascendency under-estimated the FCI. All functions except the mean function under-estimated the internal relative Ascendency. For the FCI and internal relative Ascendency, the mean function resulted in the smallest difference from the reference values of indices. The LS and TST functions showed a similar tendency and a similar difference from the reference for these two indices.

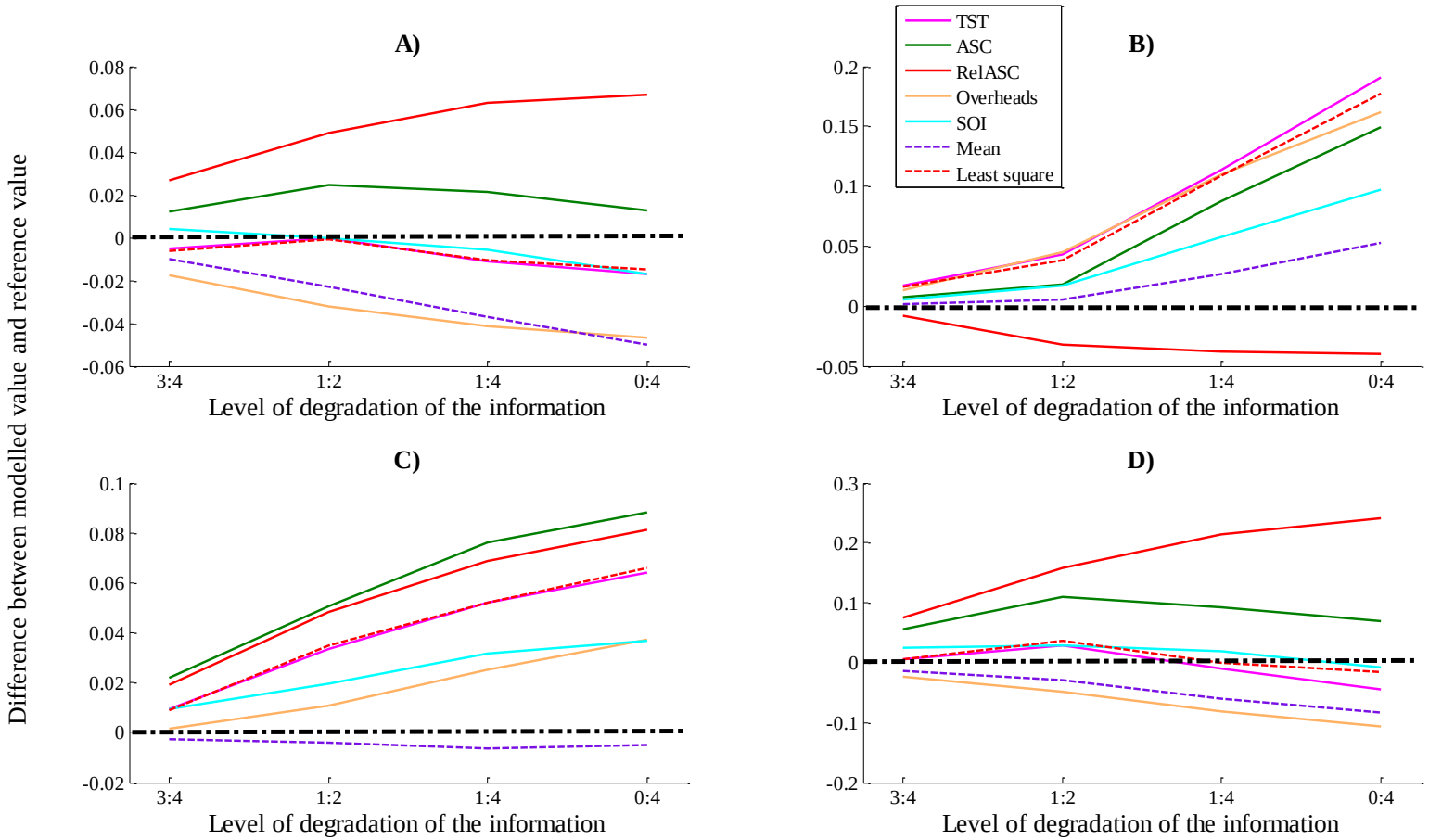


Figure III-5: Plot that represents the absolute difference between the values of 4 indices calculated either from the estimated value of flows or from the reference value of flows. The subplot (A) shows the relative Ascendency index, the second one (B) presents the FCI, the plot (C) presents the internal relative Ascendency index and the last one the AMI index (D). The dash-dot line corresponds to the estimated values of indices, which was equal to the reference value of indices. A curve located above a dash-dot line corresponds to an over-estimation of the considered index.

Discussion

1. Inverse modelling robustness according to the level of information incorporated in the model.

The performance of linear inverse modelling in reconstructing an increasing number of unknown flows depends on the metric used. The percentage of error, which measures the percent change in the estimated flows from the reference flows, suggests a strong impact of information loss on inverse reconstructions. The degradation of the information in the inverse model caused a progressive increase in the difference from the reference model measured by the percentage of error. For the first level of information loss, corresponding to a ratio known/unknown flow equal to 3:4, errors inferior to 1% were dominant and frequencies of larger percentage errors increased with information degradation until errors superior to 100% became dominant. However, there are a few factors to consider in assessing the significance of this result.

First, the degradation of the information in these models was pushed toward extreme levels. For the last level of degradation, only the mass balances, the equations of GPP and of the imports remained. Considering that about 1 in 4flows are known in most studies(Vézina and Pahlow, 2003), the third level of degradation of information (1:4) is probably more representative. For this level, approximately 40 % of flows were estimated with an error lower than 20%. In a sensitivity analysis, Richardson et al. (2006) modified data up to 20% to determine the dependence of results to the input data. Richardson et al. (2006) replaced the known flows by a random value issued from a normal distribution realized from the mean and standard deviation estimated with the original data and observed that in most cases the standard deviation is equal to about 20% of the mean. The maximal tolerance of 20% corresponds to the maximal variation of the field measurement due to natural and analytic variation (Richardson et al., 2006). Thus about 40% of flows were estimated by inverse modelling with a precision similar to the precision of field measurement.

Another large proportion of flows, about 40%, corresponded to those estimated with an error more than 100%. However, the majority of these flows had a low absolute value, inferior to 1 $mgC.m^2.d^{-1}$. A low absolute error becomes a high relative error when divided by a similarly

low original value. The high percentage of error on small flows probably had only minor consequences on the reconstruction of the network and on its ecological interpretation. Indeed, generally high Spearman correlation coefficients were observed for every level of information degradation and for every habitat, irrespective of the function used to select the solution. In spite of the high proportion of large relative errors, the inverse modelling had much less impact on the order of the flow values. The ascent order of value of flows was preserved, as was the organisation of the reconstructed network. Moreover, the values of the network indices for reconstructed food webs, which describe their structure and their functioning, remained consistent with the reference network values. In this study, the ranges of values for the inequalities constraining the linear inverse modelling were large. For example, the maximal respiration rate of birds was equal to 14 times the minimal respiration rate. Inequalities were often used to limit processes to realistic values and this was not sufficient in the case of high degradation of information. Such large ranges were necessary for a set of inequalities applicable to different systems like the 7 habitats considered in the study. For a better use of inverse modelling, inequalities should be refined to better fit to the reality of the studied habitat and the species present. Applying a more fitted set of inequalities, related to the species present at each site, will allow a reduction of the solution space and presumably an increased robustness of the method.

2. Choice of function

We based the selection of good goal functions on the similarity to reference values of both the resulting magnitude of flows and the resulting flow structure and organization. In this section, we consider each goal function and its impact on the performance for these two goals.

The minimization of the quadratic norm was proposed by Vézina and Platt (1988) to select a unique solution from the numerous possible solutions of inverse modelling. Later, Vézina and Palhow (2003) proposed the use of goal functions that correspond to *a priori* assumptions on the structure and functioning of the ecosystems, such as Ascendency and cycling indices. Vézina et al. (2004) proposed the use of the maximization of the TST and the maximization of the Ascendency instead of the least square solution. The most recent method proposed

randomly sampling the solution space (Kones et al., 2006; Van den Meersche et al., 2009), and the mean was used to summarize the possible solutions for the flows (Kones et al., 2006; van Oevelen et al., 2010). We tested the use of ecological indices, which are derived from theories on the maturity of the ecosystem, to select a single solution among all possible solutions. The Ascendency and the TST had already been evaluated but not with our numerical scheme and without definite conclusions (Vézina et al., 2004). The other ecological functions (FCI, AMI, relative Ascendency, Overheads and SOI) and the median were tested for the first time in this study.

Although both the mean and the median appeared to provide the most robust functions for selecting a unique solution from inverse modelling. However, the median did not respect the steady state mass balance condition, as suggested by van Oevelen et al. (2010). A sum of incoming flows that differs from the sum of out-going flows means an over- and under-estimation of inputs and outputs for each compartment. The median function estimated the value of flows by calculation of the median of the 100000 solutions proposed by the MCMC-LIM for each flow independently, while the ecological functions and the LS solution considered flows as a set of dependent elements. Thus, incoherence appeared when the flow network was reconstituted from the individual median estimates. Like the median, the mean was calculated for each flow independently,. but the mean calculation is a linear operation on the set of solutions which always gives a valid solution (van Oevelen et al., 2010). If the sums of the values of each vector solution (here 100000 vectors) respect the mass balance, the sum of the values of the mean flow vector will balance because the total of the values does not change. In the context of management of ecosystems and their comparison, mistakes which over- or under-estimate the energy flowing through the system and such variability in results are not acceptable. The median thus is not recommended as the function used to select a single value of each flow.

The LS solution was the least robust function, indicated by its high RMS and low correlation coefficient relative to the other functions tested. The LS solution estimated a higher proportion of flows within the range of error 50% to 100%. LS, defined as the minimization of sum of squared flows, led to the underestimation of the sum of flows through the system (Vézina and Pahlow, 2003; Johnson et al., 2009). This underestimation of the sum of flows does not involve underestimation of every flow; some flows are underestimated and others are

overestimated. This adds an artificial structure to the reconstructed food web (Stukel et al., 2012). In this study, the proportion of overestimated flows was either equal to or larger than the proportion of the underestimated flows. The slope of regression between the reference and the estimated values being superior to 1 suggested a tendency to overestimate the value of high flows. Observations of Vézina & Palhow (2003) suggesting that the small flows are overestimated and the large flows are underestimated are not verified in this study. No general rules on what flows were overestimated could be discerned; it depended on the type of equation that was removed. The value of respiration flows and value of export flow were often, but not systematically, overestimated as previous results have shown (Eldridge and Jackson, 1993). Previous studies have shown that the Ecological Network Analysis (ENA) indices, which are used to determine the emergent properties of the ecosystems, are underestimated by the LS solution (Johnson et al., 2009; Kones et al., 2009). In this study, some indices, specifically the relative Ascendency and the AMI were faithfully estimated by the LS function, but both the internal relative Ascendency and the FCI were overestimated by the LS. The over-estimation of the two latter indices, which are powerful indices in the case of comparison of ecosystems (Baird et al., 1991), led to an over-estimation of the energy flowing through the reconstructed network and to an over-estimation of the organization of internal flows. The reconstructed food web thus appeared to be more efficient. As a consequence, the LS cannot be accepted as a good criterion for selecting the single solution.

The ecological goal functions TST, ASC, relative ASC, and overheads, produced higher RMS than other ecological functions and did not provide robust results of estimated flow values by inverse modelling. These three ecological functions had consequences on the values of flows similar to the LS solution. The majority of flows were overestimated, especially export and respiration. Moreover, the slope of the regression of these functions followed the same tendency that LS did, that is a slope superior to 1. The TST solution overestimated the value of the flows and pushed them towards the upper limits of the solution space. The RMS of the ASC (the product of the AMI and TST) is closer to the TST than the AMI, which suggests that the ASC is largely determined by the TST. The maximization of the ASC was obtained by a maximization of the TST and thus also overestimated the majority of flows. The maximization of the overheads led to the overestimation of the respiration values and the export values. Among the ecological functions, the relative Ascendency showed one of the lowest RMS and one of the lowest Spearman coefficients of correlation. The relative

Ascendency is opposed to the overheads and measures the organized part of the ecosystem. The lower RMS value of the relative Ascendency suggests a relative error on the values of flows less important for the relative Ascendency than the overheads. In spite of this observation, the correlation between reference and flow values estimated by the relative Ascendency function was lower than the correlation with values estimated by overheads, especially at the high level of degradation. This suggests a stronger impact of the relative Ascendency on the rank of flows. These ecological functions (TST, ASC, relASC and Overheads) do not generate a faithful reconstruction of the magnitude of flows.

These previous ecological functions had differential impact on the ecological indices, used this time to describe the ecological properties of the obtained food web. The use of MCMC-LIM with the TST goal function gave results that presented values of the AMI and of the relative Ascendency similar to the reference values. On the contrary the Ascendency and the relative Ascendency goal functions over-estimated the relative Ascendency, the AMI and the overheads function underestimated both these indices. The FCI and the internal relative Ascendency were overestimated by the overheads and TST goal functions. A high value of the internal relative Ascendency value refers to a greater efficiency in the ecosystem (Mann et al., 1989) and a higher FCI corresponds to a greater amount of the energy and matter remaining inside the ecosystem. As expected, using the Ascendency or the relative Ascendency goal functions for choosing the unique solution led to a food web with an over-estimation of the internal relative Ascendency. In this study the Ascendency was maximized via a maximization of the TST, which maximizes cycling, leading to an increase in the cycling inside the reconstructed food webs. On the contrary, the maximization of the relative Ascendency is due to a maximization of the AMI and thus the cycling was under-estimated. To conclude, the Ascendency, the relative Ascendency, the Overheads and the TST goal functions cannot be used to select a unique solution for the MCMC-LIM due to their impact on the internal relative Ascendency and FCI indices and their impact on flows.

Omnivory, measured by the System Omnivory Index (SOI), is the ecological goal function that provided the highest robustness to the MCMC-LIM. In this study, the SOI increased as the quantity of information in the model decreased. For each habitat, the trophic group with the highest potential of omnivory was the benthic omnivorous macrofauna (BOM) because they fed on autotrophs, on meiofauna, on macrofauna and on detritus. The omnivory index of

the BOM increased and moved away from the original omnivory index as the level of information decreased irrespective of the considered habitat (Appendix A, fig.6). Flows between the BOM and the species at low trophic level were among the flows with high error. From the first level of degradation up to the second, the contribution of the low trophic levels to the diet of BOM was multiplied by about 3. The loss of information at the first level led to an increase of the omnivory index of the BOM via a maximization of the consumption on the lowest trophic level (TL=1). For other levels of degradation the omnivory index of BOM tended to increase via the consumption on other trophic level.

The relative Ascendency and the AMI indices calculated for the SOI solution were the closest to the reference value of these indices. The maximization of the system omnivory index involved some feeding preference within a diversified diet. The maximization of the SOI had consequences on the structure of the food webs, especially by increasing the AMI. In spite of this increase in the AMI, the relative Ascendency estimated from the SOI function was similar to the reference value. The balance between the organized part and unorganized part of the food web was respected. The SOI function over-estimated the internal relative Ascendency and FCI, as did the other ecological functions, providing a more efficient reconstructed network than in the reference model. In spite of its low RMS, the SOI function is not a good candidate for a unique solution because of its biases in the context of the comparison of the ecosystems.

The mean appeared the most robust function due to its lowest RMS and thus its minimal error relative to the reference. From an ecological point of view, scientists expect central position for the values of flows. This central position would bring flexibility to ecosystems in the case of perturbation (Ulanowicz et al., 2009). The mean tended to underestimate the values of the relative Ascendency and of the AMI. Averaging values of flows, the mean function tended to increase the redundancy in the ecosystem and thus decrease the AMI value. Consequently the relative Ascendency was lower than in the reference but remained at the almost perfect balance between organized and unorganized part of the system. When only the internal flows were considered (by the internal relative Ascendency index), the mean function gave index values almost identical to the reference values. The estimation of the FCI was excellent until the second level of degradation and did not increase appreciably over the next levels. The

mean solution provides reconstructed food webs with a structure and a functioning which are the closest to the reference food web.

The mean was the most powerful function to estimate indices involved in the comparison of the ecosystems. The mean solution provided food webs where the values of flows are averaged and gave central position to the value of flows and thus equilibrium between organized and unorganized part to the ecosystem. The most robust function was a function that pushed the ecosystem to a balanced organization between Ascendency and the unorganized part. The part in disorder constitutes the reserves of the organisation (Conrad, 1983) that provides flexibility of the structure to the ecosystems. Thus, a sustainable ecosystem should have a value of Ascendency between both these extremes (Ulanowicz et al., 2009). Indeed, an ecosystem with a maximal Ascendency is prone to a collapse in the case of new perturbation. On the contrary, an ecosystem with a low Ascendency cannot survive (Ulanowicz et al., 2009). The reconstructed food web that is the closest to the reference food web presents a balance between efficiency, organization and the inefficient part of the ecosystem and thus confirms the Ulanowicz suggestions (Ulanowicz et al., 2009).

Combining the findings above that the mean provides robust estimation of the flows and of the structural indices leads us to consider the mean in the context of parsimony arguments for reconstructing flow networks. The mean function embodies the parsimony principle, as originally defined by the Occam's razor philosophical principle: "The best solution is supposed to be the one obtained with the fewest hypotheses". In this sense, the mean is the most parsimonious function. The functions that thus make the fewest a *priori* suppositions on the food web structure are the most robust when subjected to degradation of the information.

3. Conclusion

1.1. Conclusion

The function used to select a single solution has a relatively low impact on the quality of reconstruction of flows relative to the degradation of the information. To insure quality results of inverse modelling, the inequalities should be as constrained as possible given the time and

the budget limits of the project. The biological constraints issued from the general biological rules should be refined in order to adapt constraints to the considered ecosystem In our study, the biological constraints include inter-habitat variability, which refers to the metabolism of similar species in different habitats. It would be preferable to consider the intra-habitat variability of the species in order to constrain the flows. The metabolism of a species in a particular habitat should studied more, especially by mesocosm experiments. On the other hand, the mean, the function that makes the fewest assumptions about the structure of food web, gives solution of flows that most closely resemble the flows in the fully measured network and its ecological interpretation.

ACKNOWLEDGEMENTS

The authors thank Galen Johnson for the critical reading and improvement of the English of the manuscript. Blanche Saint-Béat's PhD work is financed by the CNRS and Région Poitou-Charentes. This work is a contribution to the ANR-blanche VASIREMI (Trophic significance of microbial biofilms in tidal flats), and to the Procope Hubert Curien programme. (Trophic significance of microbial biofilms in tidal flats), and to the Procope Hubert

Appendix

The SOI varied according to the habitat considered; the trend of it was similar independent of the habitat considered. The value of the SOI increased as the quantity of information decreased. The Omnivory Index (OI) of the compartment BOM followed a similar tendency. The contribution of low trophic levels to the diet of the BOM compartment hardly increased between the reference and the first level of degradation of information. Between the first and the third level of degradation the contribution of low trophic level remained constant. For the last level of degradation the value of contribution was lower except for the Densenoltii and Mudflat habitats.

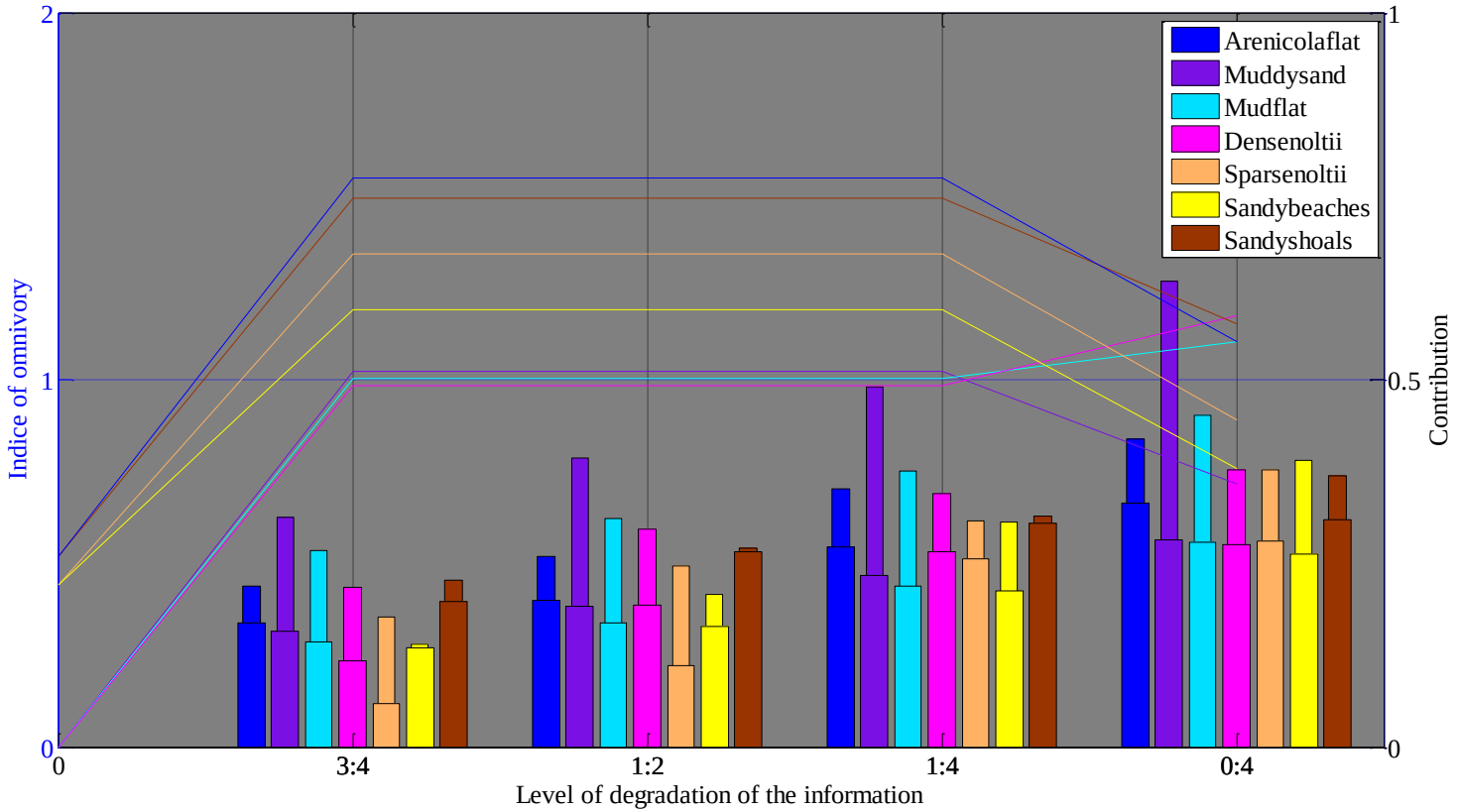


Figure III-6: Histogram representing the evolution of the SOI and the Omnivory Index (OI) of the trophic compartment BOM according to the level of degradation. The different colors correspond to the habitats. The largest bars represent the OI of the BOM and the narrowest bars represent the SOI. The curves show the contribution of low trophic level to the diet of BOM. 0 refers to the level with all information (even-determined model).

Chapitre 4

Key features of intertidal food webs that support migratory shorebirds: The case of the bare mudflat in Marennes-Oléron Bay (NE Atlantic).

Blanche Saint-Béat[1], Christine Dupuy[1], Pierrick Bocher[1], Julien Chalumeau[1], Margot De Crignis[1], Camille Fontaine[1], Katell Guizien[2], Johann Lavaud[1], Sébastien Lefebvre[3], Hélène Montanié[1], Jean-Luc Mouget[4], Pierre-Yves Pascal[5], Gwenael Quaintenne[1], Gilles Radenac[1], Pierre Richard[1], Frédéric Robin[1], Alain Vézina[6], Nathalie Niquil[1,7].

[1] Université de la Rochelle-CNRS, UMR 7266, Littoral Environnement et Sociétés (LIENSs), La Rochelle, France

[2] Laboratoire d'Océanographie Biologique de Banuyls, Banyuls, France

[3] Laboratoire d'Océanographie et de Géoscience, Université Lille 1, Wimereux, France

[4] Ecophysiologie et Métabolisme des Microalgues, Université du Maine, Le Mans, France

[5] Département de Biologie, UFR SEN, Pointe à Pitre, France

[6] Bedford Oceanographic Institute, Dartmouth, Canada

[7] CNRS, UMR 7208 BOREA, Laboratoire BioMea (FRE 3484), Caen, France

Principales caractéristiques des réseaux trophiques intertidaux qui soutiennent les oiseaux limicoles migrateurs : cas d'une vasière nue dans la baie de Marennes-Oléron (Atlantique NE).

Les oiseaux migrateurs de la route Atlantique-Est s'arrêtent massivement sur la côte Atlantique française pour une pause migratoire ou pour un hivernage. La vasière de Brouage est un des sites d'accueil principal de la côte Atlantique française. L'activité de cette vasière est liée au développement d'un biofilm microbien à basse mer, qui soutient le réseau trophique benthique. Chaque réseau trophique est caractérisé par une structure et un fonctionnement qui assure une plus ou moins grande efficacité de transfert du carbone. La structure et le fonctionnement de la vasière de Brouage est essentiel pour la conservation des espèces s'arrêtant sur cette zone, puisque les oiseaux doivent y trouver la nourriture nécessaire pour atteindre leur zone de reproduction au nord de l'Europe. Le but de cette étude est de décrire et comprendre les caractéristiques du réseau trophique qui permettent à la vasière de Brouage de subvenir aux besoins des oiseaux.

Quelles caractéristiques du réseau trophique benthique de la vasière de Brouage permettent de supporter la pression de prédation exercée par les oiseaux en hiver ?

Réalisation de deux modèles de réseaux trophiques à basse mer considérant deux saisons différentes, l'été où les oiseaux sont absents et l'hiver ou les oiseaux sont présents.
Utilisation de la modélisation inverse par échantillonnage aléatoire.
Les solutions calculées par la modélisation inverse sont utilisées pour calculer certains indices ENA permettant d'accéder à la structure et au fonctionnement du réseau trophique. Pour ces indices, une comparaison statistique entre l'été et l'hiver est alors possible, ce qui constitue une innovation essentielle dans l'application des méthodes numériques couplées modélisation inverse - ENA. Une analyse plus approfondie des réseaux trophiques faite grâce à EcoNetwrk (panel plus complet d'indices ENA) nécessite le choix d'une unique solution par flux. Les conclusions du chapitre précédent sont alors appliquées, c'est-à-dire que c'est la moyenne des flux qui est utilisée comme solution pour chaque flux.

Le réseau trophique hivernal se différencie de celui de l'été par une plus grande activité du système et un plus fort recyclage induit par une activité bactérienne plus importante. Les deux saisons présentent des caractéristiques similaires comme la longueur moyenne des chaines et la spécialisation des voies trophiques. La faible production primaire en été est compensée par un transfert très efficace vers les herbivores, conduisant à une efficacité moyenne de transfert supérieure en été. Cette forte activité du système hivernal associée à un fort recyclage et à une organisation interne inchangée entre les deux saisons soutient l'activité hivernale des oiseaux migrateurs.

Abstract

The migratory shorebirds of the East Atlantic flyway land in huge numbers during a migratory stopover or wintering on the French Atlantic coast. The Brouage bare mudflat (Marennes-Oléron Bay, NE Atlantic) is one of the major stopover sites in France. The particular structure and function of a food web affects the efficiency of carbon transfer. The structure and functioning of the Brouage food web is crucial for the conservation of species landing within this area because it provides sufficient food, which allows shorebirds to reach the north of Europe where they nest. The aim of this study was to describe and understand which food web characteristics support nutritional needs of birds. Two food-web models were constructed, based on *in situ* measurements that were made in February 2008 (the presence of birds) and July 2008 (absence of birds). To complete the models, allometric relationships and additional data from the literature were used. The missing flow values of the food web models were estimated by Monte Carlo Markov Chain – Linear Inverse Modelling. The flow solutions obtained were used to calculate the ecological network analysis indices, which estimate the emergent properties of the functioning of a food-web.

The total activities of the Brouage ecosystem in February and July are significantly different. The specialisation of the trophic links within the ecosystem does not appear to differ between the two models. In spite of a large export of carbon from the primary producer and detritus in winter, the higher recycling leads to a similar retention of carbon for the two seasons. It can be concluded that in February, the higher activity of the ecosystem coupled with a higher cycling and a mean internal organization, ensure the sufficient feeding of the migratory shorebirds.

Introduction

The French Atlantic coast constitutes one of the southernmost attractive areas for shorebird populations wintering in Europe. This is the case of the Pertuis Charentais, where birds use the network of estuarine bays as a stopover or wintering area along the East Atlantic flyway. The Pertuis Charentais is composed of various habitats, largely dominated by intertidal mudflats, which are among the largest in Europe (Verger, 2005). One of the largest and most-

studied sites in the Pertuis Charentais is the eastern mudflat (Brouage mudflat) inside the Marennes-Oléron Bay, which is important for oyster and mussel farming. The central part of the mudflat and adjacent marshlands are included in the National Nature Reserve of Moëze-Oléron (about 6,700 hectares).

Every year, c. 66,000 shorebirds use the Marennes-Oléron Bay in mid-winter, with most of them foraging within the limits of the nature reserve. Among the 18 species present in the bay, six are common and represent c. 85% of all individuals in winter (Red Knot, *Calidris canutus;* Dunlin, *Calidris alpina*; Black-tailed Godwit, *Limosa limosa*; Common Redshank, *Tringa totatnus*; Grey Plover, *Pluvialis squatarola*; and Curlew, *Numenius arquata*) (Mahéo, 2008). The Shelduck, *Tadorna tadorna* is the only anatidae common on bare mudflats. The intertidal mudflat serves one of two functions for shorebirds, depending on the migrating schedules of the considered populations. Shorebirds might use the area for winter survival and stay in the region for most of the non-breeding season or they might use it for refuelling during stopover when migrating further south. The Marennes-Oléron Bay appears to be one of the most attractive sites for coastal shorebirds in the Pertuis Charentais, due to the easy access to huge bare mudflats used as a foraging area and to the presence of a high tide roost in nearby marshland. Moreover, the nature reserve is a classified protected area where hunting is strictly forbidden (Bocher et al., 2012). Most of the shorebird species wintering in the bay breed in northern Europe, Siberia, Greenland or the Canadian Arctic (Delany et al., 2009). Consequently, birds are present in the bay from August to May, with a peak number around January. During the winter, birds feed to fulfil their daily energy needs for survival and to refuel at the end of winter before flying towards their breeding areas. They feed on the tidal Brouage mudflat on macrofauna species, particularly molluscs and annelids. For instance, the gastropods *Hydrobia ulvae* (new name: *Peringia ulvae*) contribute to about 85% of the diet of the Common Shelduck (*T tadorna*) (Viain et al., 2011) and the Red Knot (Quaintenne et al., 2010).

The Brouage mudflat is a bare mudflat (i.e. no seagrass or macroalgae grows on this site) and its primary production is mainly due to the microphytobenthos composed of benthic diatoms (Cariou-Le Gall and Blanchard, 1995). At low tide, diatoms and associated bacteria are concentrated in the first few centimeters of the sediment (Herlory et al., 2004) and form a biofilm that supports the benthic food web. Meiofauna and deposit feeders (e.g. *Hydrobia*),

comprising herbivorous and bacterivorous species, feed on the biofilm. In summer, there is less predation on the benthic macrofauna and their biomass accumulates. In winter, birds feed on macrofaunal species.

The aim of this study was to understand which ecosystem characteristics support the wintering of the birds. To do this, the structure and functioning of this ecosystem were modelled in two seasons; one with a large number of shorebirds (winter) and the other one when shorebirds were absent (summer). This comparative study aims to highlight which features of the ecosystem are crucial in sustaining such a high predator biomass. In regard to the previous result models on the Brouage mudflat, the lower primary and secondary productions observed during winter (Degré et al., 2006; Leguerrier et al., 2007) suggested two main features for the winter food web: 1) a higher efficiency in the transfer of carbon via a higher specialization of trophic links, 2) a stronger cycling in order to increase the stock of carbon available for the shorebirds and thus sustain their nutritional needs.

The ecosystem flows that were not estimated *in situ* during field campaigns, were estimated using Monte Carlo Markov Chain – Linear Inverse Modelling (MCMC-LIM) (Kones et al., 2009; Van den Meersche et al., 2009; Niquil et al., 2011). The set of possible solutions for each flow of the benthic food web in winter and summer, resulting from the MCMC-LIM method, was used to calculate indices of ecological network analysis (ENA). The ENA indices are used to characterise the overall structural properties of food webs, including activity, recycling, specialisation, trophic efficiency, and mean path length (e.g. Ulanowicz, 1997). ENA indices constitute a set of indices that describe the connections between compartments through an analysis of the input and output flows of a compartment, the trophic structure based on a linearisation of the network and the degree of redundancy or specialisation of the flows (Baird et al., 1991; Ulanowicz, 1997; Tortajada et al., 2012). The set of solutions of flows obtained by MCMC-LIM, allowed the calculation of ranges and confidence intervals for some of these indices and thus facilitated statistical tests to compare the two seasonal food webs.

Material and methods

1. Study area

The Brouage intertidal mudflat is located on the French Atlantic coast in the bay of Marennes-Oléron (Fig. IV-1). The bay covers 150 km² and the Brouage mudflat, which is located in the eastern part of the bay, occupies 68 km² at low tide. The bottom slope is relatively flat (1:1,000) and the tidal area is large (up to 4 km). The sediment consists of silt and clay particles (95% < 63 µm) (Pascal et al., 2009). The sampling zone for this study was located in the centre of the Brouage mudflat and is characterised by a typical ridge and runnel structure (Gouleau et al., 2000). It is located at about 1.5 km from the lower part of this intertidal zone, an area covered by oysters from both abandoned and active oyster farms.

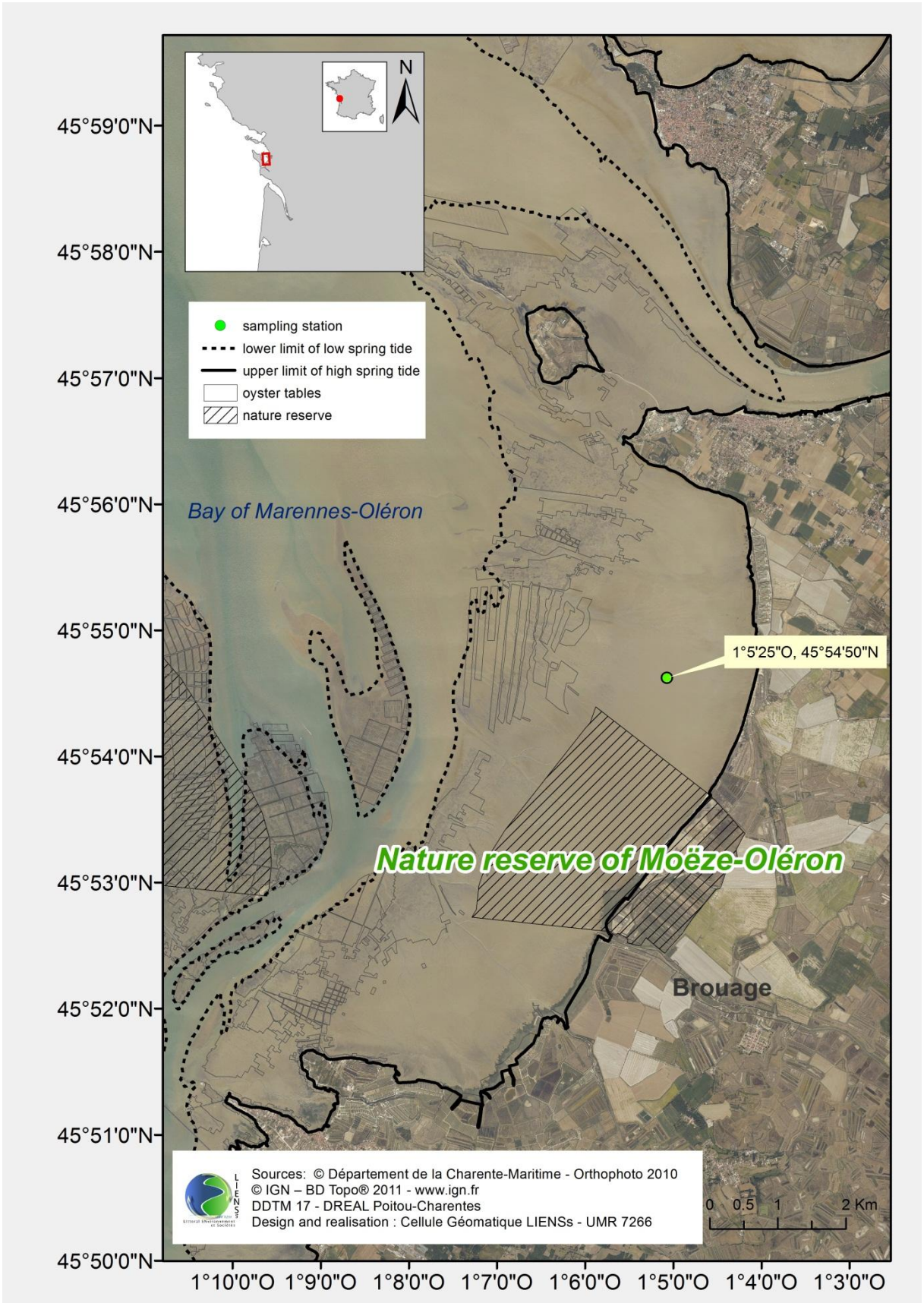


Figure IV-1: Study site: the Brouage mudflat that includes a part of the nature reserve of Moëze-Oléron.

2. Field measurements

Two field campaigns were performed; in winter (from 16 February to 24 February 2008) and in summer (from 13 July to 26 July 2008). Measurements were taken at low tide during the neap-spring cycle. No specific permission was required for the field sampling because the sampling site was located outside the nature reserve of Moëze Marennes-Oléron. Moreover, no endangered or protected species were involved in the field sampling. The species included the categories described below.

2.1. Microphytobenthos

Algal biomass in the sediment was estimated using chlorophyll *a* as a proxy, measured using fluorometry. The carbon algal biomass was estimated from the chlorophyll *a* biomass by the carbon/chlorophyll *a* ratio of 45 (De Jonge, 1980). Irradiance at the mudflat surface (µmol photons m^{-2} s^{-1}) was estimated from Meteo France records and a Licor quantameter.

The mean fluxes of gross primary production and exudation of microphytobenthos were calculated from fortnightly simulations of the coupled dynamics of microphytobenthos, bacteria and extracellular polymeric substances (EPS) under tide, light and temperature. The simulations were performed using a dynamic model adapted from Guarini et al. (2000b), regulating the migratory dynamics of the microphytobenthos in the sediments by nitrogen and carbon internal quotas (Guizien pers. comm.).

2.2. Bacteria

To estimate bacterial abundance, bacteria were extracted from cores of sediment by dilution with sodium pyrophosphate (0.01 mol L^{-1} for >30 min at 4°C). Bacteria were stained with DAPI (2.5 mg L-1) for 15 min in darkness, filtered through 0.2 µm Nucleopore black filters and counted with an epifluorescence microscope (x1,000, Axioskop 2 mot plus, Zeiss). The bacterial biovolume (V) was estimated from the length and the width using Fuhrman's formula (Fuhrman, 1981). The carbon contained in a bacterium was calculated based on the formula $133.754*V^{0.438}$(Vin μm^3) (Romanova and Sazhin, 2010) and was estimated as equal

to 79 fg C. cell^{-1} for a mean biovolume of 0.28 µm^3. This estimate was used to determine the biomass of bacteria in carbon equivalents. The production of sediment-inhabiting bacteria was estimated from their biomass and the ratio of production/biomass, which was previously determined in 2006 for February and July (Pascal et al., 2009).

The *in situ* viral production was estimated as the change in viral abundance after 3 h divided by the time elapsed, for three replicates. The bacterial mortality induced by the viral lysis was determined from the viral production divided by a burst-size of 36 (Corinaldesi et al., 2010), corresponding to the number of virus particles produced per bacterium.

2.3. Meiofauna

The abundance of the meiofauna (foraminifera, copepods and nematodes) in the sediment was estimated at the slack water tide; three replicates were performed each time. The meiofauna was extracted using Ludox HS40 and was counted using a Motoda-box to split samples and obtain aliquots with a number of individuals exceeding 500. The biomass of the meiofauna and its bacterivory were taken from a previous seasonal study at the Brouage mudflat (Pascal et al., 2009). The bacterivory was measured with *in situ* experiments based on ^{15}N-enriched bacteria (Pascal et al., 2008a). The grazing rate of the microphytobenthos by the nematodes was previously estimated using a culture of diatoms, *Navicula jeffreyi*, pre-labeled with ^{14}C (Rzeznik-Orignac and Fichet, 2012).

2.4. Macrofauna

The abundance and biomass of the macrofauna were estimated by randomly choosing three quadrants of 4 m² for sampling, using three sediment cores (30.5 cm in diameter). The resulting nine replicates were sieved over a 1 mm mesh and preserved in ethanol 70%. Determination to the species level and counting were performed following rose Bengal staining under a binocular microsope. The samples were then dried in an incubator (50°C) for 24 h and incinerated at 540°C, to estimate the biomass as ash-free dry mass. The comparison of the isotope signatures (δ^{13}C, δ^{15}N) of sources (microphytobenthos, the benthic and pelagic detrital organic matter) with those of the macrofauna allows the determination of the contribution of each resource to the diet of macrofauna. Samples were analysed using an

elemental analyser (Flash EA 1112, Thermo Scientific, Milan, Italy), coupled to an isotope ratio mass spectrometer (Delta V Advantage with a Conflo IV interface, Thermo Scientific, Bremen, Germany). Results are expressed in the δ unit notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$), following the formula: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard})-1] \times 10^3$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Reference gas calibration was performed using reference materials (USGS-24, IAEA-CH6, IAEA-600 for carbon; IAEA-N1, -N2, -N3, -600 for nitrogen). Analytical precision based on isotope values of acetanilide (Thermo Scientific) was used to estimate the C and N content for each sample series and was <0.1% both for carbon and nitrogen.

2.5. Shorebirds

Shorebird abundance in the Marenne–Oléron Bay was established by counts in January 2008, according to the International Wetland Census (Mahéo, 2008). Further studies on the diet and the time budget, defined as the time birds spent feeding, were performed for the Black-tailed Godwit, the Red Knot, the Curlew and the Shelduck. The diet of the birds was determined from dropping analysis following the methods in Dekinga and Piersma (1993) or Scheiffarth (2001).

Recent studies have shown that some shorebird species, especially the Dunlin and the Western Sandpipers, can graze on microphytobenthos (Kuwae et al., 2008; Kuwae et al., 2012). However, no trophic link between the microphytobenthos and the shorebird species present on the Brouage mudflat during winter could be demonstrated by isotopic analysis (Bocher, pers. comm.). For that reason, grazing of the microphytobenthos by shorebirds was not considered in the food web models in this study.

3. Food-web construction

Two food webs were constructed, either with shorebirds (in winter) or without (in summer). Compared to previous models published for the Brouage mudflat (Leguerrier et al., 2003; Leguerrier et al., 2004; Degré et al., 2006), the current models consider shorter time spans and spatial scales. The food webs represent the trophic interactions between species during a mean

daily low tide in February and July in the mid-zone of the mudflat. The unknown flows were reconstructed based on the Monte Carlo Markov Chain – Linear Inverse Modelling (MCMC-LIM) method. Four successive steps were necessary for the construction of the food web models (Niquil et al., 2011).

3.1. Topology of the food web

The first step determined all the compartments and the flows linking the species. The summer food web was composed of 12 compartments (Table IV-1). The seven bird species present on the mudflat during winter were combined into a single so that the winter food web contained a total of 13 compartments (Table IV-1). Fourteen macrofauna species were assembled into five groups (deposit feeder, carnivorous, omnivorous, suspension feeder and facultative suspension feeder), according to their diet and their trophic behaviour (Baird et al., 2004a; Johnson et al., 2009).

Compartments	**Abbreviations**
Microphytobenthos	mpb
Benthic bacteria	bcb
Foraminifera and copepods	mfb
Nematodes	nem
Deposit feeders (mainly *Hydrobia ulvae**)	dep
Suspension feeders (mainly *Cerastoderma edule and Ruditapes philippinarum***)	sus
Facultative suspension feeders (*Macoma balthica*)	suf
Omnivorous species (mainly H*ediste diversicolor*)	omn
Carnivorous species (mainly *Nephtys hombergii*)	car
Carnivorous birds	cbr
Benthic viruses	vrb
Benthic particulate carbon	bpc
Benthic dissolved carbon	bdc

Table IV-1: Compartments composing the winter and summer food webs.
*New name: *Peringia ulvae* **: new name: *Venerupis philippinarum*

The natural mortality of microphytobenthos and benthic bacteria was considered as negligible, based on the importance of the grazing observed in the field. Only the EPS (Exopolysaccharide) exudation of the microphytobenthos to the dissolved organic carbon (BDC) via secretion was considered. A flow of dissolved organic carbon exudation by bacteria was included; part of this flow corresponds to the loss of bacterial carbon via viral lysis. Part of the carbon originating from bacteria was considered as available for consumers during the high tide. The consumption by the five macrofauna groups was considered as equal over the 24 h diurnal cycle, irrespective of the tidal level, even for the deposit feeders (mainly composed of *H. ulvae* (Vieira et al., 2010)). As consequences, links corresponding to unconsumed production between high and low tides were considered as imports. The summer and winter food web models were composed of 62 and 70 flows, respectively.

3.2. Equations

The second step consisted of establishing a set of linear equations (Table IV-2). The mass balances that correspond to the sum of the inflows and outflows for each of the compartments constitute the first part of the linear equations. The variations in the compartment biomasses are generally considered negligible, compared to the flow values, which provide mass balances equal to zero. The second part of the linear equations was composed of the flows that were locally estimated in the sampling area. The resulting set of linear equations was written in the form $A * x = b$, where x is the vector that contains the possible flows, A is the matrix that expresses the mass balance and the field observation as a combination of coefficients of the carbon flows, and b is the vector that contains the values of mass balances and the values of the known flows (Vézina, 1989).

Mass balances		
1-Microphytobenthos	(gppTOmpb)-(mpbTOres+mpbTObdc+mpbTOmfb+mbpTOnem+mpbTOdep+mpbTOomn+mpbTOsuf+mpbTOexp)=0	
2-Benthic bacteria	(bdcTObcb)-(bcbTOres+bcbTObdc+bcbTOmfb+bcbTOnem+bcbTOdep+bcbTOomn+bcbTOsuf+bcbTOvrb)=0	
3-Foraminifera	(mpbTOmfb+bcbTOmfb+bpcTOmfb)-(mfbTOres+mfbTOcar+mfbTOomn+**mfbTOcbr**+mfbTObpc)=0	
4-Nematodes	(mpbTOnem+bcbTOnem+bpcTOnem)-(nemTOres+nemTOcar+nemTOomn+nemTObpc)=0	
5-Carnivorous	(impTOcar+mfbTOcar+nemTOcar+depTOcar+susTOcar+sufTOcar)-(carTOres+carTObpc+**carTOcbr**+carTOexp)=0	
6-Deposit feeders	(impTOdep+mpbTOdep+bcbTOdep+bpcTOdep)-(depTOres+depTOcar+depTOomn+**depTOcbr**+depTObpc+depTOexp)=0	
7-Omnivorous	(impTOomn+mfbTOomn+nemTOomn+depTOomn+susTOomn+sufTOomn+bcbTOomn+bcpTOomn)-(omnTOres+omnTOcbr+omnTObpc+omnTOexp)=0	
8-Suspension feeders	(impTOsus)-(susTOres+susTOcar+susTOomn+**susTOcbr**+susTObpc+susTOexp)=0	
9-Facultative suspension feeders	(impTOsuf+mpbTOsuf+bcbTOsuf+bpcTOsuf)-(sufTOres+sufTOcar+sufTOomn+**sufTOcbr**+sufTObpc+sufTOexp)=0	
10-Carnivorous birds	(mfbTOcbr+carTOcbr+depTOcbr+omnTOcbrsusTOcbr+sufTOcbr)-(cbrTOres+cbrTObpc+cbrTOexp)=0	
11-Benthic viruses	(bcbTOvrb)-(vrbTObdc+vrbTOext)=0	
12-Benthic particular carbon	(mfbTObpc+nemTObpc+carTObpc+depTObpc+omnTObpc+susTObpc+sufTObpc+**cbrTObpc**)-(bcpTOmfb+bcpTOnem+bpcTOdep+bpcTOomn+bpcTOsuf+bpcTOexp)=0	
13-Benthic disolve carbon	(mpbTObdc+bcbTObdc+bpcTObdc)-(bdcTObcb+bdcTOexp)=0	
Processes\ Season	**Winter**	**Summer**
14-gppTOmpb	413.09	183.6
15-mpbTObdc	110.75	51
16-Production of bcb (bdcTObcb-bcbTOres)	169.32	93.94
17-bcbTOmfb	0.086	0.035
18-bcbTOnem	0.107	0.11
19-bcbTOdep	6.11	11.25
20- bcbTOvrb	1.88	3.58

Table IV-2: Mass balances (1-13) and values of flows measured in the field (14-20). Flows that were only present in the winter model are in bold. The values of flows were expressed in $mgC.m^{-2}$ per low tide. The flows were coded by 8 letters (e.g. mpbTOmfb): the three first letters correspond to the compartment 'source', letters after the TO described the compartment 'sink' (see table IV-1 for compartment abbreviations). For instance the flow mpbTOmfb is the flow of carbon that leaves the compartment mpb to come into the compartment mfb. gpp= gross Primary Production, res=respiration, imp=imports and exp= exports.

3.3. Inequalities

The third step consisted of adding constraints determined from the literature, experiments, or field measurements from comparable intertidal mudflats, to obtain biologically and ecologically realistic flow values.. The biological constraints were expressed as a set of linear inequalities in the form: $G * x \leq h$, where G is the matrix that contains the coefficients of the biological constraints and h is the vector which was composed of the values of these biological constraints (Vézina, 1989).

For all the compartments, the respiration, consumption, excretion and import flows were constrained by lower and upper limits. The inequalities, which corresponded to the physiological rates (e.g. assimilation efficiency) or the diet contribution, are listed in Table 3. The other inequalities, which corresponded to the absolute values of the biological processes, are described below. Two different densities of birds were considered, to determine the maximum and minimum values of the previously cited processes (i.e. consumption, respiration and egestion). The minimum and maximum densities of shorebirds per m² mudflat were based on the following hypotheses: 1) the lower density was based on the assumption that the birds covered the whole mudflat at low tide, 2) the maximum density was based on the assumption that the birds followed the ebbing tide covering only a limited area of the mudflat.

Respiration	Microphytobenthos	Lower limit	0.05*gpp-resp	<0	Vézina and Platt, 1988
		Upper limit	-0.3*gpp+resp	<0	
Net Growth Efficiency	Meiofauna	Lower limit	0.5*CTOmfb-0.5*mfbTOE-resp	<0	van Oevelen et al., 2006
		Upper limit	-0.7*CTOmfb+0.7*mfbTOE+resp	<0	
	Nematods	Lower limit	0.1*CTOnem-0.1*nemTOE-resp	<0	van Oevelen et al., 2006
		Upper limit	-0.4*CTOnem+0.4*nemTOE+resp	<0	
	Macrofauna	Lower limit	0.3*CTOmac+0.3*ITO mac-0.3*macTOE-resp	<0	van Oevelen et al., 2006
		Upper limit	-0.5*CTOmac-0.5*ITO mac+0.5*macTOE+resp	<0	
	Benthic bacteria	Lower limit	$0.39*U_{doc}$-resp	<0	delGiogio and Cole, 1998
		Upper limit	$-0.89*U_{doc}$+resp	<0	
Egestion	Nematods	Lower limit	0.7*CTOnem-nemTOE	<0	van Oevelen et al., 2006
		Upper limit	-0.94*CTOnem+nemTOE	<0	
	Meiofauna	Lower limit	0.23*CTOmfb-mfbTOE	<0	van Oevelen et al., 2006
		Upper limit	-0.43*CTOmfb+mfbTOE	<0	
	Macrofauna	Lower limit	0.25*CTOmac-macTOE	<0	van Oevelen et al., 2006
		Upper limit	-0.6*CTOmac+macTOE	<0	
Contribution of mpb to the diet of macrofauna	***In summer***				
	Deposit feeders	Upper limit	0*mpbTOdep-1*bpcTOdep	<0	in this study
	Omnivorous species	Lower limit	-0.74*mpbTOomn+0.26*bpcTOomn	<0	
		Upper limit	0.09*mpbTOomn-0.91*bpcTOomn	<0	
	Suspension feeders	Lower limit	-0.35*mpbTOsuf+0.65*bpcTOsuf	<0	
		Upper limit	0.18*mpbTOsuf-0.82*bpcTOsuf	<0	
	In winter				
	Deposit feeders	Lower limit	-0.5*mpbTOdep+0.5*bpcTOdep	<0	in this study
		Upper limit	-1*bpcTOdep	<0	
	Omnivorous species	Lower limit	-0.35*mpbTOomn+0.65*bpcTOomn	<0	
		Upper limit	0.14*mpbTOomn-0.86*bpcTOomn	<0	
	Suspension feeders	Lower limit	-0.24*mpbTOsuf+0.76*bpcTOsuf	<0	
		Upper limit	0.01*mpbTOsuf-0.99*bpcTOsuf	<0	
Contribution of bpc to the diet of macrofauna	***In summer***				
	Deposit feeders	Upper limit	0.89*bpcTOdep-0.11*mpbTOdep	<0	in this study
	Omnivorous species	Lower limit	-1*bpcTOomn	<0	
		Upper limit	0.56*bpcTOomn-0.44*mpbTOomn	<0	
	Suspension feeders	Lower limit	-1*bpcTOsuf	<0	
		Upper limit	0.71*bpcTOsuf-0.29*mpbTOsuf	<0	
	In winter				
	Deposit feeders	Lower limit	-1*bpcTOdep	<0	In this study
		Upper limit	0.69*bpcTOdep-0.31*mpbTOdep	<0	
	Omnivorous species	Lower limit	-1*bpcTOomn	<0	
		Upper limit	0.76*bpcTOomn-0.24*mpbTOomn	<0	
	Suspension feeders	Lower limit	-1*bpcTOsuf	<0	
		Upper limit	0.83*bpcTOsuf-0.17*mpbTOsuf	<0	

Table IV-3: Set of inequalities used (biological rates, contribution of the microphytobenthos (mpb) and of the benthic particulate carbon (bpc) to the diet of macrofauna). Gpp= gross primary production, resp=respiration, C=consumption, E=egestion. For compartments' abbreviations see table IV-1.

3.3.1. Respiration

The respiration of the sediment-inhabiting bacteria was constrained by the bacterial growth efficiency (BGE) between 0.11 and 0.61 as previously determined for a coastal bay (delGiorgio and Cole, 1998). The meiofauna respiration (nematodes, copepods and foraminifera) was constrained by the organic carbon biomass-specific respiration rate, which ranged between 1.6 and 2.5 µl O_2 h^{-1} mg C^{-1}. The O_2 content was converted into carbon based on the following equality: 1 mL O_2 = 0.4 mg C (derived from Crisp, 1971; in Warwick and

Price, 1979). The macrofauna respiration was estimated from the range of values given by the virtual handbook of Thomas Brey (http://www.thomas-brey.de/science/virtualhandbook; Brey (2001; 2010)), using the biomasses of the macrofauna groups and the mean temperatures derived from the field measurements (8°C and 21°C in winter and summer, respectively). In this model, the energetic expenditure of the birds was considered to be equal to the basal metabolic rate, due to the low activity of shorebirds during wintering. Shorebird respiration was estimated by an allometric relation of the basal metabolic rate (BMR) (Kersten and Piersma, 1987; Scheiffarth and Nehls, 1997). The respiration rate per m² depends on the density of shorebirds on this area. The maximum and minimum respiration values per m² mudflat were derived from the above-described limits of the shorebird densities.

3.3.2. Consumption

The total consumption by nematodes was determined from the ranges of total ingestion per individual determined by Schiemer (1987). The maximum and minimum limits of macrofauna consumption were determined from its production. Production was estimated from the production/biomass (P/B) ratio, which ranged from 0.01 to 0.05 (van Oevelen et al., 2006b). Consumption was estimated by the production/consumption ratio, with a maximum value of 0.87 (Brey, 2001). The respective contributions of microphytobenthos and benthic particulate carbon to the macrofauna diet were obtained by isotope signatures. For each resource, the maximum and minimum obtained values limited their respective contribution to the macrofauna diet. The diet contribution of each trophic group was obtained by averaging the diet contribution (generated by the ISOSOURCE model), weighted by the biomass for each of the species forming a given group. In winter, shorebirds are energy minimisers and their consumption is balance by their energy expenditure (van Gils et al., 2005; Nolet et al., 2006). The consumption by the shorebirds was estimated from the daily energetic requirement ($C = n*3*BMR*(1/AE)$, where n is the number of individuals and AE is the assimilation efficiency (Kersten and Piersma, 1987; Scheiffarth and Nehls, 1997)). Because the maximum and minimum consumption limits for the shorebirds were derived from the above-described density limits, they were expressed per m² of mudflat. Shorebirds cannot feed all day and are constrained by the time of emersion (i.e. the hourly consumption is higher than if they could or would feed the whole day). The time devoted to feeding varies according to the species (Table IV-4), thus, the predation pressure applied by the shorebirds per m² per hour differs

according to the species. Moreover, each species has a particular diet (Table IV-4). Knowing the contribution of the different macrofauna species to the diet of the shorebird species allowed determination of the maximum and minimium consumption of each macrofauna group by the shorebirds. The diet composition of four species (Red Knot, Black-tailed Godwit, Common Shelduck and Curlew) was determined within the study area (Quaintenne et al., 2010; Boileau and Delaporte, 2011; Viain et al., 2011; Robin et al., in press). The contribution of the macrofauna to the diet of these species was expressed according to the total consumption by the shorebirds and was considered as the minimum contribution of macrofauna to the total consumption by shorebirds. The diets of the three other species, which remained unknown for the study area, were not extracted from the literature due to their great variability between sites in Europe and were consequently not used to define any constraints.

Species	**Time budget**	**References**	**Diet**	**References**
Black-tailed Godwit (*Limosa limosa*)	10 hours	Robin et al., in press	Macoma balthica: 100%	Robin et al., in press
Common Redshank (*Tringa totanus*)	70% during the night, 50% during the day	Dwyer, 2010	Not determined for this area	-
Common Shelduck (*Tadorna tadorna*)	14 hours	Viain et al., 2011	Hydrobia ulvae: 85% Others: 15%	Viain et al., 2011
Curlew (*Numenius arquata*)	7 hours	Stilmann et al., 2007	Scrobicularia plana: 22.2% Nephtys hombergii + Hediste diversicolor: 65.52% Carcinus maenas: 9.9%	Boileau and Laporte, 2011
Dunlin (*Calidris alpina*)	10 hours	Zwarts and Wanink, 1993	Not determined for this area	-
Grey Plover (*Pluvialis squatarola*)	40% of the consumption during the night	Turpie and Hockey, 1993	Not determined for this area	-
Red Knot (*Calidris canutus*)	10 hours	Quaintenne et al., 2010	Hydrobia ulvae: 86% Macoma balthica: 13% Cerastoderma edule: 1%	Quaintenne et al., 2010

Table IV-4: Time spent to feed by each shorebirds species and their diet.

3.3.3. Egestion

The egestion of the nematodes and meiofauna was constrained by the assimilation efficiency and by the net growth efficiency rates, which are defined in Table IV-3. For the macrofauna, a maximum egestion value was determined from the maximum value of the consumption and the minimal coefficient of the AE. The range of excretion was determined from the maximum and minimum values of consumption, considering an AE equal to 0.80 for the shorebirds (Scheiffarth and Nehls, 1997).

3.3.4. Imports

The imports for the macrofauna were considered as the production available before the diurnal low tide. In summer, this represented the macrofauna production at high tide (diurnal and nocturnal) and nocturnal low tide. In winter, only the macrofauna production generated by the previous high tide was considered as an import, because shorebirds can feed on the mudflat during the night (Lourenço et al., 2008). The maximum and minimum values of the imports were estimated from the maximum and minimum values of macrofauna production obtained as described above.

3.4. Calculation of the solutions

The MCMC-LIM, based on the mirror technique defined by Van Den Meersche et al. (2009), calculates several solutions and allows a direct characterization of the uncertainty. This modelling technique brings the advantage of calculating a range of possible values for each flow (i.e. a probability density function) This mirror technique reflected the proposed solutions inside the walls of the solution space until one was found to respect all the defined boundaries. The walls of the solution space corresponded to the equations and the inequalities defined in the model. This application required the definition of two parameters: the jump and the number of iterations. The jump corresponds to the length between two solutions and the number of iterations is the number of solutions sampled in the solution space (Van den Meersche et al., 2009). In this study, a jump equal to one and 500,000 iterations were chosen to obtain an optimal coverage of the solution space. All simulations were performed using

MATLAB© software and with an algorithm based on a translation (made by Alain Vézina and Lauriane Campo) of the R-CRAN project package LIM-Solve (Van den Meersche et al., 2009).

4. Ecological Network Analysis

Ecological network analysis is a set of numerical indices that describe the overall structure and function of a food web (Table IV-5). For the Total System Throughput (TST), Average Mutual Information (AMI), Average Path Length (APL), Internal Relative Ascendency (IRA), Finn Cycling Index (FCI), and Comprehensive Cycling Index (CCI), a MATLAB© routine was written by Carole Lebreton and Markus Schartau (GKSS Research Centre, Geesthacht, Germany), to calculate the index value for every solution estimated by MCMC-LIM. The significance of the differences between the values for the two seasons was determined by the Wilcoxon test ($\alpha = 0.01$). The tested hypothesis stated that the two data sets result from a continuous distribution with similar medians.

For the Lindeman spine, the relative redundancy, relative overheads, number of cycles and system trophic efficiency, the software EcoNetwrk, developed by Ulanowicz and Kay (Ulanowicz and Kay, 1991), was used with a unique set of solutions. This solution set corresponded for each flow, to the mean value of the whole set of possible solutions (Saint-Béat et al., Chap 3) .

Indices	Calculation	Definition	Sources
Total System Throughput (TST)	sum of all flows	activity of the whole ecosystem	a
Average Path Length (APL)	(TST-sum of imports)/ sum of imports	the average number of compartments that an atom of carbon passes through between its entry into the system and its exit	b
Finn Cycling Index (FCI)	T_c/ TST	proportion of cycled flow in a system	c
Average Mutual Information (AMI)	-	degree of specialisation of flows in the network	d
RelativeAscendency	A/DC	fraction of the network that is organized	a
Internal reltive Ascendency	A_i/DC_i	fraction of the internal exchanges that is organized	
Overheads (O)*	DC-A	fraction of the network that is not yet organized	
Relative redundancy	R/DC	proportion of the redundancy in the network	
System trophic efficiency	logarithmic mean of the all level efficiencies	globale efficiency of transfer trhough the network	e

Table IV-5: List of ENA indices calculated on the set of 500, 000 solutions from the MCMC-LIM implementation. T_c: quantity of carbon that is involved in cycling. A: the Ascendency (=TST*AMI). DC: Development Capacity corresponds to the maximal value of Ascendency. Ai: internal Ascendency. DC_i: Internal development capacity. A_i and DC_i only consider internal exchanges, and thus respiration exports and imports are excluded. *: Overheads are divided into three groups: 1-Overheads on the imports, 2- Overheads on the exports and 3- Dissipative overheads. All of them were expressed in percentage of the DC.

[a]:Ulanowicz, 1986,

[b]: Kay et al., 1989, Baird et al.,1991

[c]: Finn, 1976

[d]: Hirata and Ulanowicz, 1984

[e]: Baird et al., 2004

The trophic analysis, based on the trophic concept of Lindeman (Lindeman, 1942), corresponded to a representation of the complex network by a concatenated trophic chain with discrete trophic levels (Baird et al., 2004a). The quantity of transferred carbon from one level to another was represented, as well as the carbon loss by respiration, exports and egestion/excretion. The Lindeman spine allowed the calculation of the transfer efficiency from one level to the next.

Results

1. Input and output flows

Shorebirds fed 7.4 $mgC.m^{-2}$ per low tide on the macrofauna (table IV-6). About 17% of the ingested carbon was egested and 0.9 $mgC.m^{-2}$per low tide was lost by respiration. Thus the shorebirds exported 5.2 $mgC.m^{-2}$ at each low tide.

A greater gross primary productivity of the microphytobenthos and a higher uptake of DOC by the benthic bacteria were observed in winter (table IV-6). Nematodes and deposit feeders were the biggest consumers of the mudflat; in contrast, the consumption of other benthic consumers was low. The consumption of the deposit-feeders was higher in winter contrary to the others species of the macrofauna, except the carnivorous species. The viral lysis was more important in summer. The exudation of DOC by benthic bacteria and microphytobenthos was more important in winter. The egestion of the macrofauna followed the trends of their consumption, with higher egestion for facultative suspension-feeders and omnivorous species and a lower egestion for carnivorous species and deposit-feeders in summer. Respiration values of microphytobenthos and of benthic bacteria were higher in winter. The respiration of the macrofauna was more important in summer. Imports of carbon to macrofauna and exports of macrofaunal production were both higher in summer. The deposit-feeders were the compartment that imported the greatest quantity of carbon. Losses of macrofauna production (difference between imports and exports) were higher in summer, except for the carnivorous species. On the other hand, exports of microphytobenthos, benthic bacteria and non-living compartments were higher in winter.

Flows	Winter		Summer	
Gross primary production of microphytobenthos	**413.1**		**183.6**	
Consumption of meiofauna	0.3	± 0.0	0.2	± 0.0
Consumption of nematodes	39.3	± 8.9	48.0	± 13.6
Consumption by carnivorous species	2.6	± 0.3	2.1	± 0.3
Consumption by deposit feeders	63.5	± 17.7	41.4	± 6.9
Consumption by omnivorous species	0.8	± 0.1	5.0	± 0.7
Consumption by facultative suspension feeders	0.8	± 0.1	1.4	± 0.6
Consumption by carnivorous birds	7.4	± 1.5	-	
doc uptake by benthic bacteria	291.9	± 11.3	162.9	± 8.1
viral lysis	**1.8**		**3.6**	
Exudation of doc by microphytobenthos	**110.8**	±	**51.0**	
Exudation of doc by benthic bacteria	147.1	± 12.0	69.7	± 7.4
Exudation of doc by benthic viruses	0.9	± 0.5	1.9	± 1.0
Egestion meiofauna	0.1	± 0.0	0.1	± 0.0
Egestion nematodes	36.4	± 8.6	44.6	± 12.9
Egestion carnivorous species	1.2	± 0.3	0.9	± 0.2
Egestion deposit feeders	31.3	± 10.6	19.4	± 5.2
Egestion omnivorous species	0.4	± 0.1	2.2	± 0.5
Egestion facultative suspension feeders	0.3	± 0.1	0.6	± 0.2
Egestion carnivorous birds	1.2	± 0.4	-	
Transformation particulate carbon to dissolved carbon	49.5	± 15.9	48.4	± 11.0
Respiration microphytobenthos	69.1	± 30.0	31.6	± 13.1
Respiration meiofauna	0.1	± 0.0	0.1	± 0.0
Respiration nematodes	1.0	± 0.1	0.7	± 0.1
Respiration carnivorous species	1.6	± 0.2	1.8	± 0.3
Respiration deposit feeders	45.5	± 5.4	63.7	± 16.1
Respiration omnivorous species	0.5	± 0.0	4.3	± 0.8
Respiration suspension feeders	0.7	± 0.1	3.8	± 0.9
Respiration facultative suspension feeders	0.4	± 0.1	2.2	± 0.6
Respiration carnivorous birds	0.9	± 0.4	-	
Respiration benthic bacteria	122.6	± 11.3	69.0	± 8.1
Import to carnivorous species	3.2	± 0.5	3.7	± 1.0
Import to deposit feeders	94.5	± 15.9	142.2	± 38.8
Import to omnivorous species	1.0	± 0.2	9.2	± 2.6
Import to suspension feeders	2.0	± 0.4	10.1	± 2.9
Import to facultative suspension feeders	2.8	± 0.9	4.9	± 1.4
Export microphytobenthos	145.1	± 35.6	31.9	± 16.7
Export carnivorous species	2.0	± 0.8	3.1	± 0.8
Export deposit feeders	76.0	± 16.7	99.6	± 27.0
Export omnivorous species	0.5	± 0.3	7.7	± 2.1
Export suspension feeders	0.5	± 0.4	5.4	± 2.2
Export facultative suspension feeders	1.7	± 1.0	2.6	± 1.1
Export carnivorous birds	5.2	± 1.6	-	
Export benthic bacteria	13.8	± 12.0	8.3	± 7.4
Export benthic viruses	0.9	± 0.5	1.7	± 1.0
Export dissolved carbon	16.3	± 13.9	8.1	± 6.9
Export particulate carbon	12.0	± 10.1	8.2	± 7.4

Table IV-6: Flow values in the winter and summer models, expressed in $mgC.m^{-2}$ per low tide. Values in bold correspond to flows estimated *in situ*. Values of flows were estimated by the average of 500,000 solutions obtained by the MCMC-LIM implementation. Values expressed in average +/- standard deviation.

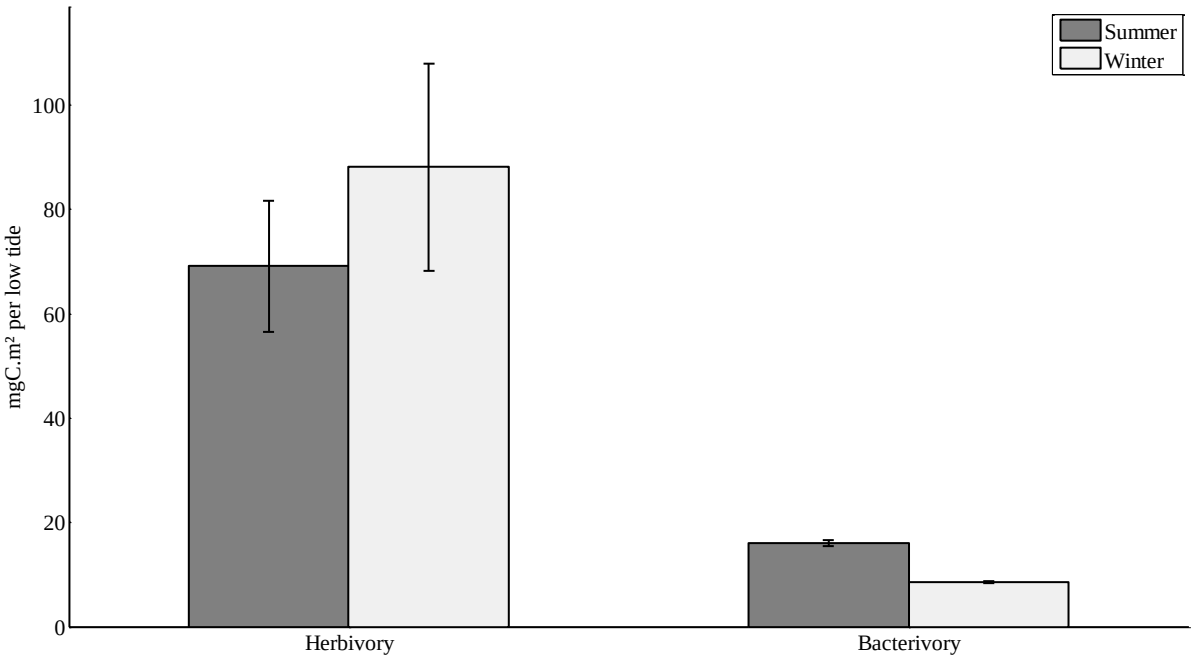


Figure IV-2: Herbivory and bacterivory in the summer and winter food webs. The herbivory and bacterivory correspond to the mean value of herbivory and bacterivory estimated for the 500,000 solutions proposed by the MCMC-LIM method. The error bars represent the standard deviation of values.

Herbivory appeared more important in winter than in summer, whereas bacterivory increased in the summer (Fig. IV-2). In summer, bacterivory represented a higher proportion of the consumption by benthic organisms, with the ratio bacterivory/herbivory being 23% in summer. Bacterivory decreased in winter, to represent only 9% of herbivory.

2. Throughputs and internal flows

The compartment throughputs (sum of inputs) of the various compartments, which quantifies their activity (Fig. IV-3) followed different tendencies. The order of the compartment activities changed according to the season considered. The activity of the biofilm (mpb, bdc and bcb) was higher in winter, in contrast to the activity of macrofauna that tended to be

higher in summer. In winter, microphytobenthos dominated the benthic activity, followed by benthic bacteria and dissolved organic carbon. The activity of deposit-feeders was the next highest, followed by that of particulate carbon and nematodes. In contrast, during summer, the four first compartments (mpb, bdb, bcb and dep) demonstrated a similar quantity of inputs. Shorebird activity was ranked between the activity of deposit-feeders and the activity of carnivorous macrofauna.

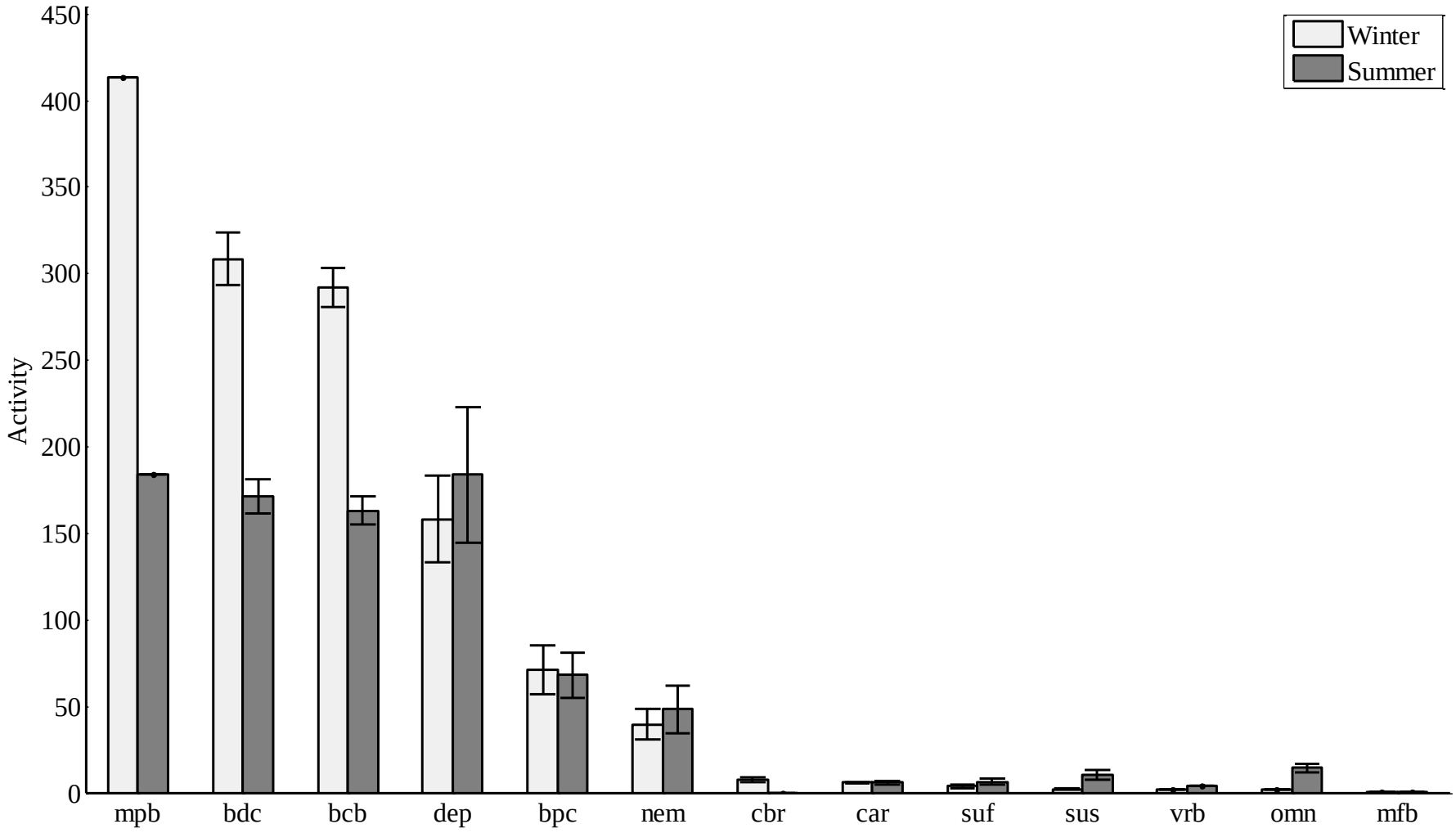


Figure IV-3: Compartment activities in $mgC.m^{-2}.LT^{-1}$ for the two seasons. The error bar represent the standard deviation on the 500, 000 simulations. See table IV-1 for compartment abbreviations.

3. Ecological network analysis

For all the ENA indices calculated for the 500,000 solutions of the MCMC-LIM, values of indices significantly differed between the two seasons (Fig. IV-4). A higher TST was observed in winter, which suggests a higher activity of the whole system. Thus, more carbon and energy flowed through the food web in the winter. A higher quantity of carbon involved in the cycling was observed in winter (i.e. high values of the FCI). The high relative ascendency (A/DC) that ranged from 0.6 to 0.7, independent of the season, suggests a well-organised ecosystem and this organisation tended to be higher in winter. This Relative Ascendency value showed that the organised part of the system was more important than the inefficient part of the network.

For the AMI, APL and A_i/DC_i the trend was less obvious (Fig. IV-4). The ranges of summer values encompassed those in winter, but the Wilcoxon test remained significant. The specialisation of pathways, measured by the AMI, only slightly changed according to the season. The internal organisation that corresponds to the A_i/DC_i value, remained very similar for the two seasons. This indicates that when the exogenous exchanges are excluded, the network showed a similar organisation. The APL defines the mean number of compartments that an atom of carbon passes through before leaving the food web. Again, the difference was small, which means that an atom of carbon passes through a similar number of compartments, irrespective of season.

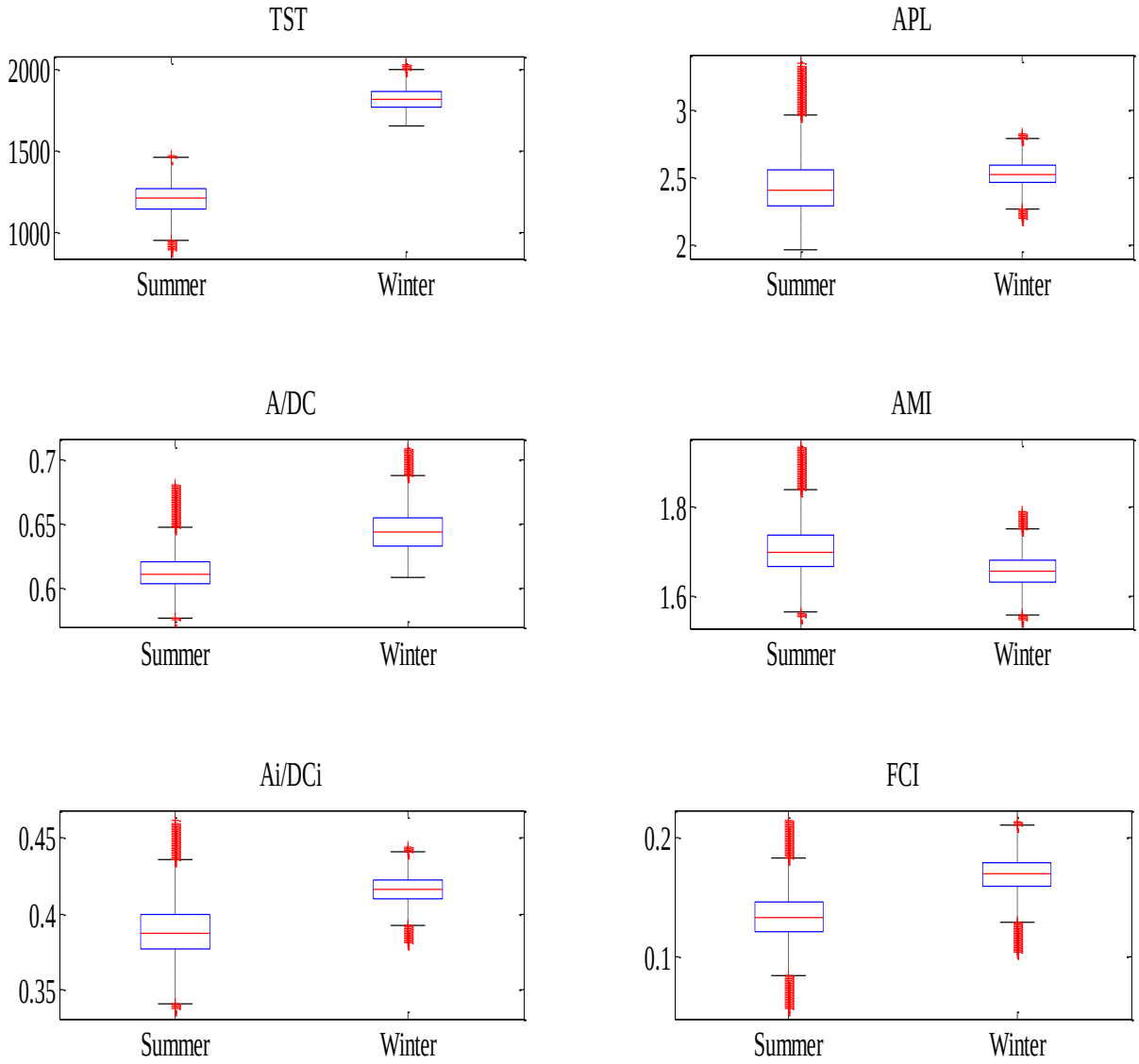


Figure IV-4: Boxplot representing the ENA indices: the Total System Throughput (TST), the Average Path Length (APL), the relative Ascendency (A/DC), the Average Mutual Information (AMI), the internal relative Ascendency (A_i/C_i) ,the Finn Cycling Index (FCI). These indices were calculated with the 500 000 solutions of the MCMC- LIM implementation. Red crosses correspond to outliers. Medians of all these indices were significantly different for the two seasons (Wilcoxon test, H_0 was rejected, p-value < 0.01).

Complementary indices calculated with the mean value of each flow (Table IV-7) confirmed the previous trends. This second set of indices was estimated from the EcoNetwrk and as a consequence, no uncertainties were estimated. More numerous flows were involved in cycling in winter, with 48, compared to 28 in summer, which confirms the higher cycling in winter. In spite of its higher activity, a lower mean trophic efficiency was observed in the winter food

web. The fraction of inefficient network associated with the relative redundancy was similar in the two food webs and thus confirmed a similar specialisation of trophic pathways. The inefficiency of the network was also measured using overheads: the loss of efficiency due to the imports of carbon into the ecosystem (i.e. overheads on imports), the loss of carbon by dissipation (i.e. dissipative overheads) and the loss of efficiency by export of carbon outside the ecosystem (i.e. overheads on exports). The loss of efficiency due to imports appeared to be lower in winter, whereas the inefficiency due to the exports tended to be higher. The loss of carbon by dissipation was similar for the two seasons.

Attributes	**Winter**	**Summer**
Mean trophic efficiency (%)	5.8	6.54
Number of cycles	48	28
Relative redundancy R/DC (%)	23.51	24.08
Overheads on imports (%)	4.97	6.08
Overheads on export (%)	13.02	11.37
Dissipative overheads (%)	10.99	10.82

Table IV-7: Parameters of trophic network for the Brouage mudflat at low tide in winter and summer. These indices were calculated from the mean of the values estimated by the MCMCIA method.

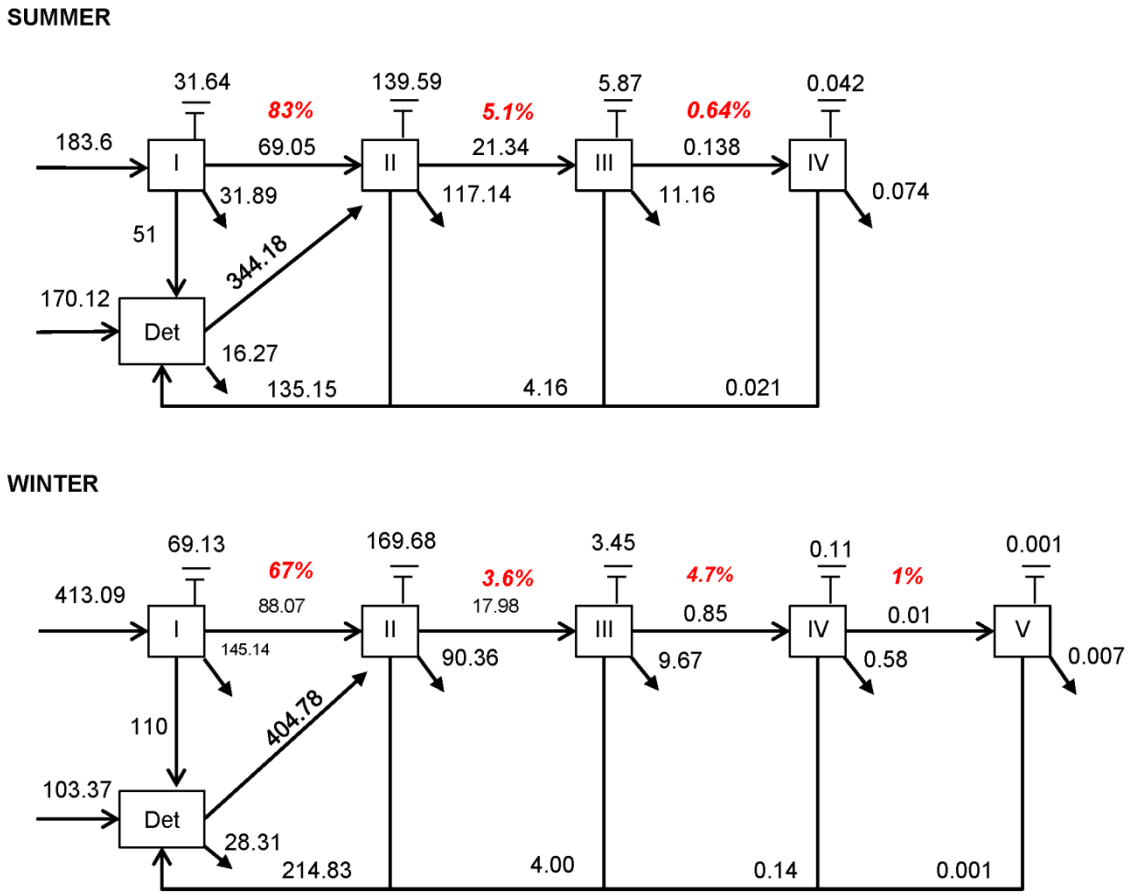


Figure IV-5: Lindeman Spine for the two seasons. The ⟶ correspond to the exchanges between trophic levels, the ↘ show the export of carbon and ⊤ symbolize the loss of carbon by respiration. Numbers in red are the transfer efficiencies between each level. Imports to macrofauna were assimilated to imports to the non-living compartment.

The Lindeman spine, which represents the complex network in the trophic chain, comprises four levels in summer and five levels in winter (Fig. IV-5). Level I contained the primary producers, which are the microphytobenthos in this model. The compartment det (detritus) regrouped all non-living compartments, which included dissolved and particulate carbon. Level II grouped herbivores (i.e. a part of the meiofauna, and macrofauna except carnivorous) and bacteria. Levels III and IV contained the macrofauna and the remaining bacterivorous species in level III and carnivorous and omnivorous species in levels III and IV. The shorebirds were in levels III, IV and V, and were the only group in level V.

The inputs to level I were higher in winter, whereas the inputs to the det compartment were higher in summer (Fig. IV-5). The exports from these levels (I and det) were higher in winter. A higher quantity of carbon passed from level I to level II in winter, but this transfer was less efficient than in summer. Detritivory, linking the Det and level II was more important in winter. The respiration of the second level was higher in winter, in contrast to the export, which was smaller in winter. The return to det was higher in winter. Trophic efficiencies between lower trophic levels (i.e. between I and II and II and III), were higher in summer. The winter food web was characterised by a contrasting pattern, with low trophic efficiencies at lower trophic levels and more efficient transfers in the upper part of the chain (between levels III, IV and V).

Discussion

1. Compartment activities

Differences in ecosystem function between winter and the summer have already been observed in the Brouage mudflat (Degré et al., 2006; Leguerrier et al., 2007). In previous works, the summer food web appeared to be the most productive season (Degré et al., 2006), whereas in the present models, winter was the most productive. This apparent contradiction might be explained by the consideration of a high primary production in summer in the previous models of Degré et al. (2006) and Leguerrier et al. (2007). In these models, the 'summer' period corresponded to seven months from March to October with a strong

heterogeneity of primary production: some months like April with a high productivity (Blanchard et al., 1997) and others (June, July) of lower productivity. The integration of this heterogeneity led to a mean production higher than the one considered in our model which is restricted to 'true' summer (July). On the Brouage mudflat, July is characterised by strong lights and temperatures that can be harmful for photosynthesis and that can inhibit the productivity of microphytobenthos (Blanchard et al., 1997; Mouget et al., 2008; Serôdio et al., in press). Additionally, high grazing in summer generates a significant depletion of the microphytobenthic biomass (Cariou-Le Gall and Blanchard, 1995; Haubois et al., 2005b). Hence, because we considered truly characteristic periods (July and February), the seasonal differences in the microphytobenthic production were different from previous studies (Degré et al., 2006; Leguerrier et al., 2007).

The biofilm activity (microphytobenthos, benthic bacteria and dissolved organic carbon i.e. EPS) dominated the benthic activity. This major finding was in agreement with a previous Brouage model developed on an annual basis (Leguerrier et al., 2004). The dominance of biofilm activity was true for both seasons and was more pronounced in winter. However, the ranking of compartment activity inside the biofilm differed from before (Leguerrier et al., 2004). In the present study, microphytobenthos showed the higher activity, whereas benthic bacteria and DOC dominated in the model from Leguerrier et al. (Leguerrier et al., 2004). Because substantial knowledge was since gained on the seasonal variation of bacterial production (Pascal et al., 2009) and on the bacterivory exerted by nematodes, meiofauna and *H. ulvae* (Pascal et al., 2008b; Pascal et al., 2008c; Pascal et al., 2008d), refined estimates of bacterial processes were used here. Shorebird activity remained low in the three models (annual, winter, and our models), and corresponded to 2.2%, 1.4%, 1.7%, respectively, of the primary production (Leguerrier et al., 2004; Degré et al., 2006). In our model, the activity of shorebirds represented a similar proportion of the primary production, 1.6%, as that found in the Sylt-Rømø Bight (Baird et al., 2004a).

The ranking of macrofaunal compartments changed in comparison with the annual model (Leguerrier et al., 2004; Degré et al., 2006). In the present models, macrofauna activity was largely dominated by deposit-feeders mainly composed of *H. ulvae*, the most abundant species of the intermediate mudflat (Orvain et al., 2007) (the sampling station in this study). The previous annual model additionally covered the lower and upper parts of the mudflat,

where some species of bivalves such as *Scrobicularia plana* and *Cerastoderma edule* are also abundant (Bocher et al., 2007). In summer, deposit feeder activity was relatively high in comparison to that of the microphytobenthos being similar to the total primary production. This high activity was due to the high value of carbon imports of 142 mgC m^{-2} per low tide to this compartment. The primary production could not sustain the carbon production of deposit-feeders from the diurnal low tide suggesting that deposit-feeders rely on other resources at high tide. Benthic bacteria can be considered as an alternative resource (Pascal et al., 2008d) and detritivory is also a plausible hypothesis: during high tide, detritus can be imported by oceanic waters and/or by two rivers (i.e. La Charente and La Seudre) as shown before (2004). The detrital carbon can be ingested at high tide and imported to the low tide food web. However, the import to deposit feeders (142 mgC m^{-2} per low tide) might be overestimated because the mean was about three times the minimum requirement of 42 mgC m^{-2} LT^{-1}. High mean was mostly driven by the high maximum value integrated as an inequality in the model (210 mgC m^{-2} per low tide). The maximum value corresponded to the production estimated from the P/B ratio ranging between 0.01 and 0.05 in the literature (van Oevelen et al., 2006b). The P/B ratio of 0.05 was an extreme value and might thus overestimated the actual daily production of the deposit-feeders.

2. Model choices for birds.

The constraints of shorebird processes were based on a range of shorebird densities and on the basal metabolic rate of each species. This choice was made because in winter, shorebird consumption only balanced energy expenditure (van Gils et al., 2005; Nolet et al., 2006). Moreover, for shorebirds that feed on the intertidal mudflat, distances between the roosts (i.e. rest areas) and the feeding areas are short and limit the energy losses (Luis et al., 2001). The P/B ratio estimated in this study was similar to ECOPATH models (Lassalle et al., 2011; Lassalle et al., 2012). A model applied to the Bay of Mont Saint Michel on the Channel coast of France showed a higher P/B ratio for shorebirds, of 0.4 (Arbach Leloup et al., 2008). In studies on seabirds, the lower P/B was equal to 0.09 (Lassalle et al., 2011; Lassalle et al., 2012) or 0.10 (Christensen et al., 2009). The ratio of production/consumption (P/C) is extremely variable and can differ by an order of magnitude and the ratio greatly depends on the losses by egestion and respiration. An assimilation efficiency of 80% is currently used

(Scheiffarth and Nehls, 1997; Ponsero and Lemao, 2011); in this study, the assimilation efficiency only exceeded this value by 3% (the absolute value of egestion was 1.2 mgC m^{-2} per low tide, compared to 1.5 mgC m^{-2} per low tide with an assimilation efficiency of 80%). Losses of carbon due to respiration vary with bird activity. For seabirds (Christensen et al., 2009; Lassalle et al., 2011; Lassalle et al., 2012), losses by respiration are important due to the flights during predation activity (i.e. the P/C ratio is low in these models). In this study, the loss of carbon by respiration was chosen to be equal to the minimum metabolic rate. This might constitute a slight underestimation of the respiration of waders and thus, their production might have been greater.

To determine a maximum and minimum consumption by shorebirds, maximum and minimum densities on the mudflat were considered. These two extremes were based on the assumption of a homogenous repartition either on the whole mudflat for the minimum density, or only on the area of the mudflat which is emerged per hour for the maximum density. Nevertheless, the distribution of shorebirds species is dependent on the prey-specific distribution on the mudflat and/or on their foraging abilities (Bocher et al., 2007). For instance, *Scrobicularia plana* is restricted only to the upper part of the mudflat, whereas *Cerastoderma edule* is located in the lower part while the prey *H. ulvae* colonises the whole area (Bocher et al., 2007). Because the intra-specific competition and the density of their prey control the spatial repartition of shorebirds on the mudflat (e.g. Sutherland, 1983; Folmer et al., 2010), it is difficult to predict precisely the shorebird densities that feed within a given area, and thus to estimate the actual predation pressure per unit area. Due to our current knowledge of the spatial distribution of shorebirds on the Brouage mudflat, there was no alternative than setting two extreme densities to define the range in which the shorebird consumption behaviour might be estimated as a whole.

3. Consumption by birds.

Considering a whole mean foraging time of 11.3 h, the estimated daily consumption was 20 mgC m^{-2} d^{-1} (or about 34.5 mgAFDW m^{-2} d^{-1}). In comparison with the previous winter model of Brouage (Degré et al., 2006), bird consumption was higher thanks to our better knowledge of bird diets (Quaintenne et al., 2010; Boileau and Delaporte, 2011; Viain et al., 2011; Robin

et al., in press). The estimated consumption in this study is close to that of shorebirds observed in the Wadden Sea, the Sylt-Rømø Bight (Scheiffarth and Nehls, 1997) and the Somme Bay (Sueur et al., 2003). Moreover, the obtained consumption corresponded to a density of birds on the Brouage mudflat close to the highest determined density, which was 2.05×10^{-4} individuals per m² (or 54 mgC m^{-2}). This biomass was in the same order of magnitude as that in the Sylt-Rømø Bight for the same assemblage of species (Baird et al., 2004a).

4. Food web function.

Whole ecosystem activity, measured by the TST, was significantly higher in winter than in summer. This can be explained by a higher gross primary production in winter (413.09 mgC m^{-2} per low tide) compared to summer (183.6 mgC m^{-2}). In summer, the strong light and the temperature conditions generated photoinhibition of the photosynthesis of microphytobenthos(Blanchard et al., 1997; Lavaud, 2007; Serodio et al., 2008) and lead to a decrease in gross primary production. Additionally, a strong decrease in microphytobenthos biomass was observed (Cariou-Le Gall and Blanchard, 1995) due to intense grazing by benthic invertebrates. The high winter TST value was linked to bacterial production which was higher in winter (169.3 mgC m^{-2} per low tide)compared to summer (93.9 mgC m^{-2} LT^{-1}). Considering the field bacterial P/B ratio, a value of 0.92 was found during summer in the Brouage mudflat and 0.77 in winter (Pascal et al., 2009). In parallel, the bacterial biomass doubled in winter and could thus sustain the high production.

The bacterivory and the herbivory of deposit feeders, meiofauna and nematodes changed according to the season. In winter, 84.8% of the carbon ingested by the three compartments came from the microphytobenthos (herbivory); in summer, the proportion decreased to 75%. Bacterivory followed the opposite tendency and was higher in summer. Even with the higher bacterial production in winter, the bacterial carbon was less ingested by primary consumers which preferentially feed on microphytobenthos, regardless of the bacterial production (Pascal et al., 2008b; Pascal et al., 2008c; Pascal et al., 2008d), except when microphytobenthos biomass drastically decreases (Pascal et al., 2009). This is what happened in summer because the gross primary production was low, as was the carbon available to upper trophic levels.

The trophic pathway lengths were similar for the two seasons (i.e. high APL values). For the winter food web, the shorebird compartment was added. Unexpectedly, an atom of carbon passed through almost the same number of compartments before leaving the system. The path length value is linked to the degree of cycling within the ecosystem (Christensen, 1995). The number of cycles was almost doubled in winter and the proportion of cycles behaved similarly (i.e. a higher FCI value). The stronger cycling can be explained by the increased detritivory behaviour (404.78 mgC m^{-2} per low tide in winter compared with 343.86 mgC m^{-2} per low tide in summer), in particular for bacteria. The bacterial biomass and production were higher in winter, with dissolved organic carbon representing 72% of the whole detritivory that was taken in larger quantity. The stronger carbon cycling lead to a higher retention of carbon inside the ecosystem without changing the carbon path compared to summer. This can be explained by a higher/faster export of carbon. Indeed, one-third of the primary production and twice more of the bacterial and detritic carbon were exported at high tide. The FCI and the number of cycles previously defined for the same seasons at the Brouage mudflat showed an opposite tendency (Leguerrier et al., 2007) with higher values in summer. In the annual model (Degré et al., 2006; Leguerrier et al., 2007), bacteria and detritus (dissolved and particulate carbon) were combined which infers strong implications for the ENA indices (Allesina et al., 2005; Niquil et al., 2012) explaining the difference with our model.

In summer, the higher sum of all imports to macrofauna (168.6 mgC m^{-2} per low tide and 103 mgC m^{-2} per low tide, respectively) suggested that macrofauna was more dependent on imports from other periods of the day than in winter. This finding was confirmed by the relative value of overheads on imports which was higher in summer (6.14%) than in winter (4.96%). The total export of carbon by macrofauna to the high tide was higher in winter as likely explained by a higher summer loss of carbon and respiration by macrofauna. For instance, summer is the recruitment for the abundant *H. ulvae*(Haubois et al., 2004) so that the individuals are smaller and their body mass lower. From the metabolic point of view, organisms with a low body mass have a higher metabolism per unit of biomass and the metabolism increases with the temperature (McNeill, 1999) well supporting why more carbon was lost by macrofauna respiration in summer.

The internal organisation and specialisation of the two food webs were similar. This is supported by the similar relative redundancy for the two seasons. The ranges of internal

Relative Ascendency, of the specialisation (i.e. AMI) and of the relative redundancy observed in the literature (e.g. Baird et al., 1991; Baird and Ulanowicz, 1993; Scharler and Baird, 2005; Baird et al., 2007), include the values for the Brouage mudflat. In winter, a higher specialisation of the trophic pathways was observed for high trophic levels because shorebirds preferentially fed on deposit feeders, and about one quarter of the production of carnivorous, omnivorous, suspension feeders and facultative suspension feeders was ingested by birds. The internal relative ascendency only considers the internal flows of the network (Ulanowicz, 1986), i.e., trophic interaction between species. The similar values of this index for the two seasons illustrate a similar organisation of the interactions between species irrespective of the season. However, a higher relative ascendency, which measures the organised and efficient part of the system (Ulanowicz, 1986), in winter suggests a higher level of organisation. This index considers all flows of the ecosystem, including internal flows and flows through the boundaries of the ecosystem. Nevertheless, the strong difference between the A/DC ratio and A_i/DC_i ratio suggests a strong dependency of the system on exchanges through the boundaries of the ecosystem (Baird and Heymans, 1996). Because this difference is higher in winter, it means a higher dependency of the winter food web to external connections explaining the higher value of relative ascendency, whereas the internal relative ascendency for the two seasons remained similar. Consequently, in winter, a large proportion of the net primary production was exported to the high tide (45%) and a lower proportion was consumed by the main grazers (only 25%). Nevertheless, a higher proportion of the secondary production was consumed due to the high shorebird density. In summer, a large proportion of the net primary production was integrated into higher trophic levels through consumption by nematodes and deposit feeders. However, a low proportion of the secondary production was ingested by secondary consumers. Noteworthy, these two different network patterns still lead to a similar internal organisation.

5. The Lindeman spine

A transfer efficiency between the level I+det and level II as high as estimated here (67% in winter and 83% in summer) is not common: the trophic efficiency in the literature tends to be lower than 50%, with a few exceptions [REF]. The transfer efficiency of the Brouage mudflat in summer was close to that found in the Baltic sea (Baird et al., 1991) and in the mud and

muddy-sand flat habitats in the Sylt-Rømø Bight (Baird et al., 2007). The high transfer efficiency of the Brouage mudflat was linked to the temporal scale. Indeed, the literature food webs consider a mean per day, whereas in this study, only low tide was integrated. Some transfer of carbon, which derived from the previous low and high tides, also appeared for macrofauna on small time-scale. These imports were assimilated as an import to the det compartment in the Lindeman spine. Thus, a part of det was, by default, transferred with an efficiency of 100% to the higher trophic levels which explains the strong transfer efficiency to level II.

The summer food web was characterised by low primary and bacterial productions . As explained above, the dominant macrofauna *H. ulvae* has a low mean body mass in summer which means that a higher quantity of carbon is necessary to satisfy its metabolic requirements for a given biomass. In winter, an increase in the transfer efficiency between the compartments III, IV, and V was observed, corresponding to an increase in shorebird carnivory. The mean transfer efficiency tended to be higher in summer, nevertheless, the two mean transfer efficiencies were close to those of the mud flat in the Sylt-Rømø Bight (Baird et al., 2007)**.** The winter food web was thus highly productive: it exported excess microphytobenthic carbon during the resuspension of the biofilm at high tide (wave and wind-induced currents). The food webs for the two seasons thus showed drastically opposite trends: the winter food web at low tide exported excess carbon, whereas the summer food web led to higher imports. The same conclusions were reached from the previous food web model (Degré et al., 2006).

Synthesis

Although the summer and winter food webs of the Brouage mudflat showed some similarities, the winter food web possessed specific characteristics that allow the sustainability of the migratory shorebird nutritional needs (Fig. 6). First, the internal organisation and specialisation of the trophic pathways were similar for the two seasons. Although the efficient part of the two networks represented the same percentage of the whole activity of the system, it did not include the same levels of the trophic chain. In summer, the strongest efficiency was found for the low trophic levels, whereas in winter, it was found for the higher trophic levels

due to the shorebird nutritional requirements. However, the winter food web was characterised by a strong activity of the whole system which was supported by high primary and bacterial productions. In winter, cycling was also stronger due to higher bacterial activity and higher detritivory. Nevertheless, the strong carbon export from microphytobenthos, bacteria and the non-living compartment, led to a similar retention of carbon for both seasons. In spite of the addition of one compartment (i.e. shorebirds) and a stronger cycling in winter, an atom of carbon passed through almost the same number of compartments as in summer. The decrease in primary production observed in summer and probably due to photo-/thermo-inhibition, was compensated for by a higher bacterivory by the meio- and macro-benthos. The strong integration of the carbon from the primary and the bacterial productions to the higher trophic levels led to a stronger mean transfer efficiency. Consequently, the Brouage mudflat showed a similar organisation and specialisation of flows for the two seasons. The efficient part was almost in equilibrium with the inefficient part of the system. In winter, the low carbon integration resulting from primary production was counterbalanced by stronger cycling. Hence, the carbon retention in the food web did not change between winter and summer. The switch to both higher production and cycling, combined with a constant organisation and specialisation of the system, are the key features that support the nutritional needs of migratory shorebirds in winter in the Brouage mudflat.

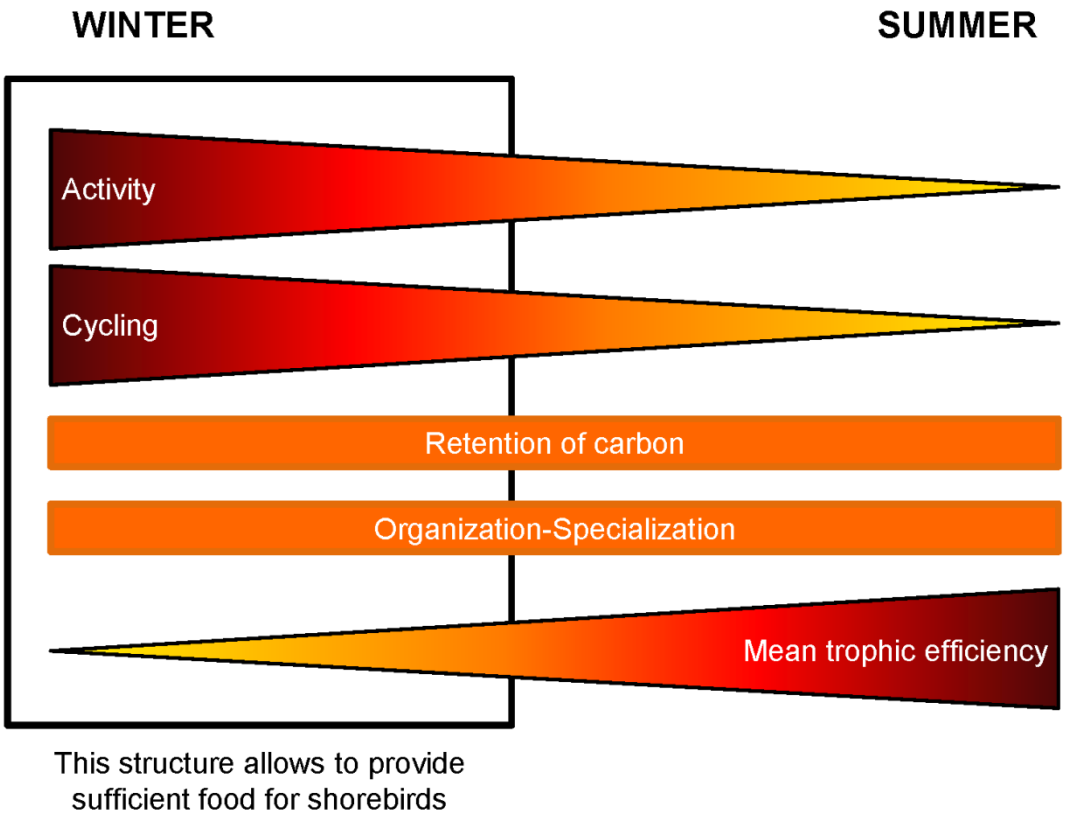


Figure IV-6: Schema to sum up the observations made on the winter and summer food webs.

Chapitre 5

How does the resuspension of the biofilm alter the functioning of the benthos-pelagos coupled food web of the bare mudflat in Marennes-Oléron Bay (NE Atlantic)?

Blanche Saint-Béat[1], Christine Dupuy[1], Hélène Agogué[1], Alexandre Carpentier[2], Julien Chalumeau[1], Serena Como[1], Valérie David[3],Margot De Crignis[1], Jean-Claude Duchêne[3], Camille Fontaine[1], Eric Feunteun[2], Katell Guizien[4], Hans Hartmann[1], Johann Lavaud[1], Sébastien Lefebvre[5], Christel Lefrancois[1], Clarisse Mallet[6], Hélène Montanié[1], Jean-Luc Mouget[7], Francis Orvain[10], Pascaline Ory[1], Pierre-Yves Pascal[8], Gilles Radenac[1], Pierre Richard[1], Alain Vézina[9], Nathalie Niquil[1,10].

[1] Université de la Rochelle-CNRS, UMR 7266, Littoral Environnement et Sociétés (LIENSs), La Rochelle, France

[2] Station marine de Dinard, Dinard, France

[3] EPOC, UMR 5805 Université Bordeaux 1 - CNRS, Arcachon, France

[4] Laboratoire d'Océanographie Biologique de Banuyls, Banyuls, France

[5] Laboratoire d'Océanographie et de Géoscience, Université Lille 1, Wimereux, France

[6] UMR-CNRS 6023, Laboratoire biologie des protistes, Université Blaise Pascal, Clermont-Ferrand, France

[7] Ecophysiologie et Métabolisme des Microalgues, Université du Maine, Le Mans, France

[8] Departement de Biologie, UFR SEN, Pointe à Pitre, France

[9] Bedford Oceanographic Institute, Dartmouth, Canada

[10] CNRS, UMR 7208 BOREA, Laboratoire BioMea (FRE 3484), Caen, France

En quoi la remise en suspension du biofilm modifie-t-elle le fonctionnement du réseau trophique couplé benthos-pélagos de la vasière nue de Marennes-Oléron (Atlantique NE) ?

Lors de l'arrivée de la pleine mer sur la vasière de Brouage, une partie du biofilm microbien présent à la surface des sédiments peut être remis en suspension. Cette remise en suspension n'est pas systématique et est contrôlée par des facteurs physiques (intensité des courants) et biologiques (état de biofilm, présence de bioturbateurs). Les micro-organismes remis en suspension dans la colonne d'eau seront intégrés au réseau trophique pélagique. A marée haute la vasière de Brouage peut être assimilée à un méta-écosystème comme le définit Loreau (2003). Un méta-écosystème est un ensemble de systèmes qui sont liés par des flux spatiaux biotique ou abiotique, induisant des changements de propriété en leur sein. Ainsi, par sa remise ne suspension, le biofilm est un élément clé de la liaison entre benthos et pelagos. L'objectif de cette étude est de déterminer d'une part l'impact de la remise en suspension sur le fonctionnement trophique des compartiments benthiques et pélagiques et d'autre part sur la stabilité du méta-écosystème que représente le système couplé benthos-pelagos.

La remise en suspension a-t-elle un effet stabilisateur sur le méta-écosystème constitué du réseau couplé benthos-pélagos, sur la vasière de Brouage à pleine mer ?

Réalisation de deux modèles de réseaux trophique considérant une pleine mer moyenne sous différentes conditions hydrologiques : une situation où la remise ne suspension du biofilm a lieu et une situation où la remise en suspension ne se produit pas, laissant alors place à la sédimentation. Certains résultats obtenus à basse mer sont utilisés comme des flux connus dans le modèle pleine mer. Il s'agit notamment des flux d'export de carbone des compartiments benthiques à basse mer qui sont considéré comme des imports à pleine mer, puisque la production non consommée à basse mer, le sera lors du retour de la pleine mer.

Utilisation de la modélisation inverse par échantillonnage aléatoire.

Les solutions calculées par la modélisation inverse sont utilisées pour calculer des indices ENA permettant de caractériser la structure et le fonctionnement du réseau trophique. Les flux sont décrits par la moyenne de l'ensemble des solutions proposées par la modélisation inverse, en accord avec les conclusions du chapitre 3.

Les indices ENA calculés dans cette étude sont mis en relation avec les théories sur la stabilité précédemment analysées dans le chapitre 2.

La remise en suspension des micro-organismes benthiques stimule la production primaire pélagique et la boucle microbienne pélagique. Le réseau trophique benthique à pleine mer est caractérisé par un développement de la bactérivorie accentué lorsque la remise ne suspension a lieu. Le remise en suspension ne stabilise pas le méta-écosystème mais au contraire le perturbe, comme l'indiquent la forte activité du système couplé à une fable spécialisation des voies trophique et le faible recyclage couplé à une forte valeur d'organisation interne caractérisant fortement stressé. Par opposition, le méta-écosystème sans remise en suspension, mais avec sédimentation, apparait stable. Les conséquences opposées de ces deux conditions peuvent être expliqué par une différence d'intensité de la liaison benthos-pelagos.

Abstract

Intertidal mudflats are ecosystems submitted to natural hydrodynamical forcings during each tide. When the offshore water flows at high tide, a proportion of the biofilm produced at low tide can be resuspended in the water column and interact with the pelagic food web. As a consequence, the resuspension creates a link between the benthos and the pelagos, modifying their properties and the stability of the meta-ecosystem they form together. The aim of this study is to describe the consequences of the microbial biofilm resuspension on the pelagic food web, and to investigate the question of the stability of the benthos-pelagos coupling resulting from the biofilm resuspension. Two food webs were considered, corresponding to different hydrodynamical conditions in summer condition: one allowing the biofilm massive resuspension, and one without resuspension, but with particle sedimentation. The Monte-Carlo Markov Chain Linear Modelling was used to estimate the unknown flows of the food web. The comparison of the Ecological Network Analysis indices for the two food webs allowed defining their respective differences of structure and functioning. The results showed that the massive resuspension of the microbial biofilm stimulates pelagic primary production and microbial food web via a higher bacterivory. The higher activity of the whole system coupled with both a drop in the specialization of the trophic pathways and a low cycling activity demonstrated that when massive resuspension occurs, the system is disturbed. In contrast, when sedimentation occurs, the food webs show functioning features pointing out to a higher stability of the whole system.

Introduction

The structure and the functioning of food webs affect the emergent properties and thus the stability of the ecosystem. As a consequence, describing the emergent properties of the ecosystem is a prerequisite for establishing their stability. The literature on the subject is diverse and can lead to controversial interpretations and conclusions. However, some trends can be observed such as equilibrium between two extremes that allows the ecosystem to act like a buffer to external perturbations. For instance, the coexistence of weak and strong interactions is assumed to bring stability to the ecosystem (McCann et al., 1998), or the asymmetry in the ecosystem ensures a higher stability (Rooney et al., 2006), or an ecosystem

that presents a balance between Ascendency and redundancy is supposed to be more stable (Ulanowicz, 2003). Moreover, Levin (1999) proposed that a stable ecosystem pattern is composed of subsystems strongly intraconnected but weakly interconnected. At larger scale, this theory is transposable to the concept of the meta-ecosystem defined by Loreau et al. (2003) as a set of ecosystems connected by spatial flows. A set of ecosystems strongly intraconnected weakly interconnected thus form a stable meta-ecosystem. In this study, we propose to consider the benthos and the pelagos as systems connected by spatial flows at high tide to form a stable meta-system. We have used this concept in order to describe and to understand the effects of the benthos-pelagos coupling on the properties of the food webs and its consequences on the stability of the Brouage mudflat meta-system.

As bare intertidal mudflat, Brouage mudflat, is characterized by the development of a microbial biofilm at the surface of the sediments at diurnal low tide. This biofilm is usually mainly composed of brown micro-algae (diatoms) which constitute the microphytobenthos (Cariou-Le Gall and Blanchard, 1995) and prokaryotes, all of them linked by a matrix of extracellular polymeric substances (EPS) (Decho, 2000). The production of the biofilm is integrated to the benthic food web via the deposit feeders, especially *Peringia ulvae* (Haubois et al., 2005a; Pascal et al., 2008b; Pascal et al., 2009), via the facultative suspension feeders and via the meiofauna (Pascal et al., 2008c; Pascal et al., 2008d; Pascal et al., 2009). The meio- and macrofauna are not only involved in the regulation of the microphytobenthos biomass via the grazing, but also via the bioturbation and the biostabilisation of the sediment whose effects are coupled with physical factors (tides and swell) (Blanchard et al., 2001).

When the tidal flow arises, the microphytobenthos biomass decreases at the surface of the sediments (Guarini et al., 2000a) for two reasons: i) the downward 'migration' of motile diatoms into the sediments (Guarini et al., 2000a; Consalvey et al., 2004; Herlory et al., 2004; Ni Longphuirt et al., 2009) and ii) the resuspension of a part of the diatom stock into the water column. The resuspension of the microphytobenthic biofilm is controlled by a complex interaction between physical and biological forcing. The physical resuspension of the microphytobenthos depends on the bed shear stress which is induced by the tidal current and/or the wind-waves (De Jonge and Van Beuselom, 1992; Blanchard et al., 2002). The erodability of the sediment is strongly variable in space and in time (Tolhurst et al., 2006) and depends on biological factor modifying sediment properties such as macrofauna activities and

microbial biofilm setting up (Herman et al., 2001a; Orvain et al., 2004). The microphytobenthos resuspension also depends on biological factors such as the ageing of the biofilm (Orvain et al., 2004) and the content of exopolysaccharids (EPS) (Orvain et al., in press). When the microphytobenthic biofilm is in its exponential growth phase, it stabilizes the sediments and counteracts the bioturbation due to macrofauna which favors its resuspension (Orvain et al., 2004). In contrast, when the biofilm reaches its senescent phase, the roughness of the biofilm as well as bacterial biofilm degradation are enhanced and the mat is more easily resuspended (Orvain et al., 2004). The microphytobenthic diatom that are resuspended in the water column are integrated to the pelagic food web and can be ingested by suspension feeders, in the case of the Brouage mudflat especially by *Crassostrea gigas*, a cultivated species (Riera and Richard, 1996) and *Cerastoderma edule* (Sauriau and Kang, 2000).

In this study new *in situ* observations and experimentations were taken into account, especially on the resuspension of the biofilm (Orvain et al., in press) and the consequences on the pelagic food web are evaluated by using a model describing trophic pathways. Erosion experiments allowed to determine the critical shear velocity necessary regarding the resuspension of benthic micro-organisms and resuspension rates (Dupuy et al., in press) . The Lagrangian and Eulerian field surveys followed the future of the resuspended particles in the water column, respectively following the water mass or at a fixed point (Guizien et al., 2013). Moreover grazing experiments and viral lysis experiments (Montanié et al., in press) were performed in order to determine the effect of resuspension of benthic organisms on the pelagic food web *sensu largo* (*i.e.* including virus). These refinements were incorporated in the framework of a trophic-flow model to better unravel the impact of the biofilm resuspension on the food web functioning by deciphering the contribution of each flow in the contribution in the functioning during high-tide phase. At high tide, the rise of the tide and the chemical/physical/biological processes associated with the increase of the water level on the Brouage mudflat create spatial flows linking benthic and pelagic parts. Consequently, it can be considered as a 'meta-ecosystem' defined by Loreau et al., (2003) as a set of ecosystems which are linked by spatial biotic and/or abiotic flows across the ecosystem boundaries. We especially focused on one question: How does the resuspension of the microbial biofilm at high tide modifies the stability of ecosystem in respect to the meta-ecosystem pattern? We explored this question by comparing the network organization of two distinct food web

models representing 2 scenarii of a summer situation. In the first model scenario, the hydrodynamic conditions were extreme and sufficient to induce the resuspension of the microphytobenthos (physical mass erosion, when bed shear stress BSS > 3 $cm.s^{-1}$ on Brouage mudflat). In this case the velocity of current stays superior to the critical sinking velocity, thus no sedimentation is possible. While in the second case the physical forcing was too weak to induce any resuspension, only limited and extremely low erosion of chl*a* (biological erosion when BSS < 3 $cm.s^{-1}$) induced by the bioturbation of the macrofauna can be observed (Orvain et al., in press). Moreover the settling of pelagic particles (organic or not) could occur and the sinking velocity enhanced by the pelletisation (Orvain et al., in press). The missing flows of the food web (i.e. flows which were not measured *in situ*) were estimated by the Monte Carlo Markov Chain Linear Inverse Modelling (MCMC-LIM) (Van den Meersche et al., 2009). This mathematical method explores a solution space defined by constraints issued from *in situ* measurement and values issued from the literature. All solutions proposed by the MCMC-LIM were used to calculate several ecological network analysis (ENA) indices, describing the emergent properties of the ecosystem.

Material and Methods

1. The study area

The Brouage intertidal mudflat is located at the French Atlantic coast in the bay of Marennes-Oléron (figure 1). The bay covers 150 km^2 and the Brouage mudflat, at the eastern part of the bay, represents 68 km^2 at low tide. The averaged bottom slope is relatively flat (1:1000) and the tidal area is large (up to 4 km). The sediment consists of silt and clay particles (95% <63 µm) (Pascal et al., 2009). The current speeds in the bay range from 0.2 to 0.6 $m.s^{-1}$ and the bed shear stress from 1.5 to 4 Pa (Bassoullet et al., 2000; Le Hir et al., 2000). The zone of interest is located in the middle of the Brouage mudflat and is characterized by a typical ridge and runnel bedform (Gouleau et al., 2000).

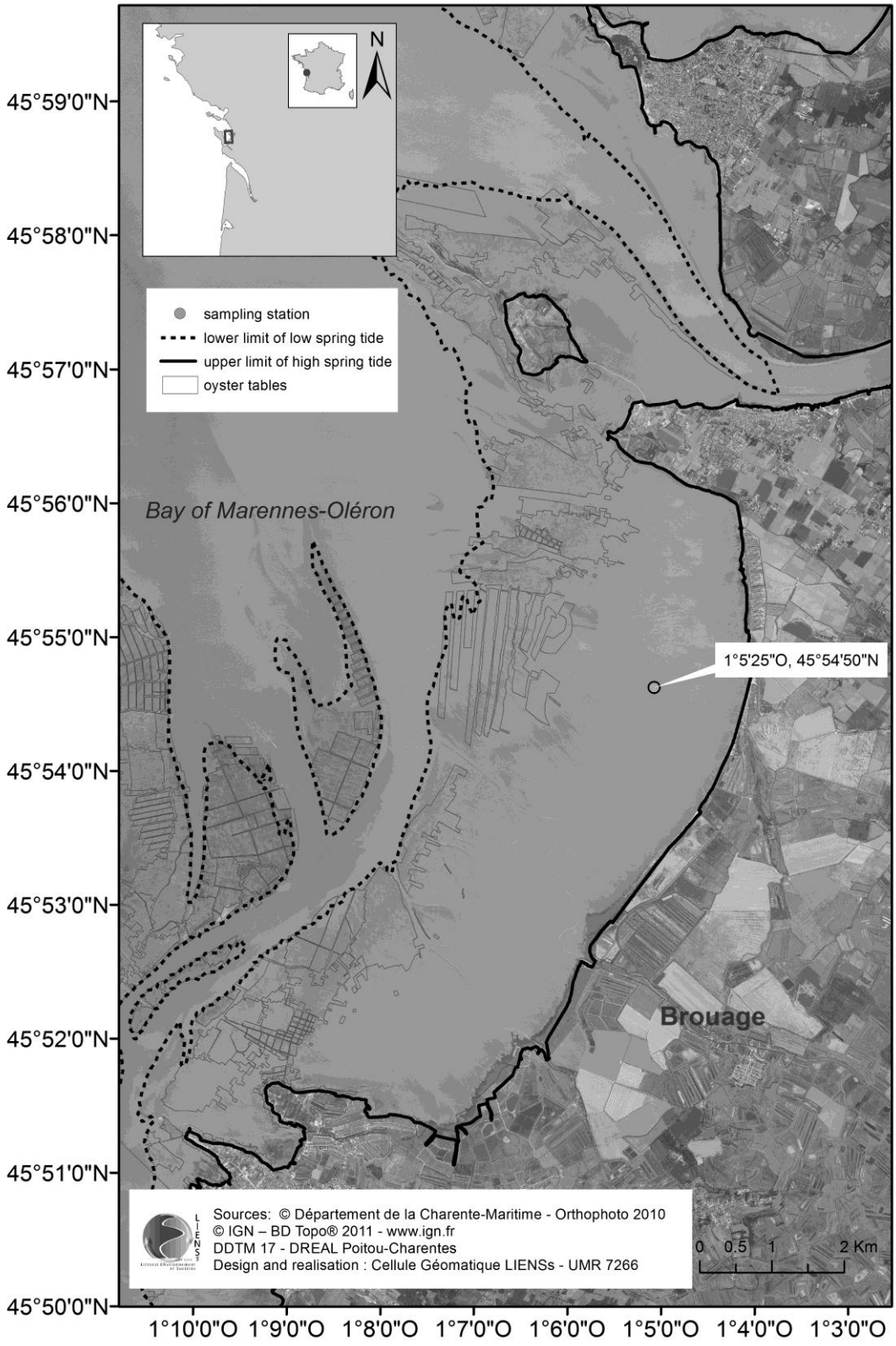


Figure V-1: Study site: the Brouage mudflat.

2. Inverse modelling

Two summer food web models were performed: the first one simulated a high-tide situation with massive suspension of micro-organisms in the water column (resuspension model), and the second one also at high tide, where the physical forcing was not sufficient to induce resuspension (sedimentation model). As a consequence, an insignificant quantity of particles is suspended via biological factors as macrofauna bioturbation and it counterparts by a strong sedimentation of organic matter.

The inverse modelling can be divided into 3 steps: (i) determine the species that compose the food web, and all possible flows between them. Twenty-one compartments were listed (Table V-1) linked by 115 or 118 flows for the models with and without resuspension, respectively. (ii) determine the mass balance of each compartment and constrains flow values by *in situ* measurements. (iii) limit possible values of flows by biological constraints.

2.1. Considered compartments and flows

2.1.1. Resuspension and sedimentation

A portable erodimeter (Guizien et al., 2012) was used to estimate the erosion shear stress of *in situ* cohesive sediments. An increased shear stress (by small steps, each timed to last about 10 minutes) was applied to the mud surface and the suspension of micro-organisms inhabiting in the sediment was monitored by changes in water column micro-organisms concentration. From these experiments, it was defined that resuspension of the microorganisms and diatoms took place when the shear bed velocity was higher or equal to 3 $cm.s^{-1}$. Sedimentation could not occur at higher current velocity.

Sedimentation was only considered in the model without resuspension, because the lower current velocity (< 3 $cm.s^{-1}$) allowed particles to settle down on the bottom during the slack water. The sedimentation rate was estimated from the formula D=Ws*C where D is expressed in $mgC.m^{-2}.h^{-1}$, C is the concentration of particles in the water column ($mgC.m^{-3}$) and Ws the

sinking velocity of particles ($m.h^{-1}$) (Krone, 1962). Concentration of both pelagic bacteria and chlorophyll *a* were measured *in situ*. The minimal limit for the concentration of the particulate carbon corresponded to the pelagic particulate carbon produced during high tide. For defining its maximal limit we considered that the import of carbon into the water column was equal to the amount of the benthic particulate carbon resuspended in the water column and not consumed. Consequently, it was assumed that the particulate carbon present in the water column at high tide, when resuspension occurred was likely to be found in a similar quantity at high tide n+1.

	Compartments	**Abbreviations**
Benthos	Microphytobenthos	mpb
	Benthic bacteria	bcb
	Meiofauna	mfb
	Nematods	nem
	Deposit-feeders	dep
	Suspension-feeders	sus
	Facultative suspension-feeders	suf
	Omnivorous species	omn
	Carnivorous species	car
	Benthic viruses	vrb
	Benthic particulate carbon	bpc
	Benthic dissolve carbon	bdc
Pelagos	Phytoplankton	phy
	pelagic bacteria	bcp
	Heterotrophic nanoflagellates	hnf
	Cilliates	cil
	Mesozooplankton	mes
	Grazing fishes	gfi
	Pelagic viruses	vrp
	Pelagic particulate carbon	ppc
	Pelagic dissolve carbon	pdc

Table V-1: List of compartments and abbreviations.

2.1.2. The microphytobenthos

Primary production of the microphytobenthos is linked to the biomass of diatoms present in the biofilm and to light conditions (Macintyre et al., 1996). During immersion, the turbidity of

the overlying water, stopping the penetration of light (Alpine and Cloern, 1988) inhibits benthic primary production (Denis and Desreumaux, 2009; Migné et al., 2009). Moreover, just before the flood return, the diatoms move down into the sediment (Round and Palmer, 1966; Herlory et al., 2004). In our models, no microphytobenthic production was considered. The only input to the microphytobenthos compartment is thus an import of carbon which comes from the production of the previous diurnal low tide by the microphytobenthos, and which was not consumed during low tide. The import of carbon to the high tide corresponded to the export of carbon determined for microphytobenthos in a low tide model and was equal to 31.9 $mgC.m^{-2}$ per high tide (Saint-Béat et al., chap 4). Moreover the secretion of EPS, related to the activity of photosynthesis and migration (Underwood and Paterson, 2003), was supposed negligible at high tide (Hanlon et al., 2006). This was confirmed by a survey of EPS concentration in a tidal mesocosm during a tidal cycle showing a fall of EPS concentration in the biofilm during high tide (Agogué et al., in press)

9.7mgC of benthic diatoms were resuspended per high tide (Dupuy et al., in press); they constitute a flow from the benthos to the pelagos that enhances the phytoplanktonic biomass after resuspension (Koh et al., 2006; Brito et al., 2012). In this way, the microphytobenthos constitutes a food resource for the secondary producers in pelagic and benthic ecosystems (Riera and Richard, 1996; Guarini et al., 1998; Yoshino et al., 2012).

2.1.3. Benthic bacteria

Biofilms (i.e an assemblage of benthic diatoms and bacteria) were reconstituted in a tidal mesocosm: the production and the biomass of the bacteria were measured during 5 days at low and high tides (Agogué et al., in press). The benthic bacterial production was estimated by tritiated thymidine incorporation (Garet and Moriarty, 1996), which was converted to numbers of cells using the ratio of $1.96*10^{17}$ cells per mol of thymidine determined for this study. A mean increase of 24.3% of the bacterial production in comparison to the bacterial production at low tide was observed in mesocosm experiments. The bacterial biomass was obtained from the mean cell volume calculated with Furhman's formula (1981) and converted in carbon units from the formula $133.754*V^{0.438}$(Vin μm^3) (Romanova and Sazhin, 2010). The carbon contain in a bacterium was thus estimated as equal to 79 fg C. $cell^{-1}$ for a mean biovolume of 0.28 μm^3. During erosion experiments at the threshold velocity considered in

this study, 58.2 mgC per high tide issued from the benthic bacteria were suspended (Dupuy et al., in press). A part of the suspended bacteria were damaged or dead during the erosion process (40%) (Mallet et al., in press), and thus they integrated the pelagic particulate organic carbon compartment. On the contrary the remaining suspended benthic bacteria, still active, were considered to increase the pelagic bacteria biomass (Mallet et al., in press).

2.1.4. Infauna (meiofauna, nematodes and macrofauna)

The microphytobenthos is the preferential resource of the benthic fauna but in case of unavailability of microphytobenthos, bacterivory becomes significant (Pascal et al., 2009). At high tide, bacterivory was supposed to be higher than the low tide values: the values of low tide used in the previous model (Saint-Béat et al., chap 4) were thus integrated to high tide models as minimal values. The obligate as well as facultative suspension feeders were assumed to feed on particles from bacteria to mesozooplankton (Taghon, 1982; Self and Jumars, 1988).

2.1.5. Phytoplankton

The primary production of the phytoplankton was estimated for six other sites in Marennes-Oléron Bay based on *in situ* measurement of chlorophyll *a* water concentration, salinity, temperature and depth profiles of light attenuation (Struski and Bacher, 2006). The phytoplanktonic primary production is influenced by the erosion of sediment, limited light penetration and by the resuspension of benthic diatoms which likely participate to the phytoplanktonic production (Macintyre et al., 1996). In order to prevent any bias in the estimation of the planktonic primary production, we constrained it by minimal and maximal primary production values measured in summer for the different stations of the bay. These stations are characterized by different hydrological conditions and are thus characterized by different resuspension and turbidity, and consequently by a different light penetration. Constraining the phytoplanktonic production by a range of possible values allowed to adjust the probability density function for gross primary production according to the needs of the food web based on the situation considered (i.e. with or without resuspension).

2.1.6. Pelagic bacteria

The summer abundance and the summer production of the pelagic bacteria were measured *in situ* (Ory et al., 2011). Bacteria were counted by epifluorescence microscopy after being fixed with 0.02µm filtered formaldehyde (2% final concentration) and staining for 30 min with Sybr Green I (for more details see Noble and Fuhrman, 1998; Ory et al., 2011). The measurement of AMPase (V_{max}), which is considered as an indicator of the bacterial production, was used to estimate the bacterial production from the equation log BP = 0.9271*log Vmax + 5.3641 (r^2=0.67, n=10, p=0.003). Pelagic bacteria being assumed to contain 16 fgC per cell (Labry et al., 2002), the bacterial production was thus expressed in carbon.

Experiments on viral lysis were conducted to test the interactions between bacteria, heterotrophic nanoflagellates (HNF) and viruses in the water column. In artificial incubations, they were re-combined to mimic the field assemblage with respect to the natural viral to bacterial ratio (VRB) and the bacteria to flagellates ratios. Fractionation allowed creating experimental recombined treatments and then differentiating between the direct and indirect interactions of the presence/absence of the virus and HNF. Through *in vitro* experiments, bacterial losses induced by viruses and flagellates were estimated by comparing the reduction of the bacteria cell production (MBP) between the different experimental assemblages.

2.1.7. Ciliates (ESD (Equivalent Spherical Diameter) <50µm) and heterotrophic Nanoflagellates (2µm<ESD<10µm)

The biomasses were expressed in carbon from a conversion factor of 19 µgC.µm-^{3} (Putt and Stoecker, 1989) by considering equivalent spherical diameter (ESD). The abundances and biomass of Ciliates (ESD < 50 µm) and heterotrophic nanoflagellates (2µm < ESD < 10µm) were estimated *in situ*. The seawater was filtered onto 0.8 µm Nucleopore black filter. The ciliates and nanoflagellates were enumerated by epifluorescence microscopy. Cells were first fixed by the glutaraldehyde and the paraformaldehyde and stained with the lugol 1% and DAPI respectively.

In the models, phytoplankton and pelagic bacteria are prey of the compartments ciliates and nanoflagellates, which are themselves the preys of ciliates. The nanoflagellates also potentially graze the viruses (Manage et al., 2002; Bettarel et al., 2005).

2.1.8. Mesozooplankton (200µm<ESD<400µm)

Mesozooplankton (200µm < ESD < 400µm) play a central role in the pelagic food web in the Marennes-Oléron Bay (Sautour and Castel, 1998) and show a variable diet (Vincent and Hartmann, 2001). The resources of mesozooplankton, as confirmed by bottle grazer experiments, in the area of Brouage mudflat are phytoplankton, either directly or indirectly via ciliates and the heterotrophic nanoflagellates (Azémar et al., 2007). This diet can be completed by the ingestion of detritic matter (David et al., 2006).

The abundance and the biomass of the mesozooplankton were estimated during study period. The mesozooplankton was sampled using a 200µm mesh WP2 net, preserved in buffered formaldehyde with $Na(Bo_3)_4$ (final concentration 5%) and counted under binocular microscope. The biomasses were expressed in carbon by multiplying the dry weight by 0.4 (Simard et al., 1985). These measurements were completed by bottle grazer experiments to test the effects of the biofilm suspension on the grazing of mesozooplankton. Water from the erodimeter (after erosion experiments) was mixed with filtered pelagic water (200 µm, in order to exclude mesozooplankton) in different proportions (20, 40 or 70%). This mix was transferred in 1.13 L Nalgene bottles and and incubated during 12 or 24 h in presence/absence (temoin) of mesozooplankton predators collected *in situ*. The resuspended biofilm in the water disturbs the trophic interactions of the mesozooplankton, especially through an inhibition of the grazing of phytoplankton and heterotrophic nanoflagellates by the mesozooplankton (Hartmann, pers. comm.). Thus in the model with the resuspension no flow between phytoplankton and nanoflagellates towards mesozooplankton was considered.

2.1.9. Grazing Fishes:

Main species able to graze on mudflat at high tide are mullets (*Liza ramada* and *Liza aurata*). Observed individuals arrive on the mudflat with an empty stomach, while they leave it with a full stomach (Carpentier et al., in press). Thus the mullets were considered as a vector of

carbon export. Since, the abundance of individuals going about the Brouage mudflat at high tide could not be measured *in situ*, grazing traces left by mullets on mudflat were considered as a proxy of their grazing pressure. Presence of traces was estimated from pictures of one square meter quadrats (expressed by surface of sediment removed by mullets by square meter). In addition, experiments on the feeding behavior of mullets were conducted in mesocoms to assess the volume of sediment ingested per individual at each tide (Como et al., in press). The coupling with field pictures finally allowed estimating the density of fishes per square meter.

2.1.10. Benthic and pelagic viruses

Viral lysis was estimated from viral production (i.e. net increase of viral abundance divided by the time of the experiment) within 2 L bottle incubations in the presence or absence of benthic particulates in order to determine the effect of the biofilm resuspension on the viral lysis. Bacterial mortality due to viral lysis was calculated from the viral production divided by the burst-size viruses (i.e. number of viruses produced by a bacterium at burst-time) which was estimated as 33 in this study (Montanié, pers. comm.). The quantity of viruses produced per time unit was converted into carbon considering that one virus contains 0.2 fgC (Suttle, 2005; Magagnini et al., 2007).

The viral lysis of benthic bacteria at high tide was considered to be similar to the one at low tide, thus we considered that 40 % of the bacterial production was lost by viral lysis (Saint-Béat et al., chap 4). At high tide, the benthic viruses were suspended and integrated into the pelagic virus compartment. 1.29 mgC per high tide of virus per m² were resuspended in the water column at the critical shear bed velocity of $3cm.s^{-1}$ (Dupuy et al., in press) determined by the erosion experiment (see above).

2.1.11. Imports and exports

For all benthic compartments, we considered that the production during the previous low tide was not totally consumed, thus imports of carbon from the diurnal low tide were taken into account. These import values corresponded to the mean export values of the low tide model (Saint-Béat et al., chap 4). Export was considered for both models regarding the

microphytobenthos and the macrofauna, while export was considered only in the model without resuspension regarding the benthic particulate carbon and the dissolved particulate carbon. For the pelagic compartment, no import from the open sea was considered in the model with resuspension and an import from the open sea of pelagic particulate carbon was considered in the model without resuspension. We supposed that the production of the pelagos was totally consumed during the high tide, thus no export from the bay to the open sea of carbon was considered except for the pelagic particulate carbon, when the suspension occurred.

2.2. Equations

The second step characterizes the mass balances of each compartment (listed in Table V-2) and flows measured in the field. These two elements (*i.e.* mass balance and equations) were written within an equation: $A * x = b$ where x was vector that contained possible flows, the matrix A expressed the mass balance and the field observation as a combination of coefficients of the carbon flows and the vector b contained value of mass balances and values of known flows (Vézina, 1989). The mass balances correspond to the report of inputs and outputs for each compartment of the food web. By default, a compartment is considered to be at the equilibrium (*i.e*. a constant biomass). Concerning the model with suspension we needed to consider standing stock of the benthic particulate carbon and the benthic dissolved carbon in deficit. Indeed, for these two compartments, there was a net change in mass equal to resuspension term for particulate carbon and equal to the minimal value necessary to the running of model for the dissolved organic carbon. In the case without resuspension, we considered that the biomass loss of pelagic bacteria was equal to the value of the sedimentation. The other sets of equations corresponded to the values of flows, which were measured *in situ*.

Mass balances of the model with supension	
Phytoplankton	(gppTOphy+**mpbTOphy**)-(phyTOres+phyTOpdc+phyTOhnf+phyTOcil+phyTOsus+phyTOsuf+phyTOppc)=0
Pelagic bacteria	(pdcTObcp+**bcbTOpcb**)-(bcpTOres+bcpTOpdc+bcpTOhnf+bcpTOcil+bcpTOsus+bcpTOsuf+bcpTOvrp)=0
Pelagic viruses	(bacTOvrp+**vrbTOvrp**)-(vrpTOhnf+vrpTOpdc+vrpTOexp)=0
Nanoflagellates	(phyTOhnf+bcpTOhnf+virTOhnf)-(hnfTOres+hnfTopdc+hnfTOcil+hnfTOmes+hnfTOppc)=0
Ciliates	(phyTOcil+bcpTOcil+hnfTOcil)-(cilTOres+cilTOpdc+cilTOmes+cilTOppc)=0
Mesozooplankton	(cilTOmes+ppcTOmes)-(mesTOres+mesTOpdc+mesTOsus+mesTOsuf+mesTOppc)=0
Grazing fisches	(mpbTOgfi+bcbTOgfi+nemTOgfi)-(gfiTOres+gfiTOdet+gfiTOexp)=0
Pelagic dissolved carbon	(phyTOpdc+hnfTOpdc+cilTOpdc+mesTOpdc+**bcbTOpdc**+bcpTOpdc+vrpTOpdc+ppcTOpdc)-pdcTObcp=0
Pelagic particulate carbon	(impTOppc+phyTOppc+hnfTOppc+cilTOppc+mesTOppc+gfiTOppc+**bcbTOppc**+**bcbTOppc**)-(ppcTOmes+ppcTOsus+ppcTOsuf+ppcTOpdc+ppcTOexp)=0
Microphytobenthos	(impTOmpb)-(mpbTOres+mpbTObdc+**mpbTOphy**+mpbTOmfb+mbpTOnem+mpbTOdep+mpbTOomn+mpbTOsuf+mpbTOgfi+mpbTOppc+mpbTOexp)=0
Benthic bacteria	(impTObcb+bdcTObcb)-(bcbTOres+bcbTObdc+bcbTOmfb+bcbTOnem+bcbTOdep+bcbTOomn+bcbTOsuf+bcbTOgfi+bcbTOvrb+**bcbTOpdc**+**bcbTObcp**)=0
Foraminifera	(mpbTOmfb+bcbTOmfb+bpcTOmfb)-(mfbTOres+mfbTOcar+mfbTOomn+mfbTObpc)=0
Nematods	(mpbTOnem+bcbTOnem+bpcTOnem)-(nemTOres+nemTOcar+nemTOomn+nemTOgfi+nemTObpc)=0
Carnivorous	(impTOcar+mfbTOcar+nemTOcar+depTOcar+susTOcar+sufTOcar)-(carTOres+carTObpc+carTOexp)=0
Deposit feeders	(impTOdep+mpbTOdep+bcbTOdep+bpcTOdep)-(depTOres+depTOcar+depTOomn+depTObpc+depTOexp)=0
Omnivorous	(impTOomn+mfbTOomn+nemTOomn+depTOomn+susTOomn+sufTOomn+bcbTOomn+bcpTOomn)-(omnTOres+omnTObpc+omnTOext)=0
Suspension feeders	(impTOsus+phyTOsus+hnfTOsus+cilTOsus+mesTOsus+bcpTOsus+ppcTOsus)-(susTOres+susTOcar+susTOomn+susTObpc+susTOext)=0
Facultative suspension feeders	(impTOsuf+phyTOsuf+hnfTOsuf+cilTOsuf+mesTOsuf+bcpTOsuf+ppcTOsuf+mpbTOsuf+bcbTOsuf+bpcTOsuf)-(sufTOres+sufTOcar+sufTOomn+sufTObpc+sufTOext)=0
Benthic viruses	(impTOvrb+bcbTOvrb)-(**vrbTOvrp**+vrbTObdc)=0
Benthic particulate carbon	(impTObpc+mfbTObpc+nemTObpc+carTObpc+depTObpc+omnTObpc+susTObpc+sufTObpc)-(bcpTOmfb+bcpTOnem+bpcTOdep+bpcTOomn+bpcTOsuf+bpcTOgfi+bpcTObdc+**bpcTOppc**)=-3584.75
Benthic dissolved carbon	(impTObdc+mpbTObdc+bcbTObdc+bpcTObdc)-(bdcTObcb)=-216
Mass balances of the model without supension	
Phytoplankton	(gppTOphy)-(phyTOres+phyTOpdc+phyTOhnf+phyTOcil+phyTOmes+**phyTOmpb**+phyTOsus+phyTOsuf+phyTOppc+phytOpdc)=0
Pelagic bacteria	(pdcTObcp)-(bcpTOres+bcpTOpdc+bcpTOhnf+bcpTOcil+bcpTOsus+bcpTOsuf+bcpTOvrp)=**bcpTObcb**
Pelagic viruses	(bacTOvrp)-(vrpTOhnf+vrpTOpdc)=0
Mesozooplankton	(phyTOmes+cilTOmes+hnfTOmes+ppcTOmes)-(mesTOres+mesTOpdc+mesTOsus+mesTOsuf+mesTOppc)=0
Pelagic dissolved carbon	(phyTOpdc+hnfTOpdc+cilTOpdc+mesTOpdc+bcpTOpdc+vrpTOpdc+ppcTOpdc)-(pdcTObcp+**pdcTObdc**)=0
Microphytobenthos	(impTOmpb+**phyTOmpb**)-(mpbTOres+mpbTObdc+mpbTOmfb+mbpTOnem+mpbTOdep+mpbTOomn+mpbTOsuf+mpbTOgfi+mpbTOppc+mpbTOexp)=0
Benthic bacteria	(impTObcb+bdcTObcb+**bcpTObcb**)-(bcbTOres+bcbTObdc+bcbTOmfb+bcbTOnem+bcbTOdep+bcbTOomn+bcbTOsuf+bcbTOgfi+bcbTOvrb)=0
Benthic viruses	(impTOvrb+bcbTOvrb)-(vrbTObdc)=0
Benthic particulate carbon	(impTObpc+mfbTObpc+nemTObpc+carTObpc+depTObpc+omnTObpc+susTObpc+sufTObpc+**ppcTObpc**)-(bcpTOmfb+bcpTOnem+bpcTOdep+bpcTOomn+bpcTOsuf+bpcTOgfi+bpcTObdc+bpcTOext)=0
Benthic dissolved carbon	(impTObdc+mpbTObdc+bcbTObdc+bpcTObdc+**pdcTObdc**)-(bdcTObcb+bdcTOexp)=0

Table V-2: List of the mass balances for the two models. Each flow is coded by a set of 8 letters. The three first letters correspond to the source compartment and three last letters to the sink compartment (for compartment abbreviations, see Table V-1). Each compartment is alternatively a sink (i.e. it refers to inputs for the considered compartment) and a source compartment (i.e. it represents outputs for the considered compartment). gpp= gross primary production, ext=export and imp=import. The mass balances that remain the same whatever the model were not written twice. The flows in bold correspond either to the flows of resuspension in the mass balances of the model with suspension or to the flows of sedimentation in the mass balances of the model without suspension.

2.3. Inequalities

At the last step, some biological constraints were added to the mass balances and flow values. These constraints were obtained from the literature and limit the possible solutions of flows to realistic values. The information was added to the model with the inequality: $G * x \leq h$, where x remains the vector containing flows, G is a matrix that contains the coefficients of the biological constraints and the vector h is composed of values of biological constraints (Vézina, 1989). For the benthic compartments the set of inequalities of the low tide model (Saint-Béat et al., chap 4) was used. When the constraints corresponded to a value of flows, the value of this constraint was updated according to the time of high tide (8h). The inequalities for the pelagic compartments were grouped in the Table V-3.

The sedimentation flows values were limited, considering two different sinking velocities, which is different according to the particle size (De La Rocha and Passow, 2007). The minimal sinking velocity corresponded to the sinking velocity of a single isolated particle. We considered a minimal sinking velocity of 0.05 $m.d^{-1}$ for free bacteria (Lapoussière et al., 2011), 0.25 $m.d^{-1}$ for chlorophyll *a* (Lapoussière et al., 2011) and 2.32 $m.d^{-1}$ for particulate carbon (Burns and Rosa, 1980). The maximal sinking velocity referred to the sinking velocity of 'marine snow', that are defined as organic aggregates with a diameter > 0.5 mm (Alldredge and Silver, 1988). The maximum sinking velocity chosen for this study was 16 $m.d^{-1}$ (Turner, 2002). We considered that pelagic dissolved carbon can fall with the aggregates formed by 'marine snow' and represents one third of the total carbon in aggregates (Alldredge, 2000).

Processes	Compartments	Lower limit	Upper limit	References
Gross Growth efficiency	HNF, CIL, MES	10%	40%	Straile, 1997
Net Growth efficiency	BCB, BCP	11%	61%	DelGiorgio and Cole, 1998
	MFB	30%	50%	
	NEM	60%	90%	van Oevelen et al. 2006
	MAC	50%	70%	
Assimilation efficiency (loss to the det)	HNF,CIL,MES	50%	90%	Vézina and Platt, 1988
	MFB	57%	97%	
	NEM	6%	30%	van Oevelen et al. 2006
	MAC	40%	75%	
	GFI	50%	90%	Leguerrier et al., 2004
Excretion (loss to doc)	HNF,CIL,MES	10% of ingestion	100% of respiration	min: Vézina and Pace, 1994 max: Vézina and Platt, 1988
	PHY	10%NPP	55%NPP	Breed et al., 2004
		5%GPP	50%GPP	Vézina and Platt, 1988
Respiration	HNF,CIL,MES	20% ingestion	-	Breed et al., 2004
	PHY, MPB	5% GPP	30%GPP	Vézina and Platt, 1988
	MES	biomass*4.8*$W^{-0.25}$	biomass*14*$W^{-0.25}$	min: Hemmingsen, 1960
	CIL, HNF	biomass*0.6*$W^{-0.25}$	biomass*1.7*W^{-025}	max: Moloney and Field,1989
Consumption / Biomass	GFI	3%	8%	Bruslé, 1981
Gross primary production (mgC.m^{-2}.h^{-1})	PHY	10	50	Struski and Bacher, 2006
Loss of doc for pelagic bacteria (mgC.m-2.h-1)	BCP	0.012	-	in this study(with suspension)
		0.005	-	
Bacterivory by HNF	HNF	-	49% of the bacterial production	in this study (with suspension)
	HNF	-	45% of the bacterial production	in this study (without suspension)
Respiration (mgC.m-2.h-1)	GFI	0.226	3.628	min: derived from Killen et al., 2010 max: derived from Brett, 1965

Table V-3: List of biologial constraints used for the food web model. NPP: Net Primary Production, GPP: Gross Primary Production. W: body mass in pgC. Net Growth Efficiency = (consumption–detritus production-respiration)/ (consumption-detritus production), Gross Growth Efficiency=(consumption-loss to det-loss to doc-respiration)/ (consumption-loss to det-loss to doc- production).

2.4. Calculation of solutions

The generated matrices (A, b, G and h) define a multi-dimensional space delimiting possible solutions of the flows (x). The MCMC-LIM mirror (Van den Meersche et al., 2009) was used to sample through that solution space in an attempt to map it completely. The MCMC-LIM, based on the mirror technique defined by Van Den Meersche et al.(2009), calculates several solutions and allows a direct characterization of the uncertainty. This modelling technique brings the advantage of calculating a range of possible values for each flow (i.e. a probability density function). For each model (with resuspension and without resuspension), 500, 000 iterations with a jump of 0.5 were calculated. The length of jump and the number of iterations were determined to cover the solution space as completely as possible. In this study the simulations were realized with a MATLAB© translation conceived by Alain Vézina and Lauriane Campo of the R-CRAN project package LIM-Solve created by Van den Meersche et al. (2009).

2.5. Network analysis

From the 500,000 solutions estimated by MCMC-LIM, seven ecological network analysis (ENA) indices were calculated. These indices allow assessing the structure and the functioning of the two food webs. The magnitude of cycling within the system was described by the Finn cycling Index (*i.e.* FCI). This index represents the fraction of flows involved in the cycling (Finn, 1976). A cycle represents a series of transfers between components in an ecosystem beginning and ending in the same compartment without going through the same compartment twice. The FCI is estimated by the ratio Tc/TST, where TST is the total system throughput (*i.e.* sum of all flows) and Tc the amount devoted to cycling. Various global indices describe the developmental and organizational state of the ecosystem (Ulanowicz, 1986). The TST measures the activity of the whole ecosystem. The TST can be considered as the total power generated within the system (Baird et al., 1998). The AMI value is indicative of the specialization of flows in the network (Ulanowicz, 2004). The probability of flows between two compartments increases with the AMI value, and thus with the specialization of flows. The Ascendency (A) which represents the state of organization within the ecosystem (Ulanowicz, 1986), is described as the product of the TST and the average mutual information

(*i.e.* AMI). The development capacity (DC) is defined as the upper limit of Ascendency. The relative Ascendency is the ratio A/DC and estimates the proportion of the network that is organized and thus efficient. The (DC – A) difference estimates the inefficient part of the network, corresponding to the overheads (*i.e.* overheads on imports, exports and dissipation) and redundancy, that measures the uncertainty associated to the presence of multiple or parallel pathways among the compartments (Ulanowicz and Norden, 1990). The internal Ascendency (A_i) and internal development capacity (DC_i) refer to internal exchanges alone and exclude the exogenous flows.

These indices were estimated using MATLAB© routine written by Carole Lebreton and Markus Schartau (GKSS Research Centre, Geesthacht, Germany) to calculate the index value for every solution estimated by the LIM-MCMC.

2.6 Statistical test

Since the distribution of the data did not follow a normal distribution a non-parametric test was used. The significance of the differences between the indices calculated for both networks with and without resuspension was controlled by the Wilcoxon test ($\alpha = 0.01$). The tested hypothesis was that the two data sets were issued from a continuous distribution with equal medians. Statistical tests is possible because using the LIM-MCMC technique on 500,000 solutions, 500,000 values of each ENA index were also calculated, as consequence we can use statistical tests which are not usually possible in such a context of food web modelling using static methods and at this level of functional diversity..

Results

1. Flow values

Some differences in flow values between the two conditions (i.e. with or without suspension) were observed (Table V-4). The pelagic primary production was higher with resuspension. On

the whole, consumption rates remained the same irrespective of the condition, except for the bacterivory of heterotrophic nanoflagellates (doubled with resuspension), the bacterivory of nematodes (consumption without resuspension was 7 times higher than the value during resuspension), as well as herbivory of deposit-feeders (about twice higher without resuspension than with resuspension) and consumption on nematodes by grazing fishes that both doubled without suspension. The exudation of DOC by benthic bacteria increased without suspension contrary to the exudation of DOC by pelagic bacteria that was five times higher during resuspension. The mortality of phytoplankton (*i.e.* phyTOppc) was higher when resuspension occurred. The egestion of nematodes without suspension was twice the egestion during resuspension. The export of carbon from benthic compartment was higher without suspension.

Processes	*Code flow*	*Without suspension*					*With suspension*				
Gross primary production phytoplankton	gpp phy	184.2	*5% perc.:*	114.3	*95% perc.:*	245.2	235.7	*5% perc.:*	107.2	*95% perc.:*	429.8
Consumption of heterotrophic nanoflagellates											
from phytoplankton	phyTOhnf	29.2	*5% perc.:*	13.7	*95% perc.:*	46.7	22.7	*5% perc.:*	6.4	*95% perc.:*	41.7
from pelagic bacteria	bcpTOhnf	4.2	*5% perc.:*	0.4	*95% perc.:*	8.1	9.6	*5% perc.:*	1.0	*95% perc.:*	17.7
from pelagic viruses	vrpTOhnf	0.0	*5% perc.:*	0.0	*95% perc.:*	0.1	0.5	*5% perc.:*	0.0	*95% perc.:*	1.1
Consumption of cilliates											
from phytoplankton	phyTOcil	2.3	*5% perc.:*	0.2	*95% perc.:*	5.8	2.2	*5% perc.:*	0.2	*95% perc.:*	5.6
from pelagic bacteria	bcpTOcil	2.2	*5% perc.:*	0.2	*95% perc.:*	5.6	2.3	*5% perc.:*	0.2	*95% perc.:*	5.9
from heterotrophic nanoflagellates	hnfTOcil	3.2	*5% perc.:*	0.5	*95% perc.:*	6.6	3.5	*5% perc.:*	0.6	*95% perc.:*	6.9
Consumption of mesozooplankton											
from phytoplankton	phyTOmzp	0.4	*5% perc.:*	0.0	*95% perc.:*	1.0	**0.0**				
from heterotrophic nanoflagellates	hnfTOmzp	0.4	*5% perc.:*	0.0	*95% perc.:*	1.0	**0.0**				
from cilliates	cilTOmzp	0.4	*5% perc.:*	0.0	*95% perc.:*	1.0	0.7	*5% perc.:*	0.1	*95% perc.:*	1.4
from pelagic particulate carbon	ppcTOmzp	0.4	*5% perc.:*	0.0	*95% perc.:*	1.0	0.7	*5% perc.:*	0.1	*95% perc.:*	1.5
Consumption of meiofauna											
from microphytobenthos	mpbTOmfb	0.1	*5% perc.:*	0.0	*95% perc.:*	0.3	0.1	*5% perc.:*	0.0	*95% perc.:*	0.3
from benthic bacteria	bcbTOmfb	0.2	*5% perc.:*	0.1	*95% perc.:*	0.4	0.2	*5% perc.:*	0.1	*95% perc.:*	0.4
from benthic particulate carbon	bpcTOmfb	0.1	*5% perc.:*	0.0	*95% perc.:*	0.3	0.1	*5% perc.:*	0.0	*95% perc.:*	0.3
Consumption of nematods											
from microphytobenthos	mpbTOnem	9.5	*5% perc.:*	0.6	*95% perc.:*	24.8	4.4	*5% perc.:*	0.3	*95% perc.:*	11.2
from benthic bacteria	bcbTOnem	47.0	*5% perc.:*	2.2	*95% perc.:*	136.9	8.8	*5% perc.:*	0.9	*95% perc.:*	19.7
from benthic particulate carbon	bpcTOnem	65.6	*5% perc.:*	9.4	*95% perc.:*	161.4	52.0	*5% perc.:*	12.2	*95% perc.:*	123.1
Consumption of deposit-feeders											
from microphytobenthos	mpbTOdep	23.3	*5% perc.:*	7.4	*95% perc.:*	37.9	12.5	*5% perc.:*	5.5	*95% perc.:*	17.2
from benthic bacteria	bcbTOdep	64.4	*5% perc.:*	45.5	*95% perc.:*	83.1	66.6	*5% perc.:*	55.6	*95% perc.:*	77.6
from benthic particulate carbon	bpcTOdep	1.5	*5% perc.:*	0.1	*95% perc.:*	3.5	0.8	*5% perc.:*	0.1	*95% perc.:*	1.7
Consumption of suspension-feeders											
from phytoplankton	phyTOsus	1.2	*5% perc.:*	0.3	*95% perc.:*	2.2	1.3	*5% perc.:*	0.3	*95% perc.:*	2.4
from heterotrophic nanoflagellates	hnfTOsus	1.8	*5% perc.:*	0.2	*95% perc.:*	4.2	2.1	*5% perc.:*	0.2	*95% perc.:*	4.7
from cilliates	cilTOsus	1.2	*5% perc.:*	0.2	*95% perc.:*	2.6	1.0	*5% perc.:*	0.1	*95% perc.:*	2.3
from mesozooplankton	mzpTOsus	0.3	*5% perc.:*	0.0	*95% perc.:*	0.5	0.2	*5% perc.:*	0.0	*95% perc.:*	0.5
from pelagic bacteria	bcpTOsus	1.4	*5% perc.:*	0.1	*95% perc.:*	3.7	1.6	*5% perc.:*	0.1	*95% perc.:*	4.0
from pelagic particulate carbon	ppcTOsus	1.7	*5% perc.:*	0.4	*95% perc.:*	3.1	1.8	*5% perc.:*	0.5	*95% perc.:*	3.3
Consumption of facultative suspension-feeders											
from phytoplankton	phyTOsuf	0.7	*5% perc.:*	0.1	*95% perc.:*	1.6	1.7	*5% perc.:*	1.3	*95% perc.:*	2.3
from microphytobenthos	mpbTOsuf	1.2	*5% perc.:*	0.4	*95% perc.:*	1.8	0.3	*5% perc.:*	0.1	*95% perc.:*	0.5
from heterotrophic nanoflagellates	hnfTOsuf	0.2	*5% perc.:*	0.0	*95% perc.:*	0.6	0.4	*5% perc.:*	0.0	*95% perc.:*	0.9
from cilliates	cilTOsuf	0.2	*5% perc.:*	0.0	*95% perc.:*	0.6	0.3	*5% perc.:*	0.0	*95% perc.:*	0.8
from mesozooplankton	mzpTOsuf	0.1	*5% perc.:*	0.0	*95% perc.:*	0.4	0.2	*5% perc.:*	0.0	*95% perc.:*	0.4
from benthic bacteria	bcbTOsuf	0.2	*5% perc.:*	0.0	*95% perc.:*	0.6	0.1	*5% perc.:*	0.0	*95% perc.:*	0.3
from pelagic bacteria	bcpTOsuf	0.2	*5% perc.:*	0.0	*95% perc.:*	0.6	0.3	*5% perc.:*	0.0	*95% perc.:*	0.8
from benthic particulate carbon	bpcTOsuf	0.2	*5% perc.:*	0.0	*95% perc.:*	0.5	0.0	*5% perc.:*	0.0	*95% perc.:*	0.1
from pelagic particulate carbon	ppcTOsuf	0.2	*5% perc.:*	0.0	*95% perc.:*	0.4	0.0	*5% perc.:*	0.0	*95% perc.:*	0.1

Table V-4: Values of flows obtained by LIM-MCMC and expressed in $mgC.m^{-2}$ per high tide. The first values correspond to the mean value of the 500,000 solutions obtained for each flow. Values in Italic represent the 5% and 95% percentiles corresponding to the value below which 5 or 95 percent of the observation are found. The bold values correspond to values measured *in situ* and thus integrated to the model in equality form.

Processes	*Code flow*	*Without suspension*				*With suspension*			
Consumption of omnivorous species									
from microphytobenthos	mpbTOomn	2.8	*5% perc.:* 0.7	*95% perc.:*	5.4	2.0	*5% perc.:* 0.4	*95% perc.:*	4.0
from meiofauna	mfbTOomn	0.1	*5% perc.:* 0.0	*95% perc.:*	0.1	0.1	*5% perc.:* 0.0	*95% perc.:*	0.1
from nematods	nemTOomn	1.2	*5% perc.:* 0.1	*95% perc.:*	3.2	1.5	*5% perc.:* 0.1	*95% perc.:*	3.7
from deposit-feeders	depTOomn	1.7	*5% perc.:* 0.1	*95% perc.:*	4.6	1.4	*5% perc.:* 0.1	*95% perc.:*	3.8
from suspension-feeders	susTOomn	0.4	*5% perc.:* 0.0	*95% perc.:*	1.2	0.4	*5% perc.:* 0.0	*95% perc.:*	0.9
from facultative suspension-feeders	sufTOomn	0.1	*5% perc.:* 0.0	*95% perc.:*	0.2	0.1	*5% perc.:* 0.0	*95% perc.:*	0.3
from benthic bacteria	bcbTOomn	2.1	*5% perc.:* 0.1	*95% perc.:*	5.4	1.4	*5% perc.:* 0.1	*95% perc.:*	3.8
from benthic particulate carbon	bpcTOomn	1.0	*5% perc.:* 0.2	*95% perc.:*	2.4	0.7	*5% perc.:* 0.1	*95% perc.:*	1.7
Consumption of carnivorous									
from meiofauna	mfbTOcar	0.1	*5% perc.:* 0.0	*95% perc.:*	0.1	0.1	*5% perc.:* 0.0	*95% perc.:*	0.1
from nematods	nemTOcar	1.4	*5% perc.:* 0.1	*95% perc.:*	3.2	1.3	*5% perc.:* 0.1	*95% perc.:*	2.8
from deposit-feeders	depTOcar	1.8	*5% perc.:* 0.2	*95% perc.:*	3.5	1.2	*5% perc.:* 0.1	*95% perc.:*	2.7
from suspension-feeders	susTOcar	0.5	*5% perc.:* 0.0	*95% perc.:*	1.2	0.4	*5% perc.:* 0.0	*95% perc.:*	0.9
from facultative suspension-feeders	sufTOcar	0.1	*5% perc.:* 0.0	*95% perc.:*	0.3	0.1	*5% perc.:* 0.0	*95% perc.:*	0.3
Consumption of grazing fishes									
from microphytobenthos	mpbTOgfi	2.9	*5% perc.:* 0.7	*95% perc.:*	5.6	1.1	*5% perc.:* 0.3	*95% perc.:*	2.2
from nematods	nemTOgfi	8.3	*5% perc.:* 5.5	*95% perc.:*	10.8	4.0	*5% perc.:* 3.3	*95% perc.:*	5.3
from benthic bacteria	bcbTOgfi	1.0	*5% perc.:* 0.1	*95% perc.:*	2.5	0.4	*5% perc.:* 0.0	*95% perc.:*	1.0
from benthic particulate carbon	bpcTOgfi	2.2	*5% perc.:* 0.2	*95% perc.:*	5.5	0.8	*5% perc.:* 0.1	*95% perc.:*	2.1
Viral lysis									
from benthic bacteria	bcbTOvrb	**8.7**				**8.7**			
from pelagic bacteria	bcpTOvrp	**0.1**				**0.2**			
Uptake of dissolve carbone by pelagic bacteria	pdcTObcp	118.6	*5% perc.:* 61.4	*95% perc.:*	164.2	301.7	*5% perc.:* 233.3	*95% perc.:*	342.6
Uptake of dissolve carbone by benthic bacteria	bdcTObcb	386.5	*5% perc.:* 374.8	*95% perc.:*	408.8	374.3	*5% perc.:* 374.2	*95% perc.:*	374.5
Transformation particular carbon									
from pelagic particulate carbon	ppcTOpdc	118.3	*5% perc.:* 64.5	*95% perc.:*	188.1	159.4	*5% perc.:* 103.7	*95% perc.:*	202.5
from benthic particulate carbon	bpcTObdc	83.9	*5% perc.:* 31.7	*95% perc.:*	173.3	48.8	*5% perc.:* 50.0	*95% perc.:*	68.2
Exudation of dissove carbon									
from phytoplankton	phyTOpdc	45.0	*5% perc.:* 15.9	*95% perc.:*	81.5	51.7	*5% perc.:* 15.4	*95% perc.:*	98.4
from heterotrophic nanoflagellates	hnfTOpdc	6.5	*5% perc.:* 2.8	*95% perc.:*	11.0	6.3	*5% perc.:* 2.7	*95% perc.:*	11.0
from cilliates	cilTOpdc	1.3	*5% perc.:* 0.7	*95% perc.:*	2.0	1.4	*5% perc.:* 0.8	*95% perc.:*	2.0
from mesozooplankton	mzpTOpdc	0.3	*5% perc.:* 0.1	*95% perc.:*	0.4	0.2	*5% perc.:* 0.1	*95% perc.:*	0.4
from benthic bacteria	bcbTObdc	234.6	*5% perc.:* 148.3	*95% perc.:*	290.6	92.2	*5% perc.:* 84.8	*95% perc.:*	103.6
from pelagic bacteria	bcpTOpdc	10.9	*5% perc.:* 5.5	*95% perc.:*	16.0	58.9	*5% perc.:* 50.0	*95% perc.:*	68.2
from benthic viruses	vrbTObdc	10.4	*5% perc.:* 10.4	*95% perc.:*	10.4	9.1	*5% perc.:* 9.1	*95% perc.:*	9.1
from pelagic viruses	vrpTOpdc	0.0	*5% perc.:* 0.0	*95% perc.:*	0.1	0.5	*5% perc.:* 0.0	*95% perc.:*	1.2
Excretion									
from phytoplankton	phyTOppc	53.9	*5% perc.:* 7.8	*95% perc.:*	106.5	124.4	*5% perc.:* 36.0	*95% perc.:*	271.5
from heterotrophic nanoflagellates	hnfTOppc	11.2	*5% perc.:* 3.0	*95% perc.:*	22.8	10.6	*5% perc.:* 2.8	*95% perc.:*	22.9
from cilliates	cilTOppc	2.6	*5% perc.:* 0.9	*95% perc.:*	4.5	2.7	*5% perc.:* 0.9	*95% perc.:*	4.5
from mesozooplankton	mzpTOppc	0.5	*5% perc.:* 0.2	*95% perc.:*	0.8	0.4	*5% perc.:* 0.1	*95% perc.:*	0.8
from meiofauna	mfbTObpc	0.2	*5% perc.:* 0.1	*95% perc.:*	0.3	0.2	*5% perc.:* 0.1	*95% perc.:*	0.2
from nematods	nemTObpc	109.6	*5% perc.:* 41.1	*95% perc.:*	184.8	57.1	*5% perc.:* 20.7	*95% perc.:*	124.9
from deposit-feeders	depTObpc	27.7	*5% perc.:* 20.9	*95% perc.:*	36.9	27.1	*5% perc.:* 18.4	*95% perc.:*	38.8
from suspension-feeders	susTObpc	2.6	*5% perc.:* 1.8	*95% perc.:*	3.7	4.3	*5% perc.:* 3.5	*95% perc.:*	4.8
from facultative suspension-feeders	sufTObpc	0.9	*5% perc.:* 0.8	*95% perc.:*	1.1	1.0	*5% perc.:* 0.8	*95% perc.:*	1.1
from omnivorous species	omnTObpc	3.8	*5% perc.:* 2.2	*95% perc.:*	5.6	4.0	*5% perc.:* 1.9	*95% perc.:*	5.3
from carnivorous species	carTObpc	1.6	*5% perc.:* 0.9	*95% perc.:*	2.4	1.5	*5% perc.:* 0.6	*95% perc.:*	2.3
from grazing fishes	gfiTOppc	4.0	*5% perc.:* 1.5	*95% perc.:*	7.3	1.7	*5% perc.:* 0.7	*95% perc.:*	3.0

Table V-4. (Continued)

Processes	*Code flow*	*Without suspension*					*With suspension*				
Respiration											
from phytoplankton	phyTOres	32.6	*5% perc.:*	10.3	*95% perc.:*	61.8	41.3	*5% perc.:*	9.1	*95% perc.:*	111.4
from microphytobenthos	mpbTOres	4.9	*5% perc.:*	1.8	*95% perc.:*	8.8	1.7	*5% perc.:*	1.6	*95% perc.:*	1.9
from heterotrophic nanoflagellates	hnfTOres	10.2	*5% perc.:*	6.1	*95% perc.:*	13.1	10.0	*5% perc.:*	5.9	*95% perc.:*	13.1
from cilliates	cilTOres	1.9	*5% perc.:*	1.4	*95% perc.:*	2.2	2.0	*5% perc.:*	1.4	*95% perc.:*	2.2
from mesozooplankton	mzpTOres	0.4	*5% perc.:*	0.3	*95% perc.:*	0.4	0.3	*5% perc.:*	0.2	*95% perc.:*	0.4
from meiofauna	mfbTOres	0.2	*5% perc.:*	0.1	*95% perc.:*	0.2	0.2	*5% perc.:*	0.1	*95% perc.:*	0.2
from nematods	nemTOres	1.4	*5% perc.:*	1.1	*95% perc.:*	1.6	1.1	*5% perc.:*	1.0	*95% perc.:*	1.4
from deposit-feeders	depTOres	53.9	*5% perc.:*	50.2	*95% perc.:*	60.4	50.0	*5% perc.:*	49.9	*95% perc.:*	50.3
from suspension feeders	susTOres	3.5	*5% perc.:*	2.9	*95% perc.:*	4.2	2.8	*5% perc.:*	2.6	*95% perc.:*	3.1
from facultative suspension-feeders	sufTOres	2.1	*5% perc.:*	2.0	*95% perc.:*	2.3	2.1	*5% perc.:*	2.0	*95% perc.:*	2.2
from omnivorous species	omnTOres	5.1	*5% perc.:*	3.8	*95% perc.:*	6.9	3.5	*5% perc.:*	3.4	*95% perc.:*	3.7
from carnivorous species	carTOres	2.1	*5% perc.:*	1.5	*95% perc.:*	2.8	1.5	*5% perc.:*	1.3	*95% perc.:*	1.7
from grazing fishes	gfiTOres	6.1	*5% perc.:*	2.2	*95% perc.:*	11.4	3.3	*5% perc.:*	1.9	*95% perc.:*	4.9
from benthic bacteria	bcbTOres	158.3	*5% perc.:*	146.6	*95% perc.:*	180.6	146.0	*5% perc.:*	145.9	*95% perc.:*	146.3
from pelagic bacteria	bcpTOres	99.6	*5% perc.:*	42.4	*95% perc.:*	145.2	263.7	*5% perc.:*	195.3	*95% perc.:*	304.6
Imports											
to microphytobenthos	impTOmpb	**31.9**					**31.9**				
to deposit-feeders	impTOdep	**99.6**					**99.6**				
to suspension-feeders	impTOsuf	**2.6**					**2.6**				
from facultative suspension-feeders	impTOsus	**5.4**					**5.4**				
to omnivorous species	impTOomn	**7.8**					**7.8**				
to carnivorous species	impTOcar	**3.1**					**3.1**				
to benthic bacteria	impTObcb	**8.3**					**8.3**				
to benthic viruses	impTOvrb	**1.7**					**1.7**				
to benthic particulate carbon	impTObpc	**8.2**					**8.2**				
to benthic dissolve carbon	impTObdc	**8.1**					**8.1**				
to pelagic particulate carbon	impTOppc	241.2	*5% perc.:*	132.8	*95% perc.:*	354.2	**0.0**				
Exports											
from microphytobenthos	mpbTOexp	6.3	*5% perc.:*	0.4	*95% perc.:*	17.0	0.1	*5% perc.:*	0.0	*95% perc.:*	0.3
from deposit-feeders	depTOexp	103.6	*5% perc.:*	99.9	*95% perc.:*	110.0	99.7	*5% perc.:*	99.6	*95% perc.:*	99.9
from suspension-feeders	susTOexp	5.9	*5% perc.:*	5.4	*95% perc.:*	6.7	5.5	*5% perc.:*	5.4	*95% perc.:*	5.7
from facultative suspension-feeders	sufTOexp	2.7	*5% perc.:*	2.6	*95% perc.:*	2.9	2.7	*5% perc.:*	2.6	*95% perc.:*	2.8
from omnivorous species	omnTOexp	8.4	*5% perc.:*	7.8	*95% perc.:*	9.1	7.8	*5% perc.:*	7.8	*95% perc.:*	8.0
from carnivorous species	carTOexp	3.3	*5% perc.:*	3.1	*95% perc.:*	3.6	3.1	*5% perc.:*	3.1	*95% perc.:*	3.3
from grazing fishes	gfiTOexp	4.3	*5% perc.:*	0.4	*95% perc.:*	9.7	1.5	*5% perc.:*	0.1	*95% perc.:*	3.1
from benthic particulate carbon	bpcTOext	193.0	*5% perc.:*	106.2	*95% perc.:*	283.3	**0.0**				
from benthic dissolve carbon	bdcTOext	14.2	*5% perc.:*	0.7	*95% perc.:*	43.2	**0.0**				
from pelagic viruses	vrpTOext	0.0	*5% perc.:*	0.0	*95% perc.:*	0.1	0.5	*5% perc.:*	0.0	*95% perc.:*	1.2
from pelagic particulate carbon	ppcTOexp	**0.0**					3562.6	*5% perc.:*	3448.1	*95% perc.:*	3693.1
Connection between benthos and pelagos											
from phytoplankton	phyTOmpb	18.9	*5% perc.:*	7.9	*95% perc.:*	24.4					
from microphytobenthos	mpbTOphy						**9.7**				
from pelagic bacteria	bcpTObcb	121.7	*5% perc.:*	94.0	*95% perc.:*	134.4					
from pelagic particulate carbon	ppcTObpc	193.0	*5% perc.:*	106.2	*95% perc.:*	283.3					
from benthic bacteria	bcbTOpdc						**23.3**				
	bcbTObcp						**34.9**				
from benthic viruses	vrbTOvrp						**1.3**				
from benthic particulate carbon	bpcTOppc						**3584.8**				
from pelagic dissolve carbon	pdcTObdc	63.7	*5% perc.:*	35.1	*95% perc.:*	93.5					

Table V-4. (Continued)

2. Compartment activities

Significant differences appeared according to the condition considered (Figure 2). The benthic activity was stimulated by the sedimentation of micro-organisms of the water column. In contrast, the resuspension of micro-organisms inhabiting in the sediment stimulated the pelagic activity.

Several pelagic compartments were affected by the resuspension of micro-organisms. The phytoplankton (phy), the pelagic non-living compartments (*i.e.* particulate compartment (ppc) and dissolved organic carbon (pdc)) as well as the pelagic bacteria (bcp) had a higher activity in the case of resuspension. On the contrary the microphytobenthos, the benthic bacteria, the benthic non-living compartments were more active when sedimentation occurred.

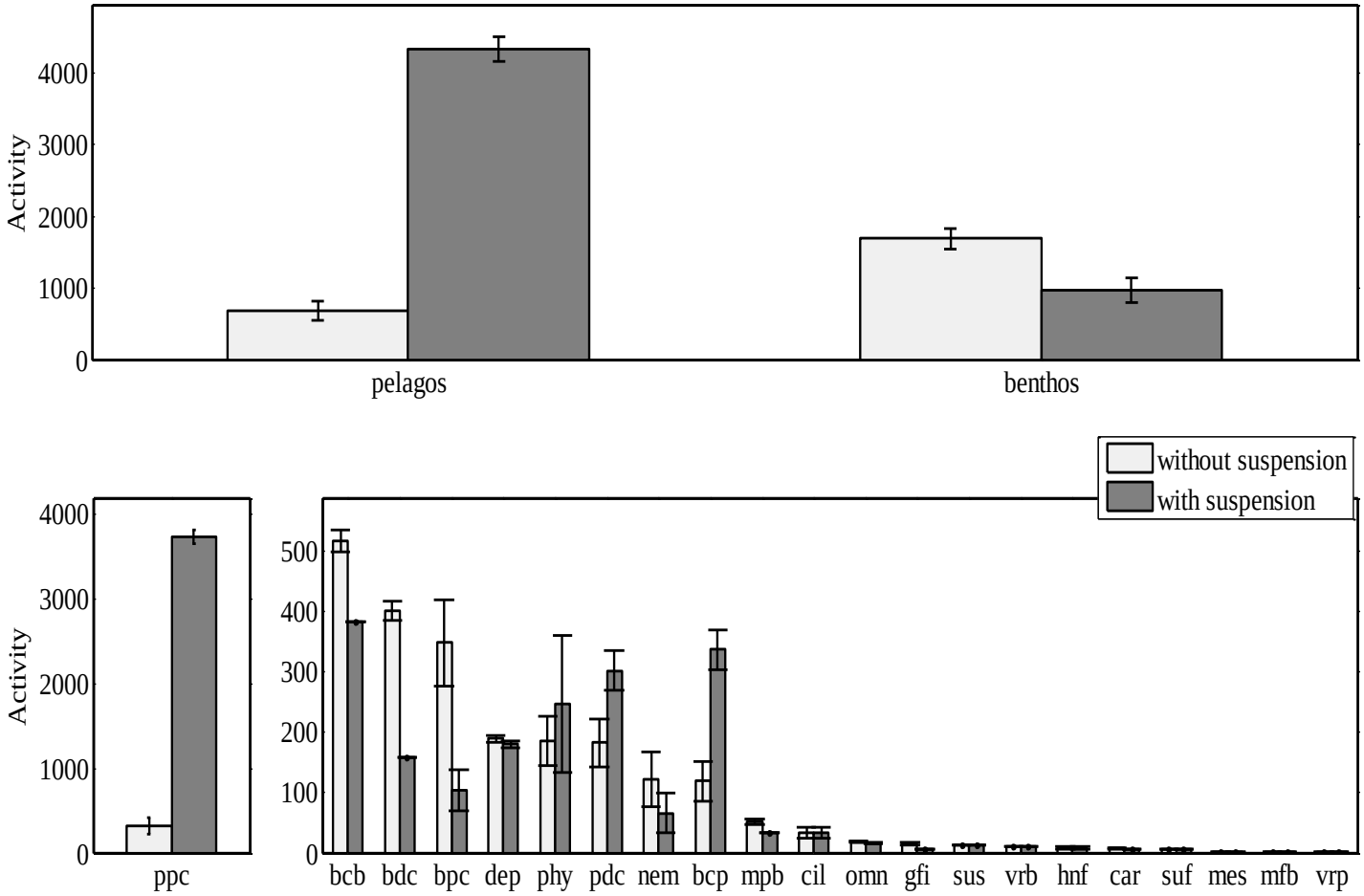


Figure V-2: Histogram presenting the activity of the compartments composing the food web. The activity corresponds to the sum of inflows and is expressed in $mgC.m^{-2}$ per high tide. A) corresponds to the sum of the activity of all compartments for the benthos and the pelagos according to the 2 modeled situations. B) and C) refer to the activity of each compartment of the benthos and of the pelagos. See table V-1 for the abbreviations of the compartments.

3. Diet and consumption

	Benthic		Pelagic	
	With Resuspension	Without resuspension	With Resuspension	Without resuspension
Herbivory ($mgC.m^{-2}.HT^{-1}$)	20.4 ± 0.1	39.7 ± 7.3	28.7 ± 11.2	33.8 ± 9.8
Bacterivory ($mgC.m^{-2}.HT^{-1}$)	85.9 ± 5.8	123.7 ± 42.7	14.3 ± 5.8	8.1 ± 3.2
Ratio herbivory/bacterivory	0.23 ± 0.01	0.35 ± 0.1	2.9 ± 3.1	5.56 ± 4.9

Table V-5: Mean values of herbivory and bacterivory in the benthos and the pelagos according to the resuspension of the biofilm. HT^{-1}= per High Tide. These values corresponded to the mean and the standard deviation calculated from the 500,000 iterations calculated by the inverse analyses. For each compartment (i.e. benthos and pelagos) values were significantly different with or without resuspension (Wilcoxon test, $p<0.05$) according to the condition considered.

Herbivory tended to represent a more important part in the pelagic system (Table V-5). In contrast, bacterivory was higher in the benthic compartment. The resuspension of the micro-organisms to the water column had an effect on bacterivory, herbivory and the ratio between them. In the pelagic part, the resuspension favored the bacterivory. On the contrary, the herbivory was favored in the case without resuspension. The herbivory and bacterivory in benthos were both higher without resuspension.

The ratios showed that the herbivory was dominant in the pelagos. Nevertheless, when resuspension occurred, the decline in the ratio (almost divided by 2) was due to a fall of herbivory as well as a rise in bacterivory. A fall in the ratio was observed regarding the benthos due to a decline in the bacterivory lower than in herbivory.

None of the compartment was affected by the resuspension (Figure V-3). Conversely, the diet of nematodes was drastically altered during the resuspension phase (B). Whatever the resuspension occurred or not, the contribution of the microphytobenthos as a food item for nematodes did not change (about 15%). On the contrary, benthic bacteria and detritus contributed to nematodes diet almost equally in the case without resuspension (40 and 30%,

respectively), while it mainly shifted to benthic particulate (about 80%) in resuspension situation.

The detritus contributed only slightly to the diet of deposit feeders. This group fed mainly on microphytobenthos and benthic bacteria. The contribution of each of these two groups changed with the resuspension. While the consumption on the benthic bacteria remained the same between resuspension and sedimentation phases, it corresponded to a higher contribution to the deposit-feeder diet during resuspension.

The facultative suspension feeders fed on the planktonic and benthic species. The contribution of the phytoplankton to the diet of this group was higher when the resuspension occurred. Consequently, the microphytobenthos was merely consumed. In contrast, in the case without resuspension, the microphytobenthos contributed to 40% of the consumption and the phytoplankton for 20%. The contribution of pelagic and particulate carbon tended to be lower with the resuspension.

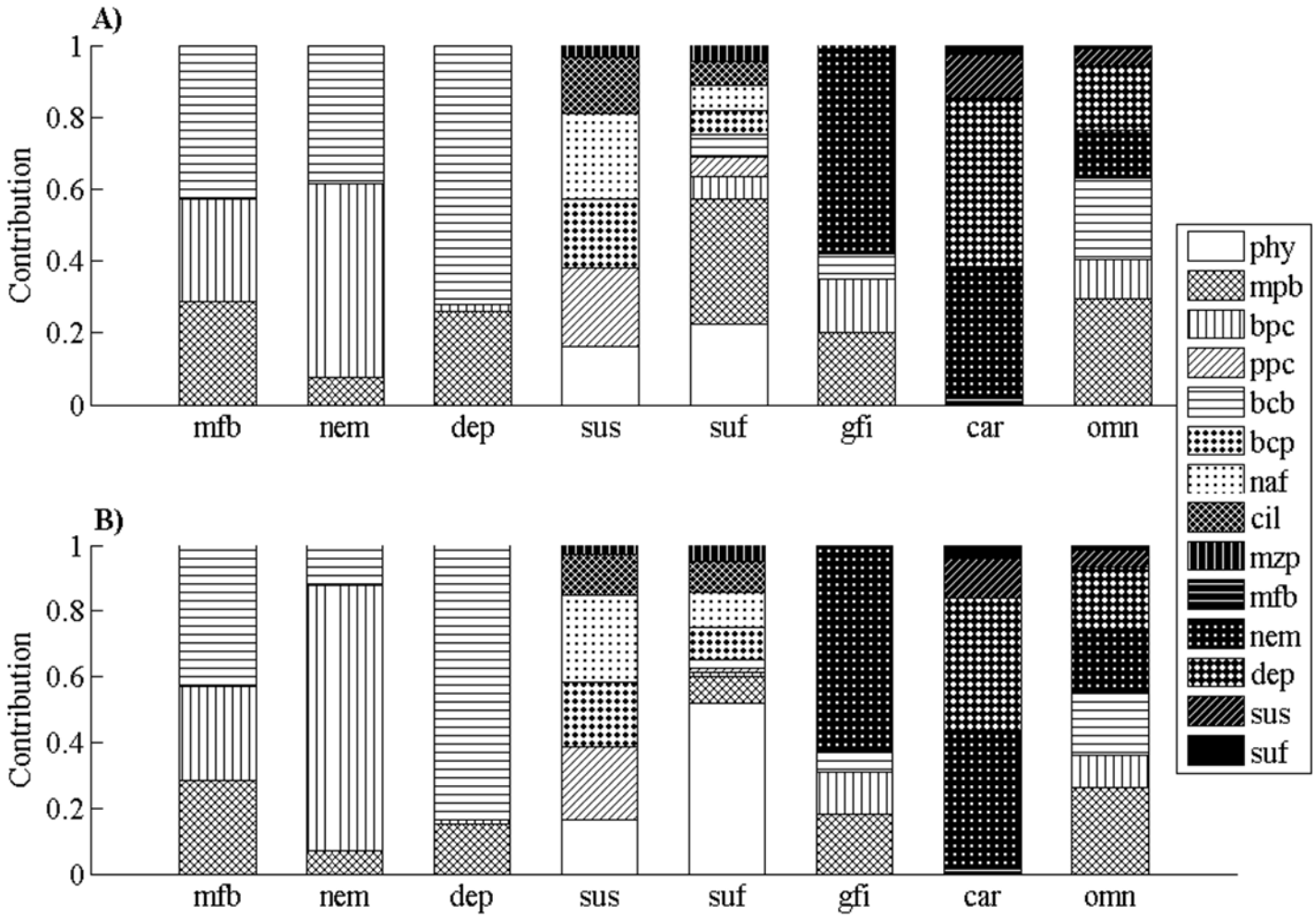


Figure V-3: Diet of the meiofauna and macrofauna. A) refers to the case without resuspension and B) to the case where the resuspension occurred. The contribution corresponds to the fraction that represents the consumption on a prey in comparison to the total consumption. The contribution of each species to the compartment consumption was estimated from the mean value of each flow.

The resuspension tended to have some consequences on the diet of the heterotrophic nanoflagellates and mesozooplankton (Figure V-4). The diet of the heterotrophic nanoflagellates was more diversified during resuspension because of the contribution of virus (vrp). The contribution of pelagic bacteria (bcp) was three times higher in the case of resuspension. Consequently the contribution of the phytoplankton (phy) decreased. The most affected compartment was the mesozooplankton. Without resuspension the mesozooplankton fed equally on the phytoplankton, heterotrophic nanoflagellates, pelagic particulate carbon (ppc) and ciliates. During the resuspension, the consumption on both heterotrophic nanoflagellates and phytoplankton was inhibited.

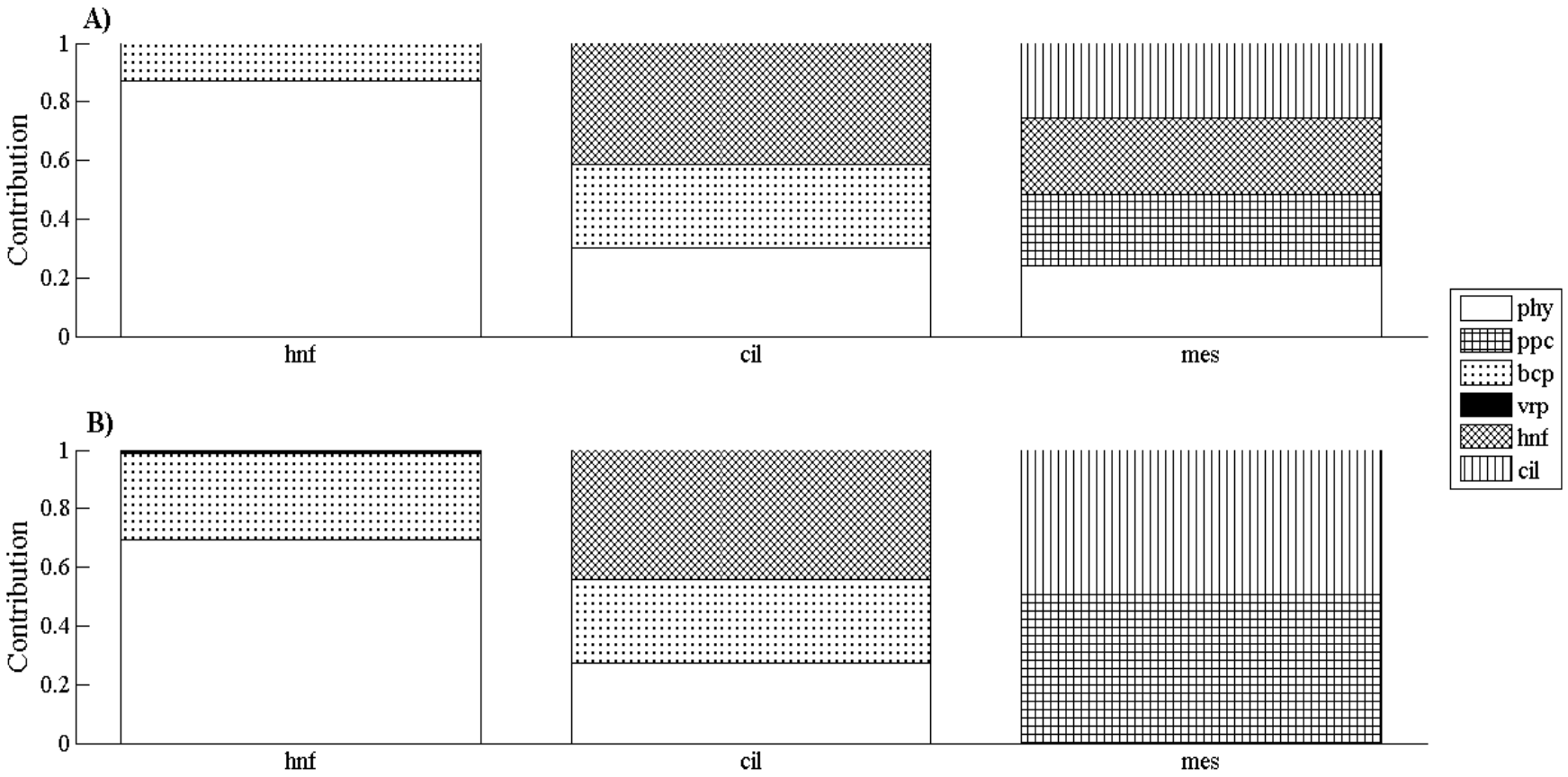


Figure V-4: Diet of heterotrophic nanoflagellates (hnf), ciliates (cil) and mesozooplankton (mes). A) refers to the case without resuspension and B) the case where the resuspension occurred. The contribution corresponds to the fraction that represents the consumption on a compartment in comparison to the total consumption. The contribution of each species to the compartment consumption was estimated from the mean value of each flow.

4. ENA indices

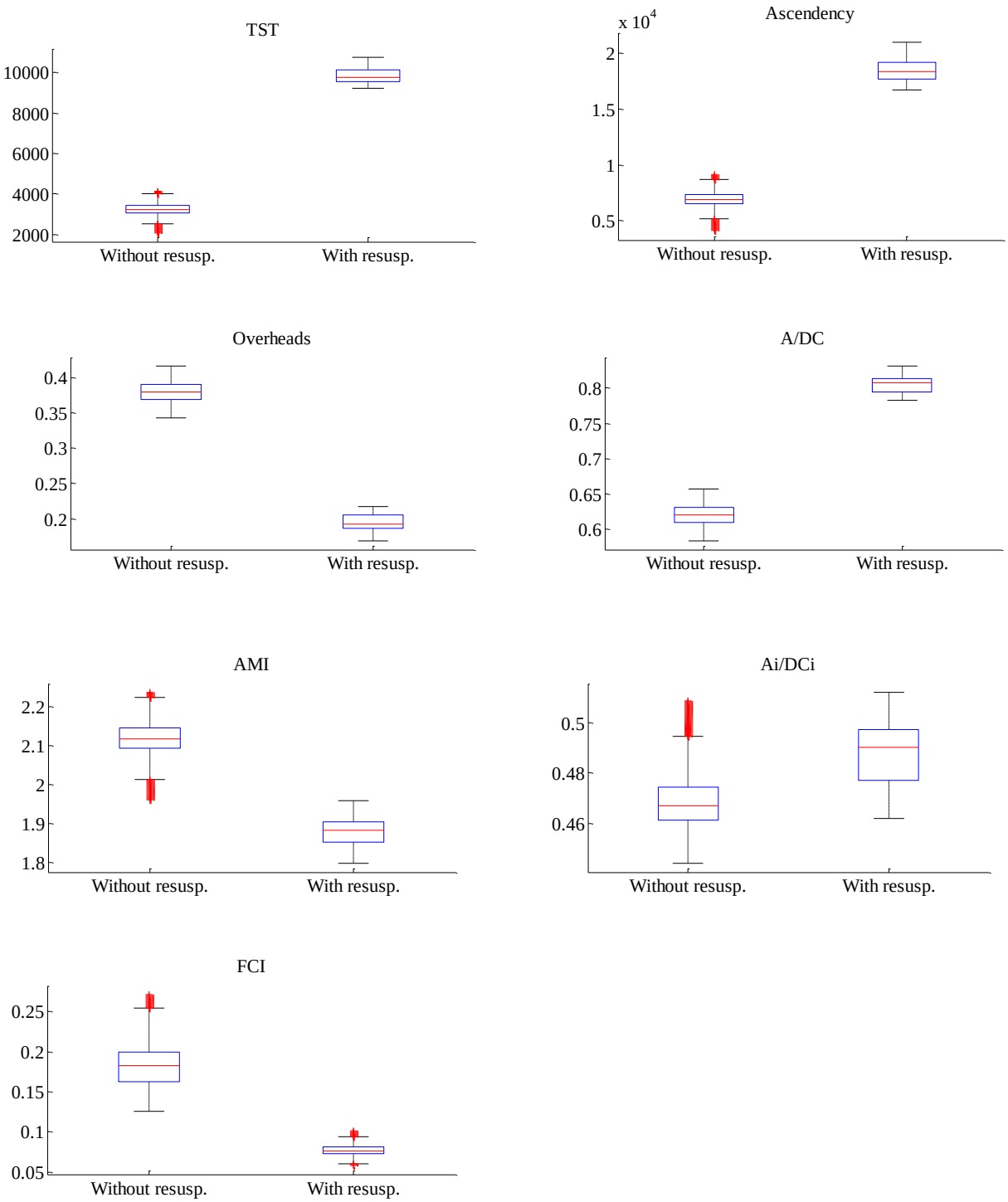


Figure V-5: Boxplots displaying the values of different ENA indices: the total System Throughput (TST), the Ascendency, the overheads, the relative Ascendency (A/DC), the Average mutual Information (AMI), the internal relative Ascendency (Ai/DCi) and the Finn Cycling index (FCI). The indices were calculated from the 500,000 solutions coming from the MCMC-LIM method. Red crosses correspond to outliers. Medians of all these indices were significantly different for the two seasons (Wilcoxon test, H_0 was rejected, p-value < 0.01).

Significant differences between values of the indices of the two situations were observed (Figure V-5). The TST was about 3 times higher when the resuspension occurred. The Ascendency followed the same trend. However, a lower organization of the system (i.e. lower AMI value) was observed. The higher relative Ascendency, coupled with a lower AMI value observed in the case of resuspension, suggested a lower diversity of flows. The overheads based on the imports, exports, respiration and redundancy of the system were lower during resuspension. The internal normalized Ascendency tended to be similar for the two situations. The proportion of flows involved in the cycling (i.e. FCI value) was lower during resuspension event.

Discussion

1. Activity of the benthic and the pelagic compartments

The benthos was more active than the pelagos regarding simulation without resuspension; in contrast the pelagic activity was higher during resuspension. This fact can be explained by a large import of particulate carbon to the pelagic particulate compartment. Without this import of pelagic carbon, the pelagic activity was equal to the benthic activity during resuspension. The higher benthic activity was previously shown in the model of the Brouage mudflat food web. In fact, the higher activity of the benthos was observed irrespective of the model considered in previous studies by regarding annual budget (Leguerrier et al., 2004) or by deciphering seasonal budgets (Degré et al., 2006). However, in our model, the ranking of the compartments was modified. The main difference concerned the benthic bacteria and the microphytobenthos. The benthic bacteria dominated the ecosystem; they were followed by the benthic non-living detritus compartments. Surprisingly, the microphytobenthos was ranked only 8^{th}. The difference with previous models is the time-scale considered: a mean year (Leguerrier et al., 2004) or a mean month (Degré et al., 2006) which is in dramatic contrast to the small scale mean immersion period integrated in our model. During immersion, because of darkness due to sediment burying, the microphytobenthos production was null (Blanchard, 2006). As a consequence, the carbon input to this compartment exclusively originated from

the photosynthesis performed during the previous diurnal low tide, which might explain its 8th rank in our model. The first pelagic compartments were ranked 4th and 5th and corresponded to the phytoplankton and the dissolved organic carbon, respectively.

The resuspension of the microbial biofilm stimulated the activity of the phytoplankton, the non-living compartments (detritus) and the pelagic bacteria. This stimulation was not only the consequence of the input of new matter in the water column. The phytoplankton showed a higher gross primary production when the resuspension of the microbial biofilm occurred. Pelagic primary production was not imposed to the model; it was only constrained by minimal and maximal values of pelagic production found for different hydrological conditions in Marennes-Oléron Bay. The higher production was somewhat surprising because the resuspension also generates a high turbidity and the reduction of the light penetration which dramatically reduces phytoplankton photosynthesis (Billerbeck et al., 2007; Porter et al., 2010). When buried in the sediments, the microphytobenthos can remove nutrients from the overlying water and the sediment pore water (Macintyre et al., 1996). Such activity tends to reduce the nutrient fluxes from the sediments to the water column which can limit the phytoplankton production (Sloth et al., 1996; Sarker et al., 2009). When the microphytobenthos resuspension occurs, the nutrient fluxes to the water column increase which has a positive effect on the phytoplankton production even if light is limiting (Porter et al., 2010). Paradoxically, the import of microphytobenthic diatoms to the water column contributes itself positively to the production of the phytoplankton (Macintyre et al., 1996). By enriching water in particulate and dissolved carbon, which sustained a higher bacterial activity as previously reported (Sloth et al., 1996; Poremba et al., 1999; Cotner et al., 2000), the resuspension also stimulated heterotrophic production.

On the contrary, the settling of pelagic micro-organisms to the bottom of the water column had smaller but significant consequences on the benthic compartments. In our model, the input of pelagic fresh matter to the benthos increased the stock of available carbon for higher trophic levels but it did not affect the production of the different compartments. The higher activity observed for the benthic compartments (mpb, bdc, bcb, bpc) (Figure V-2) was linked to the deposit of pelagic diatoms, dissolved carbon, pelagic bacteria and particulate carbon respectively at the surface of the sediments. The photosynthetic production of the pelagic diatoms settled at the bottom of the water column during immersion is more probably limited

by the penetration of light than by the nutrient availability. It is supposed that, in contrast to the light reaching the surface of the sediments (Macintyre et al., 1996; Billerbeck et al., 2007), nutrients are often not a limiting factor for the photosynthesis in the intertidal sediments (Serôdio and Catarino, 2000; Migné et al., 2004). The high turbidity reported in the bay of Marennes-Oléron (Raillard and Mesenguen, 1994) likely stops the light penetration to the sediment surface and strongly impairs the photosynthesis of pelagic diatoms. The effect of the settling on the benthic bacterial production is more obvious. The bacterial production depends on the substrate supply including organic carbon (Sander and Kalff, 1993). For instance in Kiel Bight, the settling of detritus stimulates the benthic bacterial production (Meyer-Reil, 1983). Consequently, it is very likely that the benthic bacterial production is stimulated in the Brouage mudflat during sedimentation.

2. Consumption of the benthic compartments

The hydrodynamics events (i.e. sedimentation and resuspension) did not affect the consumption rate of the macrofauna but it could modify its diet. The contribution of the microphytobenthos to the diet of the deposit-feeders was about twice higher during the sedimentation *vs*. the resuspension. This was due to the settling of phytoplankton which enriched the stock of available microalgal carbon. On the contrary, during resuspension, part of the microphytobenthos was exported to the water column thus decreasing the carbon available for the benthic herbivorous species. In such situation, the deposit-feeders tended to feed on an alternative resource: the benthic bacteria (van Oevelen et al., 2006a; Pascal et al., 2009). While the consumption on the benthic bacteria remained the same between resuspension and sedimentation phases, it corresponded to a higher contribution to the deposit-feeder diet during resuspension. The diet of facultative suspension-feeders was also affected, especially the ratio microphytobenthos/phytoplankton. The resuspension of the microphytobenthos enriched the phytoplankton. The facultative suspension-feeders doubled their consumption of phytoplankton and thus it contributed to 50% to the diet of this compartment to the detriment of the direct microphytobenthos contribution.

3. Herbivory *versus* bacterivory

The massive resuspension event impacted the pelagic microbial food web. It stimulated the bacterivory of the pelagos as reported before for heterotrophic nanoflagellates (Garstecki et al., 2002). A higher quantity of carbon flowed through the virus (viral lysis was doubled) and consequently more virus were consumed by heterotrophic nanoflagellates. The increase of pelagic bacterial abundance and production doubled the bacterivory rate of heterotrophic nanoflagellates. In contrast, the resuspension tended to decrease the pelagic herbivory. In spite of a higher gross primary production and a direct input of benthic diatoms biomass to the water column, the phytoplankton was integrated to a lower proportion to the pelagic food web. Indeed, the grazing of phytoplankton by the mesozooplankton had been shown to be inhibited during catastrophic erosion event (Hartmann, pers.comm.). Consequently, our models showed that a lower part of the phytoplankton was consumed in the model with resuspension, inducing a greater mortality of this comportment. This result of the models (*i.e.* higher phyTOppc when resuspension occurs) is coherent with previous results of resuspension experiments (Porter et al., 2010). It thus appears that in conditions of resuspension, the phytoplankton indirectly participated to the enrichment of the water column in dissolved organic carbon and to the pelagic bacterial production.

The bacterivory dominated the benthic compartment during immersion irrespective of the resuspension. At high tide, benthic diatoms moves down the sediment and cannot perform photosynthesis because of the absence of light (Cartaxana et al., 2011). Hence, the benthic food web must be sustained by the input of carbon coming from the photosynthetic production of the previous emersion and by the bacterial production. In our model, we supposed that the meiofauna and the macrofauna showed a constant consumption along the day irrespective of immersion/emersion periods. This hypothesis was based on the assumption that the meiofauna and the deposit feeders had alternative resources since the microphytobenthos was not sufficient to sustain their respective metabolism. Detritus (van Oevelen et al., 2006a) bacteria were possible alternative resource for benthic fauna (van Oevelen et al., 2006a; Pascal et al., 2009). Some isotopic analyses at the Brouage mudflat showed that the benthic detritus contributes to 11% in maximum to the deposit-feeders consumption (Richard, comm. pers.). We supposed that the alternative feeding resource was the benthic bacteria (see result section .

Previous studies on the bacterivory rates of the nematodes, the foraminifera and *Peringia ulvae* in the Brouage mudflat indeed showed that bacteria can constitute a significant alternative resource to the microphytobenthos under some conditions (Pascal et al., 2008b; Pascal et al., 2008c; Pascal et al., 2008d). When there was no resuspension, the herbivory and the bacterivory were both stimulated, although the bacterivory was stimulated in a larger proportion due to the higher activity of the nematodes. The bacterivory thus remained dominant in the benthic compartment irrespective of the physical forcing.The Sylt- Rømø Bight in the North of Germany is composed of a mosaic of habitats including a mudflat. Its benthic food web is based on microphytobenthos and macrophytes. In this benthic ecosystem, the herbivory dominates the bacterivory (Baird et al., 2004). Indeed, herbivory is more than two times higher than bacterivory. Thus the ratio herbivory/bacterivory of the Sylt-Rømø Bight displays an opposite tendency than the ratio estimated for the Brouage mudflat. This opposite tendency may be linked to the fact that this ratio was obtained from the food web for the whole bay on a long term. As a consequence, habitats with high and low primary production were associated, thus the available carbon issued from the primary production was more important. Moreover, the food web considered in Baird et al. (2004a) represents a mean day as a consequence the difference between low tide and high tide was not visible and the effect of the season was not considered contrary to present simulations, which focused on summer conditions and high tide only In this study, that considered the summer period, little carbon issued from the primary production at low tide was available. The consideration of the food web for the whole year at the Brouage mudflat should abate the seasonal difference and change the trend of herbivory/bacterivory ratio.

4. Functioning of the Brouage food web

For comparing the functional indices from our model to others, we took care of selecting ecosystem models that coupled the pelagic and benthic compartments. Moreover the non-living compartments must be separated from bacteria, otherwise the ENA indices would be biased (Johnson et al., 2009). Values of relative Ascendency and internal relative Ascendency were in general higher to those previously reported. Relative Ascendency ranged from 33.4 (Monaco and Ulanowicz, 1997) to 49.5 for the Chesapeake Bay (Baird et al., 1991) and the internal Ascendency from 31.2 for the Delaware (Monaco and Ulanowicz, 1997) to 44.1 for

the Sundays Bay (Scharler and Baird, 2005). The cycling estimated without resuspension was higher to the FCI (i.e. Finn Cycling Index) estimated in the Sylt- Rømø Bight (= 17.2%) and close to the value of Sundays Estuary (Scharler and Baird, 2005). The differences between our study and previous ones are most probably based on the shorter time scale in our models. In the aforementioned studies, the ecosystems considered are estuaries which are subjected to the tidal rhythm and thus which are controlled by strong temporal/physical forcing. It was demonstrated how physical parameters can influence the ecological properties described by the ENA indices (Niquil et al., 2012). The consequences of physical forcing like the resuspension are smoothed when the considered networks use flows averaged over a mean day, more representative of normal conditions without waves. Additionally, the biological processes change according to the immersion and the emersion periods which impacts the carbon budget (Migné et al., 2009). Consequently, when emersion and immersion are considered separately (i.e. short time scale), it allows more precisely deciphering the biological and physical processes that control the functioning of the food web.

When the massive resuspension of the microbial biofilm occurred, the enrichment of the water column by the benthic particulate carbon (i.e. 3.584gC.m^{-2}.per high tide) mainly supported the increased activity of the whole system and the decreased organization of the network decreased. The higher value of Ascendency (2*10^{4} mgC.m^{-2}.per high tide against 0.6*10^{4} mgC.m^{-2}.per high tide during sedimentation) was the consequence of a higher TST (10000 mgC.m^{-2}.per high tide during resuspension and 3500 mgC.m^{-2}.per high tide during sedimentation), in spite of a drop down in the specialization of the trophic way (measured by AMI)This is a characteristic observation for a so-called “pulse eutrophication”, an intermittent increase of organic matter supply combined with physical factors (Patrício et al., 2004). Moreover a high value of Ascendency derived from a very high TST, could disturb the internal stability of the system (Ulanowicz, 2003). The lower overheads suggest a lower resistance to the perturbation as proposed by Ulanowicz (2003). Thus the resuspension decreased the resistance of the system to a perturbation. We propose that the massive resuspension event in the Brouage mudflat could be defined as a “pulse eutrophication” event that regularly disturbs the meta-ecosystem. On the contrary the biological erosion coupled with a high sedimentation tended to reduce the perturbation in the meta-system.

During the massive resuspension, the lower proportion of cycling (i.e. lower value of FCI) coupled with a high internal relative Ascendency (close to 50%) can be explained by the limited integration to the planktonic food web of the non-living carbon suspended in the water column. Indeed, in spite of a higher pelagic bacterial production and a higher detritivory, a low quantity of carbon was recycled. As a consequence, almost all the carbon suspended in the water column (i.e. 3.534 $gC.m^{-2}$.per high tide) was exported. Note that the export value was not constrained in the model, thus this value reflected a real property of the network. The larger the difference between the cycling and the internal relative Ascendency, the less organized and more under pressure a system would be (Baird et al., 1991; Baird et al., 2007). Thus the Brouage mudflat was less organized (confirmed by lower value of AMI) and submitted to a higher stress during the resuspension. A similar relation (i.e. great difference) between FCI and internal relative Ascendency was found for the mussel-bed in the Sylt-Rømø Bight (Baird et al., 2007) and in an upwelling area (Baird et al., 1991). Baird et al (1991) brought a significant nuance to the stress sense, by the distinction between ecosystems which are under physically or chemically pressure. Indeed, the two constraints do not refer to the same time scale. A chemical stress is in general recent and it has an exogenous origin to the considered ecosystem. In contrast, physical perturbations are older and the ecosystem can have adapted to it. These differences explain how a low cycling value can be coupled with a high internal relative Ascendency (Baird et al., 1991). During the massive resuspension phase, and as expected, the Brouage mudflat obviously showed the characteristics of a system that is physically perturbed.

When massive resuspension did not occur, the Brouage mudflat was characterized by a high specialization (i.e. high AMI) and by a relative Ascendency close to 60%. Such value illustrates a state closed to the equilibrium between the efficient and the fraction of the network that has not yet been organized (Bodini and Bondavalli, 2002); it is based on redundancy in the imports, the exports, the dissipation and on internal redundancy (Baird et al., 2004a). The equilibrium between both parts (relative Ascendency and overheads) is supposed to bring sustainability to the ecosystem (Ulanowicz et al., 2009); the inefficient part being used as a reserve that brings the necessary flexibility for the ecosystem sustainability. Moreover the high internal relative Ascendency is a strong sign that the system is relatively mature (Baird et al., 1991). The lower difference between internal relative Ascendency and FCI supposed a higher organization and a less disturbed system (Baird et al., 2007). Hence,

without massive resuspension of the microbial biofilm, the Brouage system seems to be relatively mature and stable.

5. Conclusion: the stability of the Brouage meta-ecosystem

As defined by Loreau (2003), a meta-ecosystem corresponds to the different ecosystems which are linked together by spatial flows of energy and matter. The rise of the tide and the chemical/physical/biological processes, which are associated with the increase of the water level on the mudflat can be considered as spatial flows. Here, we considered two different events according to the hydrodynamical conditions: 1) the massive resuspension of benthic matter in the water column 2) the sedimentation of pelagic matter on the mudflat sediments associated to a biological resuspension induced by macrofauna activities. As described above, their respective impact on the functioning of the benthic and the pelagic food webs strongly differs. The massive resuspension tends to disturb the Brouage meta-system while the sedimentation stabilizes it. These opposite consequences can be explained by the difference in the intensity of the flows. When the massive resuspension occurs, the sum of flows from the sediments to the water column was strong (about 3654 $mgC.m^{-2}$ per immersion) while during the sedimentation, it was only 10%of the flow during resuspension. The interaction between the benthic and the pelagic compartments also appeared weaker during sedimentation than during massive resuspension. As suggested by Levin (1999), a highly modular system (composed of strongly connected sub-systems which are connected by weak links) is a stable system. This concept could be transposed to the meta-ecosystem. We observed that the sedimentation constitutes a weak link between the two subsystems benthos and pelagos. In contrast the massive resuspension constitutes a strong link between benthos and pelagos. To conclude the stabilizing pattern of Levin is observed when sedimentation occurs and not during massive resuspension event. This conceptual step appears essential for the better understanding of (meta-)ecosystem structure and functioning in order to improve our prediction for their sustainability.

Despite its visible destabilizing effect, the massive resuspension brought some benefits to the Brouage meta-system. It stimulated the pelagic microbial food web by increasing both phytoplanktonic and bacterial production, and by stimulating bacterivory. Because of the

coupling of beneficial and destabilizing effects, massive resuspension show features characteristic of an intermediate disturbance (reviewed in Shea et al., 2004). An intermediate disturbance can be defined as an event that alters the specific niche availability, for instance by removing the biomass or changing the nutrient availability, while it maintains the general biodiversity (Shea et al., 2004). A complementary and extensive study of the long term massive resuspension frequency and its consequences on the Brouage meta-system would allow to confirm the intermediate disturbance hypothesis.

Chapitre 6

Discussion générale

La reconstruction des réseaux trophiques par la modélisation inverse, couplée au calcul d'indices de l'analyse des réseaux écologiques (ENA) a mis en évidence les propriétés émergentes du réseau trophique de la vasière intertidale de Brouage et a ainsi permis la compréhension de son fonctionnement. D'une part, le travail méthodologique sur la modélisation inverse linéaire de Monte Carlo en Chain de Markov a défini un algorithme qui permet d'optimiser l'estimation des flux manquant des réseaux trophiques. D'autre part, la réalisation des modèles et leur caractérisation par les indices de réseaux ENA ont caractérisé le fonctionnement des réseaux trophiques considérés (i.e. basse mer, pleine mer). Replacée dans le contexte de l'ANR VASIREMI, cette thèse a intégré toutes les observations faites sur le devenir du biofilm microbien dans le réseau trophique couplé benthos-pélagos, pour en avoir une vision synthétique. De plus, les observations faites à l'échelle des processus, que ce soit par des expérimentations en mésocosmes ou par des mesures de terrain, ont été intégrées dans une vision couvrant l'ensemble du réseau trophique, ce qui permet d'appréhender l'effet des observations à petite échelle sur le fonctionnement d'ensemble de l'écosystème.

Aspects méthodologiques

L'étude méthodologique réalisée sur la modélisation inverse a optimisé la méthode. La méthode d'échantillonnage aléatoire conçue par Van den Meersche (2009), a apporté des solutions aux défauts de la méthode originale de la modélisation inverse de Vézina et Platt (1988). De manière intuitive, la moyenne de l'ensemble des solutions était choisie lorsqu'une seule solution était nécessaire, comme par exemple pour le calcul de certains indices ENA. Cette utilisation de la moyenne ne reposait sur aucun fondement écologique, ainsi nous nous sommes demandés si des critères basés sur des théories de maturité des écosystèmes ne seraient pas mieux adaptés à la reconstruction des réseaux trophiques. L'analyse méthodologique réalisée par dégradation/reconstruction d'un jeu de données très complet a donné des éléments de réponse. Les résultats ont confirmé les lacunes de l'estimation par la méthode déterministe basée sur le critère de choix du moindre carré des flux, lacunes déjà soulevées dans des études précédentes (e.g. Niquil et al., 1998; Donali et al., 1999; Vézina and Pahlow, 2003; Johnson et al., 2009). Lorsque l'échantillonnage aléatoire de l'espace des solutions selon la méthode des miroirs décrite par Van den Meersche (2009) est utilisé, nous

démontrons dans le chapitre 3 que c'est la moyenne qui apparait comme la meilleure fonction pour choisir une seule valeur pour chaque flux. La fonction « moyenne des flux » est la fonction qui estime au mieux les valeurs des flux quel que soit le niveau d'information. De plus elle impacte le moins les valeurs des indices ENA, caractérisant le fonctionnement des réseaux trophiques ainsi reconstruits. Les fonctions écologiques (i.e. l'Ascendence, les Overheads, le FCI, le SOI, le TST, l'Ascendence relative et AMI) basées sur les théories de maturité des écosystèmes, sont moins performantes que la moyenne. En effet, l'erreur sur l'estimation de la valeur des flux est plus importante et elle est fortement dépendante de la quantité d'informations intégrées au modèle. Grâce à cette étude il a été montré que la solution basée sur la moyenne est robuste face à la quantité d'information entrée dans le modèle. Ces résultats vont avoir une large répercussion sur les utilisateurs de la modélisation inverse puisque la preuve que la moyenne est la meilleure fonction pour reconstruire les réseaux trophiques a été apportée. Les travaux réalisés au cours de cette thèse m'ont permis de mettre en avant d'autre questionnements méthodologiques sur la modélisation inverse, notamment sur l'influence du type et de la nature de l'information intégrée au modèle. Par type d'information, il faut comprendre l'origine des données : données issues de la littérature, données expérimentales ou mesures de terrain. La nature de l'information caractérise le type de processus considéré. Dans un réseau trophique, différents processus peuvent être considérés : la respiration, la consommation, l'égestion, l'excrétion, les imports et les exports.

1. Développer les contraintes pour réduire l'incertitude de l'estimation des flux

Le développement méthodologique récent apporté à la modélisation inverse (Van den Meersche et al., 2009) apporte de nombreux avantages à la reconstruction des réseaux. L'échantillonnage aléatoire de l'ensemble de l'espace des solutions permet d'obtenir une distribution de probabilité pour chacun des flux (van Oevelen et al., 2010). Le principal avantage à cela est d'obtenir un étalement des valeurs possibles et donc une estimation de l'incertitude associée à la valeur estimée pour chaque flux, ce qui n'était pas possible avec la méthode déterministe d'origine (Vézina and Platt, 1988). De plus, l'incertitude de l'estimation peut être appréhendée par l'étalement des valeurs de flux obtenues. Un modèle fortement contraint présentera un petit espace de solutions et donc un faible étalement des valeurs. Si les connaissances le permettent, il est préférable de favoriser les espaces de solutions fortement

contraints afin d'obtenir une incertitude faible sur les valeurs estimées, ce qui donne plus de pertinence au réseau trophique ainsi reconstruit. L'intervalle des contraintes biologiques (i.e. limites minimale et maximale) a donc un impact direct sur l'incertitude des résultats mais on peut également noter un impact indirect sur les valeurs estimées comme solution unique. En effet, la solution choisie comme la meilleure estimation pour chaque flux est basée sur le calcul de la moyenne de l'ensemble des solutions obtenues pour décrire l'espace de solutions (conclusion du chapitre 3). La moyenne sera alors dépendante des bornes minimales et maximales imposées au modèle (comme vu dans le chapitre 4), c'est-à-dire des données qui forment l'espace des solutions. Ceci souligne et accentue le constat de l'importance des contraintes biologiques (i.e. le jeu d'inéquations) dans le modèle déjà argumenté dans de précédentes études (Niquil et al., 1998). Ainsi, un espace bien contraint, obtenu par un ensemble de bornes minimales et maximales sur chaque flux, et traduisant au mieux l'ensemble de l'information disponible dans la littérature, mène à une estimation de la valeur des flux présentant une plus faible incertitude. Le but du modélisateur est de bien délimiter son espace de solutions puisque toute la qualité de son travail repose sur cet espace. Ainsi, au cours de la thèse j'ai développé le jeu de contraintes biologiques couramment utilisées afin que chaque processus (e.g. respiration, égestion…) soit limité par des bornes inférieures et supérieures. J'ai essayé autant que possible de considérer des valeurs de processus estimées à partir des relations allométriques faisant intervenir la taille individuelle moyenne, la biomasse, la température, ainsi que des taux physiologiques associant plusieurs flux entre eux, comme par exemple l'efficacité d'assimilation qui associe l'égestion à x% de la consommation. Par l'étude méthodologique réalisée chapitre 3 le jeu d'inéquations intégré au modèle a été très développé de manière à ce que tous les flux du réseau trophique soient contraints. Or, les articles précédents concentraient généralement les contraintes sur les flux inconnus. La liste des contraintes ainsi définie pourra être utilisée dans les futures études de modèles couplés benthos-pélagos.Ce travail sur une détermination précise et réaliste de l'espace des solutions peut-être amélioré par une attention particulière au type de données (i.e. littérature, expériences, mesures terrain) entré dans le modèle.

2. Développer le couplage observation-expérimentation-modélisation

A l'heure actuelle les modélisateurs s'appuient sur des données issues de la littérature pour définir leurs contraintes biologiques. Ces valeurs correspondent dans la majorité des cas à des connaissances très généralistes sur un groupe trophique. Par exemple, une même gamme d'efficacité d'assimilation est considérée pour l'ensemble de la macrofaune (van Oevelen et al., 2006b). Parfois, cette gamme peut être réduite à un groupe taxonomique et à mode de nutrition, par exemple l'efficacité d'assimilation d'un annélide suspensivore ou déposivore ne sera pas la même (Gontikaki et al., 2011). La question se pose de savoir si des contraintes biologiques aussi peu spécifiques sont suffisantes pour contraindre un modèle et surtout rendre compte de la réalité trophique de chaque compartiment de l'écosystème considéré. Une amélioration envisageable serait le couplage de manipulations *ex situ* (i.e. 'au laboratoire') et *in situ* afin d'obtenir des contraintes biologiques spécifiques au milieu considéré. Les conditions abiotiques, comme la température, la lumière, etc. régissent le fonctionnement d'un écosystème. La première étape est donc de connaitre les fluctuations abiotiques auxquelles est soumis un écosystème, afin de pouvoir les appliquer aux expérimentations en laboratoire. L'avantage de ces expériences est qu'elles sont réalisées en milieu contrôlé, ainsi les effets de différents facteurs abiotiques sur un processus spécifique peuvent être testés, soit séparément, dans un premier temps, soit ensemble. Prenons un exemple concernant la vasière de Brouage. L'hydrobie est connue pour être une espèce dominante, en particulier en milieu de vasière (Orvain et al., 2007). Elle est donc un compartiment essentiel du réseau trophique, par lequel transite une quantité de carbone importante. La consommation par cette espèce est influencée par son besoin métabolique et donc les pertes métaboliques de carbone associées (respiration). Il pourrait être envisageable de prélever des hydrobies *in situ* (afin de bien considérer la réalité de la communauté), de les placer dans un mésocosme tidal afin de mesurer leur respiration en fonction de la température et du cycle tidal (émersion/immersion). Finalement, une fois la méthodologie mise au point et le métabolisme des hydrobies compris, des mesures *in situ* peuvent confirmer les observations *ex situ.* Grâce à ce couplage, un intervalle de valeurs spécifiques à cette espèce pour la vasière de Brouage peut être obtenu. Ce couplage a déjà fait ses preuves pour la détermination de la bactérivorie de la méiofaune et d'*Hydrobia ulvae*, réalisée par Pierre-Yves Pascal lors de sa thèse (Pascal, 2008; Pascal et al., 2008a; Pascal et al., 2008b; Pascal et al., 2008c; Pascal et al., 2009). Si ce couplage ne peut pas être réalisé pour tous les compartiments d'un réseau trophique, il apparait essentiel pour les

espèces dominantes de l'écosystème considéré ou celles ayant un rôle important dans le réseau trophique (figure VI-1). La particularité de l'échelle propre à cette thèse, pour les modèles du réseau trophique de la vasière de Brouage, a mis en avant des lacunes sur les connaissances des processus benthiques lors de l'immersion. La respiration du microphytobenthos est–elle plus forte lors de l'immersion ? La consommation de la macrofaune est-elle constante tout au long du cycle tidal ? La respiration bactérienne est-elle influencée par l'immersion ? Ce manque d'information nous oblige à considérer, par défaut, des contraintes biologiques semblables à celles utilisées pour les modèles de basse mer (en émersion). Dans ce cas précis, le couplage expériences/mesures terrain serait indispensable, afin d'affiner les contraintes biologiques.

3. Caractériser l'effet de la nature des flux considérés dans un modèle : vers la réalisation d'un guide des flux prioritaires à estimer *in situ*.

Un modèle de réseau trophique est construit de manière à obtenir une vision globale de l'écosystème considéré afin de répondre à une problématique précise. Par exemple, dans cette thèse le réseau trophique à pleine mer a été construit afin de déterminer l'impact de la remise en suspension sur le fonctionnement du couplage benthos-pelagos. La problématique est définie en amont afin de construire un modèle adapté. Elle peut être définie en l'absence de modélisateur mais les étapes suivantes du processus de modélisation doivent être réalisées en étroite collaboration avec lui pour deux raisons. Premièrement, les mesures terrain ou les expérimentations réalisées *ex situ* doivent être adaptées aux besoins du modélisateur pour répondre à la problématique donnée. Deuxièmement, il est toujours plus facile d'intégrer des données à un modèle quand les expériences et les mesures réalisées sont bien appréhendées, notamment quand les biais ou les faiblesses potentiels des données sont connues en amont. Les besoins du modélisateur sont liés à l'obtention d'un espace de solutions suffisamment contraint pour une estimation des flux manquants de faible incertitude.

Lors de l'étude méthodologique qui s'est concentrée sur le choix de la meilleure fonction, des variations de la qualité de l'estimation par la modélisation inverse ont été observées selon la quantité mais aussi selon la nature de l'information intégrées au modèle. Ainsi la nature du flux (e.g. respiration, égestion, import, etc.) est susceptible d'avoir un impact sur la qualité

d'estimation des flux manquants du réseau trophique. Un travail complémentaire, envisagé après cette thèse, consiste à utiliser le jeu de données complet décrivant la baie de Sylt- Rømø en Allemagne (Baird et al., 2004a, 2007) afin de mener une étude complémentaire sur cette problématique. La même méthode de dégradation/estimation est utilisée afin de tester l'effet de la nature du flux retiré et de répondre à la question : Quels sont les flux absolument nécessaires à la bonne estimation des flux manquants par la modélisation inverse ? Le but serait de créer un guide des mesures indispensables à réaliser sur le terrain ou en expérimentations en conditions contrôlées, dans l'optique de construire un modèle de réseau trophique. Ceci permettrait aux expérimentateurs de concentrer leurs efforts sur les flux ayant le plus fort impact sur l'estimation des flux manquants. Les flux considérés comme 'accessoires' pourront alors seulement être considérés dans un deuxième temps, via des mesures/expérimentations, ou tout simplement laissés de côté s'ils sont vraiment négligeables et contraints par les données de la littérature (figure VI-1).

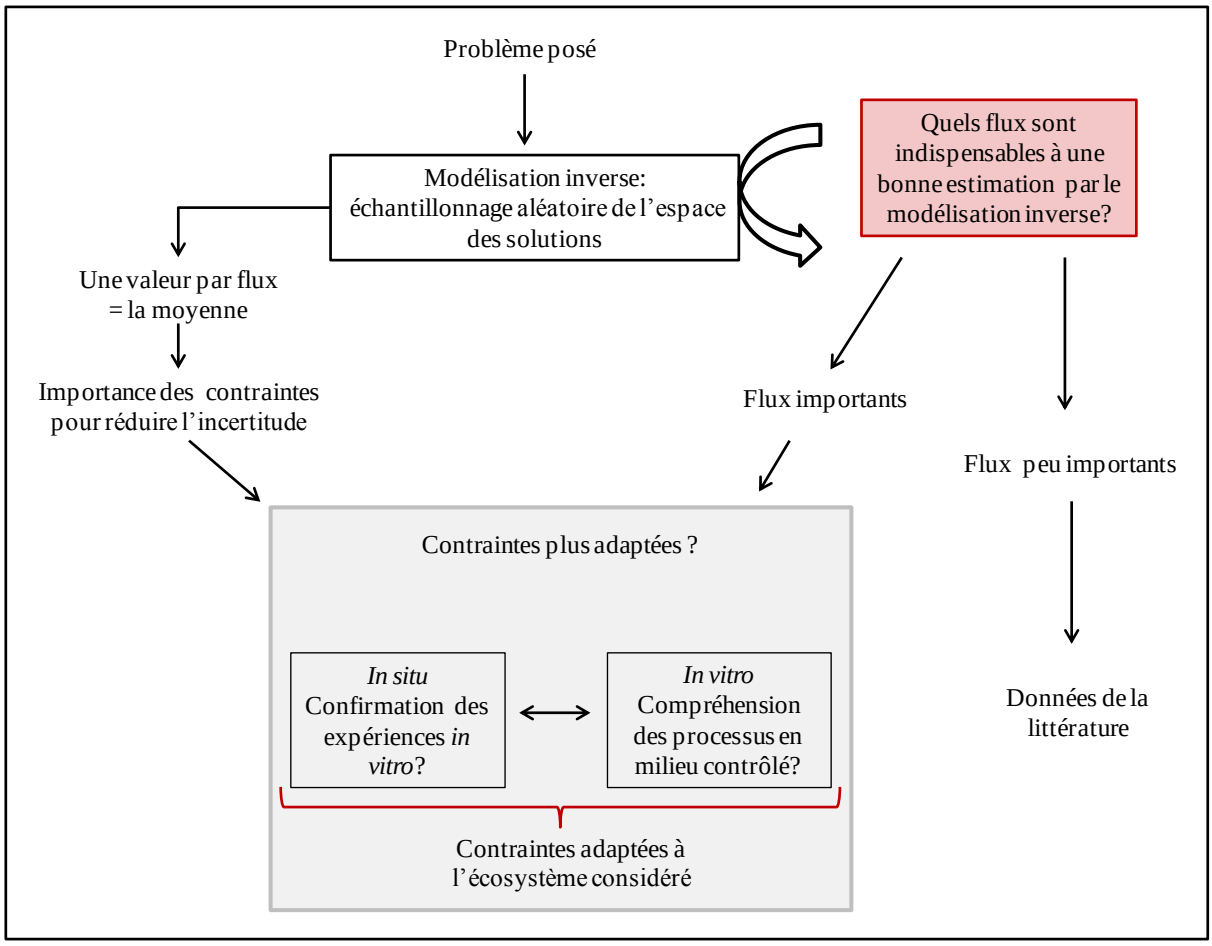


Figure VI-1 : Schéma conceptuel de synthèse d'un processus de construction d'un réseau trophique. Le modèle, soumis à la modélisation inverse, doit s'adapter à un problème. En sortie de modélisation inverse, si l'on souhaite une seule solution, c'est la moyenne qui doit être choisie. Une estimation de qualité nécessite des contraintes adaptées à l'écosystème considéré, mais comment les obtenir ? Le couplage d'expérimentations en laboratoire et de mesures *in situ* apparait comme la meilleure solution. Ce travail ne peut pas être fait sur tous les flux du réseau trophique. Il est donc nécessaire de déterminer les flux indispensables à une bonne estimation. Pour les flux importants des efforts seront déployés, pour les flux non importants des données issues de la littérature seront suffisantes.

Modélisation de la vasière de Brouage

Au cours de cette thèse quatre modèles de réseaux trophiques ont été réalisés : deux qui considèrent une basse mer à deux saisons distinctes (été-hiver), et deux qui intègrent une pleine mer estivale selon deux situations hydrologiques différentes (avec ou sans remise en suspension). Les différents modèles de réseaux trophiques réalisés dans cette thèse ont pour originalité d'utiliser une échelle de temps différente des modèles statiques trouvés dans la littérature (Savenkoff et al., 2004; Richardson et al., 2006; Marquis et al., 2007; Grami et al., 2008; Tortajada et al., 2012) et notamment de ceux réalisés précédemment sur le vasière de Brouage (Leguerrier et al., 2003; Leguerrier et al., 2004; Degré et al., 2006; Leguerrier et al., 2007). Les premiers modèles de la vasière de Brouage considéraient une année moyenne (Leguerrier et al., 2003; Leguerrier et al., 2004), puis des modèles mensuels saisonniers ont vu le jour (Degré et al., 2006; Leguerrier et al., 2007). Les modèles de cette thèse se placent à une échelle beaucoup plus fine, puisque deux périodes de basse mer et de pleine mer ont été considérées. Ces modèles ont mis en exergue des propriétés de fonctionnement du réseau trophique de la vasière de Brouage spécifiques à la basse mer ou à la pleine mer, et qui ne sont pas visibles lorsque l'on se place à une échelle temporelle plus grande.

1. Echelle considérée

Les modèles de cette thèse se basent sur les données récoltées lors de l'ANR VASIREMI qui avait pour objectif de répondre à certains questionnements soulevés par les précédents modèles de la vasière de Brouage (Leguerrier et al., 2004; Degré et al., 2006): la quantification de l'export de matière par les poissons, la remise en suspension du biofilm microbien et les flux liés à la méiofaune. Le jeu de données intégré à mes modèles est donc plus complet que pour les précédents même si quelques lacunes persistent. Comme décrit ci-dessus, la principale différence entre l'ensemble de ces modèles est l'échelle temporelle considérée.. Un effet de cette échelle doit être envisagé pour expliquer les différences de propriétés écologiques observées. Les habitats intertidaux sont soumis à de fortes contraintes biologiques et physiques au cours du cycle tidal (Raffaelli and Hawkins, 1996; Herman et al., 2001b) entrainant de grandes variations journalières retrouvées tout au long de l'année (Morris and Taylor, 1983). Au niveau des vasières intertidales et plus particulièrement de la

vasière de Brouage, la basse mer est caractérisée par une forte production primaire du microphytobenthos (Blanchard et al., 1997; Guarini et al., 2000b; Blanchard, 2006). Elle s'intègre au réseau trophique benthique par broutage direct par la méiofaune (Rzeznik-Orignac and Fichet, 2012) et par les déposivores, notamment *Hydrobia ulvae* (Haubois et al., 2005a). A pleine mer, la production microphytobenthique est inhibée (Blanchard, 2006) ce qui engendre des changements au sein de la communauté benthique. On peut donc s'attendre à des propriétés du réseau trophique benthique variables entre la basse mer et la pleine mer. Le fait de se placer à une échelle supérieure à la marée comme dans les modèles précédents, ne permet pas d'appréhender les variations liées au cycle tidal journalier. Dans un objectif de compréhension fine du fonctionnement d'une vasière intertidale soumise à un cycle émersion/immersion, il parait essentiel de considérer les contraintes imposées par le rythme des marées à une échelle adaptée à celui-ci. Les modèles (comme ceux de cette thèse) doivent donc se placer à l'échelle d'une marée ce qui implique non seulement une connaissance précise des processus à basse mer (production, broutage, etc.) et à pleine mer (remise en suspension, sédimentation, broutage par les poissons, etc.) mais aussi des études plus poussées de l'effet de l'immersion sur le réseau trophique benthique.

2. Réseau trophique benthique à basse mer

Les réseaux trophiques intégrant une basse mer considèrent deux saisons : l'été et l'hiver, dont ce dernier est caractérisé par la présence d'oiseaux migrateurs. La comparaison des réseaux trophiques estival et hivernal de basse mer (chapitre 4) a mis en avant une différence de fonctionnement qui réside principalement dans le fait que l'activité globale du système et le recyclage sont plus forts en hiver. Les propriétés d'organisation et de spécialisation (Ascendence relative interne, AMI, etc.) des flux trophiques restent les mêmes quelle que soit la saison considérée. L'association de cette forte production et de ce fort recyclage à une organisation et une spécialisation indépendantes de la saison permet de subvenir aux besoins nutritionnels des oiseaux limicoles migrateurs.

Le réseau trophique hivernal, centré sur les oiseaux, avait pour but de déterminer les propriétés de structure et de fonctionnement permettant au réseau trophique de subvenir aux besoins des oiseaux. Ce modèle a intégré de nouvelles connaissances sur les oiseaux,

notamment au niveau de leur régime alimentaire, du temps consacré à leur alimentation et de l'abondance des oiseaux faisant une halte migratoire dans la Baie de Marennes-Oléron. Cependant, une inconnue demeure : la distribution des oiseaux sur la vasière. Afin de construire le modèle hivernal de basse mer, des hypothèses ont dû être posées quant à la distribution des oiseaux sur la vasière puisque leur distribution est encore inconnue. Des densités minimales et maximales ont été déterminées afin de contraindre les flux de consommation calculés à partir d'équations métaboliques impliquant le nombre d'individus (Scheiffarth and Nehls, 1997). En effet, si des comptages d'oiseaux existent, il est difficile d'en tirer des informations sur les flux pour une zone donnée de la vasière puisque la distribution des oiseaux est dépendante de la distribution des proies (Bocher et al., 2007) mais elle est également contrôlée par la compétition intra-spécifique entre les individus (Sutherland, 1983; Triplet et al., 1999). Une densité d'individus trop importante va générer des interférences entravant leur prédation et diminuant ainsi leur efficacité d'ingestion (Sutherland, 1983). La distribution des oiseaux est une information pourtant essentielle pour construire un réseau trophique impliquant des oiseaux, puis que la densité des individus par unité de surface détermine la prédation par unité de surface. Une des solutions possible pour estimer la distribution des oiseaux sur la vasière de Brouage est l'utilisation de survols aériens. Les photos aériennes prises lors du survol sont ensuite traitées et analysées afin de déterminer la répartition des oiseaux par hectare. Cette technique ayant déjà fait ses preuves pour le suivi des mammifères marins ou pour estimer la fréquentation des plages par les touristes en été (programme QualiPlage), elle pourrait être transposée aux oiseaux. La connaissance de la répartition des individus sur la vasière permettrait alors d'affiner les contraintes du modèle et d'obtenir une incertitude moins importante sur les résultats.

Les différences de structure et de fonctionnement observées entre les réseaux trophiques benthiques en été et en hiver sont principalement dues à une différence de production primaire. En effet, la production du microphytobenthos est plus forte en hiver. Cependant, elle est intégrée au réseau trophique benthique avec une plus faible efficacité qu'en été (67% contre 82%). La production primaire en été, du fait de la forte demande en carbone de la macrofaune, est efficacement transmise aux niveaux trophiques supérieurs, ce qui aboutit à une efficacité trophique moyenne supérieure. En hiver, une forte part de cette production est exportée (35%) vers la pleine mer suivante. Cet export ne représente que 17% de la production primaire en période estivale. L'hypothèse d'une remise en suspension plus

fréquente en hiver est raisonnablement envisageable. La remise en suspension du microphytobenthos est liée à la remise en suspension des sédiments (Lucas et al., 2000). L'érosion des sédiments est contrôlée par des facteurs physiques (Le Hir et al., 2000) et biologiques (Orvain et al., 2003b; Orvain et al., 2004; Orvain et al., 2006). Tout d'abord, l'érosion des sédiments dépend du frottement sur le fond induit par les courants de marée et/ou les courants de vagues (Le Hir et al., 2000) et du coefficient de rugosité du sédiment. La rugosité du sédiment est influencée par des facteurs biologiques tel que la densité du biofilm microalgal qui augmente la cohésion du sédiment (Underwood and Paterson, 2003; Orvain et al., 2004) et qui modifie ainsi les propriétés d'érosion du sédiment. De plus, l'activité de la macrofaune benthique favorise la remise en suspension du microphytobenthos via la bioturbation (Orvain et al., 2003b; Orvain et al., 2007). L'enrichissement de la colonne d'eau en diatomées benthiques par une remise en suspension en hiver est conforté par deux observations. Premièrement, la communauté de diatomées planctoniques de la baie de Marennes-Oléron présente une forte proportion de diatomées pennées caractéristiques du benthos en hiver (Guarini et al., 2004). D'autre part, l'apparition des diatomées benthiques dans le compartiment pélagique est corrélée à une augmentation de la turbidité. Au contraire, la communauté phytoplanctonique est caractérisée par les diatomées centrique (spécifique du pélagos) et des dinoflagellés durant l'été. Ceci témoigne d'une remise en suspension plus limitée durant cette période (Guarini et al., 2004). Ainsi, en hiver, la vasière de Brouage produit une grande quantité de carbone à basse mer dont une grande partie est exportée à pleine mer par remise en suspension dans la colonne d'eau. Elle enrichie ainsi la communauté planctonique peu productive en cette saison (Struski and Bacher, 2006). Les observations faites à partir des modèles à basse mer pour les deux saisons (été-hiver) semblent alors être en adéquation avec les observations faites sur les communautés de diatomées planctoniques faites dans la baie de Marennes-Oléron.

3. Réseau trophique benthique à pleine mer

Le réseau trophique de la vasière de Brouage à pleine mer n'a pu être considéré que pendant la période estivale. Lorsque le réseau trophique benthique de la vasière de Brouage est considéré à pleine mer, il présente des caractéristiques différentes avec notamment un développement important de la bactérivorie par la méiofaune et la macrofaune. D'après la

modélisation, les bactéries benthiques constituent 40% de la consommation des foraminifères, 10 à 40% de la consommation des nématodes, et 70 à 80% de la consommation des hydrobies. Ainsi, environ 35% de la production bactérienne est transférée vers les niveaux trophiques supérieurs. En été, une faible quantité de carbone issue de la production du microphytobenthos est importée à pleine mer (voir ci-avant). De plus la biomasse algale est faible, du fait de la forte pression de broutage exercée à la basse mer précédente (Cariou-Le Gall and Blanchard, 1995). Néanmoins, la production bactérienne est stimulée et forte à pleine mer. Or les bactéries constituent une ressource trophique alternative à la méiofaune et au déposivores (principalement *Hydrobia ulvae*) lorsque la biomasse algale est faible (Pascal et al., 2008b; Pascal et al., 2008c; Pascal et al., 2008d). Un réseau trophique où la bactérivorie représente 35% de la production bactérienne et où les bactéries peuvent participer jusqu'à 80% à la consommation de la macrofaune et méiofaune est-il réaliste ?

Les précédentes études réalisées sur la bactérivorie de ces groupes montrent un faible transfert du carbone bactérien vers les niveaux trophiques supérieurs (van Oevelen et al., 2006a; Pascal et al., 2009). La part de la production bactérienne ingérée par les organismes benthiques varie selon les études de 3 à 6% (Pascal et al., 2009) et jusqu'à 27% (van Oevelen et al., 2006a) pour des vasières intertidales. En général, les bactéries ne représentent qu'une faible part de la demande en carbone des organismes benthiques puisqu'ils se nourrissent préférentiellement sur le microphytobenthos (Sundbäck et al., 1996; Pascal, 2008). Les bactéries contribuent de 10% (Sundbäck et al., 1996) à 18% (van Oevelen et al., 2006a) à la consommation de la macrofaune benthique. Toutes ces études ont été menées sur des habitats intertidaux. Si un autre habitat tel qu'un ruisseau est considéré, les bactéries participent à plus de 20% à la consommation des invertébrés (Hall and Meyer, 1998). Ainsi, dans les systèmes où l'assimilation directe de détritus n'est pas possible, les bactéries sont consommées de façon plus importante que lorsque d'autres ressources sont disponibles. Van Oevelen et al. (2006a) en ont conclu que dans les sédiments intertidaux où les phyto-détritus, les microalgues et les bactéries sont directement assimilables, la macrofaune se nourrit préférentiellement sur les phyto-détritus et les microalgues. En été, sur la vasière de Brouage, il a été estimé par analyse isotopique, que les détritus benthiques contribuent au maximum à 11% de la consommation des déposivores. On peut ainsi supposer que les déposivores, de par la faible biomasse algale et la faible contribution des phyto-détritus, consomment préférentiellement les bactéries car elles sont alors leur seule ressource alternative. Afin de vérifier notre hypothèse, il serait

intéressant de mesurer le niveau de la bactérivorie en hiver, sachant que les microalgues sont plus abondantes à pleine mer et que les détritus benthiques contribuent jusqu'à 31% à la demande en carbone des déposivores (Richard, comm. pers.).

Suite à cette thèse, où seul un modèle de pleine mer estival a été réalisé, il est prévu de travailler sur un modèle de pleine mer d'hiver. Ceci permettra de vérifier l'hypothèse posée ci-dessus et de déterminer si le couplage benthos-pelagos présente les mêmes caractéristiques en été et en hiver.

4. Remise en suspension et sédimentation

Deux réseaux trophiques à pleine mer ont été considérés, l'un intègre la remise en suspension du biofilm et l'autre considère la sédimentation des particules pélagiques. Le but de cette opposition entre les deux réseaux trophiques était de vérifier l'hypothèse selon laquelle la remise en suspension du biofilm pourrait avoir un effet stabilisateur sur le réseau couplé benthos-pelagos. Contrairement à l'hypothèse de départ, la remise en suspension des micro-organismes dans la colonne d'eau n'a pas un effet stabilisateur (chapitre 4). Cependant, et malgré l'observation de marqueurs d'un pulse d'eutrophisation (Patrício et al., 2004), c'est-à-dire une forte activité du système couplée à une faible organisation des voies trophiques, ce couplage benthos-pelagos présente les caractéristique d'un réseau mature (i.e. avec une forte valeur d'Ascendence interne relative) (Baird et al., 1991). Ceci suggère que le système est adapté à cette perturbation physique régulière d'origine naturelle. Cependant, la grande différence entre le recyclage et l'Ascendance relative interne indique un stress important (Baird et al., 1991). Le système soumis à la sédimentation, phénomène lui-aussi naturel, présente les caractéristiques d'un système stable : une forte maturité (Baird et al., 1991), un équilibre entre une partie efficace (Ascendence) et une partie inefficace (OverHeads) du réseau (Ulanowicz, 2009). Cette dernière propriété lui confère une flexibilité face à de nouvelles perturbations et donc une bonne résistance. La caractérisation de deux réseaux trophiques couplés benthos-pélagos et 'opposés', l'un caractérisé par la remise en suspension et l'autre par la sédimentation, nous a permis d'illustrer la théorie de Levin (1999) sur la modularité. Cette théorie suppose qu'une structure stabilisante associe des systèmes fortement connectés en leur sein mais faiblement connecté entre eux. Une telle structure est observée

dans le cas du modèle sans remise en suspension, où benthos et pélagos sont couplés par la sédimentation. L'utilisation des indices ENA dans cette étude est originale de par l'échelle considérée. En effet, les indices ENA et les interprétations qui leurs sont associées en termes de stabilité s'appliquent de manière générale à des écosystèmes considérant une année moyenne (e.g. Baird et al., 1998; Christian et al., 2005; Baird et al., 2007). Comme décrit précédemment, nos modèles se placent à une échelle de temps beaucoup plus courte (basse et pleine mers moyennes). La considération d'une année moyenne correspond finalement à une succession de basses mers et de pleines mers intégrées et considérées comme un tout. Cependant, la succession de pleines mers doit être considérée avec et sans remise en suspension plus ou moins régulière en fonction des saisons. Pour compléter le présent travail, la question essentielle du changement d'échelle temporelle doit être approfondie : Quelles sont les conséquences du passage à une année moyenne sur l'interprétation des propriétés émergeantes de l'écosystème en termes de stabilité ?

D'autres perspectives sont à envisager. Premièrement, ces résultats concernent la période estivale. Comme mentionné précédemment, les modèles sur la période hivernale devront être réalisés afin de vérifier les hypothèses émises à partir des modèles estivaux . Il a déjà été montré que le réseau trophique benthique en été et en hiver ne présentent pas les mêmes caractéristiques. Est-ce que les caractéristiques du réseau trophique hivernal vont modifier les conclusions sur l'effet de la remise en suspension trouvées pour le couplage benthos-pelagos en été ? D'autre part, les processus de sédimentation et de remise en suspension ont été étudiés à l'échelle d'une pleine mer. Quelles seraient les conclusions si on se place à l'échelle d'un mois, d'une saison ou d'une année ? La remise en suspension est un phénomène à considérer lorsque le couplage benthos-pelagos des zones peu profondes est étudié. Le changement de l'intensité ou de la fréquence de ces évènements devrait être étudié avec plus d'attention (Porter et al., 2010). Dans la continuité de cette thèse, une étude de la fréquence de remise en suspension sur la vasière de Brouage est envisagée. Un suivi à long terme de la remise en suspension (sur les 20 dernières années) nécessite la connaissance des courants de vagues et de marée sur la période d'intérêt. Cette étude ne peut s'effectuer que dans le cadre d'un projet transdisciplinaire entre des hydrodynamiciens et des écologues. Par le couplage des résultats de modélisation des courants de vagues et de marée, les vitesses de frottement sur le fond, la fréquence de remise en suspension du biofilm microbien sur cette période sera obtenue (travail initié par Camille Geimer, stagiaire de M1, collaboration avec Xavier Bertin).

Grâce à la modélisation des forçages physiques, des schémas temporels (variation interannuelle, intra-annuelle, cyclique) de la remise en suspension pourront être dégagés. L'analyse de la fréquence de remise en suspension du biofilm dans la colonne d'eau permettra d'estimer un flux net de remise en suspension sur une période donnée. Prenons un exemple, considérons une période de temps de 15 jours. Si sur ces 15 jours, il n'y a qu'un événement de remise en suspension, le flux net de remise en suspension sera très faible voire négatif, car la sédimentation sera plus importante. Au contraire, si, sur cette même période, une dizaine d'événements de remise en suspension a lieu, le flux net de remise en suspension sera largement positif. Ces deux cas de figure n'auront pas les mêmes conséquences sur la stabilité du méta-écosystème, basée en partie sur le couplage benthos-pelagos, puisque l'intensité des liens entre benthos et pelagos sera différente.

5. Propriétés de stabilité des réseaux trophiques de pleine mer : rôle du couplage benthos-pélagos

La stabilité des écosystèmes reste une notion très complexe et difficile à appréhender. Ceci réside principalement dans le fait que les écosystèmes sont uniques et donc les conclusions pour l'un sont difficilement transposables à un autre ; d'où la difficulté ressentie en rédigeant la synthèse bibliographique (chapitre 2), de tirer des règles générales d'une littérature aux conclusions contradictoires, du fait de la spécificité de chaque écosystème. Par exemple, deux écosystèmes présentant le même niveau de diversité, n'ont pas nécessairement la même stabilité du fait d'une 'connectance' et/ou de forces d'interactions différentes. Cependant, certaines théories, même si les mots employés sont différents, mènent aux mêmes conclusions. Une notion, retrouvée dans de nombreuses théories, est la flexibilité ou l'adaptabilité de l'écosystème. Ceci se traduit par une structure alliant liens faibles-liens forts (McCann et al., 1998), ou présentant une asymétrie de structure (Rooney et al., 2006), par un écosystème où l'omnivorie est importante (Fagan, 1997; McCann and Hastings, 1997), ou encore par un système présentant un équilibre entre une partie organisée et efficace et une partie non-organisée et peu efficace (Ascendence relative intermédiaire Ulanowicz, 2003, 2009). Par exemple, une spécialisation extrême des voies trophiques mène l'écosystème à changer d'état en cas de fortes perturbations (Ulanowicz, 2009). Toutes ces théories s'accordent sur le fait que la structure d'un écosystème, en termes d'organisation et de

fonctionnement, ne doit pas être poussée vers des extrêmes. L'écosystème doit trouver un équilibre en associant deux paramètres opposés. Reprenons l'exemple de l'organisation du système : la partie organisée (Ascendence) doit être en équilibre avec la partie non (encore) organisée (les overheads) afin d'assurer la stabilité de l'écosystème. Cette structuration non homogène, asymétrique de l'écosystème peut être trouvée à une échelle plus grande, notamment au niveau saisonnier, comme par exemple dans l'écosystème de la Gironde (Lobry et al., 2008). L'intégration des connaissances à petite échelle temporelle sur une échelle de temps supérieure ou égale à la saison permettrait-elle de mettre en évidence une asymétrie saisonnière sur la vasière de Brouage ?

Comme vu dans la section 4, les simulations des courants de vagues et de marées sur les 20 dernières années permettront de définir la fréquence de remise en suspension des micro-organismes dans la colonne d'eau. Au vu de l'étude sur la contribution des diatomées benthiques à la communautés de diatomées pélagiques menées dans la baie de Marennes-Oléron (Guarini et al., 2004), une fréquence supérieure de remise en suspension du biofilm est attendue en hiver. L'hypothèse d'un schéma saisonnier est raisonnablement envisageable (figure VI-2) : l'hiver serait caractérisé par un flux net de remise en suspension afin d'alimenter le pelagos, qui est alors faiblement productif (du fait de la forte turbidité de l'eau et des faibles températures). Au contraire, l'été serait caractérisé par un flux net de sédimentation soutenant le réseau trophique benthique faiblement productif (du fait de la thermo-/-photoinhibition et de la forte pression de broutage).

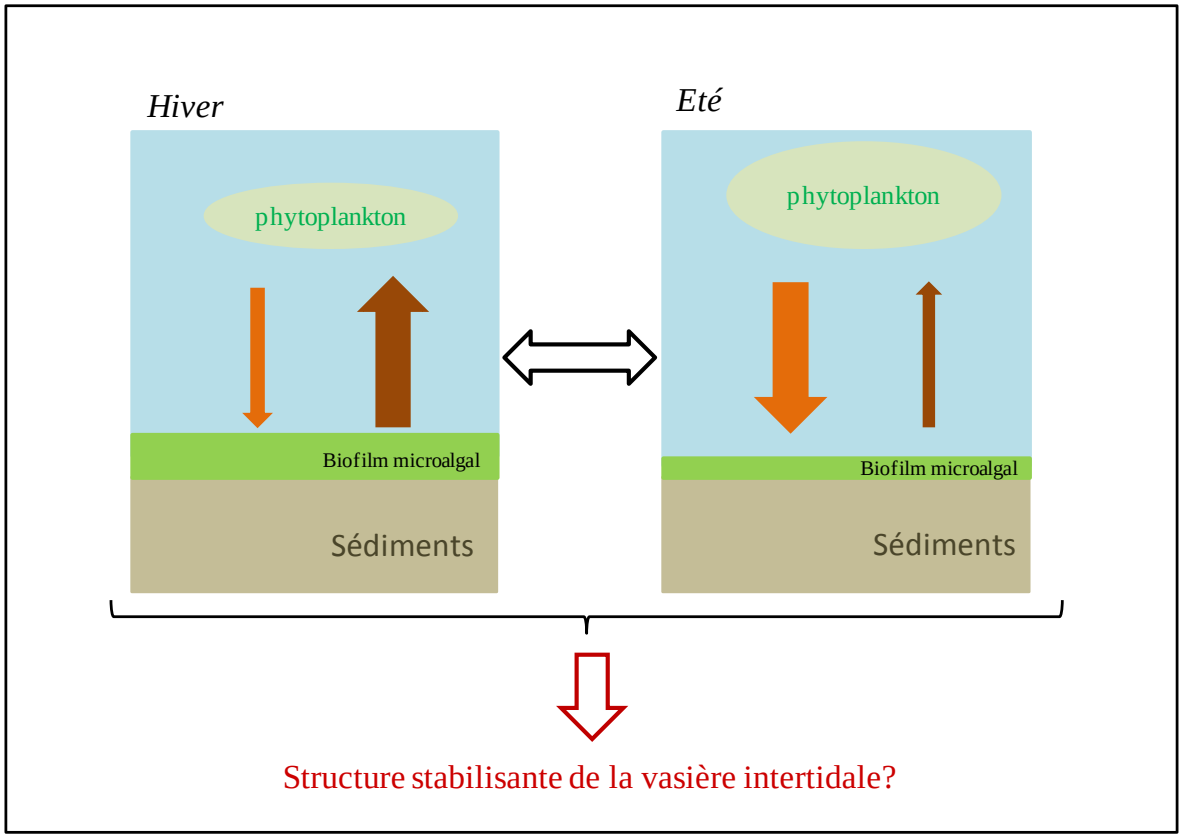


Figure VI-2 : Schéma bilan. Hypothèse d'une saisonnalité de la remise en suspension apportant de la stabilité à l'écosystème vasière intertidale.

La modélisation du réseau trophique intégrant les données hydrodynamiques pourrait ainsi être affinée pour chaque saison. Ceci permettrait de mieux comprendre et d'analyser les conséquences sur le couplage benthos-pelagos (comme réalisé ici à petite échelle temporelle) et sur le fonctionnement saisonnier de la baie de Marennes-Oléron. Pour finir, la réalisation d'un réseau trophique couplé benthos-pelagos et été-hiver permettrait de vérifier l'hypothèse (soulevée ci-dessus) de la stabilité de l'écosystème assurée par une asymétrie saisonnière. L'intégration de la saisonnalité de l'écosystème dans un modèle de réseau trophique n'est pas évidente. Une méthodologie avait été mise en place par Degré et al., (2006) mais cette méthode s'appliquait seulement à la méthode déterministe d'origine de l'analyse inverse (Vézina and Platt, 1988). L'intégration de la saisonnalité en utilisant la technique de la modélisation inverse par échantillonnage aléatoire (MCMC-LIM, Van den Meersche et al., 2009) sera probablement très lourde et très gourmande en temps de calcul. Afin d'obtenir une méthode plus performante des ajustements de l'algorithme de calcul seront certainement nécessaires.

Conclusion

Les modèles de cette thèse se sont appuyés sur des données issues de l'ANR VASIREMI qui présentait plusieurs originalités. Ce projet de grande envergure a eu la volonté d'étudier simultanément le benthos et le pélagos ainsi que l'ensemble des organismes occupant la vasière intertidale de Brouage, des virus aux oiseaux en passant par la méiofaune, la macrofaune, les poissons et bien sûr le biofilm microbien (bactéries, archées et microphytobenthos). Une autre originalité réside dans le couplage d'observation *in situ* et d'expérimentations en mésocomes et en laboratoire. Par exemple, les traces laissées par les poissons ont été suivies en mésocosmes afin de déterminer l'aire moyenne broutée par un individu, puis les observations des traces sur le terrain ont permis d'estimer la fréquentation des poissons sur la vasière à partir des résultats obtenus en mésocosmes. La détermination du flux d'érosion par les expériences d'érodimétrie réalisées à partir d'une carotte de sédiment prélevée sur le terrain constitue, elle-aussi, une innovation et une originalité de ce programme de recherche.

Les modèles de cette thèse créés à partir des données VASIREMI sont eux aussi originaux de par les échelles de temps (une basse mer, une pleine mer) et d'espace (un mètre carré moyen en milieu de vasière) considérées. C'est la première fois qu'un modèle statique de réseau trophique est réalisé à de si petites échelles spatiales et temporelles. La considération d'une échelle si fine a demandé d'ajuster de nombreuses étapes de la méthode inverse et une réflexion importante sur les liaisons entre basse mer et pleine mer. La construction de ces modèles a également fait suite à une optimisation de l'approche numérique par un travail méthodologique approfondi. En effet, à partir du jeu de données très riche de la baie de Sylt-Rømø (Allemagne), nous avons déterminé que la meilleure des solutions à considérer à la sortie de la modélisation inverse par échantillonnage aléatoire correspond à la moyenne des flux échantillonnés dans l'espace des solutions possibles. Cette étude est la première à le prouver et devrait donc faire référence dans le domaine. Une étude supplémentaire prévue à l'issue de la thèse envisage d'utiliser les données de la baie de Sylt- Rømø pour définir les flux essentiels (e.g. respiration, égestion, etc.) à une estimation de qualité par la modélisation inverse. Le but est de créer un guide des mesures terrain ou des expérimentations à réaliser dans l'optique de la construction de réseaux trophiques couplés benthos-pélagos. Cette future étude répond à un manque de la littérature et à un besoin fort des chercheurs.

La partie méthodologique de cette thèse et l'interprétation des modèles de réseaux trophiques de la vasière de Brouage en termes de stabilité a demandé une analyse approfondie 1) des théories sur la maturité des écosystèmes (liée à la thermodynamique), 2) des théories associant les propriétés émergentes de l'organisation et du fonctionnement des écosystèmes à certaines propriétés de stabilité (résistance, résilience, etc.). Cette synthèse comble elle aussi un manque dans la littérature, elle constitue une base d'informations très riche pour la compréhension des écosystèmes. De plus, cette synthèse définit un contexte théorique nécessaire à la comparaison des écosystèmes. Dans le contexte actuel de recherche d'indicateurs de santé des réseaux trophiques (par exemple au niveau européen dans le cadre de la mise en place de la Directive Cadre Stratégie pour le Milieu Marin), un tel contexte théorique est indispensable.

Références

Agogué, H., Mallet, C., De Crignis, M., Orvain, F., Mornet, F., Dupuy, C., in press. Bacterial dynamics in a microphytobenthic biofilm: a tidal mesocosm approach. Journal of Sea Research.

Alldredge, A.L., 2000. Interstitial dissolved organic carbon (DOC) concentrations within sinking marine aggregates and their potential contribution to carbon flux. Limnology & Oceanography 45, 1245-1253.

Alldredge, A.L., Silver, M.W., 1988. Characteristics, dynamics and significance of marine snow. Progress in Oceanography 20, 41-82.

Allesina, S., Bodini, A., 2004. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. Journal of Theoretical Biology 230, 351-358.

Allesina, S., Bodini, A., Pascual, M., 2009. Functional links and robustness in food webs. Philosophical Transactions of the Royal Society B: Biological Sciences 364, 1701-1709.

Allesina, S., Bondavalli, C., Scharler, U.M., 2005. The consequences of the aggregation of detritus pools in ecological networks. Ecological Modelling 189, 221-232.

Allesina, S., Ulanowicz, R.E., 2004. Cycling in ecological networks: Finn's index revisited. Computational Biology and Chemistry 28, 227-233.

Alpine, A.E., Cloern, J.E., 1988. Phytoplankton growth rates in a light-limited environment, San Francisco Bay Marine Ecology Progress Series 44, 167-173.

Aoki, I., 2008. Entropy law in aquatic communities and the general entropy principle for the development of living systems. Ecological Modelling 215, 89-92.

Arbach Leloup, F., Desroy, N., Le Mao, P., Pauly, D., Le Pape, O., 2008. Interactions between a natural food web, shellfish farming and exotic species: The case of the Bay of Mont Saint Michel (France). Estuarine, Coastal and Shelf Science 76, 111-120.

Aschoff, J., Pohl, H., 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. J. Ornithol. 111, 38-47.

Azémar, F., Boulêtreau, S., Lionard, M., Muylaert, K., Vyverman, W., Meire, P., Tackx, M., 2007. Looking for general trends in trophic interactions among estuarine micro-and mesozooplankton. Journal of Plankton Research 29, i135-i147.

Baird, D., 2011. Assessment of observed and perceived changes in ecosystems over time, with special reference to the Sylt-Rømø Bight, German Wadden Sea. Estuarine, Coastal and Shelf Science.

Baird, D., Asmus, H., Asmus, R., 2004a. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series 279, 45-61.

Baird, D., Asmus, H., Asmus, R., 2007. Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. Marine Ecology Progress Series 351, 25-41.

Baird, D., Asmus, H., Asmus, R., 2008. Nutrient dynamics in the Sylt-Rømø Bight ecosystem, German Wadden Sea: An ecological network analysis approach. Estuarine, Coastal and Shelf Science 80, 339-356.

Baird, D., Asmus, H., Asmus, R., 2011. Carbon, nitrogen and phosphorus dynamics in nine sub-systems of the Sylt-Rømø Bight ecosystem, German Wadden Sea. Estuarine, Coastal and Shelf Science 91, 51-68.

Baird, D., Christian, R.R., Peterson, C.H., Johnson, G.A., 2004b. Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. Ecological Applications 14, 805-822.

Baird, D., Heymans, J.J., 1996. Assessment of ecosystem changes in response to freshwater inflow of the Kromme River estuary, St. Francis Bay, South Africa: a network analysis approach. Water SA 22, 307-318.

Baird, D., Luzckovich, J., Christian, R.R., 1998. Assessment of spatial and temporal variability in ecosystem properties of the St Marks National Wildlife Refuge, Apalachee Bay, Florida. Estuarine, Coastal and Shelf Science 47, 329-349.

Baird, D., McGlade, J.M., Ulanowicz, R.E., 1991. The Comparative Ecology of Six Marine Ecosystems. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 333, 15-29.

Baird, D., Ulanowicz, R.E., 1989. The Seasonal Dynamics of The Chesapeake Bay Ecosystem. Ecological Monographs 59, 329-364.

Baird, D., Ulanowicz, R.E., 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Marine Ecology Progress Series 99, 221-237.

Bassoullet, P., Le Hir, P., Gouleau, D., Robert, S., 2000. Sediment transport over an intertidal mudflat: Field investigations and estimation of fluxes within the 'Baie de Marennes-Oleron' (France). Continental Shelf Research 20, 1635-1653.

Baum, J.K., Worm, B., 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78, 699-714.

Beisner, B.E., Hovius, J., Hayward, A., Kolasa, J., Romanuk, T.N., 2006. Environmental productivity and biodiversity effects on invertebrate community invasibility. Biological Invasions 8, 655-664.

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature 429, 827-833.

Berlow, E.L., Neutel, A.M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M., Petchey, O., 2004. Interaction strengths in food webs: Issues and opportunities. Journal of Animal Ecology 73, 585-598.

Bettarel, Y., Sime-Ngando, T., Bouvy, M., Arfi, R., Amblard, C., 2005. Low consumption of virus-sized particles by heterotrophic nanoflagellates in two lakes of the French Massif Central. Aquatic Microbial Ecology 39, 205-209.

Billerbeck, M., Røy, H., Bosselmann, K., Huettel, M., 2007. Benthic photosynthesis in submerged Wadden Sea intertidal flats. Estuarine, Coastal and Shelf Science 71, 704-716.

Blanchard, G., 2006. Analyse conceptuelle du système de production primaire microphytobenthique des vasières intertidales. Océanis 32, 215-235.

Blanchard, G.F., Guarini, J.M., Gros, P., Richard, P., 1997. Seasonal effect on the relationship between the photosynthetic capacity of intertidal microphytobenthos and temperature. Journal of Phycology 33, 723-728.

Blanchard, G.F., Guarini, J.M., Orvain, F., Sauriau, P.G., 2001. Dynamic behaviour of benthic microalgal biomass in intertidal mudflats. Journal of Experimental Marine Biology and Ecology 264, 85-100.

Blanchard, G.F., Simon-Bouhet, B., Guarini, J.M., 2002. Properties of the dynamics of intertidal microphytobenthic biomass. Journal of the Marine Biological Association of the United Kingdom 82, 1027-1028.

Bocher, P., Piersma, T., Dekinga, A., Kraan, C., Yates, M.G., Guyot, T., Folmer, E.O., Radenac, G., 2007. Site- and species-specific distribution patterns of molluscs at five intertidal soft-sediment areas in northwest Europe during a single winter. Marine Biology 151, 577-594.

Bocher, P., Quaintenne, G., Robin, F., Doumeret, A., Delaporte, P., 2012. Origins and age structure of Red Knot Calidris canutus staging and wintering on the Atlantic coast of France. Journal of Ornithology 153, 103-114.

Bodini, A., Bondavalli, C., 2002. Towards a sustainable use of water resources: a whole-ecosystem approach using network analysis. International Journal of Environment and Pollution 18, 463 - 485

Boileau, N., Delaporte, P., 2011. Différences liées au sexe dans le comportement alimentaire du courlis cendré *Numenius arquata* en zone intertidale. Alauda 80, 13-21.

Borrvall, C., Ebenman, B., Jonsson, T., 2000. Biodiversity lessens the risk of cascading extinction in model food webs. Ecology Letters 3, 131-136.

Brando, V.E., Ceccarelli, R., Libralato, S., Ravagnan, G., 2004. Assessment of environmental management effects in a shallow water basin using mass-balance models. Ecological Modelling 172, 213-232.

Brett, J.R., 1965. The Relation of Size to Rate of Oxygen Consumption and Sustained Swimming Speed of Sockeye Salmon (Oncorhynchus nerka). Journal of the Fisheries Research Board of Canada 22, 1491-1501.

Brey, T., 2001. The virtual hand book on population dynamics of benthic invertebrates.

Brey, T., 2010. An empirical model for estimating aquatic invertebrate respiration. Methods in Ecology and Evolution 1, 92-101.

Brito, A.C., Fernandes, T.F., Newton, A., Facca, C., Tett, P., 2012. Does microphytobenthos resuspension influence phytoplankton in shallow systems? A comparison through a Fourier series analysis. Estuarine, Coastal and Shelf Science 110, 77-84.

Brose, U., 2008. Complex food webs prevent competitive exclusion among producer species. Proceedings of the Royal Society B: Biological Sciences 275, 2507-2514.

Burns, N.M., Rosa, F., 1980. In situ measurement of the settling velocity of organic carbon particles and 10 species of phytoplankton. Limnology & Oceanography 25, 855-864.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59-67.

Cariou-Le Gall, V., Blanchard, G., 1995. Monthly HPLC measurements of pigment concentration from an intertidal muddy sediment of Marennes-Oléron Bay, France. Marine Ecology Progress Series 121, 171-179.

Carpentier, A., Como, S., Dupuy, C., Lefrançois, C., Feunteun, E., in press. Foraging strategy of Liza spp. in an intertidal mudflat: evidence of the importance of the primary production (biofilm) for the species. Journal of Sea Research.

Cartaxana, P., Ruivo, M., Hubas, C., Davidson, I., Serôdio, J., Jesus, B., 2011. Physiological *versus* behavioral photoprotection in intertidal epipelic and epipsammic benthic diatom communities. Journal of Experimental Marine Biology and Ecology 405, 127-137.

Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. Nature 405, 234-242.

Chen, X.I.N., Cohen, J.E., 2001. Global Stability, Local Stability and Permanence in Model Food Webs. Journal of Theoretical Biology 212, 223-235.

Christensen, V., 1995. Ecosystem maturity - Towards quantification. Ecological Modelling 77, 3-32.

Christensen, V., Walters, C.J., Ahrens, R., Alder, J., Buszowski, J., Christensen, L.B., Cheung, W.W.L., Dunne, J., Froese, R., Karpouzi, V., Kaschner, K., Kearney, K., Lai, S., Lam, V., Palomares, M.L.D., Peters-Mason, A., Piroddi, C., Sarmiento, J.L., Steenbeek, J., Sumaila, R., Watson, R., Zeller, D., Pauly, D., 2009. Database-driven models of the world's Large Marine Ecosystems. Ecological Modelling 220, 1984-1996.

Christian, R.R., Baird, D., Luczkovich, J., Johnson, J.C., Sharler, U.M., Ulanowicz, R.E., 2005. Role of network analysis in comparative ecosystem ecology of estuaries, in: Belgrano, A., Scharler, U.M., Dunne, J.A., Ulanowicz, R.E. (Eds.), Aquatic Food Webs an Ecosystem Approach. Oxford University press, New York, pp. 25-40.

Coll, M., Lotze, H.K., Romanuk, T.N., 2008. Structural degradation in mediterranean sea food webs: Testing ecological hypotheses using stochastic and mass-balance modelling. Ecosystems 11, 939-960.

Como, S., Lefrançois, C., Maggi, E., Antognarelli, F., Dupuy, C., in press. Behavioral responses of juvenile *Liza aurata* to changes in coastal temperatures and consequences for benthic food resources. Journal of Sea Research.

Conrad, M., 1983. Adaptability: The significance of Variability from Molecule to Ecosystem. Plenum Press, New-York.

Consalvey, M., Paterson, D.M., Underwood, G.J., 2004. The ups and downs of life in a benthic biofilm: migration of benthic diatoms. Diatom Research 19, 181-202.

Corinaldesi, C., Dell'Anno, A., Magagnini, M., Danovaro, R., 2010. Viral decay and viral production rates in continental-shelf and deep-sea sediments of the Mediterranean Sea. FEMS Microbiology Ecology 72, 208-218.

Cotner, J.B., Johengen, T.H., Biddanda, B.A., 2000. Intense winter heterotrophic production stimulated by benthic resuspension. Limnology & Oceanography 45, 1672-1676.

Cottingham, K.L., Brown, B.L., Lennon, J.T., 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4, 72-85.

Crisp, D.J., 1971. Energy flows measurements., in: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell Oxford pp. 197-279.

Dame, J., Christian, R., 2007. A Statistical Test of Network Analysis: Can it Detect Differences in Food Web Properties? Ecosystems 10, 906-923.

David, V., Sautour, B., Galois, R., Chardy, P., 2006. The paradox high zooplankton biomass-low vegetal particulate organic matter in high turbidity zones: What way for energy transfer? Journal of Experimental Marine Biology and Ecology 333, 202-218.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88, 528-534.

De Angelis, D.L., 1975. Stability and Connectance in Food Web Models. Ecology 56, 238-243.

De Angelis, D.L., 1980. Energy Flow, Nutrient Cycling, and Ecosystem Resilience. Ecology 61, 764-771.

De Jonge, V.N., 1980. Fluctuations in the organic carbon to chlorophyll-a ratios for estuarine benthic diatom populations. Marine Ecology Progress Series 2, 345-353.

De Jonge, V.N., Van Beusekom, J.E., 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnology and oceanography 40, 766-778.

De Jonge, V.N., Van Beuselom, J.E.E., 1992. Contribution of resuspended microphytobenthos to total phytoplankton in the EMS estuary and its possible role for grazers. Netherlands Journal of Sea Research 30, 91-105.

De La Rocha, C.L., Passow, U., 2007. Factors influencing the sinking of POC and the efficiency of the biological carbon pump. Deep-Sea Research Part II: Topical Studies in Oceanography 54, 639-658.

Decho, A.W., 2000. Microbial biofilms in intertidal systems: an overview. Continental Shelf Research 20, 1257-1273.

Degré, D., Leguerrier, D., Armynot du Chatelet, E., Rzeznik, J., Auguet, J.C., Dupuy, C., Marquis, E., Fichet, D., Struski, C., Joyeux, E., Sauriau, P.G., Niquil, N., 2006. Comparative analysis of the food webs of two intertidal mudflats during two seasons using inverse modelling: Aiguillon Cove and Brouage Mudflat, France. Estuarine, Coastal and Shelf Science 69, 107-124.

Dekinga, A., Piersma, T., 1993. Reconstructing diet composition on the basis of faeces in a mollusc- eating wader, the knot Calidris canutus. Bird Study 40, 144-156.

Delany, S., Scott, D., Dodman, T., Stroud, D., 2009. An Atlas of Waders Populations in Africa and Western Eurasia. Wetlands International, Wageningen, The Netherlands.

delGiorgio, P.A., Cole, J.J., 1998. Bacterial Growth Efficiency in Natural Aquatic Systems. Annual Review of Ecology and Systematics 29, 503-541.

Denis, L., Desreumaux, P.E., 2009. Short-term variability of intertidal microphytobenthic production using an oxygen microprofiling system. Marine and Freshwater Research 60, 712-726.

Diehl, S., Feißel, M., 2000. Effects of Enrichment on Three-Level Food Chains with Omnivory. The American Naturalist 155, 200-218.

Donali, E., Olli, K., Heiskanen, A.S., Andersen, T., 1999. Carbon flow patterns in the planktonic food web of the Gulf of Riga, the Baltic Sea: A reconstruction by the inverse method. Journal of Marine Systems 23, 251-268.

Downing, A.L., Leibold, M.A., 2002. Ecosystem consequences of species richness and composition in pond food webs. Nature 416, 837-841.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: Robustness increases with connectance. Ecology Letters 5, 558-567.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2004. Network structure and robustness of marine food webs. Marine Ecology Progress Series 273, 291-302.

Dupuy, C., Mallet, C., Guizien, K., Montanié, H., Bréret, M., Mornet, F., Fontaine, C., Nérot, C., Orvain, F., in press. Sequential resuspension of components (virus, prokaryotes and protists) of biofilm by erodimetry experiments in the Brouage mudflat (French Atlantic coast): subsurface vertical distribution of microorganisms into the sediment. Journal of Sea Research.

Eldridge, P.M., Jackson, G.A., 1993. Benthic trophic dynamics in California coastal basin and continental slope communities inferred using inverse analysis. Marine Ecology Progress Series 99, 115-135.

Elton, C., 1927. Animal Ecology. Sidgwick & Jackson, London.

Elton, C.S., 1958. The ecology of invasions of animals and plants. Methuen, London London.

Emmerson, M., Yearsley, J.M., 2004. Weak interactions, omnivory and emergent food-web properties. Proceedings of the Royal Society B: Biological Sciences 271, 397-405.

Emmerson, M.C., Solan, M., Emes, C., Paterson, D.M., Raffaelli, D., 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. Nature 411, 73-77.

Fagan, W.F., 1997. Omnivory as a stabilizing feature of natural communities. American Naturalist 150, 554-567.

Fath, B.D., Halnes, G., 2007. Cyclic energy pathways in ecological food webs. Ecological Modelling 208, 17-24.

Fath, B.D., Patten, B.C., 1999. Review of the foundations of network environ analysis. Ecosystems 2, 167-179.

Fath, B.D., Scharler, U.M., Baird, D., in press. Dependence of network metrics on model aggregation and throughflow calculations: demonstration using the Sylt-Romo Bight Ecosystem. Ecological Modelling.

Fath, B.D., Scharler, U.M., Ulanowicz, R.E., Hannon, B., 2007. Ecological network analysis: network construction. Ecological Modelling 208, 49-55.

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. Journal of Theoretical Biology 56, 363-380.

Folmer, E.O., Olff, H., Piersma, T., 2010. How well do food distributions predict spatial distributions of shorebirds with different degrees of self-organization? Journal of Animal Ecology 79, 747-756.

Forest, A., Tremblay, J.T., Gratton, Y., Martin, J., Gagnon, J., Darnis, G., Sampei, M., Fortier, L., Ardyna, M., Gosselin, M., Hattori, H., Nguyen, D., Maranger, R., Vaqué, D., Marrasé, C., Pedrós-Alió, C., Sallon, A., Michel, C., Kellogg, C., Deming, J., Shadwick, E., Thomas, H., Link, H., Archambault, P., Piepenburg, D., 2011. Biogenic carbon flows through the planktonic food web of the Amundsen Gulf (Arctic Ocean): A synthesis of field measurements and inverse modeling analyses. Progress in Oceanography 91, 410-436.

Fridley, J.D., 2001. The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93, 514-526.

Frontier, S., Pichod-Viale, D., Leprêtre, A., Davoult, D., Luczak, C., 2004. écosystèmes, Structure, Fonctionnement, évolution, Dunob ed, Paris.

Fuhrman, J.A., 1981. Influence of method on the apparent size distribution of bacterioplankton cells: Epifluorescence microscopy compared to scanning ellectron microscopy. Marine Ecology Progress Series 5.

Garcia, C., Chardy, P., Dewarumez, J.M., Dauvin, J.C., 2011. Assessment of benthic ecosystem functioning through trophic web modelling: The example of the eastern basin of the English Channel and the Southern Bight of the North Sea. Marine Ecology 32, 72-86.

Garet, M.J., Moriarty, D.J.W., 1996. Acid extraction of tritium label from bacterial DNA in clay sediment. Journal of Microbiological Methods 25, 1-4.

Garstecki, T., Wickham, S.A., Arndt, H., 2002. Effects of Experimental Sediment Resuspension on a Coastal Planktonic Microbial Food Web. Estuarine, Coastal and Shelf Science 55, 751-762.

Gascuel, D., Morissette, L., Palomares, M.L.D., Christensen, V., 2008. Trophic flow kinetics in marine ecosystems: Toward a theoretical approach to ecosystem functioning. Ecological Modelling 217, 33-47.

Gilbert, A.J., 2009. Connectance indicates the robustness of food webs when subjected to species loss. Ecological Indicators 9, 72-80.

Gontikaki, E., van Oevelen, D., Soetaert, K., Witte, U., 2011. Food web flows through a sub-arctic deep-sea benthic community. Progress in Oceanography 91, 245-259.

Goto, N., Mitamura, O., Terai, H., 2001. Biodegradation of photosynthetically produced extracellular organic carbon from intertidal benthic algae. Journal of Experimental Marine Biology and Ecology 257, 73-86.

Gough, L., Grace, J.B., 1998. Herbivore effects on plant species density at varying productivity levels. Ecology 79, 1586-1594.

Gouleau, D., Jouanneau, J.M., Weber, O., Sauriau, P.G., 2000. Short-and long- term sedimentation on Montportail-Brouage mudflat, Marennes-Oléron Bay, France. Continental Shelf Research 20, 1513-1530.

Grami, B., Niquil, N., Sakka Hlaili, A., Gosselin, M., Hamel, D., Hadj Mabrouk, H., 2008. The plankton food web of the Bizerte Lagoon (South-western Mediterranean): II. Carbon steady-state modelling using inverse analysis. Estuarine, Coastal and Shelf Science 79, 101-113.

Grami, B., Rasconi, S., Niquil, N., Jobard, M., Saint-Béat, B., Sime-Ngando, T., 2011. Functional effects of parasites on food web properties during the spring diatom bloom in lake pavin: A linear inverse modeling analysis. PLoS ONE 6.

Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109, 323-334.

Guarini, J.-M., Blanchard, G.F., Gros, P., Gouleau, D., Bacher, C., 2000a. Dynamic model of the short-term variability of microphytobenthic biomass on temperate intertidal mudflats. Marine Ecology Progress Series 195, 291-303.

Guarini, J.-M., Gros, P., Blanchard, G., Richard, P., Fillon, A., 2004. Benthic contribution to pelagic microalgal communities in two semi-enclosed, European-type littoral ecosystems (Marennes-Oléron Bay and Aiguillon Bay, France). Journal of Sea Research 52, 241-258.

Guarini, J.M., Blanchard, G.F., Bacher, C., Gros, P., Riera, P., Richard, P., Gouleau, D., Galois, R., Prou, J., Sauriau, P.G., 1998. Dynamics of spatial patterns of microphytobenthic biomass: Inferences from a geostatistical analysis of two comprehensive surveys in Marennes-Oleron Bay (France). Marine Ecology Progress Series 166, 131-141.

Guarini, J.M., Blanchard, G.F., Gros, P., 2000b. Quantification of the microphytobenthic primary production in european intertidal mudflats - A modelling approach. Continental Shelf Research 20, 1771-1788.

Guizien, K., Dupuy, C., Ory, P., Montanié, H., Hartmann, H., Chatelain, M., Karpytchev, M., 2013. Microorganism dynamics during a rising tide: Disentangling effects of resuspension and mixing with offshore waters above an intertidal mudflat. Journal of Marine Systems.

Guizien, K., Orvain, F., Duchêne, J.-C., Le Hir, P., 2012. Accounting for Rough Bed Friction Factors of Mud Beds as a Result of Biological Activity in Erosion Experiments. Journal of Hydraulic Engineering 138, 979-984.

Hall, R.O., Meyer, J.L., 1998. The trophic significance of bacteria in a detritus-based stream food web. Ecology 79, 1995-2012.

Hanlon, A., Bellinger, B., Haynes, K., Xiao, G., Hofmann, T., Gretz, M., Ball, A.S., Osborn, A., Underwood, G., 2006. Dynamics of extracellular polymeric substance (EPS) production and loss in an estuarine, diatom-dominated, microalgal biofilm over a tidal emersion-immersion period. Limnology and oceanography 51, 79-93.

Harrison, G.W., 1979. Stability under Environmental Stress: Resistance, Resilience, Persistence, and Variability. The American Naturalist 113, 659-669.

Haubois, A.G., Guarini, J.M., Richard, P., Blanchard, G.F., Sauriau, P.G., 2002. Spatio-temporal differentiation in the population structure of Hydrobia ulvae on an intertidal mudflat (Marennes-Oléron Bay, France). Journal of the Marine Biological Association of the United Kingdom 82, 605-614.

Haubois, A.G., Guarini, J.M., Richard, P., Fichet, D., Radenac, G., Blanchard, G.F., 2005a. Ingestion rate of the deposit-feeder Hydrobia ulvae (Gastropoda) on epipelic diatoms: Effect of cell size and algal biomass. Journal of Experimental Marine Biology and Ecology 317, 1-12.

Haubois, A.G., Guarini, J.M., Richard, P., Hemon, A., Arotcharen, E., Blanchard, G.F., 2004. Differences in spatial structures between juveniles and adults of the gastropod Hydrobia ulvae on an intertidal mudflat (Marennes–Oléron Bay, France) potentially affect estimates of local demographic processes. Journal of Sea Research 51, 63-68.

Haubois, A.G., Sylvestre, F., Guarini, J.M., Richard, P., Blanchard, G.F., 2005b. Spatio-temporal structure of the epipelic diatom assemblage from an intertidal mudflat in Marennes-Oléron Bay, France. Estuarine, Coastal and Shelf Science 64, 385-394.

Hector, A., Dobson, K., Minns, A., Bazeley-White, E., Hartley Lawton, J., 2001. Community diversity and invasion resistance: An experimental test in a grassland ecosystem and a review of comparable studies. Ecological Research 16, 819-831.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E.M., Bazeley-White, E., Weilenmann, M., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Mulder, C.P.H., Palmborg, C., Pereira, J.S., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Schmid, B., Loreau, M., 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. Ecology 91, 2213-2220.

Herendeen, R., 1989. Energy intensity, residence time, exergy, and ascendency in dynamic ecosystems. Ecological Modelling 48, 19-44.

Herlory, O., Guarini, J.-M., Blanchard, G.F., 2004. Microstructure of microphytobenthic biofilm and its spatio-temporal dynamics in an intertidal mudflat (Aiguillon Bay, France). Marine Ecology Progress Series 282, 33-44.

Herman, P.M.J., Middelburg, J.J., Heip, C.H.R., 2001a. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. Continental Shelf Research 21, 2055-2071.

Herman, P.M.J., Middelburg, J.J., Heip, C.H.R., 2001b. Benthic community structure and sediment processes on an intertidal flat: Results from the ECOFLAT project. Continental Shelf Research 21, 2055-2071.

Hewson, I., O'Neil, J.M., Heil, C.A., Bratbak, G., Dennison, W.C., 2001. Effects of concentrated viral communities on photosynthesis and community composition of co-occurring benthic microalgae and phytoplankton. Aquatic Microbial Ecology 25, 1-10.

Heymans, J.J., Guénette, S., Christensen, V., 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. Ecosystems 10, 488-502.

Heymans, J.J., Ulanowicz, R.E., Bondavalli, C., 2002. Network analysis of the South Florida Everglades graminoid marshes and comparison with nearby cypress ecosystems. Ecological Modelling 149, 5-23.

Higashi, M., Patten, B.C., Burns, T.P., 1993. Network trophic dynamics: the modes of energy utilization in ecosystems. Ecological Modelling 66, 1-42.

Hirata, H., Ulanowicz, R.E., 1984. Information theoretical analysis of ecological networks. International Journal of Systems Science 15, 261-270.

Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. Science 277, 1302-1305.

Hosack, G.R., Eldridge, P.M., 2009. Do microbial processes regulate the stability of a coral atoll's enclosed pelagic ecosystem? Ecological Modelling 220, 2665-2682.

Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J., Steneck, R.S., 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology and Evolution 25, 633-642.

Ieno, E.N., Solan, M., Batty, P., Pierce, G.J., 2006. How biodiversity affects ecosystem functioning: Roles of infaunal species richness, identity and density in the marine benthos. Marine Ecology Progress Series 311, 263-271.

Ives, A.R., Cardinale, B.J., 2004. Food-web interactions govern the resistance of communities after non-random extinctions. Nature 429, 174-177.

Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. Science 317, 58-62.

Jacobs, R.P.W.M., Den Hartog, C., Braster, B.F., Carriere, F.C., 1981. Grazing of the seagrass Zostera noltii by birds at terschelling (Dutch Wadden Sea). Aquatic Botany 10, 241-259.

Jiang, L., Morin, P.J., 2004. Productivity gradients cause positive diversity–invasibility relationships in microbial communities. Ecology Letters 7, 1047-1057.

Johnson, G.A., Niquil, N., Asmus, H., Bacher, C., Asmus, R., Baird, D., 2009. The effects of aggregation on the performance of the inverse method and indicators of network analysis. Ecological Modelling 220, 3448-3464.

Jordan, C.F., Kline, J.R., Sasscer, D.S., 1972. Relative Stability of Mineral Cycles in Forest Ecosystems. The American Naturalist 106, 237-253.

Jordán, F., Scheuring, I., 2004. Network ecology: Topological constraints on ecosystem dynamics. Physics of Life Reviews 1, 139-172.

Jørgensen, S.E., 1992. Exergy and ecology. Ecological Modelling 63, 185-214.

Jørgensen, S.E., 2000. A General Outline of Thermodynamic Approaches to Ecosystem Theory, in: Jørgensen, S.E., Müller, F. (Eds.), Handbook of Ecosystem Theories and Management. Lewis Publishers, Boca Raton, London, New York, Washington D.C., pp. 113-134.

Jørgensen, S.E., Fath, B.D., 2004. Application of thermodynamic principles in ecology. Ecological Complexity 1, 267-280.

Jørgensen, S.E., Fath, B.D., 2006. Examination of ecological networks. Ecological Modelling 196, 283-288.

Jørgensen, S.E., Patten, B.C., Straškraba, M., 2000. Ecosystems emerging: 4. Growth. Ecological Modelling 126, 249-284.

Kay, J.J., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide to network analysis. Coastal and Estuarine Studies 32.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D., Reich, P., 2002. Biodiversity as a barrier to ecological invasion. Nature 417, 636-638.

Kersten, M., Piersma, T., 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. Ardea 75, 175-187.

Killen, S.S., Atkinson, D., Glazier, D.S., 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecology Letters 13, 184-193.

Kleidon, A., Malhi, Y., Cox, P.M., 2010. Maximum entropy production in environmental and ecological systems. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 1297-1302.

Klepper, O., Van De Kamer, J.P.G., 1987. The use of mass balances to test and improve the estimates of carbon fluxes in an ecosystem. Mathematical Biosciences 85, 37-49.

Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E., Groth, J., 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecology Letters 2, 286-293.

Koh, C.H., Jong, S.K., Araki, H., Yamanishi, H., Mogi, H., Koga, K., 2006. Tidal resuspension of microphytobenthic chlorophyll a in a Nanaura mudflat, Saga, Ariake Sea, Japan: Flood-ebb and spring-neap variations. Marine Ecology Progress Series 312, 85-100.

Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. Science 299, 1388-1391.

Kondoh, M., 2005a. Is biodiversity maintained by fod-web complexity? The adaptative food-web hypothesis, in: Belgrano, A., Scharler, U.M., Dunne, J.A., Ulanowicz, R.E. (Eds.), Aquatic Food Webs An Ecosystem Approach. Oxford University Press, pp. 130-142.

Kondoh, M., 2005b. Is biodiversity maintained by food-web complexity? The adaptative food-web hypothesis, in: Belgrano, A., Scharler, U.M., Dunne, J.A., Ulanowicz, R.E. (Eds.), Aquatic Food Webs An Ecosystem Approach. Oxford University Press, pp. 130-142.

Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. Ecological Modelling 220, 370-382.

Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., Mavuti, K., 2006. Gaining insight into food webs reconstructed by the inverse method. Journal of Marine Systems 60, 153-166.

Krone, R.B., 1962. Flume studies of the transport of sediment in estuarine shaoling processes., Hydraulic Engineering Laboratory and Sanitery Engineering Research Laboratory. University of California, Berkeley, CA.

Kuwae, T., Beninger, P.G., Decottignies, P., Mathot, K.J., Lund, D.R., Elner, R.W., 2008. Biofilm grazing in a higher vertebrate: the western sandpiper, Calidris mauri. Ecology 89, 599-606.

Kuwae, T., Miyoshi, E., Hosokawa, S., Ichimi, K., Hosoya, J., Amano, T., Moriya, T., Kondoh, M., Ydenberg, R.C., Elner, R.W., 2012. Variable and complex food web structures

revealed by exploring missing trophic links between birds and biofilm. Ecology Letters 15, 347-356.

Labry, C., Herbland, A., Delmas, D., 2002. The role of phosphorus on planktonic production of the Gironde plume waters in the Bay of Biscay. Journal of Plankton Research 24, 97-117.

Lapoussière, A., Michel, C., Starr, M., Gosselin, M., Poulin, M., 2011. Role of free-living and particle-attached bacteria in the recycling and export of organic material in the Hudson bay system. Journal of Marine Systems 88, 434-445.

Laska, M.S., Wootton, J.T., 1998. Theoritical concepts and empirical approaches to measuring interaction strength. Ecology 79, 461-476.

Lassalle, G., Gascuel, D., Le Loch, F., Lobry, J., Pierce, G.J., Ridoux, V., Santos, M.B., Spitz, J., Niquil, N., 2012. An ecosystem approach for the assessment of fisheries impacts on marine top predators: The Bay of Biscay case study. ICES Journal of Marine Science 69, 925-938.

Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., Hily, C., Labry, C., Le Pape, O., Marquis, E., Petitgas, P., Pusineri, C., Ridoux, V., Spitz, J., Niquil, N., 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management. Progress in Oceanography 91, 561-575.

Lavaud, J., 2007. Fast Regulation of Photosynthesis in Diatoms: Mechanisms, Evolution and Ecophysiology. Functional Plant Science and Biotechnology 1, 268-287.

Le Hir, P., Roberts, W., Cazaillet, O., Christie, M., Bassoullet, P., Bacher, C., 2000. Characterization of intertidal flat hydrodynamics. Continental Shelf Research 20, 1433-1459.

Le Mao, P., Pasco, P.Y., Provost, S., 2006. Estimation of benthic macrofauna consumption by water birds in the Mont-Saint-Michel bay. Consommation de la macro-faune invertébrée benthique par les oiseaux d'eau en baie du Mont-Saint-Michel 74, 23-36.

Leguerrier, D., 2005. Construction et étude d'un modèle de réseau trophique de la vasière de Brouage (bassin de Marennes-Oléron, France). Prise en compte de la saisonnalité et des échanges physiques pour la synthèse constructive des connaissances sur une zone intertidale d'une région tempérée. University of La Rochelle, p. 655.

Leguerrier, D., Degré, D., Niquil, N., 2007. Network analysis and inter-ecosystem comparison of two intertidal mudflat food webs (Brouage Mudflat and Aiguillon Cove, SW France). Estuarine, Coastal and Shelf Science 74, 403-418.

Leguerrier, D., Niquil, N., Boileau, N., Rzeznik, J., Sauriau, P.G., Le Moine, O., Bacher, C., 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. Marine Ecology Progress Series 246, 17-37.

Leguerrier, D., Niquil, N., Petiau, A., Bodoy, A., 2004. Modeling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France). Marine Ecology Progress Series 273, 147-161.

Levin, 1999. Fragile dominion: complexity and the commons. Reading, MA:Perseus Books.

Levine, J.M., 2000. Species diversity and biological invasions: Relating local process to community pattern. Science 288, 852-854.

Lindeman, R.L., 1942. The Trophic-Dynamic Aspect of Ecology. Ecology 23, 399-417.

Link, J.S., Stockhausen, W.T., Methratta, E.T., 2005. Food-Web theory in marine ecosystems, in: Belgrano, A., Scharler, U.M., Dunne, J.A., Ulanowicz, R.E. (Eds.), Aquatic Food Webs An Ecosystem Approach. Oxford University Press, pp. 98-113.

Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B., Rochard, E., 2008. Diversity and stability of an estuarine trophic network. Marine Ecology Progress Series 358, 13-25.

Loeuille, N., 2010. Consequences of adaptive foraging in diverse communities. Functional Ecology 24, 18-27.

Loreau, M., 1994. Material Cycling and the Stability of Ecosystems. The American Naturalist 143, 508-513.

Loreau, M., Downing, A., Emmerson, M., Gonzalez, A., Hughes, J., Inchausti, P., Joshi, J., Norberg, J., Sala, O., 2002. A new look at the relationship between diversity and stability., in: Loreau, M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and ecosystem functionning. Oxford University press, Oxford, pp. 77-91.

Loreau, M., Mouquet, N., Holt, R.D., 2003. Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. Ecology Letters 6, 673-679.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Ecology: Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294, 804-808.

Lourenço, P.M., Silva, A., Santos, C.D., Miranda, A.C., Granadeiro, J.P., Palmeirim, J.M., 2008. The energetic importance of night foraging for waders wintering in a temperate estuary. Acta Oecologica 34, 122-129.

Lucas, C.H., Widdows, J., Brinsley, M.D., Salkeld, P.N., Herman, P.M.J., 2000. Benthic-pelagic exchange of microalgae at a tidal flat. 1. Pigment analysis. Marine Ecology Progress Series 196, 59-73.

Luis, A., Goss-Custard, J.D., Moreira, M.H., 2001. A method for assessing the quality of roost used by waders during high tide. Wader Study Group Bulletin 96, 71-73.

MacArthur, R., 1955. Fluctuations of Animal Populations and a Measure of Community Stability. Ecology 36, 533-536.

Macintyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: The ecological role of the 'secret garden' of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19, 186-201.

Magagnini, M., Corinaldesi, C., Monticelli, L.S., De Domenico, E., Danovaro, R., 2007. Viral abundance and distribution in mesopelagic and bathypelagic waters of the Mediterranean Sea. Deep-Sea Research Part I: Oceanographic Research Papers 54, 1209-1220.

Mageau, M.T., Costanza, R., Ulanowicz, R.E., 1998. Quantifying the trends expected in developing ecosystems. Ecological Modelling 112, 1-22.

Mahéo, R., 2008. Limicoles séjournant en France (littoral): Reports Wetlands International/ONCFS.

Mallet, C., Agogué, H., Bonnemoy, F., Guizien, K., Orvain, F., Dupuy, C., in press. Resuspension of benthic prokaryotic communities during physical erosion process: an experimental approach. Journal of Sea Research.

Manage, P.M., Kawabata, Z., Nakano, S.I., Nishibe, Y., 2002. Effect of heterotrophic nanoflagellates on the loss of virus-like particles in pond water. Ecological Research 17, 473-479.

Mann, K.H., 1965. Energy Transformations by a Population of Fish in the River Thames. Journal of Animal Ecology 34, 253-275.

Mann, K.H., Field, J.G., Wulff, F., 1989. Network analysis in marine ecology: an assessment. Coastal and Estuarine Studies 32, 259-282.

Marleau, J.N., Guichard, F., Mallard, F., Loreau, M., 2010. Nutrient flows between ecosystems can destabilize simple food chains. Journal of Theoretical Biology 266, 162-174.

Marques, J.C., Jørgensen, S.E., 2002. Three selected ecological observations interpreted in terms of a thermodynamic hypothesis. Contribution to a general theoretical framework. Ecological Modelling 158, 213-221.

Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A., Labry, C., Sautour, B., Laborde, P., Vézina, A., Dupuy, C., 2007. Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. Estuarine, Coastal and Shelf Science 73, 223-235.

May, R.M., 1972. Will a large complex system be stable? Nature 238, 413-414.

May, R.M., 1973. Stability and complexity in Model Ecosystems. Princeton University Press.

May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269, 471-477.

McCann, K., Hastings, A., 1997. Re-evaluating the omnivory-stability relationship in food webs. Proceedings of the Royal Society B: Biological Sciences 264, 1249-1254.

McCann, K., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. Nature 395, 794-798.

McCann, K.S., 2000. The diversity-stability. Nature 405, 228-233.

McCann, K.S., Rasmussen, J.B., Umbanhowar, J., 2005. The dynamics of spatially coupled food webs. Ecology Letters 8, 513-523.

McCann, K.S., Rooney, N., 2009. The more food webs change, the more they stay the same. Philosophical Transactions of the Royal Society B: Biological Sciences 364, 1789-1801.

McNaughton, S.J., 1977. Diversity and Stability of Ecological Communities: A Comment on the Role of Empiricism in Ecology. The American Naturalist 111, 515-525.

McNeill, A.R., 1999. Energy for animal life. Oxford University Press, New York.

Meyer-Reil, L.A., 1983. Benthic response to sedimentation events during autumn to spring at a shallow water station in the Western Kiel Bight. Marine Biology 77, 247-256.

Meysman, F.J.R., Bruers, S., 2010. Ecosystem functioning and maximum entropy production: A quantitative test of hypotheses. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 1405-1416.

Michalski, J., Arditi, 1999. The complexity-stability problem in the food webs theory. What can we learn from exploratory models?, in: Blasco, F., Weill, A. (Eds.), In Advances in Environmental and Ecological Modelling. Elsevier, Paris, pp. 91-119.

Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T., Heip, C.H.R., 2000. The fate of intertidal microphytobenthos carbon: An in situ 13C-labeling study. Limnology and oceanography 45, 1224-1234.

Migné, A., Spilmont, N., Boucher, G., Denis, L., Hubas, C., Janquin, M.A., Rauch, M., Davoult, D., 2009. Annual budget of benthic production in Mont Saint-Michel Bay considering cloudiness, microphytobenthos migration, and variability of respiration rates with tidal conditions. Continental Shelf Research 29, 2280-2285.

Migné, A., Spilmont, N., Davoult, D., 2004. In situ measurements of benthic primary production during emersion: seasonal variations and annual production in the Bay of Somme (eastern English Channel, France). Continental Shelf Research 24, 1437-1449.

Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being: synthesis. Island Press, Washington.

Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Marine Ecology Progress Series 161, 239-254.

Montagna, P.A., Blanchard, G.F., Dinet, A., 1995. Effect of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. Journal of Experimental Marine Biology and Ecology 185, 149-165.

Montanié, H., Ory, P., Orvain, F., Delmas, D., Dupuy, C., Hartmann, H.J., in press. Microbial interactions in marine water amended by eroded benthic biofilm: A case study from an intertidal mudflat Original Research Article. Journal of Sea Research.

Montoya, J.M., Pimm, S.L., Solé, R.V., 2006. Ecological networks and their fragility. Nature 442, 259-264.

Montoya, J.M., Solé, R.V., 2002. Small world patterns in food webs. Journal of Theoretical Biology 214, 405-412.

Moore, J.C., Berlow, E.L., Coleman, D.C., De Suiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., Wall, D.H., 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7, 584-600.

Morowitz, H.J., 1968. Energy flow in biology: bological organization as a problem in thermal physics. Academic Press, New York.

Morris, S., Taylor, A.C., 1983. Diurnal and seasonal variation in physico-chemical conditions within intertidal rock pools. Estuarine, Coastal and Shelf Science 17, 339-355.

Mouget, J.L., Perkins, R., Consalvey, M., Lefebvre, S., 2008. Migration or photoacclimation to prevent high irradiance and UV-B damage in marine microphytobenthic communities. Aquatic Microbial Ecology 52, 223-232.

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H., 2007. Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean. Science 315, 1846-1850.

Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., Gale, S., 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91, 97-108.

Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. Nature 390, 507-509.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., Woodfin, R.M., 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368, 734-737.

Neutel, A.M., Heesterbeek, J.A.P., De Ruiter, P.C., 2002. Stability in real food webs: Weak links in long loops. Science 296, 1120-1123.

Ni Longphuirt, S., Lim, J.H., Leynaert, A., Claquin, P., Choy, E.J., Kang, C.K., An, S., 2009. Dissolved inorganic nitrogen uptake by intertidal microphytobenthos: nutrient concentrations, light availability and migration. Marine Ecology Progress Series 379, 33-44.

Nielsen, S.N., Ulanowicz, R.E., 2000. On the consistency between thermodynamical and network approaches to ecosystems. Ecological Modelling 132, 23-31.

Nienhuis, P.H., Groenendijk, A.M., 1986. Consumption of eelgrass (Zostera marina) by birds and invertebrates: an annual budget Marine Ecology Progress Series 29, 29-35.

Niquil, N., Chaumillon, E., Johnson, G.A., Bertin, X., Grami, B., David, V., Bacher, C., Asmus, H., Baird, D., Asmus, R., 2012. The effect of physical drivers on ecosystem indices derived from ecological network analysis: Comparison across estuarine ecosystems. Estuarine, Coastal and Shelf Science 108, 132-143.

Niquil, N., Jackson, G.A., Legendre, L., Delesalle, B., 1998. Inverse model analysis of the planktonic food web of Takapoto Atoll (French Polynesia). Marine Ecology Progress Series 165, 17-29.

Niquil, N., Saint-Béat, B., Johnson, G.A., Soetaert, K., Van Oevelen, D., Bacher, C., Vézina, A.F., 2011. Inverse Modeling in Modern Ecology and application to Coastal Ecosystems., in: Wolanski, E., McLusky, D.S. (Eds.), Treatise on Estuarine and Coastal Science. Waltham: Academic press, pp. 115-133.

Noble, R.T., Fuhrman, J.A., 1998. Use of SYBR Green I for rapid epifluorescence counts of marine viruses and bacteria. Aquatic Microbial Ecology 14, 113-118.

Nolet, B.A., Gyimesi, A., Klaassen, R.H.G., 2006. Prediction of bird-day carrying capacity on a staging site: a test of depletion models. Journal of Animal Ecology 75, 1285-1292.

O'Connor, N.E., Crowe, T.P., 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. Ecology 86, 1783-1796.

Odum, E.P., 1953. Fundamentals of ecology. Saunders, Philadelphia.

Odum, E.P., 1969. The Strategy of Ecosystem Development Science 164, 262-270.

Odum, H.T., 2002. Explanations of ecological relationships with energy systems concepts. Ecological Modelling 158, 201-211.

Orvain, F., Galois, R., Barnard, C., Sylvestre, A., Blanchard, G., Sauriau, P.G., 2003a. Carbohydrate production in relation to microphytobenthic biofilm development: An integrated approach in a tidal mesocosm. Microbial Ecology 45, 237-251.

Orvain, F., Guizien, K., Lefebvre, S., Bréret, M., Dupuy, C., in press. Relevance of biofilm features to understand the dynamic behavior of sediment erodability and microphytobenthos resuspension. Journal of Sea Research.

Orvain, F., Le Hir, P., Sauriau, P.G., 2003b. A model of fluff layer erosion and subsequent bed erosion in the presence of the bioturbator, Hydrobia ulvae. Journal of Marine Research 61, 823-851.

Orvain, F., Sauriau, P.-G., Sygut, A., Joassard, L., Hir, P.L., 2004. Interacting effects of Hydrobia ulvae bioturbation and microphytobenthos on the erodibility of mudflat sediments. Marine Ecology Progress Series 278, 205-223.

Orvain, F., Sauriau, P.G., Bacher, C., Prineau, M., 2006. The influence of sediment cohesiveness on bioturbation effects due to Hydrobia ulvae on the initial erosion of intertidal sediments: A study combining flume and model approaches. Journal of Sea Research 55, 54-73.

Orvain, F., Sauriau, P.G., Le Hir, P., Guillou, G., Cann, P., Paillard, M., 2007. Spatio-temporal variations in intertidal mudflat erodability: Marennes-Oléron Bay, western France. Continental Shelf Research 27, 1153-1173.

Ory, P., Palesse, S., Delmas, D., Montanié, H., 2011. In situ structuring of virioplankton through bacterial exoenzymatic activity: Interaction with phytoplankton. Aquatic Microbial Ecology 64, 233-252.

Paine, R.T., 1988. Road Maps of Interactions or Grist for Theoretical Development? Ecology 69, 1648-1654.

Parker, R.L., 1977. Understanding inverse theory. Annual Review of Earth and Planetary Sciences 5, 35-64.

Pascal, P.Y., 2008. Devenir des bactéries dans les réseaux trophiques des vasières intertidales: le cas de Brouage (Baie de Marennes-oléron). Université de La Rochelle.

Pascal, P.Y., Dupuy, C., Mallet, C., Richard, P., Niquil, N., 2008a. Bacterivory by benthic organisms in sediment: Quantification using 15N-enriched bacteria. Journal of Experimental Marine Biology and Ecology 355, 18-26.

Pascal, P.Y., Dupuy, C., Richard, P., Haubois, A.G., Niquil, N., 2008b. Influence of environment factors on bacterial ingestion rate of the deposit-feeder Hydrobia ulvae and comparison with meiofauna. Journal of Sea Research 60, 151-156.

Pascal, P.Y., Dupuy, C., Richard, P., Mallet, C., Châtelet, E.A.D., Niquil, N., 2009. Seasonal variation in consumption of benthic bacteria by meio- And macrofauna in an intertidal mudflat. Limnology and Oceanography 54, 1048-1059.

Pascal, P.Y., Dupuy, C., Richard, P., Niquil, N., 2008c. Bacterivory in the common foraminifer Ammonia tepida: Isotope tracer experiment and the controlling factors. Journal of Experimental Marine Biology and Ecology 359, 55-61.

Pascal, P.Y., Dupuy, C., Richard, P., Rzeznik-Orignac, J., Niquil, N., 2008d. Bacterivory of a mudflat nematode community under different environmental conditions. Marine Biology 154, 671-682.

Patrício, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2004. Ascendency as an ecological indicator: A case study of estuarine pulse eutrophication. Estuarine, Coastal and Shelf Science 60, 23-35.

Patten, B.C., Higashi, M., 1984. Modified cycling index for ecological applications. Ecological Modelling 25, 69-83.

Patten, B.C., Higashi, M., Burns, T.P., 1990. Trophic dynamics in ecosystem networks: Significance of cycles and storage. Ecological Modelling 51, 1-28.

Pérez-España, H., Arreguín-Sánchez, F., 2001. An inverse relationship between stability and maturity in models of aquatic ecosystems. Ecological Modelling 145, 189-196.

Pimm, S.L., 1982. Food webs.

Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307, 321-326.

Pimm, S.L., 1991. The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities. The University of Chicago Press, Chicago and London.

Pimm, S.L., Lawton, J.H., 1978. On feeding on more than one trophic level. Nature 275, 542-544.

Pinnegar, J.K., Blanchard, J.L., Mackinson, S., Scott, R.D., Duplisea, D.E., 2005. Aggregation and removal of weak-links in food-web models: System stability and recovery from disturbance. Ecological Modelling 184, 229-248.

Pomeroy, L.R., 1970. The Strategy of Mineral Cycling. Annual Review of Ecology and Systematics 1, 171-190.

Ponsero, A., Lemao, P., 2011. Estimation of benthic macrofauna consumption by water birds in the bay of Saint-Brieuc (France). Revue d'écologie, Terre et Vie 66, 383-398.

Poremba, K., Tillmann, U., Hesse, K.J., 1999. Tidal impact on planktonic primary and bacterial production in the German Wadden Sea. Helgoland Marine Research 53, 19-27.

Porter, E.T., Mason, R.P., Sanford, L.P., 2010. Effect of tidal resuspension on benthic-pelagic coupling in an experimental ecosystem study. Marine Ecology Progress Series 413, 33-53.

Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon: volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnology & Oceanography 34, 1097-1103.

Quaintenne, G., Van Gils, J.A., Bocher, P., Dekinga, A., Piersma, T., 2010. Diet selection in a molluscivore shorebird across Western Europe: Does it show short- or long-term intake rate-maximization? Journal of Animal Ecology 79, 53-62.

Raffaelli, D.G., Hawkins, S.J., 1996. Interdital ecology. Chapman & Hall, London, UK.

Raillard, O., Mesenguen, A., 1994. An ecosystem box model for estimating the carrying capacity of a macrotidal shellfish system. Marine Ecology Progress Series 115, 117-130.

Rejmanek, M., 1989. Invasibility of plant communities., in: Drake, J.A., Di Castri, F., Groves, R.H., Kruger, F.J., Mooney, H.A., Rejmanek, M., Williamson, M.H. (Eds.), Ecology of Biological Invasion: a Global Perspective. Wiley & Sons, New York, pp. 369-388.

Richardson, T.L., Jackson, G.A., Ducklow, H.W., Roman, M.R., 2006. Spatial and seasonal patterns of carbon cycling through planktonic food webs of the Arabian Sea determined by inverse analysis. Deep-Sea Research Part II: Topical Studies in Oceanography 53, 555-575.

Riera, P., Richard, P., 1996. Isotopic determination of food sources of Crassostrea gigas along a trophic gradient in the estuarine bay of Marennes-Oleron. Estuarine, Coastal and Shelf Science 42, 347-360.

Robin, F., Piersma, T., Meunier, F., Bocher, P., in press. Expanding into a herbivorous niche by a customary carnivore: Zostera-rhizome feeding by black-tailed godwits at a newly established site. Condor.

Romanova, N., Sazhin, A., 2010. Relationships between the cell volume and the carbon content of bacteria. Oceanology 50, 522-530.

Rooney, N., McCann, K., Gellner, G., Moore, J.C., 2006. Structural asymmetry and the stability of diverse food webs. Nature 442, 265-269.

Round, F., Palmer, J., 1966. Persistent, vertical-migration rhythms in benthic microflora. J Marine Biol Assoc UK 46, 191-214.

Round, F.E., Crawford, R.M., Mann, D.G., 1990. The Diatoms. Biology and Morphology of the Genera. Cambridge University Press,Cambridge, UK., Cambridge, UK.

Rzeznik-Orignac, J., Fichet, D., 2012. Experimental estimation of assimilation rates of meiofauna feeding on 14C-labelled benthic diatoms. Journal of Experimental Marine Biology and Ecology 432-433, 179-185.

Rzeznik-Orignac, J., Fichet, D., Boucher, G., 2003. Spatio-temporal structure of the nematode assemblages of the Brouage mudflat (Marennes Oléron, France). Estuarine, Coastal and Shelf Science 58, 77-88.

Salomonsen, J., 1992. Examination of properties of exergy, power and ascendency along a eutrophication gradient. Ecological Modelling 62, 171-181.

Salonen, K., Sarvala, J., Hakala, I., Viljanen, M.L., 1976. The relation of energy and organic carbon in aquatic invertebrates. Limnology and oceanography 21, 724-730.

Sander, B.C., Kalff, J., 1993. Factors controlling Bacterial Production in Marine and Freshwater Sediments. Microbial Ecology 26, 79-99.

Sankaran, M., McNaughton, S.J., 1999. Determinants of biodiversity regulate compositional stability of communities. Nature 401, 691-693.

Sarker, M., Yamamoto, T., Hashimoto, T., 2009. Contribution of benthic microalgae to the whole water algal biomass and primary production in Suo Nada, the Seto Inland Sea, Japan. Journal of Oceanography 65, 311-323.

Sauriau, P.-G., Kang, C.-K., 2000. Stable isotope evidence of benthic microalgae-based growth and secondary production in the suspension feeder Cerastoderma edule (Mollusca, Bivalvia) in the Marennes-Oléron Bay. Hydrobiologia 440, 317-329.

Sautour, B., Castel, J., 1998. Importance of microzooplanktonic crustaceans in the coastal food chain: Bay of Marennes-Oleron, France. Oceanologica Acta 21, 105-112.

Savenkoff, C., Castonguay, M., Vézina, A.F., Despatie, S.P., Chabot, D., Morissette, L., Hammill, M.O., 2004. Inverse modelling of trophic flows through an entire ecosystem: The northern Gulf of St. Lawrence in the mid-1980s. Canadian Journal of Fisheries and Aquatic Sciences 61, 2194-2214.

Savenkoff, C., Vézina, A.F., Roy, S., Klein, B., Lovejoy, C., Therriault, J.C., Legendre, L., Rivkin, R., Bérubé, C., Tremblay, J.E., Silverberg, N., 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 1. Seasonal variations. Deep-Sea Research Part II: Topical Studies in Oceanography 47, 585-607.

Scharler, U.M., Baird, D., 2005. A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. Journal of Marine Systems 56, 283-308.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591-596.

Scheiffarth, G., 2001. The diet of Bar-tailed Godwits, *Limosa lapponica* in the Wadden Sea. Combining visual observations and faeces analyses. Ardea 89, 481-494.

Scheiffarth, G., Nehls, G., 1997. Consumption of benthic fauna by carnivorous birds in the Wadden Sea. Helgolander Meeresuntersuchungen 51, 373-387.

Schiemer, F., 1987. Nematoda, in: Pandian, T.J., Vernberg, F.J. (Eds.), Animal Energetics. Academic Press, San Diego, pp. 185-211.

Schurmann, H., Steffensen, J.F., 1997. Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. Journal of Fish Biology 50, 1166-1180.

Self, R.F.L., Jumars, P.A., 1988. Cross-phyletic patterns of particle selection by deposit feeders. Journal of Marine Research 46, 119-143.

Serôdio, J., Catarino, F., 2000. Modelling the primary productivity of intertidal microphytobenthos: time scales of variability and effects of migratory rhythms. Marine Ecology Progress Series 192, 13-30.

Serôdio, J., Ezequiel, J., Barnett, A., Mouget, J.L., Méleder, V., Laviale, M., Lavaud, J., in press. Efficiency of photoprotection in microphytobenthos: the role of vertical migration and the xanthophyll cycle against photoinhibition. Aquatic Microbial Ecology.

Serodio, J., Vieira, S., Cruz, S., 2008. Photosynthetic activity, photoprotection and photoinhibition in intertidal microphytobenthos as studied< i> in situ</i> using variable chlorophyll fluorescence. Continental Shelf Research 28, 1363-1375.

Shea, K., Roxburgh, S.H., Rauschert, E.S., 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters 7, 491-508.

Simard, Y., Lacroix, G., Legendre, L., 1985. In situ twilight grazing rhythm during diel vertical migrations of a scattering layer of Calanus finmarchicus. Limnology & Oceanography 30, 598-606.

Sime-Ngando, T., Colombet, J., 2009. Virus and prophages in aquatic ecosystems. Revue canadienne de microbiologie 55, 95-109.

Sloth, N.P., Riemann, B., Nielsen, L.P., Blackburn, T., 1996. Resilience of Pelagic and Benthic Microbial Communities to Sediment Resuspension in a Coastal Ecosystem, Knebel Vig, Denmark. Estuarine, Coastal and Shelf Science 42, 405-415.

Smith, R.L., 1984. Efficient Monte Carlo procedures for generating points uniformity. Operations Research 32, 1296-1308.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and ecosystem function in the marine benthos. Science 306, 1177-1180.

Solé, R.V., Montoya, J.M., 2001. Complexity and fragility in ecological networks. Proceedings of the Royal Society B: Biological Sciences 268, 2039-2045.

Soletchnik, P., Le Moine, O., Faury, N., Razet, D., Geairon, P., Goulletquer, P., 1999. Mortalité de l'huître Crassostrea gigas dans le bassin de Marennes-Oléron: étude de la variabilité spatiale de son environnement et de sa biologie par un système d'informations géographiques (SIG). Aquatic Living Resources 12, 131-143.

Stachowicz, J.J., Fried, H., Osman, R.W., Whitlatch, R.B., 2002. Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83, 2575-2590.

Struski, C., Bacher, C., 2006. Preliminary estimate of primary production by phytoplankton in Marennes-Oléron Bay, France. Estuarine, Coastal and Shelf Science 66, 323-334.

Stukel, M.R., Landry, M.R., Ohman, M.D., Goericke, R., Samo, T., Benitez-Nelson, C.R., 2012. Do inverse ecosystem models accurately reconstruct plankton trophic flows?Comparing two solution methods usinf field data from the California Current. Journal of Marine Systems 91, 20-33.

Sueur, F., Desprez, M., Fagot, C., Triplet, P., 2003. La baie de Somme: un site sous-exploité par les oiseaux d'eau. Alauda 71, 49-58.

Sundbäck, K., Nilsson, P., Nilsson, C., Jönsson, B., 1996. Balance Between Autotrophic and Heterotrophic Components and Processes in Microbenthic Communities of Sandy Sediments: A Field Study. Estuarine, Coastal and Shelf Science 43, 689-706.

Sutherland, W.J., 1983. Aggregation and the `Ideal Free' Distribution. Journal of Animal Ecology 52, 821-828.

Suttle, C.A., 2005. Viruses in the sea. Nature 437, 356-361.

Taghon, G.L., 1982. Optimal foraging by deposit-feeding invertebrates: Roles of particle size and organic coating. Oecologia 52, 295-304.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300-1302.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294, 843-845.

Tolhurst, T., Defew, E., De Brouwer, J., Wolfstein, K., Stal, L., Paterson, D., 2006. Small-scale temporal and spatial variability in the erosion threshold and properties of cohesive intertidal sediments. Continental Shelf Research 26, 351-362.

Tortajada, S., Niquil, N., Blanchet, H., Grami, B., Montanié, H., David, V., Glé, C., Saint-Béat, B., Johnson, G.A., Marquis, E., Del Amo, Y., Dubois, S., Vincent, D., Dupuy, C., Jude, F., Hartmann, H.J., Sautour, B., 2012. Network analysis of the planktonic food web during the spring bloom in a semi enclosed lagoon (Arcachon, SW France). Acta Oecologica 40, 40-50.

Triplet, P., Stillman, R.A., Goss-Custard, J.D., 1999. Prey abundance and the strength of interference in a foraging shorebird. Journal of Animal Ecology 68, 254-265.

Turner, J.T., 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquatic Microbial Ecology 27, 57-102.

Uchida, S., Drossel, B., 2007. Relation between complexity and stability in food webs with adaptive behavior. Journal of Theoretical Biology 247, 713-722.

Ulanowicz, R.E., 1980. An hypothesis on the development of natural communities. Journal of Theoretical Biology 85, 223-245.

Ulanowicz, R.E., 1986. Growth and Development. Ecosystems Phenomenology. Excel Press.

Ulanowicz, R.E., 1997. Ecology, the Ascendent perspective. Colombia University Press, New-York.

Ulanowicz, R.E., 2000. Ascendency: A Measure of Ecosystem Performance, in: Jørgensen, S.E., Müller, F. (Eds.), Handbook of Ecosystem Theories and Management. Lewis Publishers, Boca Raton, London, New York, Washington D.C., pp. 303-314.

Ulanowicz, R.E., 2003. Some steps toward a central theory of ecosystem dynamics. Computational Biology and Chemistry 27, 523-530.

Ulanowicz, R.E., 2004. Quantitative methods for ecological network analysis. Computational Biology and Chemistry 28, 321-339.

Ulanowicz, R.E., 2009. The dual nature of ecosystem dynamics. Ecological Modelling 220, 1886-1892.

Ulanowicz, R.E., Goerner, S.J., Lietaer, B., Gomez, R., 2009. Quantifying sustainability: Resilience, efficiency and the return of information theory. Ecological Complexity 6, 27-36.

Ulanowicz, R.E., Hannon, B.M., 1987. Life and the Production of Entropy. Proceedings of the Royal Society of London. Series B. Biological Sciences 232, 181-192.

Ulanowicz, R.E., Jørgensen, S.E., Fath, B.D., 2006. Exergy, information and aggradation: An ecosystems reconciliation. Ecological Modelling 198, 520-524.

Ulanowicz, R.E., Kay, J.J., 1991. A package for the analysis of ecosystem flow networks. Environmental Software 6, 131-142.

Ulanowicz, R.E., Norden, J.S., 1990. Symmetrical overhead in flow networks. International Journal of Systems Science 21, 429-437.

Underwood, G.J.C., Paterson, D.M., 2003. The importance of extracellular carbohydrate production by marine epipelic diatoms, pp. 183-240.

Van den Meersche, K., Soetaert, K., Van Oevelen, D., 2009. xsample(): An R Function for Sampling Linear Inverse Problems. Journal of Statistical Software 30, 1-15.

van Gils, J.A., Battley, P.F., Piersma, T., Drent, R., 2005. Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. Proceedings of the Royal Society Biological Sciences Series B 272, 2609-2618.

van Oevelen, D., Moodley, L., Soetaert, K., Middelburg, J.J., 2006a. The trophic significance of bacterial carbon in a marine intertidal sediments: Results of an in situ stable isotope labeling study. Limnology & Oceanography 51, 2349-2359.

van Oevelen, D., Soetaert, K., Middelburg, J.J., Herman, P.M.J., Moodley, L., Hamels, I., Moens, T., Heip, C.H.R., 2006b. Carbon flows through a benthic food web: Integrating biomass, isotope and tracer data. Journal of Marine Research 64, 453-482.

van Oevelen, D., van den Meersche, K., Meysman, F.J.R., Soetaert, K., Middelburg, J.J., Vézina, A.F., 2010. Quantifying food web flows using linear inverse models. Ecosystems 13, 32-45.

Vandermeer, J., 2006. Omnivory and the stability of food webs. Journal of Theoretical Biology 238, 497-504.

Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: A comparative analysis. Ecological Modelling 100, 125-134.

Verger, F., 2005. Marais et estuaires du littoral français. Belin, Paris.

Vézina, A.F., 1989. Construction of flow networks using inverse methods., in: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology. Springer, Berlin, pp. 62-81.

Vézina, A.F., Berreville, F., Loza, S., 2004. Inverse reconstructions of ecosystem flows in investigating regime shifts: Impact of the choice of objective function. Progress in Oceanography 60, 321-341.

Vezina, A.F., Pace, M.L., 1994. An inverse model analysis of planktonic food webs in experimental lakes. Canadian Journal of Fisheries and Aquatic Sciences 51, 2034-2044.

Vézina, A.F., Pahlow, M., 2003. Reconstruction of ecosystem flows using inverse methods: How well do they work? Journal of Marine Systems 40-41, 55-77.

Vézina, A.F., Platt, T., 1988. Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Marine Ecology Progress Series 42, 269-287.

Vézina, A.F., Savenkoff, C., 1999. Inverse modeling of carbon and nitrogen flows in the pelagic food web of the northeast subarctic Pacific. Deep-Sea Research Part II: Topical Studies in Oceanography 46, 2909-2939.

Vézina, A.F., Savenkoff, C., Roy, S., Klein, B., Rivkin, R., Therriault, J.C., Legendre, L., 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. Deep-Sea Research Part II: Topical Studies in Oceanography 47, 609-635.

Viain, A., Corre, F., Delaporte, P., Joyeux, E., Bocher, P., 2011. Numbers, diet and feeding methods of Common Shelduck Tadorna tadorna wintering in the estuarine bays of Aiguillon and Marennes-Oléron, western France. Wildfowl 61, 121-141.

Vieira, S., Coelho, H., Nolasco, R., Serôdio, J., Barnes, R., Queiroga, H., 2010. The circatidal rhythm of the estuarine gastropod *Hydrobia ulvae* (Gastropoda: Hydrobiidae). Biological Journal of the Linnean Society 100, 439-450.

Vincent, D., Hartmann, H.J., 2001. Contribution of ciliated microprotozoans and dinoflagellates to the diet of three copepod species in the bay of Biscay. Hydrobiologia 443, 193-204.

Virgo, N., Law, R., Emmerson, M., 2006. Sequentially assembled food webs and extremum principles in ecosystem ecology. Journal of Animal Ecology 75, 377-386.

Wardle, D.A., Bonner, K.I., Barker, G.M., 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. Oikos 89, 11-23.

Warwick, R.M., Price, R., 1979. Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. Estuarine and Coastal Marine Science 9, 257-271.

Wiback, S.J., Famili, I., Greenberg, H.J., Palsson, B.Ø., 2004. Monte Carlo sampling can be used to determine the size and shape of the steady-state flux space. Journal of Theoretical Biology 228, 437-447.

Williams, R.J., Martinez, N.D., 2004. Limits to trophic levels and omnivory in complex food webs: Theory and data. American Naturalist 163, 458-468.

Witte, J.I., Zijlstra, J.J., 1984. The meiofauna of a tidal flat in the western part of the Wadden sea and its role in the benthic ecosystem. Marine Ecology Progress Series 14, 129-138.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences of the United States of America 96, 1463-1468.

Yoshino, K., Tsugeki, N.K., Amano, Y., Hayami, Y., Hamaoka, H., Omori, K., 2012. Intertidal bare mudflats subsidize subtidal production through outwelling of benthic microalgae. Estuarine, Coastal and Shelf Science 109, 138-143.

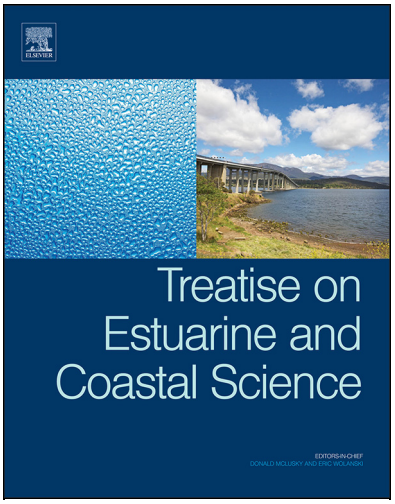
Annexes

Annexe 1

Niquil, N., Saint-Béat, B., Johnson, G.A., Soetaert, K., Van Oevelen, D., Bacher, C., Vézina, A.F.
2011.

Inverse Modeling in Modern Ecology and application to Coastal Ecosystems.

In: Wolanski, E., McLusky, D.S. (Eds.), Treatise on Estuarine and Coastal Science. Waltham: Academic press, pp. 115-133.



Niquil N, Saint-Béat B, Johnson GA, Soetaert K, van Oevelen D, Bacher C and Vézina AF (2011) Inverse Modeling in Modern Ecology and Application to Coastal Ecosystems. In: Wolanski E and McLusky DS (eds.) *Treatise on Estuarine and Coastal Science*, Vol 9, pp. 115–133. Waltham: Academic Press.

9.07 Inverse Modeling in Modern Ecology and Application to Coastal Ecosystems

N Niquil and B Saint-Béat, Université de La Rochelle – CNRS, La Rochelle, France
GA Johnson, Université de La Rochelle – CNRS, La Rochelle, France; Northwest Indian Fisheries Commission, Olympia, WA, USA
K Soetaert and D van Oevelen, The Netherlands Institute of Ecology (NIOO-KNAW), Yerseke, The Netherlands
C Bacher, Institut Français de Recherche pour l'Exploitation de la Mer, Plouzané, France
AF Vézina, Bedford Institute of Oceanography, Dartmouth, NS, Canada

Abstract

Quantitative estimates of energy or material flows within food webs are increasingly viewed as essential to progress on a number of questions in ecosystem science. Inverse analysis has been used since the 1980s to estimate all flows within plankton food webs originally based on incomplete information. Its application to many aquatic environments, including the coastal zone, has led to a variety of methodological improvements. This chapter explains the methodology of inverse modeling and illustrates its application in modern ecosystems ecology. This relatively new approach also provides rigorous statistical comparisons of food web properties across ecosystems.

9.07.1 Introduction

Organisms in a habitat or ecosystem interact in a number of ways, mostly through competition and predation; the ensemble of trophic flows that describes the exchange of matter between ecosystem compartments is called a food web. Food webs are central to many questions in ecosystem science, for example, productivity, capacity to support harvesting, and resilience to disturbance (e.g., Polis and Hurd, 1996; Pauly et al., 1998, 2002; Polis, 1999; Dambacher et al., 2003; Hughes et al., 2003; Heymans et al., 2004). Interdisciplinary studies of coastal and estuarine ecosystems have recently led to the compilation of data sets that make it possible to quantify complex food web flows. Whereas the feeding rate of large animals can be directly measured, this becomes problematic for smaller organisms, or for organisms that live in environments that are not easily accessible or observable. For such systems, the quantification of food webs by measurement alone can be a daunting task. With a few notable exceptions (e.g., Sylt-Rømø Bight; Baird et al., 2007), the direct determination of a complete set of flows characterizing an ecosystem or habitat is generally not possible. Most data sets will provide only a snapshot of the complexity of the food web that may contain many gaps, not only in coverage of interactions but also in the sampling of flows in space and over time. However, inverse modeling can fill in these gaps, and can provide estimates of the missing flows. When applied to estimate unknown quantities (i.e., model parameters from the realized values of the model's system state), a model is said to be inverse. This sets it apart from forward applications where the model is used to

Treatise on Estuarine and Coastal Science, 2011, Vol.9, 115-133, DOI: 10.1016/B978-0-12-374711-2.00906-2

describe the time evolution of a system using known parameters and relations.

From a mathematical point of view, three different inverse problems can be distinguished. The most familiar situation is the estimation of unknown parameters describing statistical relationships between different variables (e.g., fitting a line through a scatter of points in dimension 2). Typically, the number of observations (more than two points observed, with a quantification of the two variables for each point) is greater than the number of unknown parameters (two for a straight line: the slope and the intercept), and the problem can be characterized as overdetermined (more equations than unknowns). This rarely applies to the problem of quantifying interactions among components of a food web or ecosystem where the flows of energy or matter, and associated parameters, rise rapidly with the number of food web compartments. The complexity of even relatively simple food webs quickly outstrips our ability to quantify all the interactions. As a result, the number of observations is typically smaller than the number of unknown parameters (the flows). In this case, the problem can be characterized as underdetermined (less equations than unknowns) and does not have a unique solution, that is, many different flow patterns can give rise to the same set of limited observations. Finding a solution to an underdetermined problem can be compared with the fitting of a straight line to one point: any line crossing that point will do. Inverse problems can also be even-determined (the number of observations equals the number of unknowns) and show a unique solution; this is equivalent to the fitting of a line through two points. However, such a situation does not arise naturally and requires subjective decisions and manipulations to match unknowns with data.

The over- and even-determined problems are preferred from a scientific and statistical point of view, but they are not realistic expectations for most food web investigations, including those that target the coastal zone. This means that a unique solution does not *a priori* exist. Researchers have taken two alternatives to overcome this problem. Either the overdeterminacy is enforced by adding unobserved data (e.g., from neighboring sites or from literature) to the model, or a single solution is selected *a posteriori*. The standard approach, detailed in this chapter, consists in associating the two, with a hierarchical organization of the information into two different levels that distinguishes the local determination of processes from more general constraints derived from studies in other ecosystems or the laboratory. We adopt linear inverse modeling (LIM) to describe a class of methods that rely on linear relations to estimate unknown flows in food webs.

The particulars of LIM are described below. At this stage, it is suffice to say that that LIM relies on the principle of conservation of mass at steady state, that is, the sum of the inflows and outflows through the components of the system equals the rate of change in their standing stocks. This allows turning the problem into a set of simple linear relations that describe mass balance. Direct measurements of mass transfer rates or other properties linked to these transfers can be expressed as linear combinations of the flows. These can include local estimations of primary production, respiration, stoichiometric relationships, and isotopic composition. These two sets of linear relationships, usually enforced as equalities, together define the local constraints on the flows. We can then add, from literature information, linear relations that bound the flows or linear combinations of the flows to fall between certain values. The inequality in relationships forms the general constraints on the problem, while linear equality and inequality relations together define a bounded multidimensional space, called a polytope, within which all realistic solutions to the problem lie. Past practice has been to select a single solution inside this space of possible solutions. The initial one, applied most often, is based on a least-squares criterion (Vézina and Platt, 1988). Most recently, new methods have been developed to describe the solution space by calculating a representative sample of all the possible solutions using the Monte Carlo approach (Kones et al., 2006, 2009; Van den Meersche et al., 2009).

This chapter aims at presenting LIM, from its early use to its most recent advance, and its applications in coastal ecology. After a brief presentation of LIM history (Section 9.07.2), the different steps of LIM (Section 9.07.3) are presented as developed by Vézina and Platt (1988). Section 9.07.4 presents recent methodological innovations. All these methods are not specific to coastal ecology and could be equally applied to freshwater and ocean systems, but they have greatly improved the quality of description of the functioning of coastal food webs. Section 9.07.5 presents methods used to analyze the results (sensitivity analysis and ecological network analysis (ENA)), with recommendations formulated in Section 9.07.6 dedicated to methodological choices for the use of LIM in coastal ecology. Section 9.07.7 presents a simple example of application to a coastal problem, comparing five states in the late winter–spring succession of the planktonic system of the Bay of Biscay.

9.07.2 Brief History of LIM

Inverse problems first surfaced in the geophysical sciences where they are still commonly used for studying wave or chemical component dispersion, and especially in subsurface studies where direct measurement is often limited. The translation of the geophysical inverse problem into the estimation of the flows in a food web was done, more or less simultaneously, by several authors in the late 1980s. The first attempts at estimating missing values of flows in a food web were based on the method proposed in geophysics (Tarantola and Valette, 1982), treating both over- and underdetermined situations. Inspired by this work, food web applications were realized (Chardy et al., 1993; Jean, 1994) in a situation of overdeterminacy by specifying a value for each flow or efficiency, taken either from the studied site or from other sites. Then the solution in which the flows and efficiencies were as close as possible to the initially set values was selected.

Klepper and Van de Kamer (1987) proposed the first underdetermined approach, by assigning only the mass balances to the equalities, while a set of inequalities corresponded to the intervals of confidence of measured flows. A combination of equalities and inequalities was also proposed by Vézina and Platt (1988), but with a different scheme. They considered that flows, estimated *in situ*, had to be considered with priority, compared to information from other systems, estimated by experiments or from theory. Thus, the set of equalities in their case comprised both the mass balances together with a set of measured flows from the study site. All other information was

taken as inequalities. Both these contributions proceeded by selecting the simplest food web from the infinite number of solutions: Klepper and Van de Kamer (1987) by minimizing a linear norm (i.e., the sum of the absolute values of the flows) and Vézina and Platt (1988) by minimizing either the linear or the quadratic norm (i.e., the sum of squared flows). These techniques share strong similarities with metabolic flux analyses that were developed at about the same time to reconstruct metabolic reaction networks in cells (Vallino and Stephanopoulos, 1993; Varma and Palsson, 1994), except that the criterion for selecting a single solution was to optimize growth rate (maximizing flux).

Later, the Ecopath (Christensen and Pauly, 1992) steady-state mass-balance model was created, and this is possibly the most well-known LIM framework. Typically, Ecopath is applied in underdetermined situations, but creates an even-determined, or overdetermined, system to fill gaps by using diet or physiological/ecological efficiencies from comparable systems. This system is obtained by specifying, for all biotic components, the diet composition as well as the consumption and production rates, trophic efficiencies, fishery harvests, etc. As the diet composition needs to be known, it is most easily applied to large-bodied organisms where this can potentially be estimated, for example, based on gut contents. Thus, Ecopath is mostly used to investigate higher trophic levels subjected to fishing (e.g., Pauly et al., 1998, 2002), with the lower trophic levels simplified to largely undifferentiated compartments.

The paper by Vézina and Platt (1988) has been most influential for investigations focused on the plankton and lower trophic levels of the food web. Because of the posterior selection method, the method of Vézina and Platt (1988), termed simply 'inverse analysis' in the original paper, can now be placed in the larger context of LIM that includes a range of methods, which is discussed subsequently (see also van Oevelen et al., 2010). This method can be termed 'linear inverse modeling with a minimum norm' (LIM-MN). The applications of LIM-MN, and other LIM methods developed on the work of Vézina and Platt (1988) basis, in coastal and estuarine studies (**Table 1** and **Figure 1**) were done either on coupled benthic and pelagic systems or on subsystems, especially the plankton and benthic microbial systems.

The LIM represents the most transparent and flexible tool for dealing with underdetermined systems. For every flow in which a value is unknown or for which only a range of values is known, the equations used to determine the value are explicit. Because such assumptions are explicit, systems for which the solutions contain multiple flows at or near their limits (minimum or maximum) can be easily identified and the likelihood that the system is properly defined can be examined. This transparency is advantageous not only for investigators in the examination of their own systems, but also for reviewers and subsequent users who can view every piece of information that went into the construction of the model. The flexibility of the LIM is limited only by the programming ability of the user; the same framework of linear equations and inequalities can be solved in any number of ways, reflecting the investigator's preferences and assumptions about ecosystem structure and function. The definition of the criterion for the choice of the best solution and the weighting scheme (whether the same importance is given to all information considered) can be set up as desired.

Because the LIM establishes a space of possible solutions (the polytope), it can also be used to calculate ranges of possible values for flows and thus allow a more flexible interpretation of the results that acknowledges the gaps in existing knowledge.

9.07.3 Methodology for LIM: The Four Steps of the LIM-MN Method

LIM is based on the definition of a single set of flow values that fulfills a set of linear equalities and linear inequalities (Vézina and Platt, 1988; Vézina, 1989). In the LIM-MN method, a final criterion is added, based on a minimum norm solution, to select a unique solution. Other criteria have been proposed, based either on deterministic methods (the matrix calculation leads directly to the best solution according to the criterion defined) or, more recently, on Monte Carlo methods, based on a sampling procedure that attempts a complete coverage of the range of possible solutions. In this case, if one solution is to be determined, a criterion has to be defined in order to select it in the sample obtained. The following steps are distinguished.

9.07.3.1 Step 1: The *A Priori* Model

The first step is to define the unknowns, that is, the flows that ought to be determined. This corresponds to the definition of the *a priori* model. At this stage, one selects the compartments of the system and hence the level of aggregation that will be acceptable, according to the objective of the study and to the available data on processes. For example, plankton ecologists usually consider one or more size classes in the phyto- and zooplankton compartment, one compartment of heterotrophic bacteria, and two compartments of nonliving material (dissolved and particulate).

At this stage, the currency that is used ought to be defined. The flows to be resolved will generally have units of mass per unit volume and unit time, or mass per unit area and unit time. The former denotes mass concentration or density change with time and the latter represents mass flux. As flows in one currency (e.g., C) are often coupled to flows in another currency (e.g., N, P, and O_2), the use of data in multiple currencies can strongly constrain food web interactions (e.g., Vézina and Platt, 1988; Jackson and Eldridge, 1992; Gaedke et al., 2002). As shown in Chapter 9.14, the coupling will give a more complete analysis, for example, of recycling properties. The unknowns are the flows that are considered as possible between the compartments defined or between one compartment and the exterior of the system. The questions asked at this point are: "Who eats whom?", "Who/what is imported into or leaves the system?", "What is the form of the rejected nonliving matter?" All these questions are constrained by what has actually been measured in any particular application.

In order to illustrate the steps of the calculation, a toy model can be defined with a very simple situation (**Figure 2**). The model is composed of three compartments (a primary producer = phytoplankton; a grazer = microzooplankton; and a nonliving compartment = dissolved organic carbon (DOC)).

Treatise on Estuarine and Coastal Science, 2011, Vol.9, 115-133, DOI: 10.1016/B978-0-12-374711-2.00906-2

Table 1 List of coastal systems modeled using linear inverse model for food webs

Site	*System*	*Period*	*Method*	*Currency*	*Reference*
Celtic Sea[1]	Plankton	Mean year	MN	C/N	Vézina and Platt (1988)
English Channel[2]	Plankton	Mean year	MN	C/N	Vézina and Platt (1988)
Santa Monica Basin[3]	Benthos	Mean year	MN	C/N	Eldridge and Jackson (1992)
Patton Escarpment[4]	Benthos	Mean year	MN	C/N	Eldridge and Jackson (1993)
Southern California[5]	Plankton	Mean year	MN	C/N	Jackson and Eldridge (1992)
Takapoto Atoll[6]	Plankton	Mean year	MN	C	Niquil et al. (1998)
Takapoto Atoll[6]	Plankton + oysters	Mean year	MN	C	Niquil et al. (2001)
Gulf of St Lawrence[7]	Plankton	Nov–Apr/May–Oct	MN	C	Vézina et al. (2000)
Gulf of Riga (Baltic Sea)[8]	Plankton	Spring/Summer/Autumn	MN	C	Donali et al. (1999)
Baltic Sea[9]	Plankton	Mean year	MN	C	Olsen et al. (2001)
Mediterranean Sea[10]	Plankton	Mean year	MN	C	Olsen et al. (2001)
NE-Atlantic[11]	Plankton	Mean year	MN	C	Olsen et al. (2001)
Florida Bay[12]	Plankton	Mean year	MN	C	Richardson et al. (2003)
Marennes-Oléron Bay (Brouage) mudflat[13]	Benthos-Pelagos	Mean year	MN	C	Leguerrier et al. (2003)
Marennes-Oléron Bay mudflat[13]	Benthos-Pelagos (oyster simulations)	Mean year	MN	C	Leguerrier et al. (2004)
Marennes-Oléron Bay mudflat[13]	Benthos-Pelagos (herbicide simulation)	Mean year	MN	C	Niquil et al. (2006)
Marennes-Oléron Bay mudflat vs. Aiguillon cove[14]	Benthos-Pelagos	Mid Oct–mid March/Mar–Oct	MN with seasonal coupling	C	Degré et al. (2006)
Nueces Bay[15]	Benthos-Pelagos		ME	C + δ^{13}C	Eldridge et al. (2005)
(Molenplaat) Scheldt estuary[16]	Benthos	Mean year	MN	C + δ^{13}C + ^{13}C tracer	van Oevelen et al. (2006b)
Arabian Sea[17]	Plankton	Three seasons (Winter, Spring, Summer)	MN	C	Richardson et al. (2006)
Bay of Biscay shelf[18]	Plankton	Five stages of the Winter/Spring succession	MN	C	Marquis et al. (2007)
Bizerte lagoon[19]	Plankton	Summer	MN	C	Grami et al. (2008)
Gulf of St. Lawrence[7]	Pelagos – demersal	1985–87	MN	C	Savenkoff et al. (2004)
Gulf of St. Lawrence[7]	Pelagos – demersal	1980s/90s/2000s	MN	Biomass	Savenkoff et al. (2007)
NE Atlantic [11]	Plankton		MN	C	Olsen et al. (2007)
Takapoto[6] + Gulf of Riga revisited[8]	Plankton	Spring/Summer/Autumn for GR	MC	C	Kones et al. (2006)
Takapoto[6] + Gulf of Riga revisited[8]	Plankton	Spring/Summer/Autumn for GR	MCMC	C	Kones et al. (2009)
Mississippi River plume[20]	Plankton	Spring–Summer and Fall	MN	C/N	Breed et al. (2004)
Rockall[21]	Cold-water coral	Mean year	MCMC	C + δ^{15}N	van Oevelen et al. (2009)
Barents Sea[22]	Plankton + fish	Two seasons	MCMC	C	De Laender et al. (2010)
Tasmania[23]	Microbial of intertidal mudflat	Mean year	MCMC	C/N	Cook et al. (2009)

MN, Minimum norm solution; ME, maximum evenness; MC, Monte Carlo inverse analysis; MCMC, Markov Chain Monte Carlo inverse analysis.
Superscript numbers in the first column refer to site number on the map of Figure 1.

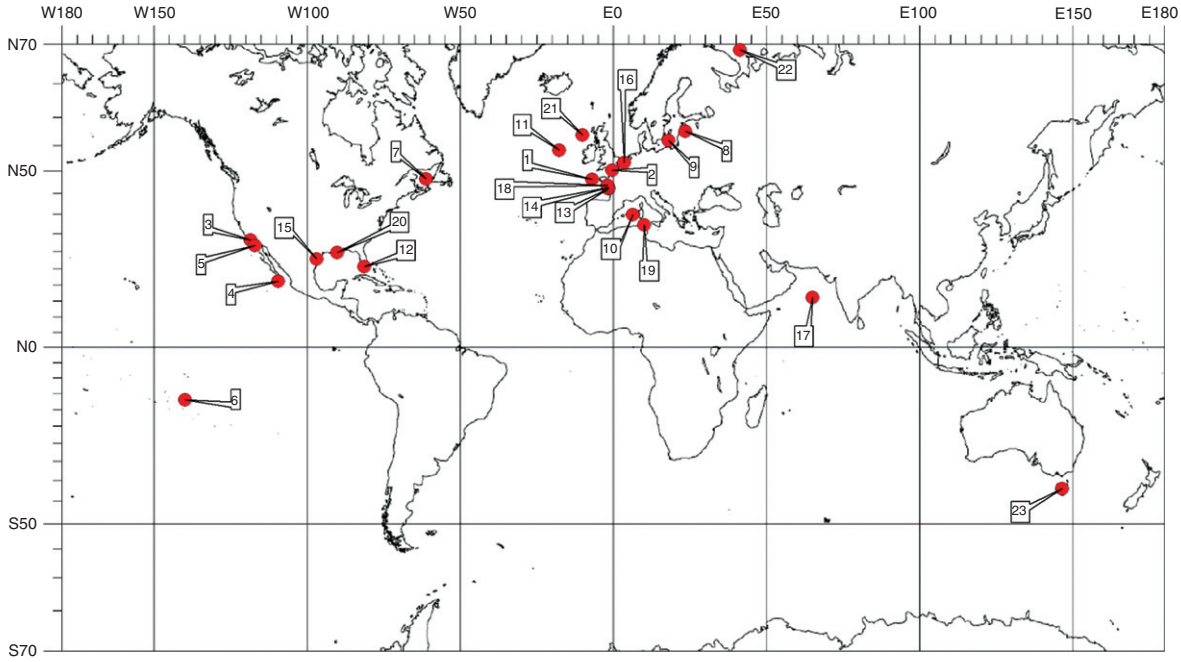
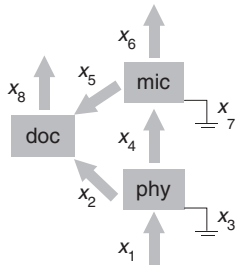


Figure 1 Map of the sites studied with LIM and detailed in Table 1.



(1) $x_1 - x_2 - x_3 - x_4 = 0$ (6) $x_3 - 0.05x_1 \geq 0$

(2) $x_4 - x_5 - x_6 - x_7 = 0$ (7) $0.3x_1 - x_3 \geq 0$

(3) $x_2 + x_5 - x_8 = 0$ (8) $x_4 \geq 167$

(4) $x_1 = 689$ (9–16) each flow ≥ 0

(5) $x_3 + x_7 = 267$

Figure 2 Toy model used for the presentation of LIM and associated linear equations (1–3 mass balance equations, 4–5 *in situ* estimates) and inequalities of the flows (6–17).

We can consider that it represents mean carbon flows for a defined habitat during a day for a defined period. The currency is carbon and the units are m-C m^{-2} day^{-1}.

In the toy model, some flows can directly be considered as improbable, such as from microzooplankton to phytoplankton and will not be considered. For certain cases, the flows to include or exclude may not be obvious; for instance, the use of DOC by hetero-mixotrophic protozoa forming the microzooplankton is a possible flow as shown by the experiments of Sherr and Sherr (1988), but it is an unlikely flow in most ecosystems. As a consequence, it will not be considered here. The vector of all possible flows forms the vector of unknowns (called $\boldsymbol{x}$ hereafter). In the example, there are eight flows,

Table 2 List of the flows of the toy model

Flow	*Compartment*	*Process*
x_1	Phytoplankton	Gross primary production
x_2	Phytoplankton	Dissolved Organic Carbon (DOC) exudation
x_3	Phytoplankton	Respiration
x_4	Microzooplankton	Consumption of phytoplankton
x_5	Microzooplankton	DOC excretion
x_6	Microzooplankton	Production, consumed by external organisms
x_7	Microzooplankton	Respiration
x_8	DOC	DOC consumption by external organisms

corresponding to gross primary production, grazing, respiration, and DOC excretion (Table 2). Gross primary production represents the only flow entering the system, while the outputs from the system are respiration, the grazing of microzooplankton production, and uptake of exuded/excreted DOC by organisms external to the system.

9.07.3.2 Step 2: The Set of Equalities

The second step consists in establishing the set of linear equalities. The mass balance of each compartment constitutes the first set of equalities. If the mass of the compartment is constant during the period considered, the sum of the flows entering into this compartment should equal to the sum of the flows leaving it. This can be modified if the compartment shows variation, in which case the rate of change is equal to the sum of inputs minus the outputs. However, as mass variations are often very low compared to the magnitude of the flows considered, neglecting them is rarely a problem. One mass-balance

equation is written for each compartment. In the example (**Figure 2**), they constitute eqns [1]–[3].

Another set of equations are those concerning the flows that have been measured from the community via *in situ* experiments. Assuming that gross primary production by phytoplankton and total respiration has been estimated, eqns [4] and [5] are obtained for the toy model (**Figure 2**). Note that if every flow value except one is estimated for each compartment, the mass balance would permit a direct estimation of the last flow and the situation would be even-determined. This is rarely the case and the ratio of unknowns to estimated flows is more often close to 4:1 (Vézina et al., 2004).

Once all the equalities have been defined, two possibilities arise. First, the equalities may be contradictory. For example, if the measured respiration for an animal exceeds its ingestion, then the set of equations has no solution. In this case, the model formulation should be reconsidered, perhaps by considering the measurements with a margin of error and adding them to the inequalities (see next step) rather than keeping them fixed. In the second situation, the equalities are plausible and the LIM, being underdetermined, has infinite solutions; thus, the solutions span a space that has as many dimensions as there are flows. In this space, it is necessary to set rules that define which solutions are considered as realistic. For example, a negative value for an ingestion flow is not realistic, nor is it realistic to assume that respiration equals ingestion. These constraints are written as linear inequalities.

9.07.3.3 Step 3: The Set of Inequalities

The third step of inverse analysis is the selection of constraints that make the solution meaningful. The constraints, written as linear inequalities, comprise, for instance, physiological efficiencies, either as ratios between flows or as ratios between a flow and a biomass. In addition, values measured with a large margin of error may be included. For systems where consumers have varied diets, diet information may be included as inequalities as well.

In the toy model, total respiration is determined but not the phytoplankton respiration. It is then possible to add the upper and lower constraints from the literature analysis that was done by Vézina and Platt (1988) stating that the respiration by phytoplankton respiration as a lower bound of 5% the gross primary production and an upper bound of 30% (inequalities 6 and 7 in **Figure 2**). The microzooplankton ingestion can also be considered as being constrained by an allometric relationship linking its maximum value to the total biomass of the compartment, the mean individual mass, and the temperature (eqn [8] in **Figure 2**), as defined in Vézina and Pace (1994) from Moloney and Field (1989). Finally, all flows must be set to be higher or equal to zero (eqns [9]–[16] in **Figure 2**).

The set of inequalities, added to the set of equalities, will set limits to the space of solutions that can be visualized as skew walls. For example, the inequalities 6 and 7 can define an angle in the space of solution. Then if the gross primary production had only one maximum value, the subspace of solutions would be triangular (**Figure 3**, left side). Generalizing this to a more complex situation leads to the definition of a subspace, generally bounded as a polytope (as shown **Figure 3**, right side).

9.07.3.4 Step 4: The Choice of a Single Vector of Flows

The last step is to represent the results and to select one solution or to define each unknown by the range of its possible solutions. In the minimum norm method, a single solution is selected from within the polytope. Vézina and Platt (1988) proposed a deterministic algorithm based on the parsimony principle, that is, the simplest flow network is selected that satisfies both the mass conservation and biological constraints. It is the network where the sum of squared flow values is lowest. The complete algorithm, from steps 1 to 4, can then be summarized as the scheme of **Figure 4**.

As stated by Vézina and Platt (1988), the choice of the solution with a minimal norm "does not imply that food webs are organized on the principle of maximum simplicity. Rather, the aim is to produce a baseline flow network that can be compared within and across food webs. At this time, the operational requirement that the flow structure be as simple as possible seems no worse than any other, and certainly better than none". Notwithstanding these reservations, the choice of the simplest solution has often been criticized afterward (Niquil et al., 1998; Donali et al., 1999; Vézina et al., 2004). The consequences of applying a minimization of the norm of the flows can be summed up as three types: (1) when several pathways of different length go from a compartment to one another, the shortest pathway from one compartment to another is favored; (2) when several pathways have the same length, the vector with the smallest norm is the one evenly

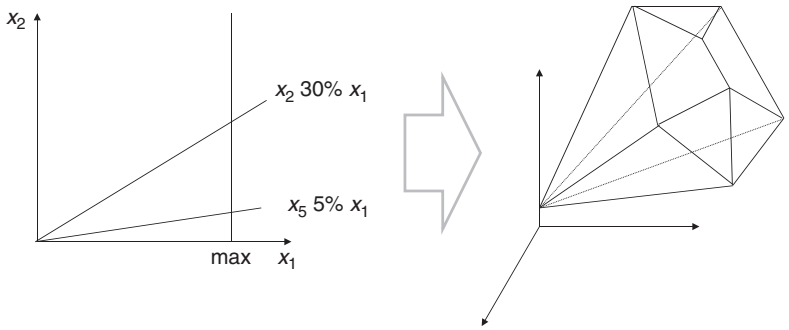


Figure 3 Visualization of the subspace of solutions defined by the set of equations plus the set of inequalities. (Left side) A triangle space of solutions defined by inequalities ($x_3 - 0.05\ x_1 \geq 0$), ($0.3\ x_1 - x_3 \geq 0$), ($x_1 \geq 0$), and ($\max \geq x_1$). (Right side) The shape of a possible polytope, defined by a more complex set of inequalities.

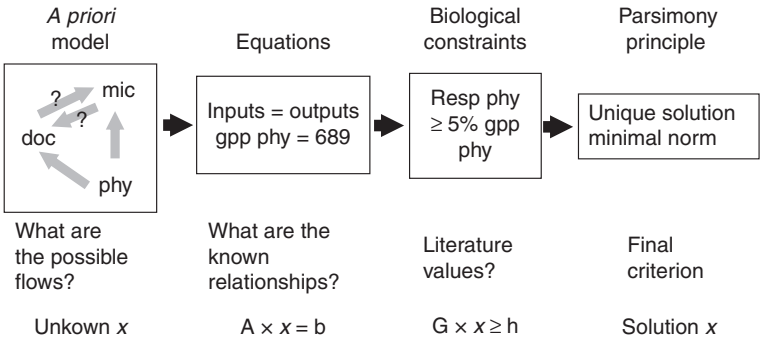


Figure 4 Scheme of the principle of LIM-MN as developed by Vézina and Platt (1988).

distributed, and (3) when a unit of matter is not required within the system, according to the constraints, the solution with the smallest norm will be the one with matter leaving the system as soon as possible. In practice, one often finds that many flows that are not directly needed in the mass-balancing procedure will be set to zero, and that flow values of the LIM-MN typically lie on the lower boundary of their possible value. The main conclusion was that the use of this criterion must be done with a maximum number of constraints translating prior knowledge. Only then can the result be considered to have some link to reality, meaning that, among all possible realistic solutions, it is the solution that introduces the least amount of structure that is required to explain the observations.

9.07.4 Recent Advances in the LIM Methodology

9.07.4.1 New Methods for Step 4: Generating Solutions Using Monte Carlo Techniques

The uncertainty surrounding the interpretation of the LIM-MN solution has led to the development of new techniques that build on the initial algorithm. These methods aim to describe the complete space of possible solutions, defined as the polytope described in **Figure 3**. The original idea of describing each flow, not just by one value, but by a range of possible values, was proposed by Donali et al. (1999). The first idea these authors proposed was to define a minimal and maximal value for each flow, given the constraints defined by the set of equalities and inequalities. Later, sampling methods were proposed in order to describe the population of solutions defined by the polytope. The first techniques (called LIM-MC for Monte Carlo) relied on a random sampling of flow values from their minimum to their maximum values (Leguerrier, 2005; Kones et al., 2006). This method samples randomly the right-angled parallelepiped (or multidimensional box) in which the polytope is inscribed. Points sampled are then accepted or rejected depending on whether they fall inside or outside of the polytope. The large number of dimensions in the polytopes usually defined in coastal areas (up to the order of magnitude of 100 in the benthos–pelagos coupled model of Leguerrier (2005)) and the complex geometry of the polytope, linked to interdependencies among many flows, led to situations where computations become intractable. Moreover, in related metabolic flux analysis, Wiback et al. (2004) showed that the algorithm would not converge to a complete coverage of the solution polytope.

This solution space can then be sampled by hit-and-run methods (Smith, 1984) where points are chosen randomly along line segments that span the space. However, our own work indicates that these hit-and-run methods can become inefficient and fail to converge under certain conditions. We noted, for example, that the variance of the reconstructed distribution for certain flows keeps rising with the number of trials. The method that seems to work for all the problems we tried (called LIM-MCMC for Markov Chain Monte Carlo) is based on a mirror technique (Van Den Meersche et al., 2009). This method consists in choosing a point within the polytope, then sampling a second point from a normal distribution centered on the first point and with a fixed standard deviation called the jump length. This is repeated from the new point to define the next one. When a new point falls outside the polytope, it is reflected along successive dimensions until it falls again within the polytype, as if mirrors were positioned on the inside walls of the polytope. This is equivalent to an MCMC Metropolis–Hastings algorithm with an acceptance ratio for the sampled solution of either 1 (inside the polytope) or 0 (outside the polytope). This method directly generates a sample of points inside the polytope. With an appropriate choice of the number of iterations and of the jump length, the polytope can be fully covered by this sampling. The selection must be done by checking that the flow values reach a steady state of their mean and standard deviation. The R-Package limSolve can be used for this procedure. The function xsample in this package provides the solution methods and can be associated with the package NetIndices that calculates network indices and food web descriptors (see below).

If the sampling parameters are appropriate, this method will converge on representative samples of the marginal probability distribution functions for each flow. These probability density functions do not account for the uncertainties related to model structure, data, and constraints. The mean of each probability density function – being a linear operation – can be combined to develop a mass-balanced solution that fits all the constraints (van Oevelen et al., 2010). However, the probability density functions are often non-normal, as – even if the underlying distribution is normal – they can either be truncated by the inequality constraints or be uniform if the model and data together are insufficient to constrain the value of a particular flow. The skewness of the probability density functions would suggest the use of other measures of central tendency such as the mode or the median; however, a solution based on combining the modes or the medians would not balance the inflows and outflows. If the goal of the exercise is to compute

one solution that is less biased than a solution based on direct optimization (such as least-squares), then the means of each probability density function should be used to construct that solution until better techniques to identify a single solution are developed. On the other hand, if the goal is to compare flows or properties of the flow network across different ecosystems, then the probability density functions should be used directly to compute credible intervals for each flow or property and assess the degree of overlap.

It is interesting to note that a similar evolution from single to multiple solutions has occurred in metabolic flux analysis (Wiback et al., 2004; Barrett et al., 2009). It is likely that direct optimization solutions will become less common and that the focus will shift to sampling the solution space and investigating the properties of these samples and determining whether solutions within these samples exist that have more descriptive or predictive value than others.

9.07.4.2 Taking into Account Spatial and Temporal Variability

LIM gives an average food web quantified for a characteristic time period and space, determined by the data available. However, natural systems are known to demonstrate strong spatial and temporal variability. Coastal areas, for example, are characterized by strong transfers of energy along an inshore–offshore gradient and between the water column and the benthic environment. There can also be strong seasonal variability in coastal areas, which has a great impact on ecosystem components and their spatial relationships. Therefore, an important addition to inverse techniques is to incorporate these spatio-temporal interactions.

In LIM, one method for incorporating temporal variability is to model a succession of periods, but this does not take into account the coupling of the biomass changes from one period to another. Consider an example from an intertidal temperate mudflat. Some properties are highly variable between seasons, whereas others can be considered invariant. A coupled procedure can be devised where certain equations operate only on the flows within a season, whereas other equations apply to the complete year. The method is presented in **Figure 5** (Degré et al., 2006) for a regime of two seasons.

The algorithm for the calculation remains the same as presented before, but the coupled method proposes another way to build the vectors and matrices of equalities and inequalities. The vector of unknowns $\mathbf{x}$ is composed of the two vectors $\mathbf{x_1}$ and $\mathbf{x_2}$, which contain the flows of the two seasons (written as transposed vectors in **Figure 5**). The mass-balance equations are established for the whole year and determine a first set of equations (matrix with the coefficients of the linear equations is A_e and constant terms of the right-hand side of the equation in $\mathbf{b_e}$). Another set of equations is built for each season and determines two matrices of coefficients (A_1, A_2) and two right-hand vectors ($\mathbf{b_1}$ and $\mathbf{b_2}$). Then a set of equations concerns annual information for observations that cannot be resolved between the seasons and defines the matrix A_g and the vector $\mathbf{b_g}$.

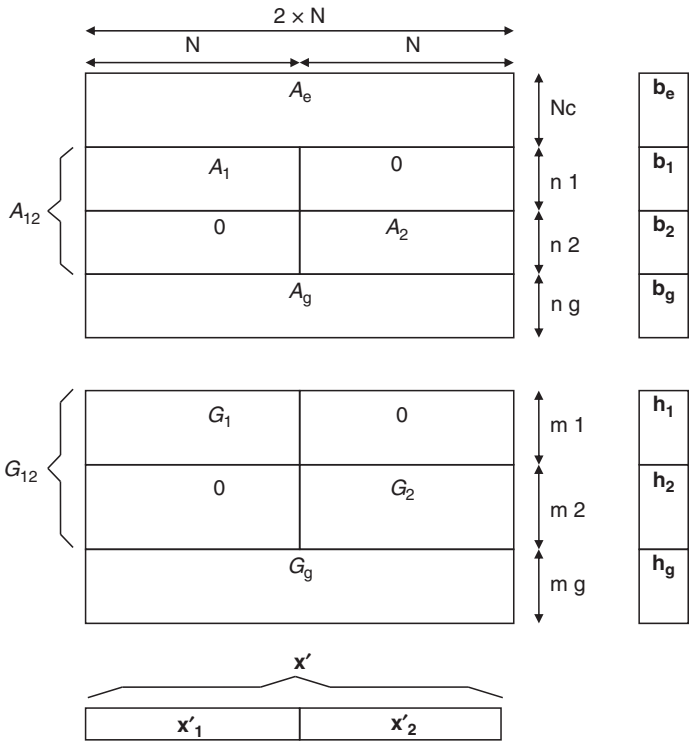


Figure 5 Introduction of spatio-temporal changes into LIM. Construction of the matrices A and G and of the vectors $\mathbf{b}$ and $\mathbf{h}$ for inverse analysis applied to a two-coupled-seasons model. A_e is the annual equilibrium equation matrix, A_1 and A_2 are the two seasonal equation matrices, A_g is the annual equation matrix. $\mathbf{b_e}$ (null vector), $\mathbf{b_1}$, $\mathbf{b_2}$, and $\mathbf{b_g}$ are the associated right-hand side constant vectors. G_1 and G_2 are the two seasonal inequality matrices; G_g is the annual inequality matrix. $\mathbf{h_1}$, $\mathbf{h_2}$, and $\mathbf{h_g}$ are the associated solution vectors. $\mathbf{x'}$ is the transposed vector of $\mathbf{x}$, the solution vector, composed of the solution vector $\mathbf{x_1}$ for season 1 and the solution vector $\mathbf{x_2}$ for season 2. These are column vectors and hence appear here in their transposed form: $\mathbf{x'}$.

All these matrices are assembled as shown in Figure 5, which allows defining an equation:

$$\mathrm{A} \times \boldsymbol{x} = \mathbf{b} \quad [1]$$

where A is the association of A_e, A_1, A_2, and A_g as in Figure 5 and $\mathbf{b}$ is an association of $\mathbf{b_e}$, $\mathbf{b_1}$, $\mathbf{b_2}$, and $\mathbf{b_g}$.

The inequalities are defined for the two seasons, which allows the building of matrices G_1 and G_2 of coefficients, and the boundary vectors $\mathbf{h_1}$ and $\mathbf{h_2}$. Some inequalities apply on an annual basis, which defines the matrix G_g of coefficients and the vector $\mathbf{h_g}$ of the boundaries. These matrices and vectors are associated as shown in Figure 5 and define the set of inequalities:

$$\mathrm{G} \times \boldsymbol{x} \geq \mathbf{h} \quad [2]$$

where G is the association of G_1, G_2, and G_g as in Figure 5 and $\mathbf{h}$ is an association of $\mathbf{h_1}$, $\mathbf{h_2}$, and $\mathbf{h_g}$.

Then the resolution is done using the inverse algorithms described previously.

Such a procedure is applied in Degré et al. (2006) for a coupled model of warm and cold seasons in two intertidal ecosystems of the Atlantic Coast of France. The seasonal or annual definition of the constraints was defined by the available information. In such a context, it is important to know the variation of the biomass of compartments between the two seasons. In this example, seasonal information was available for primary production, respiration of some compartments, DOC exudation, and some grazing flows, whereas only annual information was available for other compartments.

9.07.4.3 Constraining the Flows Using Tracers

Adding new, independent information reduces the model's solution space and leads to better-constrained results. Whereas the most commonly available data in food web models consist of biomasses and occasional rate measurements, stable isotope data provide integrated diet information and information of trophic position, and have proven to give valuable information on food webs (e.g., van Oevelen et al., 2006b, 2009). However, their usefulness depends on at least two requirements: (1) the different food sources should have different isotope signatures and (2) the isotope signature of a food should be measurable. For instance, it is not straightforward to measure the isotope composition of benthic algae that are mixed with sedimentary organic material. A way to overcome this limitation is to experimentally manipulate the isotopic signature of a food source. For instance, injection of labeled bicarbonate will isotopically enrich algae (Middelburg et al., 2000); adding labeled glucose will label bacteria (van Oevelen et al., 2006a). As organisms consume the labeled material, they also become isotopically enriched, and the timing and magnitude of label incorporation provide information about the importance of the food in the consumer's diet. Transient simulations combined with LIM were pioneered by Jackson and Eldridge (1992), who simulated the fate of a tracer introduced in a pelagic food web inferred by LIM-MN.

Starting from an inverse solution, it is relatively straightforward to derive a tracer model that simulates tracer dynamics in each compartment of the food web. The dynamic model is developed by categorizing the food web interactions into interactions that are source based (e.g., mortality, excretion, dissolution of detritus, and export) and interactions that are source–sink based such as predation and grazing. In a source–sink based interaction, the intensity of the flow depends on both the stock of the source and the sink; in a source-based interaction, there is only dependence on the source.

For each interaction, a rate constant is then calculated by dividing the magnitude of the flows by the size of the source compartment or of the product of the size of the source by the size of the sink compartment (note that the units of the rate parameters differ):

Source based

$$r^{S}_{i\to j} = \frac{\mathrm{Flow}_{i\to j}}{C_i} \quad [3]$$

Source–sink based

$$r^{SS}_{i\to j} = \frac{\mathrm{Flow}_{i\to j}}{C_i \cdot C_j} \quad [4]$$

where C_i is the stock size (in mass) of compartment i.

The feces production and respiration can be modeled as a function of the grazing, by assuming that a fixed part of the uptake flows to the detritus pools as feces (through the assimilation efficiency formulation) and that part of the assimilated food is respired as growth respiration (through the net growth efficiency formulation).

During transient simulation, the rate constants are multiplied with the tracer concentration of the source compartment (if source based), or of the product of source and sink compartment (source–sink based flows). Thus, the rate coefficients enter the dynamic model equations by describing the rate of change of component i as

$$\frac{\mathrm{d}C_i}{\mathrm{d}t} = \sum_j r^{S}_{j\to i}\cdot C_j - \sum_j r^{S}_{i\to j}\cdot C_i + \sum_j r^{SS}_{j\to i}\cdot C_i\cdot C_j - \sum_j r^{SS}_{i\to j}\cdot C_i\cdot C_j \quad [5]$$

The model is initialized by injection of the tracer in the relevant compartment.

It is quite natural to combine these transient simulations with the LIM-MCMC sampling techniques. Starting from an inverse modeling solution (as generated by an LIM-MCMC step), the transient simulation is run and the probability of this model, given the data, estimated. The probability obtained from the dynamic model is then used to define the acceptance ratio of the sampled LIM solution.

A somewhat simplified version of the combined use of LIM and transient simulation was used by van Oevelen et al. (2006b) to better quantify the food web from an intertidal mudflat. These authors first made a traditional LIM model based on carbon biomass and stable isotopic data. Then, MCMC sampling of this LIM was combined with a transient simulation, reproducing the data from a pulse-chase labeling of microphytobenthic carbon (Middelburg et al., 2000). It was shown that using both these types of data significantly improved the quality of the inverse food web reconstruction.

9.07.5 Analyzing the Results from LIM

Depending on the method selected, one can obtain a single solution from direct optimization, a single solution from averaging a sample of plausible solutions, or work directly from a

multivariate probability density function of the plausible solutions. In any case, the result characterizes a food web over a time span and a spatial area defined by the investigator, constrained by the available data and the variability of the studied system. Sensitivity analysis is used to characterize the robustness of the results obtained using LIM. Further analysis of the results can be direct by comparing the magnitude of the different flows, or indirect using indices calculated for characterizing the properties of the system. ENA indices are often used at this stage for comparing systems between temporal stages or spatial zones.

9.07.5.1 Sensitivity Analysis

The motivation behind sensitivity analysis is to assess how dependent the result is to the quality or precision of the input data. These techniques apply similarly to the types of solution defined above. Several methods exist for assessing the sensitivity of the reconstructed food web to changes in the assumptions. The impact of adding or removing links in the *a priori* model can be investigated. The inequalities can be modified. However, the most often used sensitivity analysis is based on the investigation of the influence of variations in the field data used as hard constraints (the equalities). The measured processes are varied by minus or plus a certain percentage. Then the consequences of this variation on the properties of the system are observed.

The question of the robustness is then: "to which field data is the result the most sensitive?" or "which LIM-determined flows are the most sensitive to variations in input data?" Then an overall characterization of the sensitivity of one system is possible for comparing sensitivity between systems. A sensitivity index was proposed (Richardson et al., 2003) to compare the sensitivity between food webs, between flows, or between input data. It relies on the computation of relative variations between each flow values, after a modification of each input data. Simulations are realized where each data are modified by plus or minus 10% or 20%. Then the value for each flow is calculated using inverse analysis and the result is compared to the value obtained with the initial value of the data. The results of inverse analysis calculated with the data value are considered as a reference and compared to the flow values obtained with the simulated variation of the input data.

The computation of the sensitivity index is as follows:

$$\mathrm{SI}(D,R) = \left\langle \frac{\frac{R(s)-R_{\mathrm{ref}}}{R_{\mathrm{ref}}}}{\frac{D(s)-D_{\mathrm{ref}}}{D_{\mathrm{ref}}}} \right\rangle_s \qquad [6]$$

where D stands for tested data, R for resulting flux, ref for reference model, and s for simulation. For each parameter and each resulting flux, SI is the mean sensitivity obtained over all simulations, which is symbolized by $\langle\rangle_s$. This index corresponds to the ratio of the relative variation of the result to the relative variation of the input data. The sum of SI over all the results R for one input data (D) variation is then computed. This index SI(D) gives the overall influence of this parameter on the results. The same principle can be applied for the computation of the global impact on one result. $R(s)$ can be a single solution from direct optimization, or an average of a sample of solutions obtained with Monte Carlo techniques.

With Monte Carlo techniques, it is possible to specify variances for the measurements from which possible values of the measurements can be sampled simultaneously with possible values of the flows from the polytope defined by the inequality constraints (Van den Meersche et al., 2009; van Oevelen et al., 2010). The resulting marginal probability density functions incorporate both the effect of measurement uncertainty and the uncertainty resulting from the lack of observations. Running the analysis again by setting the observational variances to zero would generate the probability density functions that account for the underdeterminacy only and would allow an assessment of the impact of observational error on the results. These techniques have not been applied yet in the literature but have the potential to account more fully for the uncertainty in the solutions to these inverse food web problems.

9.07.5.2 Ecological Network Analysis

Pimm (1982) compared a quantified scheme of a food web to a spaghetti plate. This underlines the fact that any result of inverse analysis with a model describing a mean state cannot easily be compared to another one, just by a discussion on the magnitude of the flow. In this context, the use of ENA is needed to advance the analysis of the results in terms of ecological function (Ulanowicz, 1997).

The historical development of LIM-MN has led to the possibility to develop comparisons between different systems or different stages (Savenkoff et al., 2007; Marquis et al., 2007; see this example developed in Section 9.07.7), based on different ENA indices. Such indices were also applied in large intersystems comparisons (cf. Leguerrier et al., 2007, who used principal component analysis based on ENA indices in order to remove the common information carried by those indices; **Figure 6**). However, such comparisons cannot have a statistical value in the context of LIM-MN that gives a unique solution. The Monte Carlo approaches that led to a sampling of the polytope defining the space of solution (see explanations in Section 9.07.4) allow the possibility of not only defining a confidence interval for the values of each flow (van Oevelen et al., 2009b) but also ENA indices (Kones et al., 2009; van Oevelen et al., 2010). Such a context opens the possibility for statistical comparisons of ENA indices between the described systems.

9.07.6 Guidelines on Methodological Choices for the Use of LIM in Coastal Ecology

In this chapter, we describe the state of the art in LIM and present recent methodological advances. The first recommendation that can be made in the general context of applying LIM to food web studies is that direct optimization, such as the LIM-MN method, is likely to be supplanted by Monte Carlo techniques that have matured recently. This methodological development is still under progress. The focus of further developments will be (1) to develop ways to characterize and synthesize the probability density functions of the inverse solutions, using multivariate analyses, and (2) to assess which

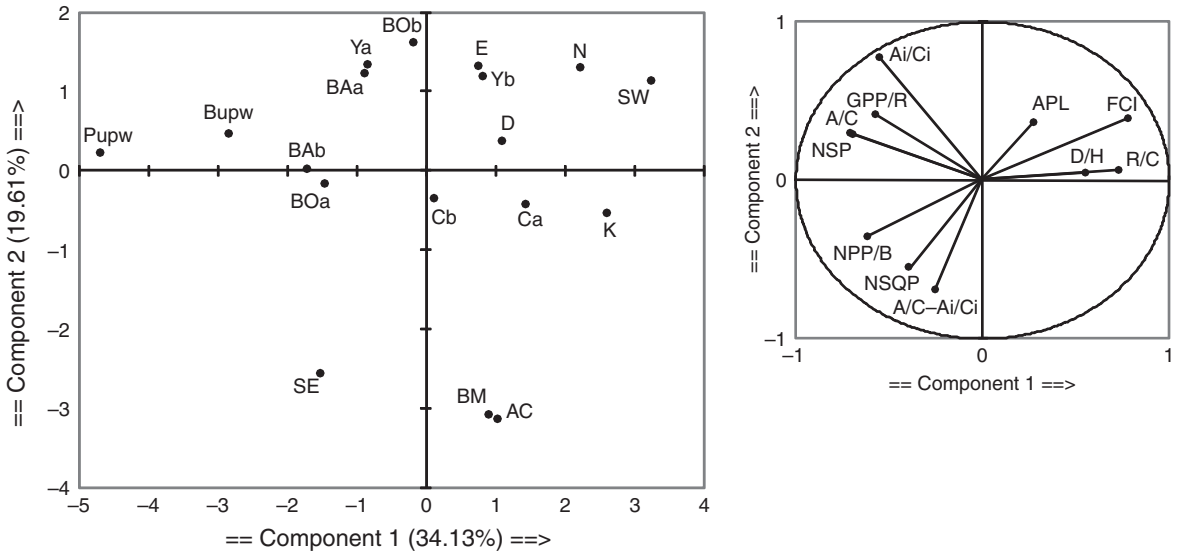


Figure 6 From Leguerrier et al. (2007), incorporation of two inverse modeled ecosystems (BM, Brouage Mudflat in Marennes-Oléron Bay and AC, Aiguillon Cove, located 40 km North from it) into a more general inter-ecosystem comparison of ecological network analysis indices of food webs built with other methods (Ecopath or direct approach), but with a relatively similar number of compartments (from 12 to 24). SE, = Seine Estuary (Ecopath; Rybarczyk and Elkaïm, 2003); Pupw, Peruvian upwelling (direct approach; Baird et al., 1991); Bupw, = Benguela upwelling southern system (Baird et al., 1991); Baa, Baltic proper (Sandberg et al., 2000); BAb, Baltic proper (Baird et al., 1991); BOa, Bothnian Bay (Sandberg et al., 2000); BOa, Bothnian Sea (Sandberg et al., 2000); Ya, Ythan Estuary (Baird and Milne, 1981); Yb, Ythan Estuary (Baird and Ulanowicz, 1993); E, Ems Estuary (Baird et al., 1991); D, Delaware Bay (Monaco and Ulanowicz, 1997: 5); N, Narragansett Bay (Monaco and Ulanowicz, 1997: 5); SW, Swartkops Estuary (Baird et al., 1991); K, Kromme estuary (Baird and Ulanowicz, 1993); Ca, Chesapeake Bay (Monaco and Ulanowicz, 1997); Cb, Chesapeake Bay (Baird et al., 1991). NSP, net system production (g-C m^{-2} yr^{-1}); NSQP, net system quality production (based on the net production of Exergy sensu Marques et al. (1997)); D/H, detritivory/herbivory; APL, average path length; FCI, Finn cycling index; A/C, relative ascendency (ascendency/development capacity); R/C, relative redundancy; Ai/Ci, internal relative ascendency (internal ascendency/internal development capacity); GPP/R, gross primary production/total respiration; NPP/B, net primary production/total biomass.

descriptors have greater predictive values. The initial optimization context gave a result corresponding to a flow vector. Any flow was then estimated by a single value. The new methods now give a probability density function that will enrich the discussions from a statistical point of view. However, the description of food webs as a network of probability density functions is difficult and it will always be useful to collapse the complex MCMC results into unique numbers or fewer dimensions. The question is then to know on which criterion this simplification should be made: the mean value, the median, the least squares, a linear combination of the flows, or any criteria from ecological theories. In the context of coastal ecology, the existence of a very complete data set as the Sylt-Rømø Bight (Baird et al., 2004, 2007), where almost every process has been quantified, is a useful foundation for further methodological developments. This data set is currently analyzed with the objective to define the best goal function for choosing a unique set of flow values (Saint-Béat et al., in preparation).

Another question in the context of LIM applications to coastal ecology is the minimum set of data required. This is still an open question as no studies have been able to strictly indentify this minimum set of data required for an estimation of all flows with a sufficient accuracy. What can be deduced from our experience in coastal ecology, and through the sensitivity analyses realized, is that exchanges with ecosystems adjacent to the one in study are of primary importance. A good local estimation of the primary production is essential and should not be deduced from production/biomass ratios, which are highly variable, especially when microorganisms are concerned. Migration, imports, and exports should also be described locally as far as possible. The use of circulation models to constrain transport in advective environments could be very useful. This variability in standing stocks should also be estimated when feasible, although most of the time the variation in biomass is small compared to the flows through the food web (inferior to the level of precision of any measurement). Sensitivity analysis associated with optimization methods such as LIM-MN, and probability density functions in the LIM-MCMC techniques can be used to address gaps in the data set. The role of the inverse modeler is then very structuring in a coastal ecology research team, as she/he can then define a priority order of the flows and processes that need to be estimated to a good level of precision in the description of the food web.

In previous applications in coastal ecology, the temporal and spatial scales considered were highly variable. Here again, there is no general rule for making this choice. The steady-state assumption does not imply that the system remains constant in the course of the period described, but only that mass accumulation or depletion between the beginning and the end of the period averaged could be neglected compared to the flow values estimated. However, the ecological conclusions will be more appropriate if the function described corresponds to a trophic state, and not an association of several different states. In this case, a nested association of temporal scales would be useful. The same is true for spatial scales.

Our final recommendations refer to the definition of compartments in the food web model. An inverse modeler must decide on a level of aggregation for compartments, and what compartments may be neglected, due to scarcity of information (e.g., microbial items). To answer this question, Johnson et al. (2009) investigated the effects of the extent and type of aggregation of food web compartments on both the results of LIM-MN and ENA of LIM-MN-determined flows and actual flows. LIM-MN was carried out on the Sylt-Rømø Bight food web (Baird et al., 2004), where some known flows were assumed unknown. By comparing flows estimated by LIM-MN on 14 different aggregations of the same food web to known values for the food web, it was determined that the use of the parsimony principle consistently underestimated both the size and the complexity of the food web. More flows were estimated as missing (had a value of 0), and the nonzero estimated flows tended to be smaller than their actual value. This, in turn, led to differences in ENA indices between estimated and actual values within differently aggregated models. For example, the herbivory/detritivory (H/D) was consistently overestimated by LIM-MN because, as discussed above, it is more efficient, or more fitting with the parsimony principle, for consumers to directly feed on plants than for consumers to feed on detritus made up of dead plant matter (which would involve two flows, one from plants to detritus and another from detritus to consumer).

The ENA indices that were least sensitive to LIM-MN were topological indices of the weighted network, especially those which were scaled by the calculated size of the system: relative ascendency and relative redundancy. It is suggested that the LIM-MN be carried out on the most disaggregated *a priori* model possible, and that any aggregation necessary for an investigation (such as comparison with systems of greater aggregation) be carried out on the LIM results. In particular, aggregation of low trophic level compartments led to profound underestimation of system size and complexity as measured by ENA. Johnson et al. (2009) suggested that care should be taken in comparing food webs where flows have been estimated by different methods or on food webs of different levels of aggregation, as bias is introduced by the method of determining unknown flows. It also suggests that the low trophic levels and especially microbial items are essential for a good description of the overall ecological functioning, when building the *a priori* model (step 1 in Section 9.07.3.1).

9.07.7 An Example of Application: A Comparison of Plankton Models in the Bay of Biscay during the Late Winter/Spring Succession Period

Here, we present a simple case (Marquis et al., 2007), with few data constraints and without coupling of seasons or tracer constraints, for pedagogical reasons. For more complex examples, see the articles from **Table 1**, especially Degré et al. (2006) for seasonal coupling, van Oevelen et al. (2006b) for tracers, and Kones et al. (2009) for LIM-MCMC applications in coastal planktonic systems with the use of ENA on the resulting probability density functions.

As compared to intertidal or nearshore zones, the available data for processes are usually scarcer when the location is further offshore. This example utilizes the available data on the continental shelf in order to reconstruct the functioning of the plankton system through the development of the winter–spring succession. The continental shelf of the Bay of Biscay is characterized by the great influence of two large river plumes, the Loire and the Gironde. At the end of winter, halostratification and a temporary increase in luminosity sometimes induce an early phytoplankton bloom (Labry et al., 2001). This bloom considerably reduces the amount of phosphate available within the surface layer of the water column (Labry et al., 2002), leading to a phytoplankton community dominated by small-size cells in spring. Gathering data from cruises that took place at different periods and sites of the Gironde and Loire plume, Marquis et al. (2007) were able to determine, from nutrient concentration, cell-size structure in the phytoplankton and thermo-halostratification at which stage of the succession the cruise took place. From a very incomplete set of information on the processes, they were able to build, with the LIM-MN method, the carbon food web at each stage of the succession. The *a priori* model was composed of three size classes of phytoplankton (ph1, ph2, and ph3), heterotrophic bacteria (bac), unicellular (pro) and multicellular (mes) zooplankton, and two non-living compartments (particular non-living carbon called detritus, det, and dissolved organic carbon, doc). The possible flows are given in **Table 3**. They constitute the 32 unknowns in each system.

For each of the eight compartments, a mass-balance equation was established for which steady state was assumed, meaning that they neglected the daily variation of each biomass, which was considered small relative to the magnitude of each flow value. Such an assumption can be violated under a seasonal succession during which daily variations can be large. If the measures had been available, it would have been possible here to incorporate a daily mean modification of the biomass for each compartment (see, e.g., Donali et al., 1999). Then, data were available for some processes and these were used to construct additional linear equalities (**Table 4**). The best-documented situation was for the late spring with eight equalities for the process rates. The minimal situation was in early spring with only four equalities, corresponding to primary production for each size class of phytoplankton and to bacterial production. This is really the minimum information possible for such a process of applying inverse analysis as only four flows were estimated out of 32. It is crucial to have precise information of the primary production in the food web, the main input of carbon, and more generally on exchanges between the system and the adjacent environment. Indeed, sensitivity analyses show that primary production is the process to which the structure inside the system is most sensitive (Niquil et al., 1998; Richardson et al., 2003; Marquis et al., 2007). The system of equations is then composed of 12–16 equations for 32 unknowns. This defines a space of solution that will be bounded by the skew walls of the set of inequalities.

The inequalities were composed of 28 bounds to different efficiencies (**Table 5**). The efficiencies expressed as ratio of flows have to be translated into linear inequalities: for example, the gross production efficiency of protozoa is usually expressed as production/ingestion that is between 25% and 50%. As production = ingestion − (respiration + excretion + ejection), the ratio can be linearized under the inequalities (because all inequalities must be in the same form, negative values are used rather than positive):

Table 3 Bay of Biscay models along the winter/spring plankton succession

		Late winter		*Spring*		*Late spring*
Symbol	*Description*	*Biomet3*	*Biomet3*	*PEL-A*	*PEL-B*	*Biomet1*
Cgpp TOph1	Gross primary production of small phytoplankton	**58.9**	**45.1**	**653.8**	**802.2**	**285.0**
Cgpp TOph2	Gross primary production of intermediate phytoplankton	**155.6**	**151.9**	**255.9**	**316.9**	**246.9**
Cgpp TOph3	Gross primary production of large phytoplankton	**281.9**	**142.3**	**756.0**	**25.5**	**99.9**
Cph1TOres	Respiration by small phytoplankton	17.7	13.5	43.6	40.1	14.3
Cph1TOpro	Grazing of small phytoplankton by protozoa	16.2	1.4	301.4	331.5	**110.2**
Cph1TOdet	Detritus production by small phytoplankton	20.9	12.8	247.8	299.4	38.5
Cph1TOdoc	DOC excretion by small phytoplankton	4.1	17.4	61.0	131.2	122.1
Cph2TOres	Respiration by intermediate phytoplankton	36.0	7.6	76.8	58.0	12.3
Cph2TOpro	Grazing of intermediate phytoplankton by protozoa	51.5	30.1	61.4	0.0	**86.8**
Cph2TOmes	Grazing of intermediate phytoplankton by mesozooplankton	**0.0**	**12.1**	92.1	131.2	**33.9**
Cph2TOdet	Detritus production by intermediate phytoplankton	56.1	41.4	7.8	101.9	15.1
Cph2TOdoc	DOC excretion by intermediate phytoplankton	12.0	60.7	17.9	25.9	98.8
Cph3TOres	Respiration by large phytoplankton	16.2	7.1	37.8	7.7	30.0
Cph3TOmes	Grazing of large phytoplankton by mesozooplankton	**26.6**	**19.0**	365.3	16.1	**25.1**
Cph3TOdet	Detritus production by large phytoplankton	143.3	48.4	281.1	0.0	6.3
Cph3TOdoc	DOC excretion by large phytoplankton	95.9	67.7	71.8	1.8	38.5
CproTOres	Respiration by protozoa	84.6	74.5	256.8	156.5	210.4
CproTOmes	Grazing of protozoa by mesozooplankton	38.4	33.9	116.7	117.1	112.0
CproTOdet	Detritus production by protozoa	15.4	13.6	46.7	87.8	44.8
CproTOdoc	DOC excretion by heterotrophic protozoa	15.4	13.6	46.7	40.2	80.8
CmesTOres	Respiration by mesozooplankton	46.8	34.0	230.4	155.3	61.3
CmesTOdet	Detritus production by mesozooplankton	26.7	19.4	131.7	88.7	**35.0**
CmesTOdoc	DOC excretion by mesozooplankton	13.4	9.7	65.8	44.4	17.5
CmesTOlos	Outflows of mesozooplankton by predation	46.8	34.0	230.4	155.3	61.2
CdocTObac	DOC absorption by bacteria	**172.2**	**208.0**	**399.0**	**331.4**	**502.0**
CbacTOres	Respiration by bacteria	86.1	84.4	348.4	293.5	190.3
CbacTOpro	Grazing of bacteria by protozoa	86.1	104.0	50.6	37.8	251.0
CbacTOdoc	DOC excretion by bacteria	0.0	19.6	0.0	0.0	60.7
CdetTOdoc	Detritus dissolution into DOC	31.5	19.3	135.7	88.0	83.7
CdetTOpro	Detritus consumption by protozoa	0.0	0.0	53.6	32.2	0.0
CdetTOmes	Detritus consumption by mesozooplankton	68.6	32.1	84.3	179.2	4.0
CdetTOlos	Outflows of detritus by sedimentation	162.4	84.1	441.5	278.4	**52.0**

Flows formulations, descriptions and values (mg-C m^{-2} day^{-1}) issued from direct measures (bold font) and from inverse analysis calculations (normal font) (adapted from Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A., Labry, C., Sautour, B., Laborde, P., Vézian, A., Dupuy, C., 2007. Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. Estuarine, Coastal and Shelf Science 73, 223–235). Symbols define the flow of carbon (C) from one compartment (that indicated by three lower case letters following C) to another (the three lower case letters following TO); thus Cph1TOres means the flow of carbon from compartment phytoplankton 1 to respiration.

$$0.5(\text{Sum of ingestion flows}) - (\text{respiration} + \text{excretion} + \text{ejection flows}) \leq 0 \quad [7]$$

and

$$-0.75(\text{Sum of ingestion flows}) + (\text{respiration} + \text{excretion} + \text{ejection flows}) \leq 0 \quad [8]$$

Some of the inequalities, especially respiration and ingestion rates, are derived from allometric equations (Moloney and Field, 1989) and combined information on biomass, average cell mass, and temperature.

The results were compared according to mainly two properties, quantified using two ENA indices: the Finn cycling index for quantifying the recycling, and the H/D ratio for quantifying the main origin of the organic carbon circulating in the food web. The result (**Figure 7**) shows great differences between these two properties during succession. The late winter, in a situation of postwinter bloom, with a high bacterial production compared to the phytoplankton primary production, is characterized by high recycling and a low H/D ratio. The spring bloom situation, however, is exactly the opposite with a high H/D ratio. The late spring situation, which is once again postbloom, is similar to the late winter situation. The recycling, quantified by the Finn cycling index, is negatively correlated with the H/D, as strong detritivory favors recycling.

This comparison is not possible from a statistical point of view as the range of variation is not defined. What can be added from the sensitivity analysis (Marquis et al., 2007) is that the comparison is robust when applying a 10% variation of the processes measured *in situ*. However, no interval of confidence can be defined at this stage, even if we know that the scarcity of the initial data should leave a large degree of uncertainty in these results.

The example presented here was built in the context of a significant lack of data, the typical situation in food web reconstructions, and the constraints defined for an application of the LIM-MN method. When applying the LIM-MCMC approach to

Table 4 Field data used as equalities to build the five systems along the plankton succession in the Bay of Biscay

		Late winter		*Spring*		*Late spring*
Data	*Equation*	*Biomet3N*	*Biomet3S*	*PEL-A*	*PEL-B*	*Biomet1*
Picophytoplankton production	CgppTOph1 – 0.5Cph1TOres	50.1	38.4	632.0	782.1	277.9
Nanophytoplankton production	CgppTOph2 – 0.5Cph2TOres	137.6	148.1	217.5	287.9	240.7
Microphytoplankton production	CgppTOph3 – 0.5Cph3TOres	273.8	138.7	737.1	21.7	84.9
Bacterial production	CbacTOpro	86.1	104.0	50.6	37.8	251.0
Mesozooplankton grazing on nano- and micro-phytoplankton	Cph2TOmes + Cph3TOmes	65.0	65.0	Not est.	Not est.	171.0
Protozoa grazing on nano- and micro-phytoplankton	Cph1TOpro + Cph2TOpro	Not est.	Not est.	Not est.	Not est.	197.0
Mesozooplankton fecal pellet sinking rate	CmesTOdet	Not est.	Not est.	Not est.	Not est.	35.0
Sedimentation of detritus	CdetTOlos	Not est.	Not est.	Not est.	Not est.	52.0

Not est. means not estimated. Values are in mg-C m^{-2} day^{-1}. Flows are defined as in the symbol column of Table 3.

Adapted from Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A., Labry, C., Sautour, B., Laborde, P., Vézina, A., Dupuy, C., 2007. Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. Estuarine, Coastal and Shelf Science 73, 223–235.

Table 5 Biological constraints used as inequalities to build the five systems along the plankton late-winter/spring succession in the Bay of Biscay

Compartment	*Process*	*Bound*	*Description*	*Inequality*	*Reference*
Phytoplankton	Respiration	Both	Respiration of phytoplankton ranges between 5% and 30% of gross primary production.	Res–0.05 GPP ≥ 0 Res–0.30 GPP ≤ 0	Vézina and Platt (1988)
	Excretion	Both	Excretion of phytoplankton ranges between 10% and 55% of net primary production(NPP)	0.10 NPP – CphTOdoc ≤ 0 0.55 NPP – CphTOdoc ≥ 0	Modified from Vézina and Pace (1994)
Bacteria	Respiration	Lower	Respiration by bacteria is at least 20% of total ingestion	0.2 (Total ingestion) – Res ≤ 0	Vézina et al. (2000)
		Upper	Respiration by bacteria does not exceed maximum specific respiration (function of cell mass (W) and temperature (T) x biomass (B))	Max spe res = $3.6W^{-0.25}$ $e^{0.0693(T-20)}$ (B × Max spe res)– Res ≤ 0	Vézina and Pace (1994) according to Moloney and Field (1989)
	Net production efficiency	Both	The sum of respiration and excretion by bacteria ranges between 50% and 75% of DOC uptake.	0.50 CdocTObac – (Res + CbacTOdoc) ≤ 0 0.75 CdocTObac – (Res + CbacTOdoc) ≥ 0	Vézina et al. (2000)
Protozoa	Respiration	Lower	Respiration by prototoza is at least 20% of total ingestion	0.2 (Total ingestion) – Res ≤ 0	Vézina and Pace (1994)
		Upper	Respiration by protozoa does not exceed maximum specific respiration (function of cell mass (W) and temperature (T) x biomass (B))	Max spe res =$14W^{-0.25}$ $e^{0.0693(T-20)}$ (B × Max spe res)– Res ≤ 0	Vézina and Pace (1994) according to Moloney and Field (1989)
	Excretion	Both	DOC excretion by protozoa is at least 10% of total ingestion and does not exceed respiration.	0.10 (Total Ingestion) – CproTOdoc ≤ 0 Res – CproTOdoc ≥ 0	Vézina and pace (1994)
	Gross production efficiency	Both	Sum of respiration, excretion, and ejection by protozoa ranges between 50% and 75% of total ingestion.	0.50 (TotIng) – (Res + CproTOdoc + CproTOdet) ≤ 0 0.75 (TotIng) – (Res + CproTOdoc + CproTOdet) ≥ 0	Vézina et al. (2000)
	Ingestion	Upper	Total ingestion of protozoa does not exceed maximum specific ingestion (function of cell mass (W) and temperature (T) x biomass (B))	Max spe ing = $63W^{-0.25}$ $e^{0.0693(T-20)}$ (B × Max spe ing) – TotIng ≤ 0	Vézina and Pace (1994) according to Moloney and Field (1989)
	Assimilation efficiency	Both	Assimilation efficiency of protozoa ranges between 50% and 90% of total ingestion	– 0.50 TotIng – CproTOder ≤ 0 – 0.10 TotIng – CproTOder ≥ 0	Vézina and Platt (1988)

(*Continued*)

Table 5 (*Continued*)

Compartment	*Process*	*Bound*	*Description*	*Inequality*	*Reference*
Mesozooplankton	Respiration	Lower	Respiration by mesozooplankton is at least 20% of total ingestion	0.2 (Total ingestion) – Res ≤ 0	Vézina and Pace (1994)
		Upper	Respiration by mesozooplankton does not exceed maximum specific respiration (function of body mass(W) and temperature (T) × biomass (B))	Max spe res $=14W^{-0.25}\ e^{0.0693(T-20)}$ (B × Max spe res) – Res ≤ 0	Vézina and Pace (1994)according to Moloney and Field (1989)
	Excretion	Both	DOC excretion by protozoa is at least 10% of total ingestion and does not exceed respiration.	0.10 (Total Ingestion) – CproTOdoc ≤ 0 Res – CmesTOdoc ≥ 0	Vézina and Pace (1994)
	Gross production efficiency	Both	Sum of respiration, excretion, and ejection by mesozooplankton ranges between 50% and 75% of total ingestion.	0.50 (TotIng) – (Res + CproTOdoc + CmesTOdet) ≤ 0 0.75 (TotIng) – (Res + CmesTOdoc + CmesTOdet) ≥ 0	Vézina et al. (2000)
	Ingestion	Upper	Total ingestion of mesozooplankton does not exceed maximum specific ingestion (function of body mass (W) and temperature (T) × biomass (B))	Max spe ing $=63W^{-0.25}\ e^{0.0693(T-20)}$ (B × Max spe ing)– TotIng≤ 0	Vézina and Pace (1994)according to Moloney and Field (1989)
	Assimilation efficiency	Both	Assimilation efficiency of mesozooplankton ranges between 50% and 80% of total ingestion	– 0.50 TotIng – CmesTOdet ≤ 0 – 0.20 TotIng – CmesTOdet ≥ 0	Vézina and Platt (1988)
DOC	Detritus dissolution	Lower	Detritus dissolution into DOC is at least 10% of the net primary production	CdetTOdoc – 0.10 NPP ≤ 0	Vézina and Pace (1994)
Detritus	Sedimentation	Upper	Detritus from cells and organisms > 2 μm can sediment	(Cph2TOdet + Cph3TOdet + CproTOdet + CmesTOdet) – CdetTOlos ≥ 0	This study

Adapted from Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A., Labry, C., Sautour, B., Laborde, P., Vézina, A., Dupuy, C., 2007. Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. Estuarine, Coastal and Shelf Science 73, 223–235.

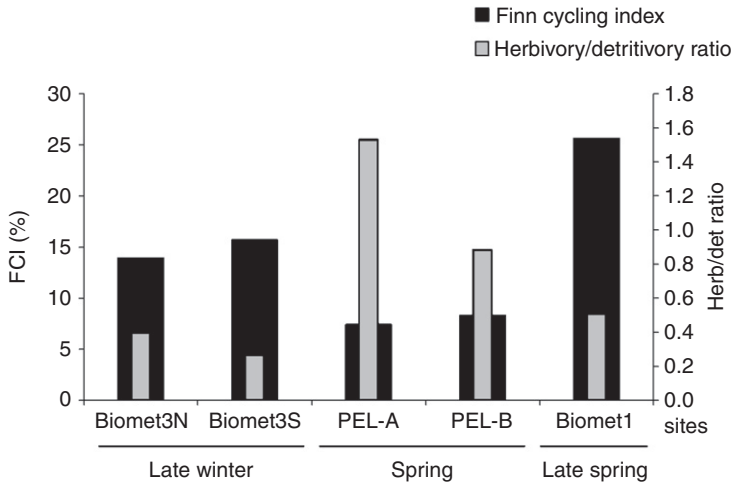


Figure 7 Dynamic of evolution of the Finn cycling index and herbivory/detritivory ratio along the development of the plankton succession in winter/spring in the Bay of Biscay (Marquis et al., 2007).

this situation, the probability density functions were determined for each flow value and then for the two indices from ENA, namely the Finn cycling index and the H/D ratio. Theses probability density functions showed that the five states described presented a high indeterminacy with wide intervals of values and that no difference appeared as statistically significant because of the overlap, for each index, of the five probability density functions. The application of the LIM-MCMC technique to this data set underlines the fact that the constraints should be reinforced in the context of statistical comparisons.

9.07.8 Conclusion

To conclude on the choice of a method for food web building, LIM combines and makes explicit many of the other commonly used methods for determining unknown flows. Most methods for estimating missing values of the flows rely on data from similar or neighboring systems. In LIM, this information is used as ranges for the constraints and the user does not need to select a specific value but let the optimization method choose the most appropriate one. One consequence of this method is full repeatability of the application. This is especially important to research, and also for potential use of ENA indices as indicators of ecosystem state or health. Using LIM-MCMC methods to take into account indeterminacies and uncertainties in the input data and determining the probability density functions of the flows, and consequently of the ENA indices calculated from them, will lead to standardized protocols and will allow a clear evaluation of competing hypotheses and conclusions on the effects of global changes on coastal ecosystems.

Acknowledgments

Nathalie Niquil was supported by the French Research Agency sponsored program ANR Blanche VASIREMI (Trophic significance of microbial biofilms in tidal flats).

References

Baird, D., Asmus, H., Asmus, R., 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series 279, 45–61.

Baird, D., Asmus, H., Asmus, R., 2007. Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. Marine Ecology Progress Series 351, 25–41.

Baird, D., McGlade, J.M., Ulanowicz, R.E., 1991. The comparative ecology of six marine ecosystems. Philosophical Transactions of the Royal Society of London, Series B 333, 15–29.

Baird, D., Milne, H., 1981. Energy flow in the Ythan Estuary, Aberdeenshire, Scotland. Estuarine, Coastal and Shelf Science 13, 455–472.

Baird, D., Ulanowicz, R.E., 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Marine Ecology Progress Series 99, 221–237.

Barrett, C.L., Herrgard, M.J., Palsson B., 2009. Decomposing complex reaction networks using random sampling, principal component analysis and basis rotation. BMC Systems Biology 3, 30.

Breed, G.A., Jackson, G.A., Richardson, T.L., 2004. Sedimentation, carbon export and food web structure in the Mississippi River plume described by inverse analysis. Marine Ecology Progress Series 278, 35–51.

Chardy, P., Gros, P., Mercier, H., Monbet, Y., 1993. Benthic carbon budget for the Bay of Saint-Brieuc (western channel). Application of inverse method. Oceanologica Acta 16, 687–694.

Christensen, V., Pauly, D., 1992. ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61, 169–185.

Cook, P.L.M., van Oevelen, D., Soetaert, K., Middelburg, J.J., 2009. Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. IV. Inverse model analysis and synthesis. Marine Ecology Progress Series 394, 35–48.

Dambacher, J.M., Li, H.W., Rossignol, P.A., 2003. Qualitative predictions in model ecosystems. Ecological Modelling 161, 79–93.

Degré, D., Leguerrier, D., Armynot du Chatelet, E., Rzeznik, J., Auguet, J.-C., Dupuy, C., Marquis, E., Fichet, D., Struski, C., Joyeux, E., Sauriau, P.-G., Niquil, N., 2006. Comparative analysis of the food webs of two intertidal mudflats during two seasons using inverse modelling: Aiguillon Cove and Brouage Mudflat, France. Estuarine, Coastal and Shelf Science 69, 107–124.

De Laender, F., van Oevelen, D., Soetaert, K., Middelburg, J.J., 2010. Carbon transfer in a herbivore-dominated and a microbial loop-dominated pelagic food web: spring and summer in the southern Barents Sea. Marine Ecology Progress Series 398, 93–107.

Donali, E., Olli, K., Heiskanen, A.S., Andersen, T., 1999. Carbon flow patterns in the planktonic food web of the Gulf of Riga, the Baltic Sea: a reconstruction by the inverse method. Journal of Marine Systems 23, 251–268.

Eldridge, P.M., Cifuentes, L.A., Kaldy, J.E., 2005. Development of a stable-isotope constraint system for estuarine food-web models. Marine Ecology Progress Series 303, 73–90.

Eldridge, P.M., Jackson, G.A., 1992. Benthic food web flows in the Santa Monica Basin estimated using inverse methodology. In: Rowe, T., Pariente, V. (Eds.), *Deep-Sea Food Chains and the Global Carbon Cycle*. Kluwer Academic Press, Amsterdam, pp. 255–276.

Eldridge, P.M., Jackson, G.A., 1993. Benthic trophic dynamics in California coastal basin and continental slope communities inferred using inverse analysis. Marine Ecology Progress Series 99, 115–135.

Gaedke, U., Hochstädter, S., Straile, D., 2002. Interplay between energy limitation and nutritional deficiency: empirical data and food web models. Ecological Monographs 72, 251–270.

Grami, B., Niquil, N., Sakka Hlaili, A., Gosselin, M., Hamel, D., Hadj Mabrouk, H., 2008. The plankton food web of the Bizerte lagoon (south-western Mediterranean): II. Carbon steady-state modelling using inverse analysis. Estuarine, Coastal and Shelf Science 79, 101–113.

Heymans, J.J., Shannon L.J., Jarre, A., 2004. Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s. Ecological Modelling 172, 175–195.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933.

Jackson, G.A., Eldridge, P.M., 1992. Food web analysis of a planktonic system off Southern California. Progress in Oceanography 30, 223–251.

Jean, F., 1994. Modélisation à l'état stable des transferts de Carbone dans le réseau trophique benthique de la rade de Brest (France). Thèse de Doctorat, Université de Bretagne Occidentale, Brest.

Johnson, G.A., Niquil, N., Asmus, H., Bacher, C., Asmus, R., Baird, D., 2009. The effect of aggregation on the performance of the inverse method and indicators of network analysis. Ecological Modelling 220, 3448–3464.

Klepper, O., Van de Kamer, J.P.G., 1987. The use of mass balances to test and improve the estimates of carbon fluxes in an ecosystem. Mathematical Biosciences 85, 37–49.

Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. Ecological Modelling 220, 370–382.

Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., Mavuti, K., 2006. Gaining insight into food webs reconstructed by the inverse method. Journal of Marine Systems 60, 153–166.

Labry, C., Herbland, A., Delmas, D., 2002. The role of phosphorus on planktonic production of the Gironde plume waters in the Bay of Biscay. Journal of Plankton Research 24, 97–117.

Labry, C., Herbland, A., Delmas, D., Laborde, P., Lazure, P., Froidefond, J.M., Jegou, A.M., Sautour, B., 2001. Initiation of winter phytoplankton blooms within the Gironde plume waters in the Bay of Biscay. Marine Ecology Progress Series 212, 117–130.

Leguerrier, D., 2005. Construction et étude d'un modèle de réseau trophique de la vasière de Brouage (bassin de Marennes Oléron, France). Prise en compte de la saisonnalité et des échanges physiques pour la synthèse constructive des connaissances sur une zone intertidale d'une région tempérée.PhDThesis, University of La Rochelle, p. 655.

Leguerrier, D., Degré, D., Niquil, N., 2007. Network analysis and inter-ecosystem comparison of two intertidal mudflat food webs (Brouage Mudflat and Aiguillon Cove, SW France). Estuarine, Coastal and Shelf Science 74, 403–418.

Leguerrier, D., Niquil, N., Boileau, N., Rzeznik, J., Sauriau, P.-G., Le Moine, O., Bacher, C., 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. Marine Ecology Progress Series 246, 17–37.

Leguerrier, D., Niquil, N., Petiau, A., Bodoy, A., 2004. Modelling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France). Marine Ecology Progress Series 273, 147–161.

Marques, J.C., Pardal, M.A., Nielsen, S.N., Jørgensen, S.E., 1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. Ecological Modelling 102, 155–167.

Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A., Labry, C., Sautour, B., Laborde, P., Vézian, A., Dupuy, C., 2007. Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. Estuarine, Coastal and Shelf Science 73, 223–235.

Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T., Heip, C.H.R., 2000. The fate of intertidal microphytobenthos: an *in situ* ^{13}C labeling study. Limnology and Oceanography 45, 1224–1234.

Moloney, C.L., Field, J.G., 1989. General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. Limnology and Oceanography 34, 1290–1299.

Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Marine Ecology Progress Series 161, 239–254.

Niquil, N., Jackson, G.A., Legendre, L., Delesalle, B., 1998. Inverse model analysis of the planktonic food web of Takapoto Atoll (French Polynesia). Marine Ecology Progress Series 165, 17–29.

Niquil, N., Kerleguer, G., Leguerrier, D., Richard, P., Legrand, H., Dupuy, C., Pascal, P.-Y., Bacher, C., 2006. How would the loss of production due to an herbicide have repercussions in the food web of an intertidal mudflat? Sensitivity analysis of an inverse model for Brouage mudflat, Marennes-Oléron Bay, France. Cahiers de Biologie Marine 47, 63–71.

Niquil, N., Pouvreau, S., Sakka, A., Legendre, L., Adessi, L., Le Borgne, R., Charpy, L., Delesalle, B., 2001. Trophic web and carrying capacity in a pearl oyster farming lagoon (Takapoto, French Polynesia). Aquatic Living Resources 14, 165–174.

Olsen, Y., Andersen, T., Gismervik, I., Vadstein, O., 2007. Protozoan and metazoan zooplankton-mediated carbon flows in nutrient-enriched coastal planktonic communities. Marine Ecology Progress Series 331, 67–83.

Olsen, Y., Reinertsen, H., Vadstein, O., Andersen, T., Gismervik, I., Duarte, C., Agusti, S., Stibor, H., Sommer, U., Lignell, R., Tamminen, T., Lancelot, C., Rousseau, V., Hoell, E., Sanderud, K.A., 2001. Comparative analysis of food webs based on flow networks: effects of nutrient supply on structure and function of coastal plankton communities. Continental Shelf Research 21, 2043–2053.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., Jr., 1998. Fishing down marine food webs. Science 279, 860–863.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689–695.

Pimm, S.L., 1982. Food Webs. Chapman and Hall, London, p. 219.

Polis, G.A., 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86, 3–15.

Polis, G.A., Hurd, S.D., 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147, 396–423.

Richardson, T.L., Jackson, G.A., Burd, A.B., 2003. Planktonic food web dynamics in two contrasting regions of Florida Bay, U.S. Bulletin of Marine Science 73, 569–591.

Richardson, T.L., Jackson, G.A., Ducklow, H.W., Roman, M.R., 2006. Spatial and seasonal patterns of carbon cycling through planktonic food webs of the Arabian Sea determined by inverse analysis. Deep-Sea Research Part II: Topical Studies in Oceanography 53, 555–575.

Rybarczyk, H., Elkaïm, B., 2003. An analysis of the trophic network of a microtidal estuary: the Seine Estuary (Eastern Channel, Normandy, France). Estuarine, Coastal and Shelf Science 58, 775–791.

Sandberg, J., Elmgren, R., Wulff, F., 2000. Carbon flows in Baltic Sea food webs – a re-evaluation using a mass balance approach. Journal of Marine Systems 25, 249–260.

Savenkoff, C., Castonguay, M., Vézina, A.F., Despatie, S.-P., Chabot, D., Morissette, L., Hammil, M.O., 2004. Inverse modelling of trophic flows through an entire ecosystem: the northern Gulf of St. Lawrence in the mid-1980s. Canadian Journal of Fisheries and Aquatic Sciences 61, 2194–2214.

Savenkoff, C., Swain, D.P., Hanson, J.M., Castonguay, M., Hammill, M.O., Bourdages, H., Morissette, L., Chabot, D., 2007. Effects of fishing and predation in a heavily exploited ecosystem: comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). Ecological Modelling 204, 115–128.

Sherr, E.B., Sherr, B.F., 1988. Role of microbes in pelagic food webs: a revised concept. Limnology and Oceanography 33, 1225–1227.

Smith, R.L., 1984. Efficient Monte Carlo procedures for generating points uniformly. Operations Research 32, 1296–1308.

Tarantola, A., Valette, B., 1982. Generalized nonlinear inverse problems solved using the least squares criterion. Reviews of Geophysics and Space Physics 20, 219–232.

Ulanowicz, R.E., 1997. *Ecology, the Ascendant Perspective*. Columbia University Press, New York, 201 pp.

Vallino, J.J., Stephanopoulos, G., 1993. Metabolic flux distributions in *Corynebacterium glutamicum* during growth and lysine overproduction. Biotechnology Bioengineering 41, 633–646.

Van den Meersche, K., Soetaert, K., van Oevelen, D., 2009. xsample (): An R function for sampling linear inverse problems. Journal of Statistical Software 30, 1–15.

van Oevelen, D., Duineveld, G.C.A., Lavaleye, M.S.S., Mienis, F., Soetaert, K., Heip, C.H.R., 2009. The cold-water coral community as hotspot of carbon cycling on continental margins: a food web analysis from Rockall Bank (northeast Atlantic). Limnology and Oceanography 54, 1829–1844.

van Oevelen, D., Moodley, L., Soetaert, K., Middelburg, J.J., 2006a. The trophic significance of bacterial carbon in a marine intertidal sediment: results of an *in situ* stable isotope labeling study. Limnology and Oceanography 51, 2349–2359.

van Oevelen, D., Soetaert, K., Middelburg, J.J., Herman, P.M.J., Moodley, L., Hamels, I., Moens, T., Heip, C.H.R., 2006b. Carbon flows through a benthic food web: integrating biomass, isotope and tracer data. Journal of Marine Research 64, 453–482.

van Oevelen, D., Van den Meersche, K., Meysman, F., Soetaert, K., Middelburg, J.J., Vézina, A., 2010. Quantifying food web flows using linear inverse models. Ecosystems, 13(1), 32–45. doi:10.1007/s10021-009-9297-6.

Varma, A., Palsson, B., 1994. Metabolic flux balancing: basic concepts, scientific and practical use. Nature Biotechnology 12, 994–998.

Vézina, A.F., 1989. Construction of flow networks using inverse methods. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology. Springer, Berlin, pp. 62–81.

Vézina, A.F., Berreville, F., Loza, S., 2004. Inverse reconstructions of ecosystem flows in investigating regime shifts: impact of the choice of objective function. Progress in Oceanography 60, 321–341.

Vézina, A.F., Pace, M.L., 1994. An inverse model analysis of planktonic food webs in experimental lakes. Canadian Journal of Fisheries and Aquatic Sciences 51, 2034–2044.

Vézina, A.F., Platt, T., 1988. Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Marine Ecology Progress Series 42, 269–287.

Vézina, A.F., Savenkoff, C., Roy, C., Klein, B., Rivkin, R., Therriault, J.-C., Legendre, L., 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. Deep-Sea Research Part II: Topical Studies in Oceanography 47, 609–635.

Wiback, S.J., Famili, I., Greenberg, H.J., Palsson, B.O., 2004. Monte Carlo sampling can be used to determine the size and shape of the steady state flux space. Journal of Theoretical Biology 228, 437–447.

Annexe 2

Grami, B., Rasconi, S., Niquil, N., Jobard, M., Saint-Béat, B., Sime-Ngando, T. 2011.

Functional effects of parasites on food web properties during the spring diatom bloom in lake pavin: A linear inverse modeling analysis.

PLoS ONE 6., e23273

OPEN ACCESS Freely available online

PLoS one

Functional Effects of Parasites on Food Web Properties during the Spring Diatom Bloom in Lake Pavin: A Linear Inverse Modeling Analysis

Boutheina Grami[1☯], Serena Rasconi[1,2☯], Nathalie Niquil[1]*, Marlène Jobard[2], Blanche Saint-Béat[1], Télesphore Sime-Ngando[2]

1 Université de La Rochelle-CNRS, UMR 6250 Littoral Environnement et Sociétés (LIENSs), La Rochelle, France, **2** LMGE, Laboratoire Microorganismes: Génome et Environnement, UMR CNRS 6023, Clermont Université, Blaise Pascal, BP 80026, Aubière, France

Abstract

This study is the first assessment of the quantitative impact of parasitic chytrids on a planktonic food web. We used a carbon-based food web model of Lake Pavin (Massif Central, France) to investigate the effects of chytrids during the spring diatom bloom by developing models with and without chytrids. Linear inverse modelling procedures were employed to estimate undetermined flows in the lake. The Monte Carlo Markov chain linear inverse modelling procedure provided estimates of the ranges of model-derived fluxes. Model results support recent theories on the probable impact of parasites on food web function. In the lake, during spring, when 'inedible' algae (unexploited by planktonic herbivores) were the dominant primary producers, the epidemic growth of chytrids significantly reduced the sedimentation loss of algal carbon to the detritus pool through the production of grazer-exploitable zoospores. We also review some theories about the potential influence of parasites on ecological network properties and argue that parasitism contributes to longer carbon path lengths, higher levels of activity and specialization, and lower recycling. Considering the "structural asymmetry" hypothesis as a stabilizing pattern, chytrids should contribute to the stability of aquatic food webs.

Citation: Grami B, Rasconi S, Niquil N, Jobard M, Saint-Béat B, et al. (2011) Functional Effects of Parasites on Food Web Properties during the Spring Diatom Bloom in Lake Pavin: A Linear Inverse Modeling Analysis. PLoS ONE 6(8): e23273. doi:10.1371/journal.pone.0023273

Editor: Jack Anthony Gilbert, Argonne National Laboratory, United States of America

Received April 4, 2011; **Accepted** July 11, 2011; **Published** August 22, 2011

Funding: This study was supported by a grant from the French ANR (Agence Nationale de la Recherche) Programme Blanc 'DREP: Diversité et Rôles des Eumycètes dans le Pélagos'; Coordinator TSN. B.G. and S.R. were supported by grants from DREP (T.S.-N., N.N.). B.S.B. was supported by a PhD fellowship from the CNRS and Région Poitou-Charentes. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: nniquil@univ-lr.fr

☯ These authors contributed equally to this work.

Introduction

Fungal parasitism is common in plankton communities [1–4], especially in the form of parasitic chytrids [5–8]. In freshwater environments, chytrids infect a wide variety of hosts including fish, eggs, zooplankton, and other aquatic fungi but primarily microalgae. Chytrids are also called 'zoosporic' fungi [9], since their life cycle includes dispersal forms, uniflagellated zoospores, and host-associated infective sporangia. Microscopic observations have provided evidence for the presence of both forms in the plankton [8,10].

Previous studies have investigated the effects of chytrid parasitism on the growth of algal species and phytoplankton successions [11–13] as well as on the genetic structure of infected populations [14]. A critical finding was that chytrids seem to preferentially infect large algae. In the absence of parasites, large and colonial microalgae species because of their inedibility are unexploited in the planktonic food web and sink from the euphotic to the benthic zone [15,13]. However, infective sporangia not only consume host biomass thereby contributing to nutrient recycling, but also produce zoospores which are potential prey for cladoceran zooplankter [16]. Thus, fungi might increase the growth of phytoplankton through releasing nutrients bound in inedible algae, and increase the growth of zooplankton by converting biomass from inedible algae to edible zoospores. Moreover, zoospores constitute upgraded food source for grazers because of their high nutritional quality [16]. This chytrid pathway was recently conceptualized in the "Mycoloop theory" [13], and in the specific case of large inedible algae, chytrid zoospores can constitute an important trophic link and prevent the loss of energy in the plankton. Thus, parasitic chytrids are potentially important in pelagic environments due to their role as trophic links and in biogeochemical cycling.

Given that food webs are central to ecological concepts [17], it is important to establish the role of parasites in the structure and function of food webs. In theory, parasites can have a variety of effects. Lafferty et al. [18–19] suggested that parasites affect food-web properties and topology since they double connectance (defined as the number of observed links divided by the number of possible links) and quadruple the number of links. Others have postulated that parasites drive an increase in species richness, trophic levels, and trophic chain length of the food web [20–21]. These properties may stabilize community structure [22]. However, the potential effects of parasites on food web stability is a complex and unresolved issue [19] since the concept of stability is the centre of a perhaps infinite debate in community

ecology [23–28]. Based on the ideas of May [29], parasites should lead to a destabilized trophic network because they increase species diversity and the connectance. In addition, adding parasites to food webs extends the length of trophic chains which can decrease food-web stability [30]. However, the addition of long loops of weak interactions, which may be a characteristic of parasites with complex life cycles, might offset the destabilizing effects of increased connectance [31].

To investigate ecosystem properties and ecological theories, the application of mathematical tools, such as models, is useful and allows trophic network representation through carbon flows. In the absence of quantification of the flows induced by fungal activity, simulations were recently realized of their potential role in the plankton food web of the Lake Biwa [32]. The presence of this indirect pathway channeling microphytoplankton production to the consumers via the fungi, leads to an enhancement of the trophic efficiency index and a decrease of the ratio detritivory/herbivory [32], when considering the fungi, compared with a model without fungi. The results suggested that the food web relies less on the consumption of detritus, and that the transfer of carbon to higher trophic levels is higher than estimated without taking into account the parasites. Due to the lack of data quantifying carbon transfer through parasitism in pelagic ecosystems no attempt was made to build model based on field estimated flows. Thus, the roles and ecological implications of chytrid infections of microphytoplankton remain to be fully explored for aquatic microbial food webs.

In this study our objective was to add parasitic chytrids as a compartment in a well-studied pelagic food web and quantify their impact on matter flow through a trophic network. We then evaluate, for the first time, the impact of chytrid parasitism on the functioning of a planktonic ecosystem using field data set collected from the euphotic zone of the oligo-mesotrophic Lake Pavin (Massif Central, France). To describe the food web, we built a model representative of carbon flow involved in chytrid parasitism and quantified the amount of primary production channelled in food web via chytrid infection. Specifically, we compared carbon flows between the complete food web including parasitic chytrids (MWC, Model with Chytrids) with the same model that did not consider the presence of chytrids and the resulting flows (MWOC, Model without Chytrid), as traditionally done in previous plankton food-web analysis [e.g. 33]. Both of them were constructed on the base of the same data set corresponding to the spring bloom period in Lake Pavin (i.e. March to June 2007).

These models were built using the Linear Inverse Modeling procedure (LIM, [34]) recently modified into the LIM-Monte Carlo Markov Chain (LIM-MCMC, [35]). This method allow reconstruction of missing flow values and alleviates the problem of under-sampling using the principle of conservation of mass, i.e. the quantity of carbon coming into each compartment considered as equal to the amount leaving it [34]. Thanks to recent development of the inverse analysis into LIM – MCMC, a probability density function covering the range of possible values, was generated for each flow. For each calculated set of flows, there is a set of calculated indices which allows application of statistical tests. The flows obtained from the models were used for calculations of Ecological Network Analysis indices that characterize the structure of the food web, and help reveal emergent properties [36–38]. The use of ecological indices moreover, allows an indirect evaluation of the effects of network properties on the stability of an ecosystem, as several authors have proposed theoretical links between structural properties and local stability. For example, Ulanowicz [39] stated that a stable ecosystem needs sufficient amounts of two mutually exclusive attributes: ecosystem organization and overheads. Ecosystem organization is characterized by the Ascendency index [40]. Overheads represent all those disorganized, inefficient and incoherent aspects of an ecosystem's activity [41]. In the absence of perturbation, ecosystem Ascendency tends to increase at the expense of the overheads and the ultimate result is a highly organized, tightly constrained and stable ecosystem [39]. On the other hand, Rooney et al. [42] proposed as a stabilizing pattern a high specialisation of the flows (comparable to the high organisation proposed by Ulanowicz) in the lowest trophic levels and a low specialisation in the high levels. The sum of these analyses revealed overlooked trophic links in a planktonic system in which parasites of microalgae are integrated including (i) the carbon flows involved in chytrid parasitism pathway, (ii) the emergent properties of a planktonic food web in which parasites are integrated, and (iii) the structural and functional properties of a parasite-containing ecosystem.

Results

1. Direct and indirect impacts of chytrids on overall flows

Calculated flows ($mgCm^{-2}\ d^{-1}$) by the LIM–MCMC method, in food webs with or without fungal compartments (i.e. MWC and MWOC), are detailed in Fig. 1 and Table 1. Carbon input into the pelagic system was from the phytoplanktonic primary producers. No allochtonous input were considered due to the small catchment area (50 ha) of Lake Pavin, and the absence of inflow river. For the two models, the major contribution to the gross primary production was provided by microphytoplankton (74%) while the nanophytoplankton and the picophytoplankton contribution were at 16% and 10% respectively. The carbon throughput calculated for sporangia and zoospores represented 5.2% and 4.2% of the total system throughput, respectively.

Carbon flowing from the microphytoplankton compartments to the parasites (i.e. sporangia and zoospores) and through them to the grazers (i.e. microzooplankton and mesozooplankton) is detailed in Fig. 2 in order to focus and compare the fate of microphytoplankton primary production for both models. Through parasitism, 21.4% of the microphytoplankton throughput was channelled to sporangia compartment (Fig. 2); 17.4% of this flow was transferred to zoospores via sporangia production and 12.5% was then channelled to microzooplankton and 2.5% to mesozooplankton by grazing on zoospores. Among fungal compartments, 81.4% of sporangia throughput was channelled to zoospores and 85% of zoospores throughput was channelled to micro- and mesozooplankton. Most of this flow was taken up by microzooplankton (71%) and only 14% by mesozooplankton. In the presence of chytrids a substantial contribution to microzooplankton diet originated from zoospores (38% of total diet).

Formation of detritus represented 9% of total sporangia compartment throughput, the losses by respiration and sedimentation were at 12 and 5%, respectively. Detritus formation from zoospores constituted 1.8% of this compartment throughput, the carbon loss by respiration was 12.6% and no loss due to sinking was considered. The total detritus formation decreased in the presence of chytrids in the food web (29% less of detritus compartment throughput) due to lower contribution of microphytoplankton (from 11 to 3%) to detritus input (Fig. 2).

Compared to the model without chytrids, microzooplankton and mesozooplankton throughput in the model with parasites exhibited higher throughput rates, 23% and 36%, respectively. Conversely, heterotrophic nanoflagellates and detritus throughputs increased (13% and 40%, respectively) when parasites were not included in the food web construction (i.e. MWOC).

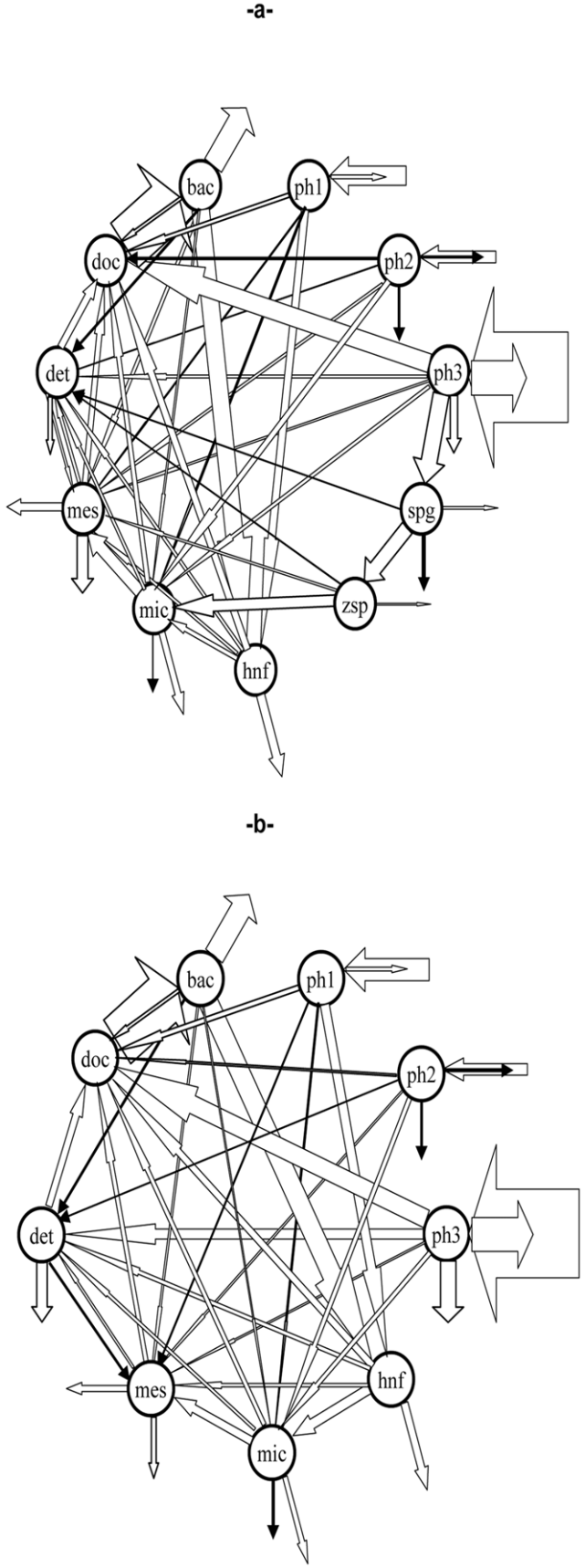


Figure 1. Food webs constructed by LIM-MCMC approach: a- Model With Chytrids and b- Model Without Chytrids. Footnotes: Used abbreviations: bac: heterotrophic bacteria; ph1, ph2 and ph3 are pico-, nano- and microphytoplankton compartments; hnf: heterotrophic nanoflagellates; mic and mes: micro- and mesozooplankton compartments; zsp: zoospores, spg: sporangia; det: detritus and doc: dissolved organic carbon. Green arrows indicate gross primary production, arrows pointing away from center of each compartment indicate respiration, and arrows pointing down represent loss by sedimentation flows. Widths of arrows indicate magnitude of carbon flow.
doi:10.1371/journal.pone.0023273.g001

Grazing insured direct transfer of 6% of microphytoplankton carbon produced to microzooplankton and 2% to mesozooplankton. As a consequence, the total input flow from microphytoplankton to grazers increased from 8% in the model without chytrids to 21% in the model with chytrids (Fig. 2). In the model without chytrids the most important contribution to microzooplankton diet was heterotrophic nanoflagellates (44%) (Fig. 3). Considering the mesozooplankton, the most important contribution was that of microzooplankton for both models (42% of total diet, Fig. 3) but the flow from micro- to mesozooplankton in term of mgC m^{-2} d^{-1} was higher in MWC (38 vs. 24 mgC m^{-2} d^{-1}).

The loss by sinking flows was lower in the MWC than in the MWOC models due to higher detritus and microphytoplankton sinking flows in the second model. For microphytoplankton compartment the sinking flow was reduced from 21% to 10% of the compartment throughput in the MWC. In addition, due to less detritus originating from microphytoplankton in the MWC model, the amount of detritus sinking in the MWOC model was almost three times higher (Fig. 2).

2. Impact of chytrid on network emerging properties

The LIM-MCMC derived flow results of each model were used to calculate the ecological network indices. Box plots of Fig. 4 show the relative positions of the median and associated dispersion of some ecological network analysis indices of the two models. For all considered indices, lower (0.5%) and upper (99.5%) quantiles did not overlap. It was straightforward to see differences in network properties of the two considered webs. Indeed, comparison (by Student test) of the same index in the two different models showed that the effect of chytrid inclusions was significant ($p<0.05$).

Chytrid increased the total activity, measured by total system throughput (TST, Fig. 4a) and the calculated averages for MWC and MWOC were respectively at 1464 and 1332 mgCm^{-2} d^{-1}. In the presence of chytrids (Fig. 4b) the average pathway length (APL) also was higher. This means that trophic chains were longer and the calculated mean number of compartments through which each inflow passed was equal to 3 in the model with chytrid (MWC) and 2.6 in the model without chytrid (MWOC).

Higher values of Ascendency (A) were calculated when chytrid were considered in the model food web (2305 and 2812 mgC m^{-2} d^{-1} respectively for MWOC and MWC). Then, parasitism led to a trophic network with higher fraction of TST efficiently transferred along specialized pathways. The relative Ascendency (A/DC), a ratio reflecting the degree of organization [40,43] was higher in the MWC (60%) compared to the MWOC (58%). Since A is calculated as the product of the TST and the average mutual information, any increase of A could be linked to an enhancement of TST with a concomitant decrease in the information factor (AMI). In this case we did observe an increase of the TST values for the MWC (Fig. 4a). Furthermore, the calculated AMI showed higher values for the MWC (1.92) compared to the MWOC (1.73). Indices relative to internal exchanges (Ai and DCi) showed higher values calculated for the MWC (Fig. 4c

Table 1. Flow description, name and corresponding value (mg C m^{-2} d^{-1}) of steady state models of the pelagic food web of Lake Pavin during spring 2007.

		Inferred value (mg C m^{-2} d^{-1})	
		Model I	**Model II**
Flow description	**Flow name**	**With Chytrid**	**Without Chytrid**
Microphytoplankton gross primary production	CgppTOph3	267.8	261.63
Nanophytoplankton gross primary production	CgppTOph2	35.27	33.94
Picophytoplankton gross primary production	CgppTOph1	57.47	64.96
Microphytoplankton respiration	Cph3TOres	**101.67**	**100.49**
Microphytoplankton doc excretion	Cph3TOdoc	**56.11**	**55.57**
Microphytoplankton grazing by mic	Cph3TOmic	**11.01**	**14.86**
Microphytoplankton grazing by mes	Cph3TOmes	**6.13**	**5.94**
Parasitism of ph3 by sporangia	Cph3TOspg	57.44	
Microphytoplankton det production	Cph3TOdet	**9.36**	**29.75**
Microphytoplankton sinking	Cph3TOlos	26.07	55.03
Nanophytoplankton respiration	Cph2TOres	**2.53**	**4**
Nanophytoplankton doc excretion	Cph2TOdoc	**3.75**	**6.03**
Nanophytoplankton grazing by mic	Cph2TOmic	**18.24**	**14.77**
Nanophytoplankton grazing by mes	Cph2TOmes	**9.71**	**6.62**
Nanophytoplankton sinking	Cph2TOlos	**0.52**	**1.28**
Nanophytoplankton det production	Cph2TOdet	**0.51**	**1.25**
Picophytoplankton respiration	Cph1TOres	**11.16**	**10.88**
Picophytoplankton doc excretion	Cph1TOdoc	**13.2**	**16.41**
Picophytoplankton grazing by hnf	Cph1TOhnf	**25.85**	**31.98**
Picophytoplankton grazing by mic	Cph1TOmic	**5.1**	**4.18**
Picophytoplankton grazing by mes	Cph1TOmes	**2.16**	**1.51**
Bacteria respiration	CbacTOres	**73.27**	**71.75**
Bacterivory by hnf	CbacTOhnf	61.59	67.24
Bacteria uptake by mes	CbacTOmes	**10.87**	**6.88**
Bacteria uptake by mic	CbacTOmic	**5.98**	**4.09**
Bacterial doc release due to viruses lysis	CbacTOdoc	9.9	9.9
Attached bacteria to det	CbacTOdet	**1.67**	**1.88**
Heterotrophic nanoplankton respiration	ChnfTOres	**29.25**	**25.1**
Heterotrophic nanoplankton doc excretion	ChnfTOdoc	**23.1**	**21.91**
Heterotrophic nanoplankton uptake by mic	ChnfTOmic	**14.41**	**29.61**
Heterotrophic nanoplankton uptake by mes	ChnfTOmes	**10.27**	**10.07**
Heterotrophic nanoplankton det production	ChnfTOdet	**10.39**	**12.54**
Microzooplankton respiration	CmicTOres	**21.87**	**16.94**
Microzooplankton doc excretion	CmicTOdoc	**16.27**	**13.94**
Microzooplankton uptake by mes	CmicTOmes	**38.14**	**24.57**
Microzooplankton egestion	CmicTOdet	**10.44**	**9.66**
Microzooplankton sinking	CmicTOlos	1.38	2.4
Mesozooplankton respiration	CmesTOres	**24.16**	**18.29**
Mesozooplankton doc excretion	CmesTOdoc	**17.88**	**14.98**
Mesozooplankton egestion	CmesTOdet	**10.7**	**7.77**
Mesozooplankton grazing by larger organisms	CmesTOlos	**39.25**	**17.1**
Sporangia respiration	CspgTOres	**6.9**	
Sporangia emission of zoospores	CspgTOzsp	46.79	
Sporangia detrital production	CspgTOdet	**0.86**	
Sporangia sinking	CspgTOlos	**2.89**	
Zoospores respiration	CzspTOres	**5.92**	

Table 1. Cont.

		Inferred value (mg C m^{-2} d^{-1})	
		Model I	**Model II**
Flow description	**Flow name**	**With Chytrid**	**Without Chytrid**
Zoospores ingestion by mic	CzspTOmic	**33.34**	
Zoospores ingestion by mes	CzspTOmes	**6.63**	
Zoospores detrital production	CzspTOdet	**0.9**	
Dissolved organic carbon uptake by bacteria	CdocTObac	**163.27**	**161.75**
Detritus dissolution	CdetTOdoc	**23.06**	**23.01**
Detritus consumption by mes	CdetTOmes	8.07	2.55
Detritus sinking	CdetTOlos	**14**	**37.3**

Model II presents no fungi while model I consider them in the model exercise. Underlined values indicate flows that were estimated or derived from processes determined *in situ* in Lake Pavin. Bold values are those constrained by one or 2 inequations and estimated by the LIM-MCMC method.
doi:10.1371/journal.pone.0023273.t001

and 4d). Indeed, higher Ai/DCi ratio reported for the MWC demonstrated its tendency to internalize most of its activity which could be an aspect of a highly organized food web [43]. In contrast, the absence of chytrids promote enhancing the internal relative redundancy (MWC: 57%; MWOC: 63%) a measure of the ecosystem degree of information loss due to parallel pathways. Also, chytrids decrease recycling as indicated by a decrease of the Finn Cycling Index (FCI, Fig. 4f).

The Lindeman spine provided more insights considering trophic analysis. According to the trophic level efficiencies and to the global trophic efficiency given in Table 2, the most efficient planktonic food web for carbon transfer was the MWC. Moreover, the grazing chain analysis highlighted a better efficiency transfer of the primary production in the MWC for each trophic level (Table 2). The food web percentage of detritivory was higher in the MWOC (67%) compared to the MWC (55%). Detritivory decrease when considering chytrids in the spring pelagic food web of Lake Pavin.

Discussion

1. Methodological choices

Using Linear Inverse Modeling coupled with the Monte Carlo Markov Chain approach applied to a complete *in situ* data set on chytrids allowed construction of the first model that quantifies and describes the implications of fungal parasitism in a pelagic ecosystem. Ecological Network Analysis (ENA), increasingly used coupled with a calculated set of flows driven from modelling exercises [33,44], allows characterisation of emergent properties and overcomes the difficulties of comparing different food webs solely on the basis of the magnitude of flows [45].

Monte Carlo approach is a technique only recently applied to the Linear Inverse Modeling (LIM) [46] to describe the whole set of possible solutions and to overcome the problem of adopting the parsimony principle [34] that was used traditionally and consistently underestimates both the size and the complexity of the food web [46–48]. The Monte Carlo Markov Chain technique was recently coupled with a new mirror algorithm (LIM-MCMC, Markov Chain Monte Carlo algorithm) to provide more robust ecological basis to the models with a high range of possible solutions [49]. Kones et al. [49] also proposed the first coupling of the LIM-MCMC with ENA indices calculation, which allows estimating a probability density function covering the whole space of possible solutions for each ENA index, for each model. This adds to the great quality of our data set concerning the parasites and the planktonic processes [50], as it allows comparing the ecological properties of the two food web properties (i.e. with and without parasites) with a statistical test. In the present paper, we indeed present the first application of this approach to an ecological question. Performing statistical tests on the calculated ENA indices has proved to be useful for our purpose to compare the classical plankton food web carbon model of the Lake Pavin with the model including the two life forms of chytrids (zoospores and sporangia).

2. Carbon flows involved in parasitism

Channeling of primary production through the food web (Fig. 2) was highly impacted by the inclusion of chytrids in the plankton ecosystem of Lake Pavin. About 21% of microphytoplankton primary gross production is involved in sporangia development and increased carbon input into the zooplanktonic compartments (i.e. micro- and mesozooplankton). In the classical food web vision with no parasites, biogenic carbon produced by phytoplankton was considered to pass through various processes including remineralisation, food wed transfer and loss by sinking. The most effective way to pass energy to consumers is via direct consumption processes, even through microbial loop pathways, i.e. DOC uptake by bacteria [51], and zooplankton grazing [52]. Another part of primary production is considered as lost by sinking without being consumed [53]. However, this study showed the importance of parasitism as an indirect pathway channelling primary produced carbon to grazers.

Grazers were directly sustained by parasitic chytrids through the consumption of their zoospores (38% of microzooplankton diet). This pathway, called 'Mycoloop' by Kagami *et al.* [13] was quantified in our study and shown to increase energy transfer from primary producers to consumers in the system. In the temperate Lake Pavin during spring period large-size diatoms sustain primary production (Fig. 1) and the principal species are the pennate genera *Asterionella* and *Synedra* and the filamentous genera *Melosira*. These large diatoms are usually too large to be eaten and thus are not considered as efficient links in a classical food web (Fig. 2b). Our model, including parasitism in the pelagic food web confirms and provides, for the first time, quantitative estimates of primary production contained in ''inedible algae'' but channeled into zooplankton (mainly microzooplankton) via the 'Mycoloop'.

Chytrids zoospores do constitute a food source of high quality; they are rich in polyunsaturated fatty acids (PUFAs) and

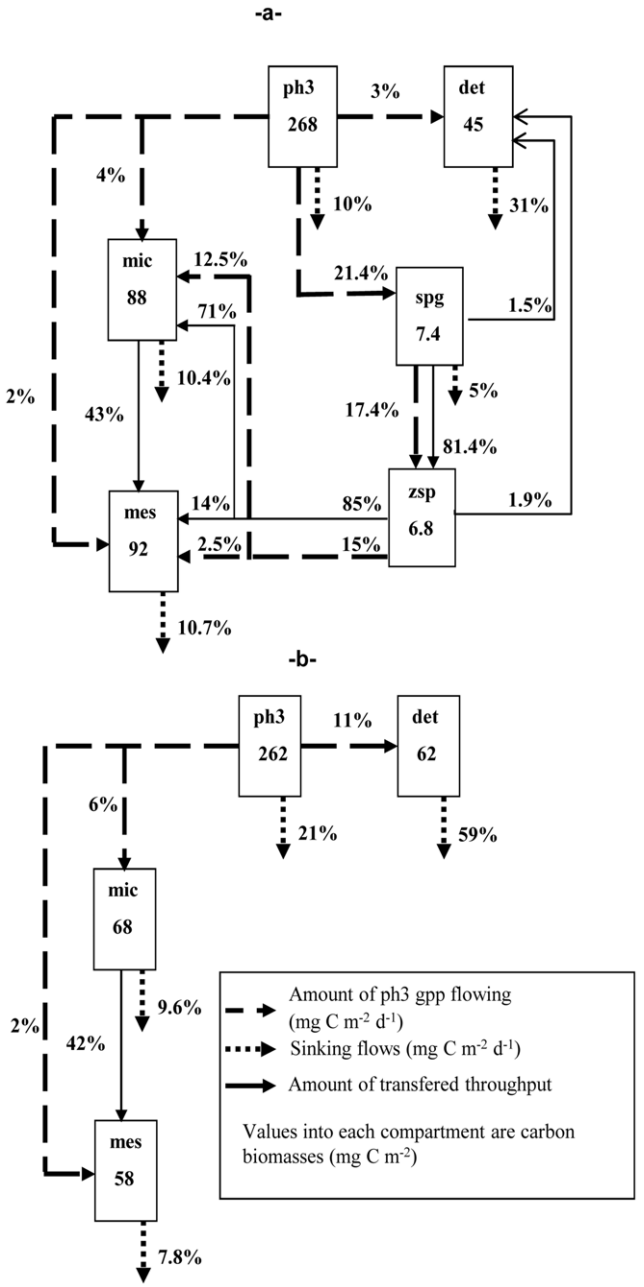


Figure 2. Highlights of the carbon sinking and flowing from ph3 gross primary production to other compartments for a- MWC, and b- MWOC.
doi:10.1371/journal.pone.0023273.g002

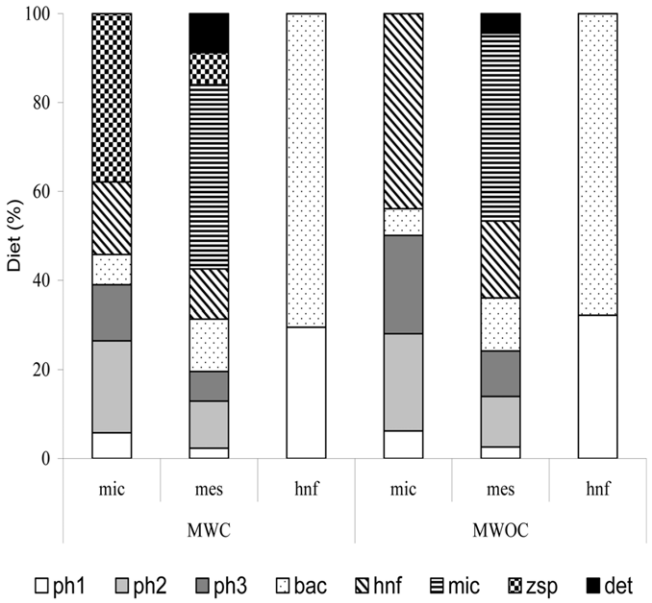


Figure 3. Diet composition of hnf, mic and mes in the two models.
doi:10.1371/journal.pone.0023273.g003

cholesterol, which are essential nutrients for crustaceans [16]. Moreover, it is also possible that grazers due to the absence of a chitinous cell wall could easily assimilate zoospores. In Lake Pavin, as in other lake environments [54,55], fungal epidemics occur when diatoms form blooms during spring period. This is a crucial moment in seasonal development of planktonic successions [56], especially for crustacean zooplankton development. It has been shown that diatoms constitute the basic fuel for higher trophic levels at the start of the growing season [57]. Experimental evidence suggests that chytrids improve survival of Cladocera [16] and Copepods [57]. Kagami *et al.* [53] remarked that cell lysis due to fungal infection of the diatom species *Staurastrum dorsidentiferum* in Lake Biwa could lead to nutrient release, supporting the production of bacteria and zooplankton, but the mechanism involved remained unclear. It is possible that, at this crucial moment for planktonic community development, grazing on chytrid zoospores might facilitate the growth of zooplankton due to their high nutritional quality.

In our model, carbon flows increased when chytrids were included and carbon transfer to higher trophic levels was improved (Table 1, Fig. 2). This pathway appears to be extremely efficient, the flow to detritus from the compartment of sporangia represented only 9% of its total throughput and it was even less for zoospores (2%). Consequently, the carbon input that passed into the zooplankton (i.e. micro- and mesozooplankton) was higher in the model with chytrids (Fig. 2) than without. Fungal zoospores represent key intermediates in food chains [58] and a very efficient link between sporangia and grazers. This could be due to the fact that they constitute more direct producer-consumer link [58]. Zoospores do not feed [58,59] and the losses by respiration are extremely low compared to equivalent compartments such as heterotrophic nanoflagellates, HNF (Fig. 1, Table 1).

The inclusion of parasitic chytrid drastically reduced the direct loss via sedimentation of large phytoplankton (50% less) and their role in the production of detritus (29% less, Fig. 1). It is known that diatoms are usually considered to sink fast due to the weight of the frustule. Especially, the species *Melosira* is known to proliferate in Lake Pavin [60,61] and was observed reaching the hypolimnion when 40–60% of the cells were still viable [62]; thus the large diatoms could not constitute an efficient trophic link. It would therefore appear that in the absence of parasites the majority of algal production is lost by sinking and is unavailable to support higher trophic levels. The consequence of parasitism on micro-phytoplankton will be that less carbon is lost from the pelagic zone. The fate of sinking organic matter will depend on the studied lake. In the studied case, a meromictic lake, the sinking organic matter constitutes an energy supply for the anoxic benthic community and will not reach the upper layers by recirculation. In a well-mixed lake, the sinking organic matter constitutes an energy

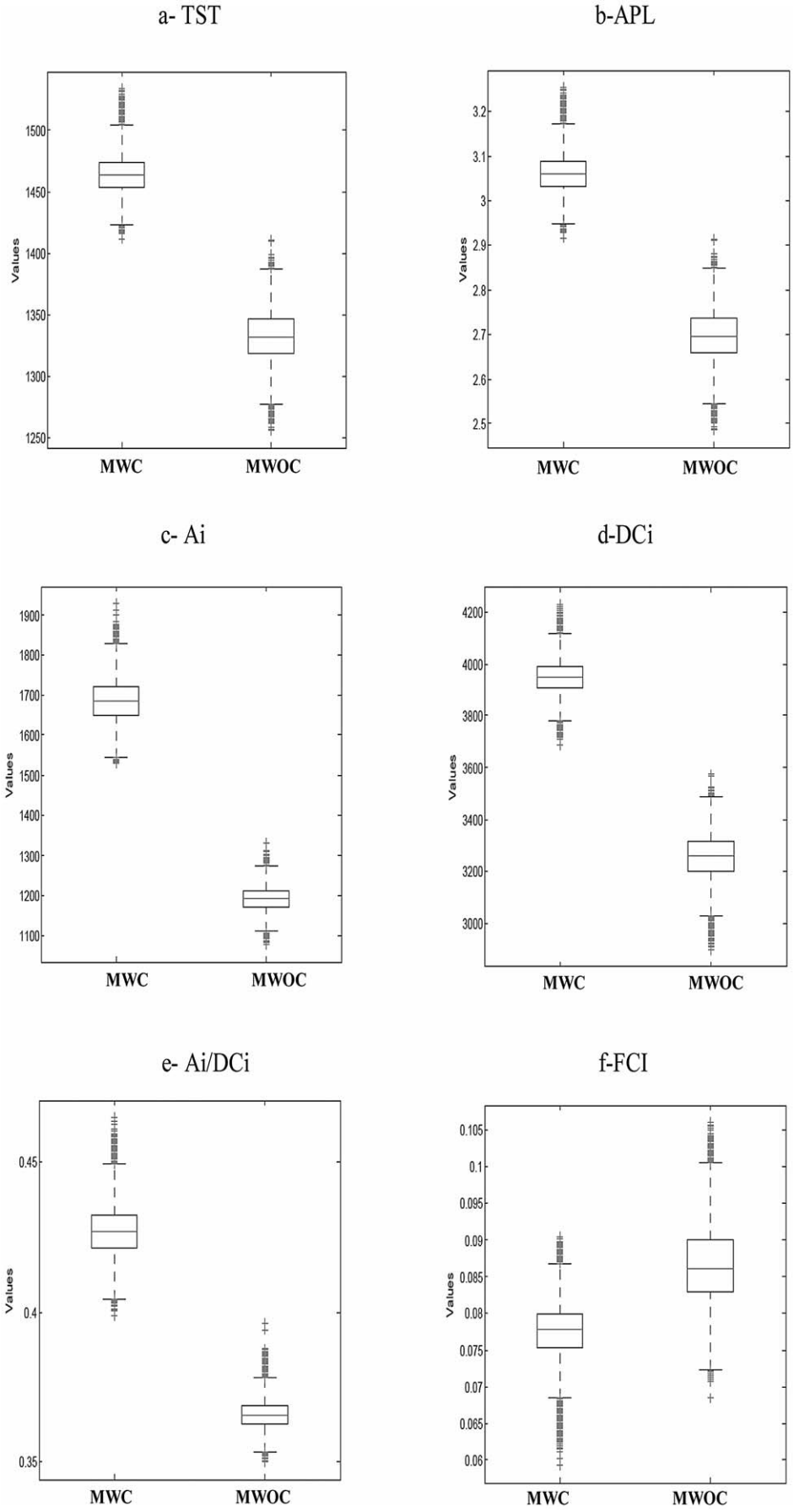


Figure 4. Comparison of Ecological Network Analysis indices across food webs with (MWC) and without (MWOC) Chytrids.
doi:10.1371/journal.pone.0023273.g004

Table 2. Indices derived from the Lindeman spine.

	Model I -With Chytrid	Model II -Without Chytrid
Trophic level (TL) efficiency (%)		
1st TL	66.4	53.9
2nd TL	48.0	42.3
3rd TL	41.9	30.8
4th TL	30.5	22.9
Global trophic efficiency	44.9	35.6
Grazing chain efficiency (%)		
1st TL	37.7	22.1
2nd TL	40.7	28.5
3rd TL	17.1	8.8
4th TL	5.2	2.0
Detritivory (%)	55.7	67.3
Herbivory (%)	44.3	32.7

doi:10.1371/journal.pone.0023273.t002

supply for benthos, and can reach the upper layers by recirculation only after being processed in benthic food webs. Thus, chytrid infections can increase the residence time of algal biomass in water column [50] and decrease the contribution of organic matter to the benthic community.Our results show that the "Mycoloop" reduces the sinking flows of inedible algae and the carbon produced by these latter is transferred to consumers via zoospores of chytrid parasites. Chytrids not only have important role in the fate of primary production, but also in the trophic upgrading necessary to boost the seasonal development of planktonic populations in a pelagic ecosystem.

3. Emergent properties of ecosystem functioning

Theoretical studies [18–19] have concluded that emergent properties of an ecosystem can be affected by parasites. Analyzing food web models with, and without, parasites was suggested by parasitologists as a means to confirm theories [21,63]. In our case, the comparison between the two models, including the range of possible values for ENA indices, clarifies the effects of parasites on ecosystem properties.

Number of flows increased in the model with chytrids (Fig. 1, Table 1) as well as the total system activity (TST, Fig. 4a). Parasites are known to add links and species to food webs [19] observed in broad variety of environments, including terrestrial [64], estuarine [18], marine [21] and freshwaters [55]. Even if this seems logical, as for the addition of any species to a food web, this is especially true for parasites that have a free-living stage that can interact with other compartment and that may be eaten, as the chytrids zoospores.

Including parasites in food web increases the number of compartments through which each inflow passes and the APL (Fig. 4b) expressed higher chain length for the MWC. This important structural property (i.e. APL) defines the number of links in food web and energy transfer through its components [65]. Increasing the number of links increases the robustness of interactions [19] of an ecosystem, a measure of its overall organization [18]. Robustness indeed is considered as a parameter linked to the stability of the system [18], and according to this theory, incorporating parasitic chytrids in pelagic food webs increases stability. According to Williams and Martinez [30], any increase in the length of trophic chains should decrease food web stability.

Parasites help the food web to reach a higher limit of development, as revealed by the DCi values. The increase of the relative Ascendency as well as the internal relative Ascendency (Ai/DCi) (Fig. 4e) point to a higher level of organization following the theory developed by Ulanowicz [36,37].The action of chytrids allowed a higher fraction of the total system throughput to pass along specialized pathways as revealed by the Ascendency values. However, to conclude on the effect of chytrids on the degree of specialization, the AMI value provided better information about the flow specialization. Indeed, this index was higher when considering the presence of chytrids in the spring food web model. This means that inclusion of parasites leads to a higher specialization corresponding to a more direct link (i.e. zoospores>microzooplankton) compared to the classical microbial chain (i.e. DOC>bacteria>HFN>microzooplankton). In a food web simulation including chytrids [32], an increase in relative ascendency was related to an observed increase in trophic efficiency. Relative to the classical microbial chain, the flows estimated showed a higher transfer of primary produced organic matter via parasitism and zoospores grazing. Major ascendency could be the consequence from this more direct link between producers and consumers. As the degree of organization and robustness of the interactions among species into a food web impacts the degree of stability [19], the presence of chytrids could be considered as a factor enhancing stability. Robustness corresponds to a measure of the quantity of perturbation that an ecosystem can support before changing to another state [66]. The higher the robustness, the more stable the food web is. Niquil *et al.* [32] suggested after simulating the probable impact of chytrids in Lake Biwa, that high relative ascendency calculated for the low trophic levels associated with lower specialisation at higher levels (i.e. structural asymmetry reported by Rooney *et al.* [42]) should confer stability to the food web. In this study, higher ascendency was apparent for the lower trophic levels; and if the compartments were based on the level of species, incorporating the specificity of chytrids should enhance the ascendency even more than what we have observed in this study.

The inclusion of chytrids enhances the overheads of the ecosystem under study, especially the internal redundancy. The difference between 1 and the relative Ascendency estimates the overhead of the system. Overheads represent all those disorganized, inefficient and incoherent aspects of an ecosystem's activity [41]. In fact, they correspond to inputs, outputs, dissipation (respiration) and functional redundancy [67]. The functional redundancy can be estimated by the difference between Internal Ascendency and internal capacity of development. A higher functional redundancy in the presence of chytrids would enhance the stability. Indeed, as proposed by Ulanowicz [68], organized (Ascendency) and non-organized (redundancy) parts of ecosystem should be in equilibrium. This configuration of ecosystem leads to a better resistance and survival to perturbations. In the case of perturbations, an ecosystem with a high Ascendency would be less vulnerable and the consequences of perturbations would be small. The coupling with a high redundancy enhances such flexibility, and the dissipation of the effects of flow fluctuation as well [69].

The FCI index was lower in the model with chytrids. FCI is a measure of the quantity of recycling in the ecosystem and its low level confirms the tendency of parasites to favour the more direct links. In terrestrial environments, a theory elaborated for macroparasites [70] stated that parasites lead to complex long-loops interactions between species. Neutel *et al.* [31] stated that the addition of long loops of weak interactions could be the

characteristic of parasites with complex life cycles. Here, the parasites studied had no significant effects on the recycling, because they only interacted with primary producers. One may consider that adding the parasites of heterotrophs would have had a different effect.

The calculated values of global trophic efficiency showed that carbon is rather efficiently transferred within the MWC. Reasons behind this high trophic efficiency are a better carbon transfer efficiency coupled with a higher grazing efficiency at each trophic level (Table 2). The MWC exhibited also a lower percentage of detritivory compared to the MWOC (Table 2), stressing the fact that in the MWC the food web is more efficient in direct use of the primary production compared with the MWOC food web. This conclusion is congruent with the conclusion made on the basis of carbon flows analysis. Moreover, detritivory decrease when parasites were involved could be related to the seasonal planktonic successions. Spring period in temperate lakes is a typical transitional system characterized by recovery of planktonic populations. Primary production is high and, in general, the community is dominated by r-strategist populations characterized by rapid growth and an important role of detritus in nutrient turnover [71]. This functional characteristic of an ecosystem is typical of immature community, as described in a previous study where during spring period detritivory value was high [72]. Including parasites was associated with a decrease in detritus consumption, enhancing the detritivory and thereby the maturity of the system. This fact related to low retention of the system (i.e. low FCI) contradicts the Odum [72] theory which states that efficient cycling of matter is a fundamental characteristic of a mature system.

4. Conclusions

This study is the first attempt to quantify the effective impact of parasitic chytrids in a pelagic food web. The improved inverse method coupled with Ecological Network Analysis allowed estimation of undetermined flows, taking into account the quantified processes from fungal infections and the emergent properties of the ecosystem. Methodological improvements allowed definition of the allowed range of values thus permitting statistical tests.

The epidemic growth of chytrids reduced the flow of sedimentation loss of large inedible algae and their contribution to detritus pool, thus less carbon is lost from the pelagic zone. Chytrid zoospores, via the Mycoloop pathway, channelled up to 20% of primary production to the higher trophic levels. The better global trophic efficiency was highlighted by a higher global trophic efficiency coupled to higher efficiency of carbon transfer through each trophic level of the grazing chain. Chytrids constituted an efficient and good quality trophic link and had important role in the flow of energy for the seasonal development of planktonic successions.

Parasitism affected also the structural and functional properties of the ecosystem. It lead to an increase in the number of the trophic links leading to longer path lengths, which in general are considered as characteristics of stable ecosystems. The increase in topological indices (i.e. A/DC, Ai/Dci and AMI) indeed indicated that parasites contribute to better organization of the ecosystem and more efficient specialization of pathways corresponding to links that are more direct. Some structural properties (i.e. FCI, detritivory) were indicative of a system based on rapid growth and turnover, thus of planktonic successions not yet mature and typical of spring period, and parasite seems to accentuate these characteristics.

Materials and Methods

1. Study site and sampling

Lake Pavin is a crater freshwater lake situated in the Massif Central of France (45° 29′ 41″N, 02° 53′ 12″E). It is an oligo-mesotrophic deep volcanic mountain lake ($Z_{max} = 92$ m) with a permanently anoxic monimolimnion from 60 m depth downwards. More details on the characteristics of the lake are available in Amblard *et al.* [73]. The data used here correspond to the recurrent spring bloom of diatom in Lake Pavin, a site that offers a unique environment with low human influences and high annual reproducibility of seasonal dynamics in the water column [5–6]. Samples were collected fortnightly in a central location of the lake from March to June 2007 by simple capillarity as described by Sime-Ngando and Hartmann [74]. This method allowed collecting integrated samples (21 L) representative of the euphotic layer (0–20 m). Samples were pre-filtered on 150 µm pore size nylon filter (except for metazooplankton samples) for the elimination of metazoan zooplankton and taken to the laboratory for immediate analysis.

2. Abundance and biomass of planktonic organisms

Sub-samples were processed for identification and quantification of picoplankton, heterotrophic nanoflagellates, phytoplankton, zooplankton and the two life stages of microphytoplankton fungal parasites (Chytridiales).

Bacteria. Sample aliquots were fixed with glutaraldehyde (1% final concentration) before counting of heterotrophic and autotrophic picoplankton by a flow cytometer (BD system) equipped with a 15-mW, 488 nm, and air-cooled argon ion laser. Environmental samples were diluted 10 times and simultaneous measurements of size light scatter (relative size), 90 degree light scatter, and SYBR green fluorescence emission (wave length 650 nm) were conducted to detect and enumerate heterotrophic and autotrophic bacteria. Cell numbers were converted to carbon biomass by adopting mean cell volume (μm^3). Carbon conversion factors of 0.35 pg C μm^{-3} and 0.22 pg C μm^{-3} were used for conversion of biovolumes to carbon biomasses of heterotrophic bacteria [75] and picophytoplankton (0.2–2 µm) [76,77], respectively.

Heterotrophic nanoflagellates (2–20 µm). Sub-samples (15 ml) were fixed and handled according to Caron [78] for quantification of heterotrophic nanoflagellates. Counts were performed using an inverted epifluorescent microscope (Leica DMIRB) equipped with a 100× objective lens, a HBO-100 W mercury lamp, and a set of different optic filters, including filters (340 to 380 nm) for UV light excitation. Mean cell biovolumes were estimated for each sample by measuring the linear dimension of at least 50 cells and equating shapes to standard geometric forms. Carbon biomass was calculated using a conversion factor of 0.22 pg C μm^{-3} [79].

Nano- and microphytoplankton (2–20 µm and 20–150 µm, respectively). Sub-samples (200 ml) were fixed with alkaline Lugol solution (1% v/v) and nano- and microphytoplankton cells counted and identified using the Utermöhl method [80] under an inverted microscope (WILD - M40). Cell biovolumes were estimated by measuring the linear dimension of at least 100 cells and equating shapes to standard geometric forms. The resulting volumes were transformed into organic carbon values by using the conversion equation of Menden-Deuer and Lessard [81] (pgC $cell^{-1} = 0.288 \times Vol^{(0,811)}$ for diatoms and pgC $cell^{-1} = 0.216 \times Vol^{(0,939)}$ for the other autotrophic genera).

Ciliates (20–150 µm). Sub-samples (200 ml) were fixed with alkaline Lugol solution (5% v/V) and ciliates were counted and

identified using the same method as for microphytoplankton. For carbon biomasses of ciliates, biovolumes were converted into organic carbon using conversion factors of 0.19 pg C μm^{-3} [82].

Metazooplankton. The metazooplankton was collected by filtering raw samples from the euphotic layer (0–20 m) through a 50 µm pore-size mesh. Retained animals were preserved in 4% formalin-sucrose to prevent any release of eggs or physical deformation [83]. Identification and counting, after addition of few drops of rose Bengal to improve detection, were conducted under a binocular microscope (Wild M3Z) using Dolfuss chambers [84]. The carbon biomass of each metazoan group was estimated by multiplying the individual carbon contents by the corresponding abundances. For Copepods the dry weight (DW, mg) was calculated as 22.5% of wet weight [85,86] and C content (mg) was estimated as 40% of DW [87]. For Cladocera the length (L, mm) of each organism was used to determine its carbon content (C_{clad}) as: µg C $ind^{-1} = 5.24 \times L - 1.08$ [88]. For rotifers, wet weights were converted to dry weight according to Pace and Orcutt [89] and McCauley [90]. Dry weights were converted to carbon biomass using carbon: DW ratio of 0.48 [91].

Chytrid parasites. Sub-samples were handled for chytrid parasites counting based on a size fraction approach and the use of the fluorochrome calcofluor white (CFW) for diagnosing, staining and counting chitinaceous fungal parasites (i.e. sporangia of chytrids) of microphytoplankton. 20 L of the integrated samples were passed through a 25 µm pore size nylon filter. Large phytoplankton cells in the >25 µm size fraction were collected and fixed with formaldehyde (2% final conc.), before staining and analysis. Nanoplanktonic cells in the <25 µm size-fraction were concentrated by ultrafiltration and 180 ml of the ultrafiltrate retentate was fixed with formaldehyde (2% final conc.), before staining and analysis. Aliquots (150 µl) of each fraction were stained by CFW (1% v/v) and drops (10 µl) of stained samples were mounted between glass slides and cover slips for observation and counting under an inverted epifluorescent microscope (more details are available in [8]). For each sample, microphytoplanktonic cells were inspected for fungal infection (i.e. the presence of fixed sporangia). Identification of chytrids was based on phenotypic keys known from classical manuals, primarily those in Sparrow [9], Canter [92], and Canter and Lund [93]. The prevalence of infection was estimated as the percentage of infection in the host population according to Bush *et al.* [94], i.e. $Pr\,(\%) = [(Ni/N) \times 100]$, where Ni is the number of infected host cells, and N is the total number of host cells. Carbon biomass of infectious sporangia was estimated using a conversion factor of 10.7 pg C $cell^{-1}$ [13].

For zoospore counting, sub-samples were processed using the CARD-FISH method of Not *et al.* [95], recently modified by Jobard *et al.* [10]. Carbon biomass of zoospores was estimated using a conversion factor of 10.7 pg C $cell^{-1}$ [13].

3. Model construction

Data from the field study were used to construct the pelagic food web model that quantitatively illustrates carbon pathways in Lake Pavin during spring in the presence of chytrids (sporangia and zoospore life stages). To estimate the unknown flows, we adopted the method LIM-MCMC, derived from the LIM of Vezina and Platt [34] to reconstruct trophic flows through the pelagic food web. The approach is based on four steps.

Compartments and a priori model. The first step consists in constructing a conceptual model including all possible flows between compartments and the outside. Living compartments included three phytoplankton compartments, three grazer compartments, one compartment for heterotrophic bacteria and two compartments for fungal parasites of microphytoplankton, while non-living compartments included dissolved organic carbon (doc) and detritus (det). We divided the phytoplankton into picophytoplankton (ph1: 0.2–2 µm); nanophytoplankton (ph2: 2–20 µm; principally Cryptophyta as *Rhodomonas sp.* and Chlorophyta as *Ankistrodesmus sp.* and *Ankyra sp.*) and microphytoplankton (ph3: 20–150 µm; essentially large and filamentous Bacillariophyceae, as *Asterionella sp.*, *Synedra sp.* and *Melosira sp.*). Grazer compartments included the heterotrophic nanoflagellates (hnf: 2–20 µm), microzooplankton (mic: 20–150 µm: Ciliates and some Rotifera: *Ascomorpha sp.*, *Keratella quadrata*, *Polyarthra platyptera* and *Conochilus unicornis*) and mesozooplankton (mes; >150 µm; Cladocera: *Bosmina coregoni*, *Daphnia longispina*; Copepoda: *Acanthodiaptomus denticornis*, *Cyclops abyssorum prealpinus* and some large Rotifera: *Brachionus sp.*, *Fillinia terminalis*, *Kellicottia longispina*). Fungal parasites of microphytoplankton compartments included infectious sporangia (spg) and free zoospores (zsp).

The food-web model contains 53 carbon flows, which correspond to the model with Chytrids (MWC). Since our aim was to highlight the role of chytrids in the pelagic food web and their impact on ecosystem properties, a second model was built with the same consideration and data set of the MWC but without incorporating the chytrids compartments and the involved flows. The second model had 44 carbon flows and was named model without chytrids (MWOC). The sole carbon inputs were gross primary productions by each phytoplankton size fraction. Carbon output from the network was driven by respiration of all living compartment and carbon loss by sinking from ph2, ph3, spg, mic, mes and det compartments. Mesozooplankton contribution to the carbon output flow considers not only their production of sinking fecal pellets but also their consumption by a higher trophic level. All living compartments, except fungal parasites, contribute to DOC production that was taken up by bacteria. In addition to ph2, ph3, mic and mes contributions to detritus production, we considered the existence of a carbon flow from bacteria and heterotrophic nanoflagellates to detritus. Attached bacteria were identified on TEP in Lake Pavin during spring [96] which sediment and create a flow from bacteria to detritus. Attached bacteria are also known to constitute preferential prey for heterotrophic nanoflagellates [97]. Detritus production by sporangia was due to chitinaeous wall dissolution or break-up during zoospore discharge [9]. Moreover, zoospores were considered as contributing to detritus production by the loss of their flagellum when they found a host to fix on. The carbon flow from microphytoplankton to sporangia represented carbon from diatom cells to infectious sporangia and the carbon flow from sporangia to zoospores was considered as the production of zoospores by sporangia. Grazing relationships were defined considering size and preferential ingestion of each identified grazer. Heterotrophic flagellates grazed on compartments of bac and ph1, microzooplankton grazed on bac, ph1, ph2, ph3, hnf and zsp, while mesozooplankton grazed on bac, ph2, ph3, hnf, mic, zsp and det.

Equalities. The second step is setting equations (equalities) to constrain the mass balance of the system and to impose measured flows. The mass balance equations for all compartments are given in the first 11 lines of Table 3. Some of the estimated flows were measured during previous studies focused on spring blooms in Lake Pavin and are introduced as additional equations; these include values for total gross and net primary production [98,99], bacterial production [99] and viral lysis of bacteria [100] considered as the value of the flux from bacteria to DOC (last 4 lines of Table 3).

Primary production was measured from ^{14}C uptake according to Steemann-Nielsen [101]. Subsamples (100 ml) from each sampling depth were drawn into two transparent and one dark

Table 3. Mass balance (1 to 11) and other linear (12 to 16) equations used for inverse analysis.

Equation number	Process concerned	Equations
1	Mass balance for microphytoplankton	(gpp-ph3)−(ph3-mic+ph3-mes+ph3-spg+ph3-doc+ph3-res+ph3-det+ph3-los) = 0
2	Mass balance for nanophytoplankton	(gpp-ph2)−(ph2-mic+ph2-mes+ph2-doc+ph2-res+ph2-det+ph2-los) = 0
3	Mass balance for picophytoplankton	(gpp-ph1)−(ph1-hnf+ph1-doc+ph1-res) = 0
4	Mass balance for heterotrophic nanoflagellates	(ph-hnf+bac-hnf)−(hnf-res+hnf-doc+hnf-mic+hnf-mes+hnf-det) = 0
5	Mass balance for bacteria	(doc-bac)−(bac-res+bac-doc+bac-hnf+bac-mic+bac-mec+bac-det) = 0
6	Mass balance for microzooplankton	(ph2-mic+ph3-mic+bac-mic+hnf-mic+zsp-mic)−(mic-mes+mic-doc+mic-res+mic-det+mic-los) = 0
7	Mass balance for mesozooplankton	(ph2-mes+ph3-mes+hnf-mes+mic-mes+det-mes+zsp-mes+bac-mes)−(mes-res+mes-doc+mes-det+mes-los) = 0
8	Mass balance for sporangia	(ph3-spg)−(spg-res+spg-zsp+spg-det) = 0
9	Mass balance for zoospores	(spg-zsp)−(zsp-res+zsp-mic+zsp-mes+zsp-det) = 0
10	Mass balance for detritus	(ph1-det+ph2-det+ph3-det+mic-det+mes-det+ext-det)−(det-doc+det-mic+det-mes+det-los) = 0
11	Mass balance for dissolved organic carbon	(ph1-doc+ph2-doc+ph3-doc+mic-doc+mes-doc+det-doc)−(doc-bac) = 0
12	Total gross primary production estimate	gpp-ph1+gpp-ph2+gpp-ph3 = 360.54*
13	Total net primary production estimate	(gpp-ph1+gpp-ph2+gpp-ph3)−(ph1-res+ph2-res+ph3-res) = 245.17*
14	Net bacterial production	doc-bac−bac-res = 90*
15	Viral lysis of bacteria	bac-doc = 9.90*

*values are in mgC m^{-2} d^{-1}.

doi:10.1371/journal.pone.0023273.t003

(control) bottles, inoculated each with 0.5 µCi of NaH1 4C03 , and incubated in situ for 4 h. After incubation, 30 ml of each subsamples were filtered onto 1 µm pore size Nuclepore filter and the radioactivity was estimated by liquid scintillation counting. Calculation of total primary production and excreted primary production for each depth are given in details in [98,99]. The value of net primary production was obtained after subtracting the value of the excreted primary production from the total primary production. Values corresponding for each depth were integrated to be representative of the 20 m water layer. Bacterial production was determined by measuring the uptake of tritiated thymidine into bacterial DNA [102], after incubating the samples for 45 min. The radioactivity was measured using a Beckman LS 5000 scintillation counter. The quantity of ^{3}H-thymidine incorporated into DNA was converted into bacterial production by using a conversion factor of 2×10^{18} cells produced per mole of thymidine incorporated. The bacterial production was converted in terms of cells into the equivalent amount of carbon produced using the equation of Simon and Azam [103]. Viral lysis of bacteria was considered as the value of the flux from bacteria to DOC. In formalin-fixed samples, bacteria contained in 5 ml subsamples were harvested by ultracentrifugation onto three grids for 30 min at 4°C. Each grid was then stained for 30 s with uranyl acetate and examined with a transmission electron microscope. Bacterial cells containing mature phages were identified and counted. To estimate the impact of viruses on bacterial mortality, the used method proposed by Weinbauer et al. [104] was considered, based on transmission electron microscopy examinations of entire cells visibly infected by viruses. The fraction of bacterial mortality from viral lysis was related to the calculated frequency of visibly infected cells, calculations are detailed in Bettarel et al. [100].

Constraints. The third step consists in imposing ecological limits (maximum and/or minimum) for each unknown flow, which means a linear system of inequalities: 75 inequalities were provided for MWC and 68 inequalities for MWOC (fungi inequalities were not needed). These latter are presented, explained and referenced in Table S1. The first set of inequalities concerned the gross primary production partitioning between the three size fractions (ph1, ph2, ph3). Earlier works reported the higher contribution of diatoms (ph3) during spring to the total primary production compared to the pico- and the nanophytoplankton in Lake Pavin [62]. The maximum and the minimum contribution of each phytoplankton size class to the phytoplankton total biomass during spring 2007 in Lake Pavin were considered as upper and lower bounds of their contribution to the total gross primary production. Upper bound for chytrids respiration was considered as 20% of their total carbon uptake. In fact, sporangia are living fixed on their hosts from which they absorb their substrate [9], implying low energy loss from sporangia. Zoospore produced by sporangia have their own resource storage (carbohydrates, proteins, fatty acids, phospholipids, sterols and other lipids and nucleic acids; [105]) which is used for swimming away and to subsist until colonizing new substrates or infect new hosts [9]. To constrain the ingestion rate flows, preferential ingestion constraints were built based on taxa dominance, grazers and predators' cell or individual size and their corresponding prey size sampled during spring 2007. Bacterivory by heterotrophic nanoflagellates was constrained by a minimum value given by Bettarel *et al.* [100] for Lake Pavin. Ingestion rates of zoospores by microzooplankton were considered at least the double of those ingested by mesozooplankton. The lowest bound of carbon transfer from sporangia to zoospores was considered equal to zoospores biomass estimated for spring 2007.

Solutions. The last step of the inverse analysis is the calculation of flow solutions. A range of possible values was given by the adopted method of the Monte Carlo Markov Chain (LIM-MCMC), based on the mirror technique defined by Van Den Meersche *et al.* [35]. The jump value was set at 10 and a number of iterations of 100,000 was applied that proved optimal coverage of the possible solutions. The program used was a Matlab© translation by Alain Vézina and Lauriane Campo of the

R-CRAN project package LIM-Solve [35,104]. More details on the method are available in Van Den Meersche *et al.* [35] and Niquil *et al.* [45].

4. Ecological Network Analysis

The resulting flows from inverse analysis were used for calculating indices from Ecological Network Analysis. We used an algorithm written for Matlab© by Carole Lebreton and Markus Schartau to calculate a set of indices that are used for describing the emergent properties of the ecosystem [36].

Total system throughput (TST). TST is a measure of the total system activity and is the sum of all the flows through all compartments [97].

Average path length (APL). APL is the average number of compartments crossed by a unit of carbon from its entry to the system to its living. It represents a measure of the system retention capacity [106].

System Ascendency (A). System Ascendency (A) merges the quantification of the activity and the degree of specialization involved into processes [107]. It is the product of the TST and the average mutual information (AMI: degree of specialization of flows in the network) [36]. This value is a more informative metric describing the organization of the system when it is expressed in relation to development capacity that as its maximum value (A/DC). High A/DC ratios are in fact, thought to reflect high degrees of organization [43,108]. The difference between A and its upper bound (DC) represents the overhead [109], which reflects the multiplicity of pathways in the network that happen for any of four reasons: uncertainty on imports (Oi), exports (Oe), dissipations (Do) and redundancy (R) [41]. The relative redundancy (R/DC, %) is a measure of the ecosystem degree of information loss due to parallel pathways.

Development capacity (DC). Development capacity (DC) is calculated as the product of TST and the upper limit of AMI, corresponding to the maximum potential ascendancy and to a food web with maximum specialization. The development capacity is the sum of ascendency, redundancy and information loss related to external exchanges.

As suggested by Ulanowicz [36], growth and development were characterized by indices calculated over only internal exchanges. The internal capacity of ecosystems development (DCi) was calculated as the sum of internal ascendency (Ai) and internal redundancy (Ri). Any decrease of Ai/DCi ratio in relation to the A/DC ratio could point to a strong dependency of an ecosystem on external inputs [110]. Ai/DCi ratio could also be another aspect of a highly organized ecosystem with its tendency to internalize most of its activity [43]. However, Rutledge et al. [111] and others [108,112] considered the internal redundancy (Ri/DCi) as a measure of ecosystem stability. Indeed, broken pathways are more easily re-established when the ecosystem exhibit higher internal stability or resilience to perturbation [43]. Resilience is the speed with which a system returns to equilibrium state after a perturbation [113,114].

Finn Cycling Index (FCI). FCI is the ratio of carbon flowing in loops to the sum of all carbon flows. It quantifies the fraction of all flows involved in recycling [115] and can be considered as a measure of the retentiveness of the system.

Trophic analysis: based on the trophic concept of Lindeman [116], maps the complex network of trophic transfers as a linear food chain (called Lindeman spine, [117]). The Lindeman spine allows calculation of the trophic efficiency for each level, i.e. the efficiency of transfer from one level to the next [107]. The global trophic efficiency is computed as the logarithmic mean of all the trophic level efficiencies. Two others indices were derived from the Lindeman spine the grazing chain efficiency and the percentage of detritivory. The mean values of the 100.000 set of flows resulting from the LIM-MCMC analysis were analyzed using the ecological network analysis package of Ulanowicz and Kay [118] to build the Lindeman spine. The program used for these analyses is available at www.glerl.noaa.gov/EcoNetwrk/.

5. Data analysis

Box plots, a widely used graphical tool introduced by Tukey [119], illustrate the location of the median and associated dispersion of the data. Box plots of all solutions per index for the model with chytrids were plotted with the model without chytrids. This method is useful as it provides visual information showing the differences in network properties of the two food-web models. The statistical comparison between the two constructed models was tested with two-tailed Student (t) tests on the sets of calculated ecological network indices.

Supporting Information

Table S1 Constraints used on different planktonic food web processes.
(DOC)

Acknowledgments

Thanks are due to Alain Vézina and Lauriane Campo for making available their LIM solve translation in Matlab package. We are grateful to Carole Lebreton and Markus Schartau for making available the ENA translation in Matlab package. We thank John Dolan for helpful comments and editing and the two anonymous reviewers for their suggestions.

Author Contributions

Conceived and designed the experiments: BG SR NN MJ TS-N. Performed the experiments: BG SR NN MJ TS-N. Analyzed the data: BG SR NN MJ BS-B TS-N. Contributed reagents/materials/analysis tools: BG SR NN BS-B TS-N. Wrote the paper: BG SR NN BS-B TS-N. Designed the software used in analysis: BS-B NN.

References

1. Huber-Pestalozzi G (1946) Der Walensee und sein Plankton. In Canter, H. M. and Lund, J. W., 1948. Studies on plankton parasites. I. Fluctuations in the numbers of *Asterionella Formosa* Hass. In relation to fungal epidemics. New phytol 47: 238–261.
2. Canter HM, Lund JWG (1969) The parasitism of planktonic desmids by Fungi. Osterr Botan Zeitschrift 116: 351–377.
3. Sigee DC (2005) Freshwater microbiology. John Wiley & Sons LTD, Chichester, England.
4. Tsui CKM, Hyde KD (2003) Freshwater mycology. Fungal diversity research series 10. Fungal diversity Press, The University of Hong Kong, Hong Kong.
5. Lefèvre E, Bardot C, Noël C, Carrias J.-F, Viscogliosi E, et al. (2007) Unveiling fungal zooflagellates as members of freshwater picoeukaryotes: evidence from a molecular diversity study in a deep meromictic lake. Environ Microbiol 9: 61–71.
6. Lefèvre E, Roussel B, Amblard C, Sime-Ngando T (2008) The molecular diversity of freshwater picoeukaryotes reveals high occurrence of putative parasitoids in the plankton. PloS One 3(6): 2324.
7. Lepère C, Masquelier S, Mangot JF, Debroas D, Domaizon I (2010) Vertical structure of small eukaryotes in three lakes that differ by their trophic status: a quantitative approach. ISME 4: 1509–1519.
8. Rasconi S, Jobard M, Jouve L, Sime-Ngando T (2009) Use of Calcofluor White for Detection, Identification, and Quantification of Phytoplanktonic Fungal Parasites. Appl Environ Microbiol 75: 2545–2553.
9. Sparrow FK (1960) Aquatic Phycomycetes. University of Michigan Press, Ann Arbor.
10. Jobard M, Rasconi S, Sime-Ngando T (2010) Fluorescence in situ hybridization of zoosporic fungi (chytrids) in aquatic environments: testing with clone-FISH and application to natural samples using CARD-FISH. J Microbiol Meth 83: 236–43.

11. Van Donk E (1989) The role of fungal parasites in phytoplankton succession, 171–194. *In* Sommer U, ed. Plankton Ecology: Succession in Plankton Communities, Springer-Verlag: Berlin.
12. Ibelings BW, de Bruin A, Kagami M, Rijkeboer M, Brehm M, et al. (2004) Host parasite interactions between freshwater phytoplankton and chytrid fungi (Chytridiomycota). J Phycol 40: 437–453.
13. Kagami M, de Bruin A, Ibelings BW, van Donk E (2007) Parasitic chytrids: their effects on phytoplankton communities and food-web dynamics. Hydrobiologia 578: 113–129.
14. De Bruin A, Ibelings BW, Kagami M, Mooij WM, van Donk E (2008) Adaptation of the fungal parasite *Zygorhizidium planktonicum* during 200 generations of growth on homogeneous and heterogeneous populations of its host, the diatom *Asterionella formosa*. J Euk Microb 55: 69–74.
15. Legendre L, Le Fèvre J (1991) From individual plankton cells to pelagic marine ecosystems and to global biogeochemical cycles. In: Demers S, ed. Particle analysis in Oceanography, Springer, Berlin. pp 261–300.
16. Kagami M, von Elert E, Ibelings BW, de Bruin A, Van Donk E (2007) The parasitic chytrid, *Zygorhizidium* facilitates the growth of the cladoceran zooplankter, *Daphnia* in cultures of the inedible algae *Asterionella*. Proceed Royal Soc Biol Sci 274: 1561–1566.
17. Pascual M, Dunne J (2006) Ecological Networks: Linking structure to dynamics in Food webs. Oxford University Press, USA.
18. Lafferty KD, Hechinger RF, Shaw JC, Whitney K, Kuris AM (2006) Food webs and parasites in salt marsh ecosystem. Chap. 9, In:, , Collinge S, Ray C (2006) Disease ecology: community structure and pathogen dynamics, Oxford University Press, Oxford. pp 119–134.
19. Lafferty KD, Allesina S, Arim M, Briggs CJ, Leo G, et al. (2008) Parasites in food webs: the ultimate missing links. Ecol Lett 11: 533–546.
20. Huxham M, Raffaelli D, Pike A (1995) Parasites and Food Web Patterns. J Anim Ecol 64: 168–176.
21. Thompson RM, Mouritsen KN, Poulin R (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. J Anim Ecol 74: 77–85.
22. Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? Trends Ecol Evol 21: 381–385.
23. Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen, London. Reprinted 2000 by The University of Chicago Press, (Chapman & Hall, London).
24. May RM (1972) Will a large complex system be stable? Nature 238: 413–414.
25. Pimm SL (1984) The complexity and stability of ecosystems. Nature 307: 321–326.
26. McCann KS (2000) The diversity-stability debate. Nature 405: 228–233.
27. O'Gorman EJ, Emmerson MC (2009) Perturbations to trophic interactions and the stability of complex food webs. Proceed Nat Acad Sci USA 106(32): 13397.
28. Hosack GR, Li HW, Rossignol PA (2009) Sensitivity of system stability to model structure. Ecol Model 220(8): 1054–1062.
29. May RM (1973) Stability and complexity in model ecosystems Princeton U.P, Princeton. 265 p.
30. Williams R, Martinez ND (2004) Simple rules yield complex food webs. Nature 404: 180–183.
31. Neutel AM, Heesterbeek JAP, de Ruiter P (2002) Stability in real food webs: weak links in long loops. Science 296: 1120–1123.
32. Niquil N, Kagami M, Urabe J, Christaki U, Viscogliosi E, et al. (2011) Potential role of fungi in plankton food web functioning and stability: a simulation analysis based on Lake Biwa inverse model. Hydrobiologia 659: 65–79.
33. Niquil N, Bartoli G, Urabe J, Jackson GA, Legendre L, et al. (2006) Carbon steady state model of the planktonic food web of Lake Biwa, Japan. Freshwater Biol 8: 1570–1585.
34. Vézina AF, Platt T (1988) Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Mar Ecol Prog Ser 42: 269–287.
35. Van den Meersche K, Soetaert K, Van Oevelen D (2009) xsample(): An R Function for Sampling Linear Inverse Problems. J Stat Soft 30: 1–15.
36. Ulanowicz RE (1986) Growth and Development: Ecosystems Phenomenology. Springer-Verlag, New York. 203 p.
37. Ulanowicz RE (1997) Ecology, the Ascendent Perspective. Columbia University Press, New York. 201 p.
38. Ulanowicz RE, Goerner SJ, Lietaer B, Gomez R (2009) Quantifying sustainability: resilience, efficiency and the return to of information theory. Ecol complex 6: 27–36.
39. Ulanowicz RE (2003) Some steps toward a central theory of ecosystem dynamics. Comput Biol Chem 27: 523–530.
40. Ulanowicz RE (1980) An hypothesis on the development of natural communities. J Theor Biol 85: 223–245.
41. Ulanowicz RE (1988) On the importance of higher-level models in ecology. Ecol Model 43: 45–56.
42. Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. Nature 442: 265–269.
43. Baird D, Mc Glade JM, Ulanowicz RE (1991) The comparative ecology f six marine ecosytems. Phill Tran Roy Soc London Ser B 333: 15–29.
44. Grami B, Niquil N, Sakka Hlaili A, Gosselin M, Hamel D, et al. (2008) The plankton food web of the Bizerte Lagoon (South-Western Mediterranean): II. Carbon steady state modeling using inverse analysis. Estuar Coast Shelf S 79: 101–113.
45. Niquil N, Soetaert K, Johnson GA, van Oevelen D, Bacher C, et al. (2012) Inverse modelling in modern ecology and application to coastal ecosystem. Chap. 9 in Vol. 9 Estuarine and coastal ecosystem modelling (D. Baird & A. Mehta Editors) In: Treatise on coastal and estuarine Science E. Wolanski, DS. Mc LuskyChief, eds. Elsevier, *In press*.
46. Kones JK, Soetaert K, van Oevelen D, Owino JO, Mavuti K (2006) Gaining insight into food webs reconstructed by the inverse method. J Marine Syst 60: 153–166.
47. Niquil N, Jackson GA, Legendre L, Delesalle B (1998) Inverse model analysis of the planktonic food web of Takapoto Atoll (French Polynesia). Mar Ecol Prog Ser 165: 17–29.
48. Johnson GA, Niquil N, Asmus H, Bacher C, Asmus R, et al. (2009) The effects of aggregation on the performance of the inverse method and indicators of network analysis. Ecol Model 220: 3448–3464.
49. Kones JK, Soetaert K, Van Oevelen D, Owino JO (2009) Are network indices robust indicators of food web functioning? A Monte Carlo Approach. Ecol model 220: 370–382.
50. Rasconi S (2010) Etude des chytrides parasites du phytoplancton dans les écosystèmes aquatiques. PhD thesis, Blaise Pascal University, Clermont Fd, France.
51. Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, et al. (1983) The Ecological Role of Water-Column Microbes in the sea. Mar Ecol Prog Ser 10: 257–263.
52. Yoshimizu C, Yoshida T, Nakanishi M, Urabe J (2001) Effects of zooplankton on the sinking flux of organic carbon in Lake Biwa. Limnology 2: 37–43.
53. Kagami M, Gurung TB, Yoshida T, Urabe J (2006) To sink or to be lysed? Contrasting fate of two large phytoplankton species in Lake Biwa. Limnol Oceanogr 51(6): 2775–2786.
54. Van Donk E, Ringelberg J (1983) The effect of fungal parasitism on the succession of diatoms in Lake Maarsseveen-I (The Netherlands). Freshwater Biol 13: 241–251.
55. Kudoh S, Takahashi M (1990) Fundal control of population changes of planktonic diatom Asterionella Formosa in shallow eutrophic lake. J Phycol 26: 239–244.
56. Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) PEG-model of Seasonal Succession of Planktonic Events in Fresh Waters. Arch Hydrobiol 106(4): 433–471.
57. Kagami M, Helmsing NR, van Donk E (2010) Parasitic chytrids could promote copepod survival by mediating material transfer from inedible diatoms. Hydrobiologia 659(1): 49–54.
58. Gleason FH, Kagami M, Marano AV, Sime-Ngando T (2009) Inoculum. Newsletter Mycol Soc Amer 59: 1–3.
59. Canter HM, Jaworski GHM (1979) The Occurrence of a Hypersensitive Reaction in the Planktonic Diatom Asterionella formosa Hassall Parasitized by the Chytrid *Rhizophydium planktonicum* Canter Emend., in Culture. New Phytol 82: 187–206.
60. Devaux J (1976) Dynamique des populations phytoplanctoniques dans deux lacs du massif central français. Ann Sta Biol Besse-en-Chandesse 10: 1–185.
61. Amblard C (1978) Application du dosage des adenosines 5′-phosphate à l'étude d'un phytoplancton lacustre (Lac Pavin). PhD thesis, Université de Clermont FD, France.
62. Amblard C, Bourdier G (1990) The spring bloom of the diatom *Melosira italica* subsp. subarctica in Lake Pavin: biochemical, energetic and metabolic aspects during sedimentation. J Plank Res 12(3): 645–660.
63. Arias-Gonzalez JE, Morand S (2006) Trophic functioning with parasites: a new insight for ecosystem analysis. Mar Ecol Prog Ser 320: 43–53.
64. Kuris AM, Hechinger RF, Shaw JC, Whitney KL, Aguirre-Macedo L, et al. (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 24: 15–18.
65. Jordán F, Sheuring I, Molnár I (2003) Persistence and flow reliability in simple food webs. Ecol Model 161: 117–124.
66. Loreau M, Downing A, Emmerson M, Gonzalez A, Hughes J, et al. (2002) A new look at the relationship between diversity and stability., in: Loreau M, Naeem S, Inchausti P, eds. Biodiversity and ecosystem functionning Oxford University press, Oxford. pp 77–91.
67. Baird D, Ulanowicz RE (1989) The Seasonal Dynamics of The Chesapeake Bay Ecosystem. Ecol Monographs 59: 329–364.
68. Ulanowicz RE, Goerner SJ, Lietaer B, Gomez R (2009) Quantifying sustainability: Resilience, efficiency and the return of information theory. Ecol Complexity 6: 27–36.
69. MacArthur R (1955) Fluctuations of Animal Populations and a Measure of Community Stability. Ecology 36: 533–536.
70. Dobson AP, Lafferty K, Kuris A (2005) Parasites and food webs. In Ecological Networks: Linking Structure to Dynamics in Food webs Dunne JA, Pascual M, eds. 119–135, Oxford University Press.
71. Odum EP (1969) The strategy of ecosystem development. Science 164: 262–270.
72. Marquis E, Niquil N, Delmas D, Hartmann HJ, Bonnet D, et al. (2007) Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. Estuar Coast Shelf S 73: 223–235.
73. Amblard C, Rachiq S, Bourdier G (1992) Photolithotrophy, photoheterotrophy and chemoheterotrophy during spring phytoplankton development (Lake Pavin). Microbial Ecol 24: 109–123.

74. Sime-Ngando T, Hartmann HJ (1991) Short-term variations of the abundance and biomass of planktonic ciliates in a eutrophic lake. Eur J Protistol 27: 249–263.
75. Bjørnsen PK (1986) Automatic determination of bacterioplankton biomass by image analysis. Appl Environ Microb 51: 1199–1204.
76. Søndergaard M, Jensen LM, Ertebrjerg G (1991) Picoalgae in Danish coastal waters during summer stratification. Mar Ecol Prog Ser 79: 139–149.
77. Mullin MM, Sloan PR, Eppley RW (1966) Relationship between carbon content, cell volume and area in phytoplankton. Limnol Oceanogr 11: 307–311.
78. Caron DA (1983) A technique for the enumeration of photosynthetic and heterotrophic nanoplankton using epifluorescence microscopy, and a comparison with other procedures. Appl Environ Microb 46: 491–498.
79. Børsheim KY, Bratbak G (1987) Cell volume to cell carbon conversion factors for a bacterivorous *Monas sp.* enriched from seawater. Mar Ecol Prog Ser 36: 171–175.
80. Utermöhl H (1931) Neue wege in der quantitativen erfassung des planktons (mit besonderer berücktingung des ultraplanktons). Verh Int Ver Theor Angew Limnol 5: 567–596.
81. Menden-Deuer S, Lessard EJ (2000) Carbon volume relationships for dinoflagellates, diatoms and other protest plankton. Limnol Oceanogr 45: 569–579.
82. Putt M, Stoecker DK (1989) An experimentally determined carbon: volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. Limnol Oceanogr 34: 1097–1103.
83. Prepas E (1978) Sugar-frosted Daphnia: an improved fixation technique for Cladocera. Limnol Oceanogr 23: 557–559.
84. Dussart B (1967) Les Copépodes des eaux continentales d'Europe occidentale. In: Boubée N, Cie, eds. Calanoides et Harpactoides, Paris 1: 500.
85. Riemann F, Ernst W, Ernst R (1990) Acetate uptake from ambient water by the free-living marine nematode Adoncholaimus thalassophygas. Mar Biol 104: 453–457.
86. Gradinger R, Friedrich C, Spindler M (1999) Abundance, Biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep-Sea Res PT II 46: 1457–1472.
87. Feller RJ, Warwick RM (1988) Energetics. In: Higgings RP, Thiel H, eds. Introduction to the study of meiofauna, Smithsonian Institution Press, Washington, DC. pp 181–196.
88. Kankaala P, Johansson S (1986) The influence of individual variation on length-biomass regressions in three crustacean zooplankton species. J Plank Res 8(6): 1027–1038.
89. Pace ML, Orcutt D (1981) The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnol Oceanogr 26: 822–830.
90. McCauley E (1984) The estimation of the abundance and biomass of zooplankton in samples. In Downing JA, Rigler FH, eds. A Manual for the Assessment of Secondary Productivity in Fresh Waters, 2nd edn, Blackwell Scientific Publications, Oxford. pp 228–265.
91. Andersen T, Hessen DO (1991) Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnol Oceanogr 36: 807–814.
92. Canter HM (1950) Fungal parasites of the phytoplankton .I. Studies on British chytrids X. Ann Bot 14: 263–289.
93. Canter HM, Lund JWG (1951) Studies on plankton parasites. III. Examples of the 399 interaction between parasitism and other factors determining the growth of diatoms. Ann Bot 15: 359–371.
94. Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasit 83: 575–583.
95. Not F, Simon N, BIegala IC, Vaulot D (2002) Application of fluorescent in situ hybridization coupled with tyramide signal amplification (FISH-TSA) to assess eukaryotic picoplankton composition. Aquat Microb Ecol 28: 157–166.
96. Carrias JF, Amblard C, Quiblier-Lloberas C, Bourdier G (1998) Seasonal dynamics of free and attached heterotrophic nanoflagellates in an oligomesotrophic lake. Freshwater Biol 39: 91–101.
97. Arnous MB, Courcol N, Carrias JF (2010) The significance of transparent exopolymeric particles in the vertical distribution of bacteria and heterotrophic nanoflagellates in Lake Pavin. Aquat Sci 72: 245–253.
98. Devaux J (1980) Contribution à l'étude limnologique du lac Pavin (France) I: facteurs abiotiques et phytoplancton. Hydrobiologia 62(2): 67–189.
99. Bettarel Y, Sime-Ngando T, Amblard C, Carrias JF, Sargos D, et al. (2002) The functional importance of bacteriophages in the microbial loop of an oligomesotrophic lake over a diel cycle. Ann Limnol 38(4): 263–269.
100. Bettarel Y, Amblard C, Sime-Ngando T, Carrias JF, Sargos D, et al. (2003) Viral Lysis, Flagellate Grazing Potential, and Bacterial Production in Lake Pavin. Microbial Ecol 45: 119–127.
101. Steemann-Nielsen E (1952) The use of radio-active carbon (l 4C) for measuring organic production in the sea. J Cons Explor Mer 18: 117–140.
102. Petit M, Servais P, Lavandier P (1999) Bacterial production measured by leucine and thymidine incorporation rates in French lakes. Freshwater Biol 42: 513–524.
103. Simon M, Azam F (1989) Protein content and protein synthesis rates of planktonic marine bacteria. Mar Ecol Prog Ser 52: 201–213.
104. Weinbauer MG, Winter C, Höfle MG (2002) Reconsidering transmission electron microscopy based estimates of viral infection of bacterioplankton using conversion factors derived from natural communities. Aquat Microb Ecol 27: 103–110.
105. Suberkropp KF, Cantino EC (1973) Utilization of endogenous reserves by swimming zoospores of *Blastocladiella emersonii*. Arch Microbiol 89: 205–221.
106. Kay JJ, Graham LA, Ulanowicz RE (1989) A detailed guide to network analysis. In Wulff F, Field JG, Mann KH, eds. Network Analysis in Marine Ecology: Methods and Applications, Springer-Verlag, Berlin. 284 p.
107. Ulanowicz RE, Wulff F (1991) Comparing ecosystem structures: the Chesapeake Bay and the Baltic Sea. In: Cole J, Lovett G, Findlay S, eds. Comparative analysis of ecosystems, pattern, mechanism, and theories, Springer-Verlag, New York. pp 140–166.
108. Baird D, Luczkovich J, Christian RR (1998) Assessment of spatial and temporal variability in system attributes of the St. Marks National Wildlife Refuge, Apalachee Bay, Florida. Estuar Coast Shelf S 47: 329–34.
109. Ulanowicz RE, Norden JS (1990) Symmetrical overhead in flow networks. Int J Syst Sci 1: 429–437.
110. Baird D, Heymans JJ (1996) Assessment of ecosystem changes in response to freshwater inflow of the Kromme River estuary, St. Francis Bay, South Africa: a network analysis approach. Water S A (Pretoria) 22: 307–318.
111. Rutledge RW, Bacore BL, Mulholland RJ (1976) Ecological stability: an information theory standpoint. J Theor Biol 57: 355–371.
112. Baird D, Asmus H, Asmus R (2004) Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Mar Ecol Prog Ser 279: 45–61.
113. De Angelis DL (1980) Energy Flow, Nutrient Cycling, and Ecosystem Resilience. Ecology 61: 764–771.
114. Pimm SL (1991) The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities. The University of Chicago Press, Chicago and London.
115. Finn JT (1976) Measures of ecosystem structure and function derived from analysis of flows. J Theor Biol 56(2): 363–380.
116. Lindeman RL (1942) The trophic dynamic aspect of ecology. Ecology 23: 399–418.
117. Ulanowicz RE, Kemp WM (1979) Toward a canonical trophic aggregation. Am Nat 114: 871–883.
118. Ulanowicz RE, Kay JJ (1991) A package for the analysis of ecosystem flow networks. Env Software 6(3): 131–142.
119. Tukey JW (1977) Exploratory Data Analysis. Reading, MA: Addison Wesley.

Annexe 3

Tortajada, S., Niquil, N., Blanchet, H., Grami, B., Montanié, H., David, V., Glé, C., Saint-Béat, B., Johnson, G.A., Marquis, E., Del Amo, Y., Dubois, S., Vincent, D., Dupuy, C., Jude, F., Hartmann, H.J., Sautour, B.
2012.

Network analysis of the planktonic food web during the spring bloom in a semi enclosed lagoon (Arcachon, SW France).

Acta Oecologica 40, 40-50.

(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

Acta Oecologica 40 (2012) 40–50

Contents lists available at SciVerse ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Network analysis of the planktonic food web during the spring bloom in a semi enclosed lagoon (Arcachon, SW France)

Sébastien Tortajada [a,1], Nathalie Niquil [a,*,1], Hugues Blanchet [b], Boutheina Grami [a], Hélène Montanié [a], Valérie David [a], Corine Glé [b], Blanche Saint-Béat [a], Galen A. Johnson [a], Elise Marquis [a,c], Yolanda Del Amo [b], Sophie Dubois [b], Dorothée Vincent [b,d], Christine Dupuy [a], Florence Jude [b], Hans J. Hartmann [a], Benoît Sautour [b]

[a] LIENSs, UMR 6250 Université de La Rochelle – CNRS, 2 rue Olympe de Gouges, 17000 La Rochelle, France
[b] EPOC, UMR 5805 Université Bordeaux 1 – CNRS, 2 rue du Professeur Jolyet, 33120 Arcachon, France
[c] Institute of Oceanography, National Taiwan University, No. 1, Section 4, Roosevelt Road, Taipei, 10617, Taiwan
[d] Laboratoire d'Océanologie et de Géosciences, UMR 8187 Université du Littoral Côte d'Opale CNRS, 32 av Foch, 62930 Wimereux, France

ARTICLE INFO

Article history:
Received 19 January 2011
Accepted 13 February 2012
Available online

Keywords:
Plankton
Trophic structure
Linear inverse model
Ecological network analysis
Northeast Atlantic
Bay of Biscay

ABSTRACT

The structure and functioning of the food web in Arcachon Bay (Bay of Biscay, Northeast Atlantic Ocean) was analyzed during the spring bloom period to evaluate the sensitivity of this ecologically and economically important ecosystem perturbation. Differences in the timing of the peaks in phytoplankton and zooplankton populations occur due to a mismatch between primary production and grazing. Using an inverse approach based on *in situ* experimental data, an ecological network analysis was carried out to characterize emergent properties of the food web and to estimate carbon flows. The data set was composed of rate measurements for net primary production, import and export of dissolved organic carbon, and grazing of heterotrophic nanoflagellates and ciliates by metazoan micro- and meso-zooplankton. Ecological network analysis indices were calculated on the estimated fluxes and compared to values from plankton models built with exactly the same method. The largest activities in the resulting model came from the nano- and microphytoplankton. The detritivory/herbivory ratio, the recycling rates and the relative redundancy of the system were very low compared to other planktonic systems, even in similar periods of bloom. These values indicate a transitional system with poor resilience that exports a large quantity of carbon either to the benthos where it is consumed by non-planktonic consumers such as oysters, or else to systems outside of the bay (outwelling).

1. Introduction

Despite their relatively very narrow surface area, coastal regions represent about 20% of the primary production of the world ocean (Duarte et al., 2004; Gattuso et al., 1998). Such high levels of primary production are sustained by continental inputs through river discharges into coastal ecosystems and a strong benthic-pelagic coupling. The effects of increasing human pressure exerted on coastal ecosystems is often difficult to assess at the level of ecosystem functioning since these areas are impacted by multiple factors [e.g. industrial fishing activities, intensive aquaculture (Héral, 1993), introduction of invasive species (Gucu, 2002), eutrophication and/or imports of pollutants (Tett et al., 2003)]. Interactions between these pressures and both physical and biological components are complex and are driven by space and time variability from micro- to macroscale (10 m–1000 km).

One of the possible approaches for understanding ecosystem functioning and its response to perturbations is the study of their trophic networks (Ulanowicz, 1986, 1997). Researchers have developed various food web models to quantify the energy and matter transfers between the different compartments of an ecosystem. Amongst the several approaches developed, static approaches (Kones et al., 2009; Vézina and Platt, 1988) favor the biological complexity inside the web. Although these models neglect the spatial and temporal variability of the trophic groups, they take into account a high number of compartments in the food web. Vézina and Platt (1988) developed an inverse analysis technique to describe marine planktonic food webs using measured carbon and nitrogen flows to estimate the unknown flow values.

* Corresponding author. Tel.: +33 (0) 546457271; fax: +33 (0) 546458264.
E-mail address: nniquil@univ-lr.fr (N. Niquil).
[1] The first two authors contributed equally to this work.

1146-609X/$ – see front matter © 2012 Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.actao.2012.02.002

This approach has been successfully applied to distinct aquatic ecosystems to analyze flows among trophic components [e.g. lakes (Niquil et al., 2006; Vézina and Pace, 1994), Mediterranean lagoons (Grami et al., 2008), atoll lagoons (Niquil et al., 2001), continental shelves (Marquis et al., 2007), and intertidal mudflats (Degré et al., 2006)]. These studies revealed that inverse analysis is a very useful and relevant tool for determining the relative importance of trophic channels within a given food web. However, substantial knowledge of the links between trophic components is required to successfully apply inverse analysis. Thus, inverse modeling is often applied in association with Ecological Network Analysis (ENA, e.g. Ulanowicz, 1997) to characterize emergent properties of the observed food web. ENA aim to characterize the structure of a food web through a set of indices that describe the connections between compartments through an analysis of the inputs and outputs flows of a compartment, the trophic structure (based on a linearization of the network), the rates of recycling, and the topology of the flows (how redundant/specialized are the flows).

The study of the Arcachon Bay ecosystem was motivated by its strong ecological (largest *Zostera noltii* seagrass bed of Europe (Auby and Labourg, 1996), and economical interests. The annual production of cultivated *Crassostrea gigas* is approximately 15.000 tons and Arcachon Bay is the main European center for oyster spats (de Montaudoin et al., 2001). Since 1998, several years have been particularly unfavorable for oyster larval recruitment. One of the possible causes of this shortage could be linked to an inadequate nutritive pool for the larvae (D. Maurer, pers. comm.). To understand the interactions between oysters and their potential prey, several studies have focused on plankton community variability (Glé et al., 2007, 2008; Vincent et al., 2002), with emphasis of the spring period during the oyster growth period (Castel and Courties, 1982; D'Elbée and Castel, 1995; Vincent et al., 2002).

The plankton succession in Arcachon Bay is characterized by an early spring bloom of large phytoplankton cells (diatoms >20 μm) in the external part of the bay, mainly caused by anticyclonic conditions (Glé et al., 2007) (Fig. 1). Temperature and incident irradiance increase during the following weeks contribute to the bloom extension into the inner part of the bay (Glé et al., 2007) (Fig. 1). This bloom plays a central role in foodweb functioning since the non-toxic chain-forming diatoms that dominate the blooms make the greatest contribution to annual primary production in the lagoon (Glé et al., 2008). Zooplankton abundance is characterized by a winter minimum, an increase during spring and a maximum in summer, with a dominating temperature control and a strong dominance of meroplankton taxa (Vincent et al., 2002). During the spring to summer transition, the long developmental time of the large zooplankton causes a time lag between phytoplankton and zooplankton dynamics. Consequently, phytoplankton could not be efficiently consumed by zooplankton because of the zooplankton's relatively low abundance, providing a large supply of organic matter which serves as a rich food source for benthic organisms as shown in other coastal ecosystems (Oviatt et al., 2002). Therefore, in such a shallow coastal ecosystem with high densities of suspension feeders (particularly due to oyster culture), studying the planktonic food web during this transition period will allow a better understanding of the organisation of the different compartments as well as an estimation of its export of carbon available for oysters. The Ecological Network Analysis (ENA) indices will then allow characterizing the emergent properties of this system (recycling, detritivory/herbivory, redundancy). This emergent properties can be linked to the concepts of ecological stability defined by the two notions of resilience (ability of an ecosystem to come back to its equilibrium after a perturbation) and resistance (ability of an ecosystem to resist to a perturbation) (McCann, 2000).

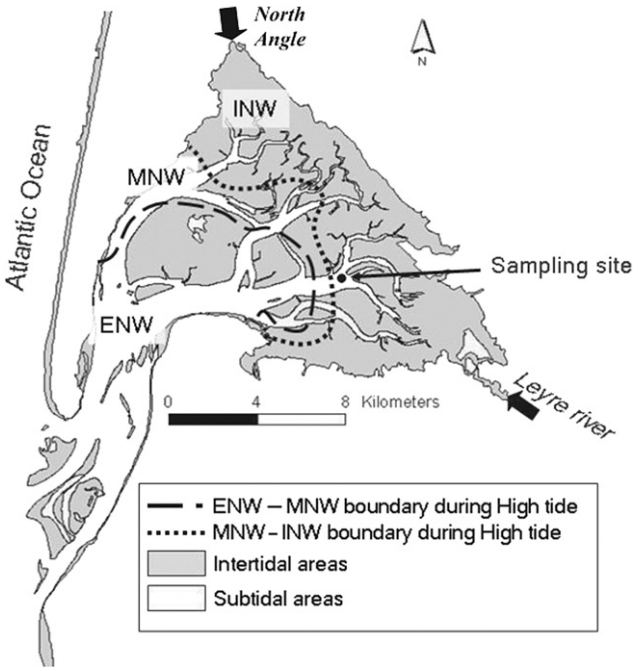


Fig. 1. Map of Arcachon Bay at low tide showing the sampling site (arrow) and the boundaries of the main water bodies during high tide. INW: Internal Neritic Water; MNW: Mean Neritic Water; ENW: External Neritic Water.

2. Experimental procedures

2.1. Study site

Arcachon Bay is located in the south-western Atlantic coast of France (44°40′N, 1°10′W). This semi-enclosed ecosystem is linked to the Atlantic Ocean by a 3-km wide and 20-km long entrance channel (Fig. 1). The surface area, excluding the entrance channel, is 155 km^2, and the average water volume is 731.10^6 m^3 at high tide. The bay is meso- to macrotidal, with a tidal range varying between 0.90 and 4.90 m. The tide is semi-diurnal. Though the oceanic component influences the water quality of the lagoon, freshwater inputs are not negligible with $1.25\ 10^9$ m^3 per year: this consists of 83% coming from rivers, 11% from rainfall and 6% from groundwater streaming. The river inputs result principally from the Leyre (80%) and from numerous small channels (20%) (Fig. 1). Both marine and freshwater inputs create a thermohaline gradient from the external to the inner parts of the bay and in a distinction of three water bodies according to their hydrological parameters (Bouchet, 1993): the external neritic waters (ENW), the median neritic waters (MNW) and the inner neritic waters (INW) (Fig. 1). The subtidal zone is characterized by channels (71 km^2) with a maximal depth of 25 m. The surface area of the intertidal zone is 110 km^2. The majority of this surface is occupied by the seagrass *Z. noltii* bed (Auby and Labourg, 1996).

2.2. Inverse analysis method

The inverse approach of Vézina and Platt (1988) was developed to estimate flow values within food webs, with a special interest for systems with a low ratio of known *versus* unknown flow values. It describes each trophic component (compartment) in terms of all the possible flows that connect them to others. A steady state assumption (i.e. first criterion of the inverse analysis method) was adopted, neglecting daily growth compared to production flows. Thus, several mass balance equations describing each compartment

are generated assuming that the sum of input flows is equal to the output flows. Plankton rate processes determined through field studies, such as primary production and grazing rates, were incorporated into the model by formulating them as additional linear equations of the flows (second criterion of the Linear Inverse Model). The k equations describing the mass balance and the field data can thus be written:

$$A \times \mathbf{r} = \mathbf{b} \quad (1)$$

Where A is the matrix of coefficients, **r** is the vector of flows (composed of n unknowns) and **b** is the solution vector of the k equations (Vézina and Platt, 1988).

Because the number of flows (unknowns, $n = 59$) exceeds the number of equations (mass balance + data estimates, $k = 11 + 9 = 20$ equations), the system is mathematically underdetermined and has an infinite number of solutions. Vézina and Platt (1988) applied two additional criteria to obtain a single solution. The first was a set of constraints limiting the rates and efficiencies of biological processes, based on literature values. These constraints were expressed as inequalities for linear combinations of flows. The system of inequalities can be written:

$$G \times \mathbf{r} \geq \mathbf{h} \quad (2)$$

Where G is a matrix of coefficients and **h** is the boundaries vector of inequalities (Vézina and Platt, 1988).

Applying such constraints reduces the domain of possible solutions, but still allows an infinite number of possible solutions. The second criterion is based on the parsimony principle which assumes that the 'best' values for the flows are those forming the smallest Euclidean norm (Vézina, 1989). This method is now called Least Square Linear Inverse Model in the literature. This criterion has been used in all previous planktonic food web studies (reviewed in (Niquil et al., accepted). These two additional criteria lead to a single solution vector describing the flows. The algorithmic technique is fully described in Vézina and Platt (1988).

2.3. Available data and their incorporation into model equations

Field sampling was carried out in the south-eastern part of Arcachon Bay at the station called Comprian (Fig. 1), in the Inner Neritic Waters (INW). Data used were collected during May 2003, 2005 and 2006. Planktonic organisms were sampled and identified with at least family-level specificity twice a week during May 2005 and 2006: monthly average values were used for estimating biomass of all the sampled planktonic organisms (Table 1). Planktonic organisms were then regrouped into nine living compartments (or functional groups) according to their size and their feeding behavior. These nine compartments were: three size-fractions of phytoplankton (ph1 to ph3, biomass estimation by cytometry and Utermöhl count), five classes of zooplankton (hnf, cil, mic, mes and cap, inverted microscope and binocular magnifying glass count) and one class of heterotrophic bacteria (bac, cytometry) (Table 1). Two non-living compartments were also identified : particulate (POC) and dissolved organic carbon (DOC). Between these compartments, all possible flows were selected and constituted the *a priori* model (Table 2). The translation of process estimates from the field into linear combinations of flows is given in Table 3.

Glé et al. (2008) estimated net primary production rates of 245 mg C m^{-2} d^{-1} for microphytoplankton (ph3), 129 mg C m^{-2} d^{-1} for nanophytoplankton (ph2) and 44 mg C m^{-2} d^{-1} for picophytoplankton (ph1) during spring 2003 at the Comprian station using measurement of incorporation of ^{14}C. The input of DOC was defined as the product between the mean annual concentration of DOC in the Leyre river and the mean daily flow for all rivers (DOC input = 13.1 mg C m^{-2} d^{-1}). The DOC export was described as the product between the DOC concentration in the entrance channel of the Bay and its mean daily flow (DOC export = 79.5 mg C m^{-2} d^{-1}) (C. Carruesco, pers. comm.).

Several grazing experiments were performed during high frequency monitoring in May 2006. Polycarbonate bottles (2.4 L) were filled with <200 μm sieved seawater containing a natural assemblage of preys (phytoplankton, heterotrophic nanoflagellates

Table 1
Descriptions and abbreviations of the eleven food web compartments used in the model. The currency is expressed as organic carbon (mg C m^{-2}).

Description	Abbreviation	Taxon	Converting factor	Counting method
Picophytoplankton (<2 μm)	ph1	Cyanobacteria Picoeucaryots	Blanchot and Rodier (1996) Zubkov et al. (1998)	Flow cytometry
Nanophytoplankton (2–20 μm)	ph2	Cryptophycea Nanoeucaryts	Com pers. Com pers.	Utermöhl count
Microphytoplankton (>20 μm)	ph3	Diatoms Dinoflagellate Silicoflagellate Others	Menden-Deuen and Lessard (2000)	Utermöhl count
Heterotrophic bacteria	bac			Cytometry flow
Heterotrophic nanoflagellates	hnf		Maixandeau et al. (2005)	Inverted microscope
Ciliates	cil	Ciliates Tintinids	Maixandeau et al. (2005) Sautour (1991)	Utermöhl count
microzooplankton Metazoans (<200 μm)	mic	Meroplanktonic larva Nauplii Foraminifera	Sautour (1991)	Stereo microscope
Mesozooplankton (>200 μm)	mes	Copepods Decopod metazoea Decapod Zoea Cladoceran	Sautour (1991)	Stereo microscope
Carnivorous zooplankton	cap	Chaetognatha Cnidera Mydisadecae Ctenophora	Sautour (1991)	Stereo microscope
Particulate organic carbon (non-living material >0.7 μm)	poc			
Dissolved organic carbon (non-living material <0.7 μm)	doc			

Table 2
Flows of the steady-state model. For each flow, the value given is obtained by the inverse analysis. Abbreviations are given in Table 1.

	Description	Flow number	Flow from	Flow to	Inferred value (mg C m^{-2} d^{-1})
Primary production	Gross phytoplankton production for ph1	1	Gpp	ph1	50,76
	Gross phytoplankton production for ph2	2	Gpp	ph2	149,10
	Gross phytoplankton production for ph3	3	Gpp	ph3	283,61
Flows from Picophytoplankton	Grazing of ph1 by hnf	4	ph1	hnf	18,40
	Grazing of ph1 by ciliate	5	ph1	cil	5,61
	Grazing of ph1 by microzooplankton metazoans	6	ph1	mic	19,83
	DOC excretion by ph1	7	ph1	doc	4,38
	Respiration by ph1	8	ph1	res	2,54
Flows from Nanophytoplankton	Grazing of ph2 by ciliate	9	ph2	cil	16,99
	Grazing of ph2 by microzooplankton metazoans	10	ph2	mic	16,30
	Grazing of ph2 by mesozooplankton	11	ph2	mes	17,37
	Export of ph2	12	ph2	los	78,12
	DOC excretion by ph2	13	ph2	doc	12,88
	Respiration by ph2	14	ph2	res	7,45
Flows from Microphytoplankton	Grazing of ph3 by microzooplankton metazoans	15	ph3	mic	32,59
	Grazing of ph3 by mesozooplankton	16	ph3	mes	44,42
	DOC excretion by ph3	17	ph3	doc	24,49
	Respiration by ph3	18	ph3	res	14,18
	ph3 detrital POC production	19	ph3	poc	49,12
	Export of ph3	20	ph3	los	118,80
Flows from heterotrophic nanoflagellate	Grazing of hnf by ciliate	21	hnf	cil	16,43
	Grazing of hnf by microzooplankton metazoans	22	hnf	mic	1,67
	Grazing of hnf by mesozooplankton	23	hnf	mes	14,10
	DOC excretion by hnf	24	hnf	doc	4,60
	Respiration by hnf	25	hnf	res	9,20
Flows from ciliate	Grazing of ciliate by microzooplankton metazoans	26	cil	mic	8,21
	Grazing of ciliate by mesozooplankton	27	cil	mes	12,33
	DOC excretion by ciliate	28	cil	doc	4,11
	Respiration by ciliate	29	cil	res	16,43
Flows from metazoans microzooplankton	Grazing of microzooplankton metazoans by mesozooplankton	30	mic	mes	23,09
	Grazing of microzooplankton metazoans by carnivorous zooplankton	31	mic	cap	6,56
	Export of metazoans microzooplankton	32	mic	los	24,01
	Respiration by metazoans microzooplankton	33	mic	res	32,20
	POC egestion of metazoans microzooplankton	34	mic	poc	10,73
	DOC excretion by metazoans microzooplankton	35	mic	doc	10,73
Flows from mesozooplankton	Grazing of mesozooplankton by carnivorous zooplankton	36	mes	cap	19,69
	Export of mesozooplankton	37	mes	los	36,96
	Respiration of mesozooplankton	38	mes	res	36,96
	POC egestion of mesozooplankton	39	mes	poc	10,31
	DOC excretion by mesozooplankton	40	mes	doc	11,55
Flows from bacteria	Respiration by bacteria	41	bap	res	36,88
	Grazing of bacteria by hnf (hnf Bacterivory)	42	bap	hnf	27,60
	Grazing of bacteria by ciliate (ciliate bacterivory)	43	bap	cil	2,05
	Grazing of bacteria by metazoans microzooplankton (bacterivory)	44	bap	mic	10,73
	DOC excretion by bacteria	45	bap	doc	3,51
Flows from carnivorous zooplankton	Export of carnivorous zooplankton	46	cap	los	2,60
	Respiration by carnivorous zooplankton	47	cap	res	20,88
	POC egestion by carnivorous zooplankton	48	cap	poc	6,04
	DOC excretion by carnivorous zooplankton	49	cap	doc	3,28
Flows from DOC	DOC consumption by bacteria	50	doc	bap	80,78
	DOC floculation to POC	51	doc	poc	30,89
Flows from POC	POC dissolution to DOC	52	poc	doc	12,02
	Grazing of POC by mesozooplankton	53	poc	mes	4,16
	Grazing of POC by metazoans microzooplankton	54	poc	mic	18,00
	Grazing of POC by carnivorous zooplankton	55	poc	cap	6,56
Import/export of DOC and POC	Export of POC → POC Export	56	poc	los	79,45
	Export of DOC → DOC Export	57	doc	los	25,29
	Import of POC → POC Import	58	los	poc	13,10
	Import of DOC → DOC Import	59	los	doc	45,40

Table 3
Values and linear equations used as complements for the mass balance equations, calculated from field observations. Abbreviations are from Tables 1and 2. NPP = Net Primary Production.

Equation number	Process	Equation	Reference
1	NPP of ph1	CgppTOph1 - Cph1TOres - Cph1TOpoc = 44	Glé et al., 2008
2	NPP of ph2	CgppTOph2 - Cph2TOres - Cph2TOpoc = 129	Glé et al., 2008
3	NPP of ph3	CgppTOph3 - Cph3TOres - Cph3TOpoc = 245	Glé et al., 2008
4	Import of DOC	ClosTOdoc = 45.4	Carruesco, 1989
5	Export of DOC	CdocTOlos = 25.3	Carruesco, 1989
6	Grazing of hnf by mic	ChnfTOmic = 1.67	H.J. Hartmann & B. Sautour, unpublished results
7	Grazing of hnf by mes	ChnfTOmes = 14.1	H.J. Hartmann & B. Sautour, unpublished results
8	Grazing of cil by mic	CcilTOmic = 8.2	H.J. Hartmann & B. Sautour, unpublished results
9	Grazing of cil by mes	CcilTOmes = 12.3	H.J. Hartmann & B. Sautour, unpublished results
10	Grazing of ph3 by mic	Cph3TOmic = 32.6	H.J. Hartmann & B. Sautour, unpublished results
11	Grazing of ph3 by mes	Cph3TOmic = 44.4	H.J. Hartmann & B. Sautour, unpublished results

and ciliates). The most abundant predators, the metazoans (copepods and cirripeds nauplii), were selected and added separately. Hence, the grazing experiments with copepods allowed estimating the mesozooplankton grazing rates, and the experiments with cirriped nauplii allowed an estimation of microzooplankton grazing rates. The density of added predators in the incubation bottles was determined in relation to their natural abundance in the study site. Three replicates for each experiment and each incubating time (12 h and 24 h) were incubated in a mesocosm (reproducing natural light and temperature conditions) with three incubators without predators as controls. The beginning of the incubation started after the addition of the predators. The biomass of each prey was estimated at the beginning and at the end of the experiment using flow cytometry and Utermöhl counting (Table 1). First, these experiments permitted estimation of metazoan microzooplankton grazing on heterotrophic nanoflagellates (1.67 mg C m^{-2} d^{-1}), heterotrophic ciliates (8.2 mg C m^{-2} d^{-1}) and microphytoplankton (32.6 mg C m^{-2} d^{-1}). Second, mesozooplankton grazing on the same preys i.e. heterotrophic nanoflagellates (14.1 mg C m^{-2} d^{-1}), heterotrophic ciliates (12.3 mg C m^{-2} d^{-1}) and microphytoplankton (44.4 mg C m^{-2} d^{-1}) was also assessed.

2.4. Inequalities

Thresholds for biological and physical processes were applied to constrain the calculated value ranges into realistic values. Vézina and Platt (1988) Vézina and Pace (1994) and Tian et al. (2000) gathered published information on different plankton processes in order to estimate their realistic limits. The values used are listed in Table 4.

Table 4
Constraints used in the inverse analysis. Abbreviations are from Table 1.

Constraint	Lower bound	Upper bound	Reference
Respiration - ph1/ph2/ph3	5% of gpp	30% of gpp	(Vézina and Platt, 1988)
Respiration - hnf/cil/mic/mes/cap	20% of total ingestion	–	(Vézina and Savenkoff, 1999)
Respiration – bacteria	20% of DOC uptake	–	(Vézina and Savenkoff, 1999)
Exsudation of DOC - ph1/ph2/ph3	10% of npp	55% of npp	(Breed et al., 2004)
Exsudation of DOC - hnf/cil/mic/mes/cap	10% of total ingestion	No more than the respiration	(Carruesco, 1989; Vézina and Pace, 1994; Vézina and Platt, 1988)
Import of POC	13 mgC m^{-2}	–	(Carruesco, 1989)
Export of POC	79 mgC m^{-2}	–	(Carruesco, 1989)
Dissolution of POC	10% of the total POC stock	–	Modified from Vézina and Platt (1988)
Floculation of DOC	1% of the total DOC stock	–	(Tian et al., 2000)
Assimilation Efficiency - mic/mes/cap	50% of total ingestion	90% of total ingestion	(Vézina et al., 2000)
Natural mortality - ph3 (POC production)	1% of the biomass	–	(Arnous et al., 2010)
Natural mortality of bacteria (DOC production)	8% of bacterial production	–	H. Montanié pers. comm.
Natural mortality of mic/mes/cap (POC production)	10% of total ingestion	No more than the respiration	(Carruesco, 1989; Vézina and Pace, 1994; Vézina and Platt, 1988)
Total ingestion of bap	–	No more than the maximum specific uptake of DOC	(Vézina et al., 2000)
Total ingestion - hnf/cil/cap	–	No more than the maximum specific ingestion	(Vézina and Savenkoff, 1999)
Trophic preferency of cap to mes and of hnf to bac	40% of total ingestion	80% of total ingestion	B Sautour pers. comm.
Trophic preferency of cil to bac	5% of total ingestion	10% of total ingestion	B Sautour pers. comm.
Trophic preferency of cil to hnf	40% of total ingestion	60% of total ingestion	B Sautour pers. comm.
Trophic preferency of mic to bac	10% of total ingestion		B Sautour pers. comm.
Trophic preferency of cap to mic	20% of total ingestion	30% of total ingestion	
Trophic preferency of cap to mes and of hnf to bac	20% of total ingestion	40% of total ingestion	
Growth efficiency - cil/mic/mes/cap	The sum of respiration, excretion and egestion is no more than 25% of their total ingestion	The sum of respiration, excretion and egestion is no more than 50% of their total ingestion	(Vézina et al., 2000)
Growth efficiency - bac	The sum of respiration, excretion and egestion is no more than 50% of their total ingestion	The sum of respiration, excretion and egestion is no more than 75% of their total ingestion	(Vézina and Pahlow, 2003)
Bacterial Production	9.08 mgC m^{-2}	–	H. Montanié pers. comm.

Some thresholds used here came from *in situ* measurement. River input of particulate organic carbon (POC), calculated as the product of river flows by river POC concentrations, was considered as a minimum value for total POC input. An additional experiment was carried out in May 2006 to evaluate the viral-mediated mortality of bacteria in presence or absence of nanoflagellates (sea-water filtered through 0.8 μm or 3 μm, respectively), evaluated from the viral production assuming a burst-size of 50 viral particles produced by lysed cell (see details in Ory et al., 2010). In the presence of small flagellates, the mean bacterial production (MBP = mean bacterial production rate calculated for the growth phases observed over a 48 h period), was estimated to around $3.60 \pm 1.06 \times 106$ cells mL^{-1} d^{-1}. In order to compare results of modeling obtained from different ecosystems, we decided to convert our abundance-based data to thymidine incorporation rate equivalents. Using the regression established between bacterial production, tBP evaluated by the thymidine method, and MBP (as log (tBP) = 2.3889 + 0.5766 log (MBP); Montanié unpublished data), tBP has been estimated to 1.46×106 cells mL^{-1} d^{-1}, on average. Because the bacterial production was only estimation, it was not used as an equation in the model but as an inequality defining the minimum value. Deduced from this experiment, virus −mediated bacterial lysis was on average 8% of BP (Montanié, unpublished), and was used as a minimum threshold for the bacterial mortality.

2.5. Ecological network analysis

The WAND Program (Allesina and Bondavalli, 2003) was used to calculate network indices from the carbon flows. The activity of a given compartment is measured by its throughput, the sum of all flows passing through it (i.e. sum of entering or sum of exiting flows, for a system at equilibrium). The throughput estimated for the whole ecosystem is the Total System Throughput (*TST*). Recycling is quantified by the Finn Cycling Index (*FCI*; (Finn, 1976) and corresponds to the ratio between the sum of carbon flowing through cyclic pathways and the sum of all carbon flows in the system. The Detritivory/Herbivory ratio is the sum of consumption flows of non-living material divided by the sum of consumption flows of autotrophic organisms. For characterizing the organization of the flows, topologic indices were computed (Ulanowicz, 1997). The Ascendency (*A*) is the product of the *TST* and the constraints inherent to the structure of the flows, which is estimated by AMI (Average Mutual Information). Constraints are linked to the probability of transfer of an atom of carbon from one compartment to another. The more specialized the system, the more constraints apply to the ecosystem. In contrast, when a system is weakly constrained, an atom of carbon is transferred through many parallel pathways. The theoretical maximum of *A* is called the development capacity (*DC*), and corresponds to a food web with maximum specialization. The ratio *A*/*DC* is called the relative Ascendency and defines the ecosystem degree of development. The internal Ascendency (A_i) and the internal development capacity (DC_i) are restricted to internal exchanges. The difference between A_i and DC_i corresponds to the internal Redundancy. It quantifies the multiplicity of parallel flows. The relative redundancy (*R*/*DC*) is also calculated to disregard the effect of the *TST*.

The different indices calculated for the Arcachon Bay food web were compared to indices derived from several coastal planktonic food webs. As it has recently been shown (Johnson et al., 2009), the least square criterion of inverse analysis causes a bias in the evaluation of some network indices. The bias is limited when the microbial items are considered (Johnson et al., 2009). However, comparisons with planktonic food webs of other ecosystems that have been built with the same approach as that of Arcachon Bay will be done with relative indices values rather than absolute values. In fact, this relative comparison assumes that the bias is constant, which has been verified with similar network structures (Johnson et al., 2009). The Network analysis was applied to the inverse analysis results of carbon flow values for the following plankton systems: Bizerte lagoon in Summer and Spring (Grami et al., 2009; Grami et al., 2008), Loire and Gironde river plumes of the Bay of Biscay during late-winter and spring succession (BB1 and BB2 in March, following the late-winter bloom, BB3, BB4 in May, during the spring bloom, and BB5 at the end of May in a post-bloom situation (Marquis et al., 2007)), Takapoto atoll in French Polynesia (Niquil et al., 2001), and the Celtic Sea and English Channel (Vézina and Platt, 1988).

2.6. Sensitivity analysis

A sensitivity analysis was performed to assess the dependence of the calculated fluxes on variations in the values of the eleven equations of the model (Table 3). Their values were varied by ±20% one at a time. A new set of flows was calculated for each perturbed situation. A sensitivity index SI (Richardson et al., 2004) was calculated for each flow of the model and each perturbation:

$$\text{SI for } i \text{ th flow} = \left(\left|f_{i,p} f_{i,o}\right| / f_{i,o}\right) \Big/ 0.2 \quad (3)$$

where $f_{i,p}$ and $f_{i,o}$ are the values for ith flow in the perturbed and original situations. A value of 1 indicated that the 20% variation of the field value leaded to a 20% variation in the considered flow value. The SI values were averaged per flow, for all the simulations realized and per simulation, for all the obtained flows.

3. Results

3.1. Input and output flows

Estimates of the integrated flows from inverse analysis are given in Table 2. From the total input to the studied system (sum of GPP and allochtonous inputs: 542 mg C m^{-2} d^{-1}), 52%, 28% and 9% were related to the primary production of the micro-, nano- and picophytoplankton, respectively. The net allochtonous inputs (13 mg C m^{-2} d^{-1} for POC and 45 mg C m^{-2} d^{-1} for DOC, Table 2) were very low compared to primary production (11% of the total input). Respiration flows accounted for only 33% of the carbon output from the system. Among the living compartments, mesozooplankton and bacteria displayed the highest respiration flows (both equal to 37 mg C m^{-2} d^{-1}, Table 2), followed by microzooplankton metazoans (32 mg C m^{-2} d^{-1}, Table 2). The remaining 67% of the outputs mainly consisted in exports of microphytoplankton (22%), POC (15%) and nanophytoplankton (14%).

3.2. Throughputs and internal flows

Six out of ten compartments displayed high throughput values, ranging from 50 to 434 mg C m^{-2} d^{-1}, Table 2) (Fig. 2, left scale). The three highest values corresponded to micro- and nanophytoplankton, and to DOC. They were followed by a lower throughput for picophytoplankton, and then POC detritus, metazoans microzooplankton, mesozooplankton and bacteria. The lowest throughput value corresponded to the activities of carnivorous zooplankton, heterotrophic ciliates and nanoflagellates. The lack of correlation between the biomass and the throughput is related to the high variability of turnover rates between compartments.

The internal flows (flows between two compartments) were dominated by herbivory on the 3 phytoplankton size classes

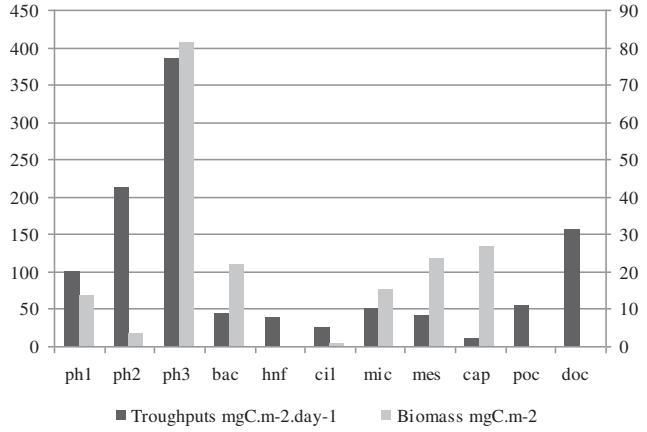


Fig. 2. Throughputs (sum of entering flows, left axis) and biomasses (right axis) of plankton components. The mass of POC and DOC were undetermined. Biomass for hnf and cil are very low ($7.1 \cdot 10^{-2}$ and 0.82 mg C m^{-2} respectively). Abbreviations for the compartments are given in Table 1.

(Fig. 3). This herbivory was essentially due to metazoans (both micro- and mesozooplankton) grazing 37% of the total net primary production (pico-, nano- and microphytoplankton). More accurately, metazoan herbivory corresponded to the grazing of micro- and nanophytoplankton by mesozooplankton (44 and 17 mg C m^{-2} d^{-1} and representing 12% and 16% of the net primary production, respectively, Table 2) and the grazing of micro-, nano- and picophytoplankton by metazoans microzooplankton (33, 16 and 20 mg C m^{-2} d^{-1} and representing 12%, 11% and 39% of the net primary production respectively, Table 2). Protozoan (hnf) herbivory was particularly relevant on picophytoplankton (18 mg C m^{-2} d^{-1}, Table 2), representing 50% of its net primary production. Phytoplankton DOC production decreased with size, at 24 mg C m^{-2} day^{-1} for microphytoplankton and only 4 mg C m^{-2} day^{-1} for picophytoplankton. Other important flows related to the uptake of DOC by bacteria (80 mg C m^{-2} d^{-1}, Table 2), the POC production by microphytoplankton (49 mg C m^{-2} d^{-1}, Table 2), the flocculation of DOC into POC (31 mg C m^{-2} d^{-1}, Table 2), the predation of bacteria by hnf (27 mg C m^{-2} d^{-1}, Table 2), the predation of microzooplankton by mesozooplankton (23 mg C m^{-2} d^{-1}, Table 2), the predation of mesozooplankton by carnivorous zooplankton (cap, 20 mg C m^{-2} d^{-1}, Table 2), the consumption of detritus by microzooplankton (18 mg C m^{-2} d^{-1}, Table 2) and the predation of heterotrophic nanoflagellates by ciliates and mesozooplankton (16 and 14 mg C m^{-2} d^{-1}, Table 2). Other flow values were very low, particularly those of detritivory on POC. Zooplankton consumed both micro- and mesozooplankton while mesozooplankton exclusively grazed on microphytoplankton, while ciliates mainly consumed nanophytoplankton.

3.3. Ecological network analysis

Microphytoplankton community was largely grazed because of their dominance in terms of primary production and biomass compared to the other primary producers which led to high herbivory in overall network properties. The Detritivory/Herbivory (D/H) ratio was 0.18, which is the lowest value when compared to other planktonic systems (Fig. 4C). This situation corresponded to an efficient use of the primary production, measured by a high value of Net Primary Production (i.e. the primary production fraction directly consumed by herbivores) equal to 37%. In parallel to this high herbivory, carbon involved in recycling was very low, indicating that only a very small part of the carbon flowed through cyclic pathways. In fact, with a value of 3%, the Arcachon Bay FCI was 2–10 times lower than values reported for the other plankton systems (Fig. 4A). Moreover, the comparison with ecosystems characterized by similar spring bloom conditions (e.g. in the Bay of Biscay and in the dilution plume of the Loire estuary) did not show such low FCI values (BB3 and BB4, Fig. 4A). As far as the total plankton system was concerned, the spring food web in Arcachon Bay presented one of the lowest values of redundancy (30.6%) (Fig. 4B). This means that the internal flows (between two compartments of the system) did not present numerous equivalent parallel pathways.

3.4. Sensitivity analysis

The sensitivity analysis (Table 5) shows that whatever the equation perturbed, the impact was low. All values of the sensitivity index were lower than 1, meaning that a 20% variation of the field data estimates caused a modification of calculated flows of less than 20%. The greatest impacts were for the GPP of micro-, nano- and picophytoplankton (0.56, 0.38 and 0.24, respectively). The grazing of heterotrophic nanoflagellate by microzooplankton had the smallest effect on the calculated flow values.

When averaging the SI by flow, for all perturbations, the most affected flows were the consumption of POC by mesozooplankton (1.95), the exportation of carnivorous zooplankton (0.96) and the grazing of picophytoplankton by ciliates (0.94). The main effect came from changes is the GPP of the three size classes of phytoplankton.

4. Discussion

4.1. Methodological choices

The inverse approach used here presents some limits that are inherent to (i) the model structure, (ii) the assumed hypothesis for the model conception and (iii) the precision of the data used for processes estimations.

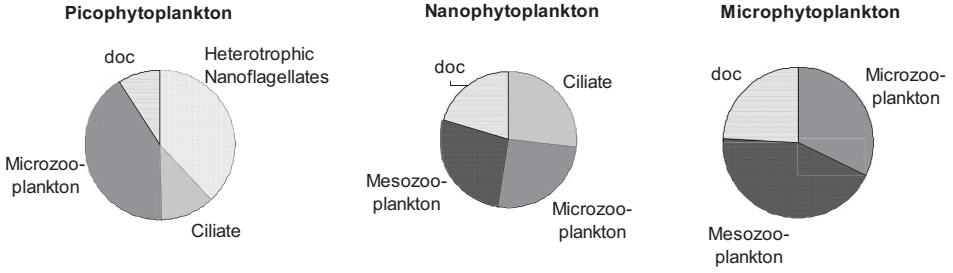


Fig. 3. Fate of the net primary production of each phytoplankton size class inside the plankton system.

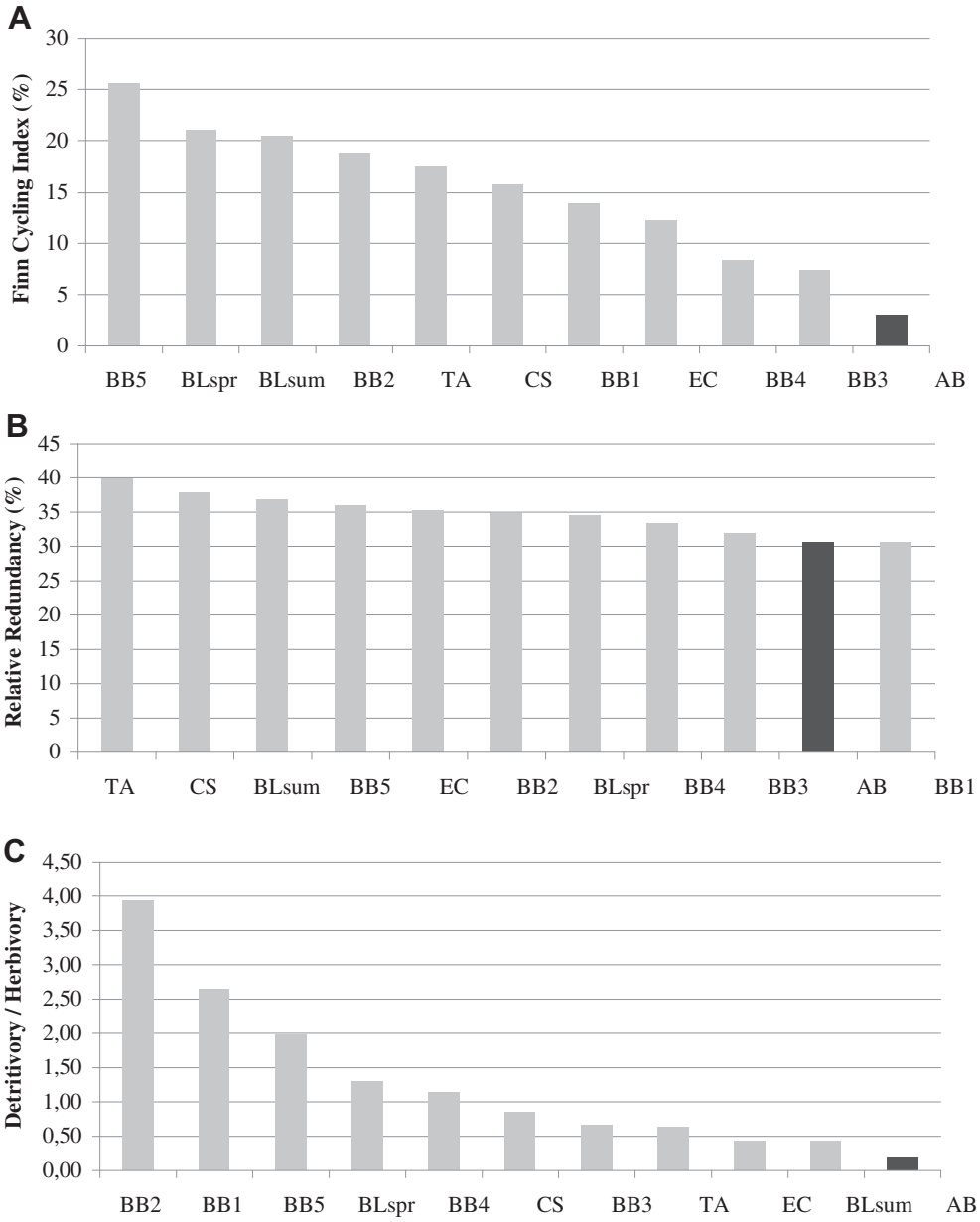


Fig. 4. Comparison of network analysis indices calculated from the Least Square Linear Inverse Models of different ecosystems - BLspr and BLsum: Bizerte Lagoon in spring and summer (Grami et al., 2008, Grami, 2009), TA: Takapoto atoll (Niquil et al., 2001), CS: Celtic Sea (Vézina and Platt, 1988), EC: English Channel (Vézina and Platt, 1988), BB1, BB2, BB3, BB4, BB5: Bay of Biscay during the succession from the post late winter bloom period, BB1, BB2, to the spring bloom development, BB3, BB4 and to the post spring bloom period, BB5 (Marquis et al., 2007), AB: Arcachon Bay in spring.

(i) Concerning the model structure, the living compartments of the model are functional units corresponding to different groups of taxa. It is assumed that all individuals involved in the model computation display the same trophic behavior although diet varies according to a large number of biological factors (e.g. age, sex and/or morphology; (Forbes, 1989); review in (Mauchline, 1998) for zooplankton). This would suggest developing a model with a greater number of compartments, but it would not fit to the level of process estimation applied on the site. The present level of aggregation was chosen to remain coherent with the level of precision of the quantification of the *in situ* processes.

(ii) Concerning the assumed hypothesis for the model conception, the model is considered as at mass-balanced. The obtained model must be considered as an instantaneous picture of the system mean state at a given period of the year (May). Ecosystems evolve naturally in both space and time and/or can be constrained by specific forcing such as human activities. For instance, in Arcachon Bay exotic species like the Japanese clam (*Ruditapes philippinarum*) and the Japanese oyster (*Crassotrea gigas*) were introduced in 1980's and 1970's, respectively, and proliferated thus inducing changes in the ecosystem structure over the last thirty years (Blanchet et al., 2005, 2004). Moreover, both species composition and abundance of planktonic communities are subject to important seasonal variations (Castel and Courties, 1982; D'Elbée and Castel, 1995; Glé et al., 2007; Vincent et al., 2002). However, at the mean day scale, values of biomass variations are negligible when compared to daily rate processes such as production and grazing. For example, a typical daily variation of microphytoplankton

Table 5
Results of the sensitivity analysis. Each equation value is modified by minus (−) or plus (+) 20%. SI: Sensitivity Index, averaged for all the flows of the simulated model. Abbreviations are from Table 1.

	SI
Gross primary production of ph1	
−	0.24
+	0.24
Gross primary production of ph2	
−	0.38
+	0.38
Gross primary production of ph3	
−	0.45
+	0.56
Input of dop	
−	0.17
+	0.17
Output of dop	
−	0.10
+	0.10
Grazing of ph3 by microzooplankton	
−	0.16
+	0.16
Grazing of ph3 by mesozooplankton	
−	0.17
+	0.17
Grazing of hnf by mesozooplankton	
−	0.19
+	0.19
Grazing of cil by mesozooplankton	
−	0.19
+	0.21
Grazing of hnf by microzooplankton	
−	0.03
+	0.03
Grazing of cil by microzooplankton	
−	0.14
+	0.14

would be lower than the 20% variation of its gross primary production that we tested in the sensitivity analysis. Consequently, considering the system as mass-balanced is justified for the purpose of describing the organization of the flows.

Another assumed hypothesis is the choice of the least square criterion for the selection of a unique solution per flow. In the absence of constraints, this least square criterion favors the shortest course inside the system, and the direct outputs from the system. Additionally, it pushes the result of inequalities towards one of the two threshold values (maximum and minimum), while in an ecological view an intermediate value would be more probable. These qualitative criticisms made by Niquil et al. (1998) are now confirmed by quantitative estimations of the biases caused by the least square criterion in the computation of Ecological Network Analysis indices (Johnson et al., 2009). This is why the models of plankton systems chosen for the comparison (Fig. 4) were built with the same approach and at a similar level of aggregation. They are selected to present exactly the same biases as the model described in the present paper. Then, even if the absolute value may be false, the relative situation in comparison with the other systems is exact.(iii) Concerning the precision of the field estimates for plankton processes (productions, grazing…). The low values of the sensitivity index values for each input data show that the model is robust. The fact that primary production of the 3 size classes has the highest SI values also means that the field estimation of the primary production is essential when applying such a food web modeling approach.

4.2. The spring pelagic food web of Arcachon Bay, a typical herbivorous chain

In pelagic ecosystems, primary production is transferred to higher levels through two main pathways, depending to the size structure of primary producers (Azam et al., 1983; Sherr et al., 1986; Thingstad and Rassoulzadegan, 1999). In the classical view of trophic food web functioning (Fig. 5 left), the grazing food chain has a herbivorous status and energy is transferred from large diatoms to metazoans zooplankton (Pomeroy, 1974). The improved means of sampling and observations in the 1970s revealed the importance of nano- (e.g. hnf) and micro-zooplanktonic grazers (e.g. ciliates) as energy and material carriers (Pomeroy, 1974) and highlighted the concept of the microbial food web (Azam et al., 1983) illustrated in Fig. 5 (right). It is now well established that nano- and micro-zooplanktonic grazers constitute an essential food link in marine environments since they remove a significant part of the energy of primary and bacterial production (Fenchel, 1988) (Sanders and Wickham, 1993) and assume the " trophic repackaging " (Gifford, 1991) of picoplankton particles (0.2–2 μm) inaccessible to mesozooplankton (Sherr et al., 1986). Metazoan zooplankton feeding on protozoans links the microbial food web and upper trophic levels predators (e.g. fish larvae (Runge, 1980)). The association of the microbial food web and the classic herbivorous chain defines the multivorous food web. In the extreme case of a bacteria/protozoan loop almost disconnected from the metazoans, the food web is called the microbial loop. This typology of planktonic food web functioning was synthesized by Legendre and Rassoulzadegan (1995), who show that, generally, large phytoplankton blooms determining the herbivorous food web are followed by a limitation

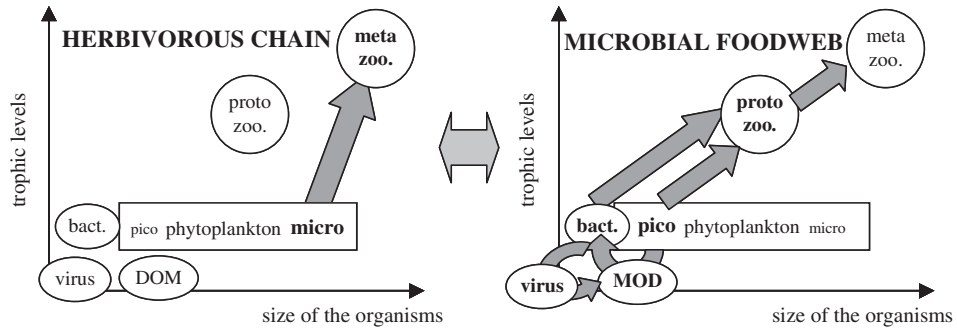


Fig. 5. Typology of planktonic food web functioning as described by Legendre and Rassoulzadegan (1995) based on 4 food web type types, the herbivorous chain and microbial food web represented here, the multivorous web, associating the two of them and the microbial loop based on bacteria and protozoa almost disconnected from the other compartments.

in nutrients leading to a multivorous or even a microbial food web. Consequently, the herbivorous food web is less persistent than the other food webs (Legendre and Rassoulzadegan, 1995).

The main characteristic of Arcachon Bay ecosystem is the spring dominance of nano- and microphytoplankton primary producers. These are within the food size spectra of most micro- and mesozooplankton grazers (e.g. Hansen et al., 1993). The dominance of large phytoplankton cells was explained by the high nutrient inputs coming from the Leyre River during the winter and spring periods (around 30 $\mu M\ L^{-1}$ in winter and 7 $\mu M\ L^{-1}$ in spring of nitrate and nitrite), which sustained great developments of diatoms (Glé et al., 2007, 2008). As shown from the model, primary production was essentially grazed by mesozooplankton and/or transferred out of the system through sedimentation or other exports. Mousseau et al. (2001) defined a herbivorous food web when the production and consumption of larger phytoplankton (>5 μm) was higher than that of smaller size (<5 μm). They proposed two ratios that should be less than 1.0 to define a herbivorous food web: the NPP by small phytoplankton (>5 μm) to NPP by large phytoplankton (>5 μm) (NPPs/NPPl), and the same ratio based on grazing (Gs/Gl). With the Arcachon values, NPPs/NPPl ratio is 0.12 with a limit between large and small at 2 μm, and 0.70 with the limit at 20 μm. The Gs/Gl ratio is 0.20 with a limit at 2 μm and 0.99 with a limit at 20 μm. Even if our phytoplankton size limits were not the same than Mousseau et al. (2001), those ratios clearly define a herbivorous food chain.

Ory et al. (2010) had considered the same period as a multivorous food web and not as a herbivorous food web like us. Their conclusions were, based on the increasing abundance of bacteria, viruses, and small and large phytoplankton, during the considered period, which may suggest an activation of the microbial food web. In contrast, our results showed that the whole microzooplanktonic community (hnf, ciliate and metazoans) consumed less bacteria than primary producers (Table 2). This can be explained by the low standing stocks of heterotrophic protozoans (heterotrophic ciliates and nanoflagellates) during this period (Fig. 2, right scale), which does not efficiently transfer the bacterial production to higher consumers. This bacterial production was essentially dissipated through respiration. As a consequence, the microbial food web in Arcachon Bay during the spring bloom presented a minor contribution to the matter/energy flows within the system and the model results favored the hypothesis of a herbivorous food web. This apparent contradiction between these two methods underlines the problem that defining the state of the planktonic food web can differ when dynamics of abundances or flows are considered.

The model shows that the high microphytoplankton production was not directly consumed by the planktonic grazers leading to a high production of detritus (POC and DOC). A small part of this organic carbon was consumed by planktonic organisms of the bay (the detritivory/herbivory ratio is only 0.18). Consequently, POC and phytoplankton were exported out of the system without being consumed as in the behavior of a typical grazing food web (Legendre and Rassoulzadegan, 1995). The theory of estuaries, salt marshes or mangroves as 'exporter systems' has developed since the 1960s (Odum, 1969). These types of ecosystems produce more organic matter than they consume. The excess is then exported toward the coastal waters where it sustains oceanic production: this constitutes the 'outwelling theory' (Costa et al., 2001). The spring herbivory food web of Arcachon Bay fits to this theory, as the export of carbon will be (i) channeled to benthos through sedimentation providing a large supply of organic matter which serves as a rich food source for benthic organisms as shown in other coastal ecosystems (Oviatt et al., 2002), and particularly, sustaining the oyster production culture of the bay or (ii) exported to adjacent areas. The precise amount of exported or sunk matter is unknown and should be assessed in order to evaluate whether the outwelling theory could be applied to the lagoon.

4.3. Emergent properties of the food web and link with stability theories

Numerous studies using ENA indices have proposed theories linking the structure of the food web with stability properties. For example, a stable system is supposed to maximize its recycling (Finn, 1976), and Vasconcellos et al. (1997) showed that the resilience (the inverse of return time to equilibrium) is correlated to the *FCI*. According to Legendre and Rassoulzadegan (1995), a herbivorous chain, as observed here, should be considered as a system of low stability. This is coherent with the very low value observed for *FCI* that indicates a low value for resilience, according to the correlation demonstrated by Vasconcellos et al. (1997). The *FCI* value observed in the present model was even lower than those observed for the late winter (BB1) and spring (BB3 and BB4) blooms in the Bay of Biscay Loire (BB3 and BB4) and Gironde (BB1) plumes (BB3 and 4) (Marquis et al., 2007).

The functioning of the Arcachon Bay spring food web is also characterized by a low Redundancy (*R%*). With regards to the theory that suggests Redundancy (*R%*) as an indicator for resilience (Heymans et al., 2007), the spring bloom period in Arcachon Bay would also correspond to a period of low resilience. If the Redundancy is high, the flows between the different compartments are not concentrated on one or two pathways, but on several alternative pathways. Consequently, a low Redundancy in a developed system such as what we observed in Arcachon Bay and in the Bay of Biscay (BB3 and BB4, corresponding to the spring bloom in May) in the Gironde plume would imply difficulties in reestablishing pathways following a disturbance. This is coherent with Legendre and Rassoulzadegan (1995) theory that an herbivorous chain is likely to switch to a multivorous or microbial food web, presenting a higher Redundancy.

In conclusion, the coherence between the typology of functioning defined as a basic concept of plankton ecology, considering herbivorous chains as highly unstable, and the emergent properties characterizing a low resilience, is noteworthy. However, the papers establishing these theories rely on models covering the ecosystem completely, and on annual models, contrary to the present one which is only for May. Further investigations should explore whether this coherence persists in larger, annual models.

Acknowledgments

We are grateful to George A. Jackson and Alain F. Vézina for providing software and advice. This research was supported by 2 projects PNEC/EC2CO named "Chantier Littoral Atlantique" and "COMPECO". Sébastien Tortajada finished the writing of this publication with a grant from the French "Ministère de l'Enseignement Supérieur et de la Recherche".

References

Allesina, S., Bondavalli, C., 2003. Steady state of ecosystem flow networks: a comparison between balancing procedures. Ecological Modelling 165, 221–229.

Arnous, M.-B., Courcol, N., Carrias, J.-F., 2010. The significance of transparent exopolymeric particles in the vertical distribution of bacteria and heterotrophic nanoflagellates in Lake Pavin. Aquatic Sciences - Research Across Boundaries 72, 245–253.

Auby, I., Labourg, P.-J., 1996. Seasonal dynamics of Zostera noltii hornem. In the bay of arcachon (France). Journal of Sea Research 35, 269–277.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. Marine Ecology Progress Series 10, 257–263.

Blanchet, H., de Montaudouin, X., Lucas, A., Chardy, P., 2004. Heterogeneity of macrozoobenthic assemblages within a Zostera noltii seagrass bed: diversity, abundance, biomass and structuring factors. Estuarine, Coastal and Shelf Science 61, 111–123.

Blanchet, H., de Montaudouin, X., Chardy, P., Bachelet, G., 2005. Structuring factors and recent changes in subtidal macrozoobenthic communities of a coastal lagoon, Arcachon Bay (France). Estuarine, Coastal and Shelf Science 64, 561–576.

Bouchet, J.M., 1993. Stratification, fronts halins dans une lagune mésotidal (Bassin d'Arcachon - France). In: Sorbe, J.-C., Jouanneau, J.-M. (Eds.), 3ème Colloque International d'Océanographie du Golfe de Gascogne, pp. 33–39. Arcachon.

Breed, G.A., Jackson, G.A., Richardson, T.L., 2004. Sedimentation, carbon export and food web structure in the Mississippi River plume described by inverse analysis. Marine Ecology Progress Series 278, 35–51.

Carruesco, C., 1989. Genèse et évolution de trois lagunes du littoral atlantique depuis l'holocène: Oualidia, Moulay Bousselham (Maroc) et Arcachon (France). Biology. Université Bordeaux-1, Bordeaux, France.

Castel, J., Courties, C., 1982. Composition and differential distribution of zooplankton in Arcachon Bay. Journal of Plankton Research 4, 417–433.

Costa, M.J., Catarino, F., Bettencourt, A., 2001. The role of salt marshes in the Mira estuary (Portugal). Wetlands Ecology and Management 9, 121–134.

de Montaudoin, X., Labarraque, D., Giraud, K., Bachelet, G., 2001. Why does the introduced gastropod Crepidula fornicata fail to invade Arcachon Bay (France)? Journal of the Marine Biological Association of the UK 81, 97–104.

Degré, D., Leguerrier, D., Armynot du Chatelet, E., Rzeznik, J., Auguet, J.-C., Dupuy, C., Marquis, E., Fichet, D., Struski, C., Joyeux, E., Sauriau, P.-G., Niquil, N., 2006. Comparative analysis of the food webs of two intertidal mudflats during two seasons using inverse modelling: aiguillon Cove and Brouage Mudflat, France. Estuarine, Coastal and Shelf Science 69, 107–124.

D'Elbée, J., Castel, J., 1995. In: de la station biologique (Ed.), Evolution spatio-temporelle du zooplancton dans le bassin d'Arcachon: le rôle des variables de milieu. Roscoff, France.

Duarte, C.M., Middelburg, J.J., Caraco, N., 2004. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences Discussions 1, 659–679.

Fenchel, T., 1988. Marine plankton food chains. Annual Review of Ecology and Systematics 19, 19–38.

Finn, 1976. Measures of ecosystem structure and function derived from analysis flows. Journal of Theoretical Biology 56, 363–380.

Forbes, T.L., 1989. The Importance of Size-dependant Processes I, the Ecology of Deposit Feeding Benthos (New-York).

Gattuso, J.P., Frankignoulle, M., Bourge, I., Romaine, S., Buddemeier, R.W., 1998. Effect of calcium carbonate saturation of seawater on coral calcification. Global and Planetary Change 18, 37–46.

Gifford, D.J., 1991. The protozoan-metazoan trophic link in pelagic ecosystems. Journal of Eurkaryotic Microbiology 38, 81–86.

Glé, C., Del Amo, Y., Bec, B., Sautour, B., Froidefond, J.-M., Gohin, F., Maurer, D., Plus, M., Laborde, P., Chardy, P., 2007. Typology of environmental conditions at the onset of winter phytoplankton blooms in a shallow macrotidal coastal ecosystem, Arcachon Bay (France). Journal of Plankton Research 29, 999–1014.

Glé, C., Del Amo, Y., Sautour, B., Laborde, P., Chardy, P., 2008. Variability of nutrients and phytoplankton primary production in a shallow macrotidal coastal ecosystem (Arcachon Bay, France). Estuarine, Coastal and Shelf Science 76, 642–656.

Grami, B., Niquil, N., Sakka Hlaili, A., Gosselin, M., Hamel, D., Hadj Mabrouk, H., 2008. The plankton food web of the Bizerte Lagoon (South-western Mediterranean): II. Carbon steady-state modelling using inverse analysis. Estuarine, Coastal and Shelf Science 79, 101–113.

Grami, B., 2009. Dynamique et fonctionnement des réseaux trophiques planctoniques dans la lagune de Bizerte: modélisation par la méthode inverse. PhD from Carthage University, Bizerte Faculty, and from La Rochelle University, La Rochelle, France, and Bizerte, Tunisia, pp. 375.

Gucu, A.C., 2002. Can Overfishing be Responsible for the Successful Establishment of Mnemiopsis leidyi in the Black Sea? Estuarine, Coastal and Shelf Science 54, 439–451.

Hansen, F.C., Reckermann, M., Klein Breteler, W.C.M., Riegman, R., 1993. Blooming enhanced by copepod predation on protozoa: evidence from incubation experiments. Mar. Ecol. Prog. Ser. 102, 51–57.

Héral, M., 1993. Why Carrying Capacity Models Are Useful Tools for Management of Bivalve Molluscs Culture.

Heymans, J.J., Guénette, S., Christensen, V., 2007. Evaluation of network analysis indicators of ecosystem status in the Gulf of Alaska. Ecosystems 10, 488–502.

Johnson, G.A., Niquil, N., Asmus, H., Bacher, C., Asmus, R., Baird, D., 2009. The effects of aggregation on the performance of the inverse method and indicators of network analysis. Ecological Modelling 220, 3448–3464.

Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. Ecological Modelling 220, 370–382.

Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in marine waters. Ophelia 41, 153–172.

Maixandeau, A., Lefèvre, D., Karayanni, H., Christaki, U., Van Wambeke, F., Thyssen, M., Denis, M., 2005. Microbial community production, respiration, and structure of the microbial food web of an ecosystem in the northeastern Atlantic Ocean. J. Geophys. Res. 110, 1–13.

Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A., Labry, C., Sautour, B., Laborde, P., Vézina, A., Dupuy, C., 2007. Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. Estuarine, Coastal and Shelf Science 73, 223–235.

Mauchline, J., 1998. The Biology of Calanoid Copepods (San Diego).

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228–233.

Menden-Deuer, S., Lessard, E.J., 2000. Carbon to Volume Relationships for Dinoflagellates, Diatoms, and Other Protist Plankton. Limnol. Oceanogr. 45, 569–579.

Mousseau, L., Klein, B., Legendre, L., Dauchez, S., Tamigneaux, E., Tremblay, J.-E., Ingram, R.G., 2001. Assessing the trophic pathways that dominate planktonic food webs: an approach based on simple ecological ratios. J. Plankton Res. 23, 765–777.

Niquil, N., Jackson, G.A., Legendre, L.B.D., 1998. Inverse model analysis of the planktonnic food web of Takapoto Atoll (French Polynesia). Mar. Ecol. Prog. Ser. 165, 17–29.

Niquil, N., Pouvreau, S., Sakka, A., Legendre, L., Addessi, L., Le Borgne, R., Charpy, L., Delesalle, B., 2001. Trophic web and carrying capacity in a pearl oyster farming lagoon (Takapoto, French Polynesia). Aquatic Living Resources 14, 165–174.

Niquil, N., Bartoli, G., Urabe, J., Jockson, G.A., Legendre, L., Dupuy, C., Kumagai, M., 2006. Carbon steady-state model of planktonic food web of lake Biwa. Japanese Freshwater Biology 51, 1570–1585.

Niquil, N., Soetaert, K., Johnson, G.A., Van Oevelen, D., Bacher, C., Saint-Béat, B., Vézina, A.F., accepted. Estuarine and Coastal Ecosystem Modelling E. Wolanski and D.S. McLusky chief editors, Elsevier, Oxford.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Ory, P., Hartmann, H.J., Jude, F., Dupuy, C., Amo, Y.D., Catala, P., Mornet, F., Huet, V., Jan, B., Vincent, D., Sautour, B., Montanié, H., 2010. Pelagic food web patterns: do they modulate virus and nanoflagellate effects on picoplankton during the phytoplankton spring bloom? Environmental Microbiology 9999.

Oviatt, C., Keller, A., Reed, L., 2002. Annual primary production in Narragansett bay with no bay-wide winter-spring phytoplankton bloom. Estuarine, Coastal and Shelf Science 54, 1013–1026.

Pomeroy, L.R., 1974. The ocean's food web, a changing paradigm. Bioscience 24, 499–504.

Runge, J.A., 1980. Effects of hunger and season on the feeding behavior of Calanus pacificus. Limnol. Oceanogr. 25, 134–145.

Sautour, B., 1991. Zooplankton in the "Marennes-Oléron" Bay (France), population dynamics, nutrition and production of dominant Copepods. Biology. University of Bordeaux 1, Talence, France, p. 326.

Sanders, R.W., Wickham, S.A., 1993. Planktonic protozoa and metazoa: predation, food quality and population control. Marine Microbial Food Webs 7, 194–223.

Sherr, E.B., Sherr, B.F., Albright, L.J., 1986. Bacteria: link or sink? Science 235, 88.

Tett, P., Gilpin, L., Svendsen, H., Erlandsson, C.P., Larsson, U., Kratzer, S., Fouilland, E., Janzen, C., Lee, J.-Y., Grenz, C., Newton, A., Ferreira, J.G., Fernandes, T., Scory, S., 2003. Eutrophication and some European waters of restricted exchange. Continental Shelf Research 23, 1635–1671.

Thingstad, T.F., Rassoulzadegan, F., 1999. Conceptual models for the biogeochemical role of the photic zone microbial food web, with particular reference to the Mediterranean Sea. Progress in Oceanography 44, 271–286.

Tian, R.C., Vézina, A., Legendre, L., Ingram, R.G., Klein, B., Packard, T., Roy, S., Savenkoff, C., Silverberg, N., Therriault, J.C., Tremblay, J.E., 2000. Effects of pelagic food-web interactions and nutrient remineralization on the biogeochemical cycling of carbon: a modeling approach. Deep Sea Research Part II: Topical Studies in Oceanography 47, 637–662.

Ulanowicz, R.E., 1986. Growth and Development: Ecosystems Phenomenology (New-York).

Ulanowicz, R.E., 1997. Ecology, Thes Ascendant Perspective (New-York).

Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: a analysis. Ecol. Model 100, 125–134.

Vézina, A., 1989. Construction of Flow Networks Using Inverse Methods (Berlin).

Vézina, A., Pace, M.L., 1994. An inverse model analysis of planktonic food webs in experimental lakes. Canadian Journal of Fisheries and Aquatic Sciences 51, 2034–2044.

Vézina, A.F., Pahlow, M., 2003. Reconstruction of ecosystem flows using inverse methods: how well do they work? Journal of Marine Systems 40-41, 55–77.

Vézina, A., Platt, T., 1988. Food web dynamics in the ocean. I. Best estimates of flow networks using inverse methods. Marine Ecology Progress Series 42, 269–287.

Vézina, A.F., Savenkoff, C., 1999. Inverse modeling of carbon and nitrogen flows in the pelagic food web of the northeast subarctic Pacific. Deep Sea Research Part II: Topical Studies in Oceanography 46, 2909–2939.

Vézina, A.F., Savenkoff, C., Roy, S., Klein, B., Rivkin, R., Therriault, J.C., Legendre, L., 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. Deep Sea Research Part II: Topical Studies in Oceanography 47, 609–635.

Vincent, D., Luczak, C., Sautour, B., 2002. Effects of a brief climatic event on zooplankton community structure and distribution in Arcachon Bay (France). Journal of the Marine Biological Association of the UK 82, 21–30.

Résumé

La vasière intertidale de Brouage, écosystème très étudié localement de longue date, a fait l'objet depuis 5 ans d'analyses plus approfondies notamment sur le devenir du biofilm microbien se formant à la surface des sédiments à marée basse. Ce travail de thèse s'inscrit dans cette optique. Il propose, par le couplage d'outils mathématiques et écologiques, d'analyser le réseau trophique de la vasière de Brouage sous différentes conditions abiotiques à partir de la synthèse des données les plus récentes. La modélisation inverse a permis d'estimer les flux manquants du réseau trophique. Les calculs d'indices d'analyse des réseaux écologiques ou ENA (Ecological Network Analysis) ont caractérisé la structure et le fonctionnement du réseau trophique.

Un premier travail méthodologique, basé sur la dégradation-reconstruction d'un jeu de données très complet, a défini la meilleure fonction, la moyenne, pour le choix d'une seule solution pour chaque flux à la sortie de la modélisation inverse. La moyenne est la meilleure fonction puisque son utilisation aboutie à une bonne estimation des flux manquants quel que soit le niveau d'information intégré au modèle. Cette fonction permet aussi une bonne préservation de la structure et du fonctionnement du réseau trophique ainsi reconstruit.

Le réseau trophique de la vasière de Brouage à basse mer a été étudié sous un aspect saisonnier par l'opposition de l'été et de l'hiver, l'hiver étant caractérisé par la présence d'oiseaux migrateurs sur la vasière. L'activité limicole des oiseaux est soutenue en hiver par une forte production du microphytobenthos et un fort recyclage de la matière. L'organisation interne et la spécialisation des flux restent cependant semblables pour les deux saisons considérées.

Dans un deuxième temps, le réseau trophique à pleine mer en été a été modélisé sous différentes conditions hydrodynamiques permettant ou pas la remise en suspension du biofilm microbien. La comparaison entre ces deux situations met en évidence l'effet de la remise en suspension sur le couplage benthos-pelagos. Le système soumis à la remise en suspension présente un très faible indice de recyclage lié à la faible intégration au réseau trophique pélagique du carbone particulaire benthique remis en suspension. De plus, la remise en suspension provoque une augmentation de l'activité du système couplée à une faible spécialisation des flux, ce qui est supposé déstabiliser le système.

Abstract

The Brouage mudflat is an intertidal ecosystem which has been studied locally for a long time. During the last 5 years, in depth studies have especially focused on the fate of the microbial biofilm which develops at the surface of the sediments at low tide. The present Ph.D. work was accomplished in this framework. It proposes, through the synthesis of the most recent data, to combine mathematical and ecological tools to analyze the Brouage food web under different abiotic conditions. The inverse modelling allowed estimating the unknown flows of the food web. The calculation of the ENA (Ecological Network Analysis) indices characterized the structure and the functioning of the food web.

A methodological work, based on the degradation/reconstruction of a complete data set from the bay of Sylt-Rømø (Germany), determined the best function, the mean, to choose a single solution for each flow among the set of values estimated by the inverse modelling. The mean is the best function because it leads to a good estimation of the unknown flows irrespective of the quantity of information integrated in the model. Moreover, this function allows a good conservation of the structure and functioning of the reconstructed food web.

The Brouage food web at low tide was investigated with a seasonal approach by the opposition of the summer and the winter food webs; is the latest being characterized by the presence of migratory shorebirds. The shorebird activity is sustained by a strong primary production and a strong recycling. Nevertheless, the internal organization and the specialization remain similar for the two seasons.

In a second step, the food web at high tide was modeled under different hydrodynamical conditions sufficient or not to induce the resuspension of the microbial biofilm. The comparison between the two food webs highlights the effect of the resuspension on the benthos-pelagos coupling. The recycling activity is low due to the low integration of the resuspended benthic particulate carbon in the pelagic food web during resuspension. Additionally, the resuspension leads to an increase of the activity of the whole system coupled with a drop of the specialization of the trophic pathways that is supposed to destabilize the system.