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Main factors favoring *Mnemiopsis leidyi* individuals growth and population outbreaks: a modelling approach

E. Alekseenko\textsuperscript{a,b,c,*}, M. Baklouti\textsuperscript{a}, F. Carlotti\textsuperscript{a}

\textsuperscript{a}Aix-Marseille Université, Université de Toulon, CNRS/INSU, IRD, MIO, UM 110, 13288, Marseille, Cedex 09, France
\textsuperscript{b}P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovsky Prospekt 36, 117997, Moscow, Russia
\textsuperscript{c}Laboratoire des Sciences du Climat et de l’Environnement (LSCE/IPSL), CEA Saclay, Gif-sur-Yvette, 91191, France

Abstract

A population model of the marine invasive ctenophore species *Mnemiopsis leidyi* (ML) including physiological and demographic processes has been included in the flexible-stoichiometry biogeochemical marine ecosystem model (Eco3M-MED). This model is used in order to define through several numerical simulations possible environmental windows favorable to ML adaptation and outbreaks in invaded habitats, such as the coastal areas of the Mediterranean Sea. One of the strengths of the ML model is that it delivers the functional response either expressed in terms of consumed individual prey or in prey biomass, however the prey are expressed, as individual abundance or biomass concentration. Numerical experiments were performed to test the functional response in various quantitative and qualitative diet conditions. Longer term experiments including starvation regimes were run to characterize the response of the ML population in terms of growth rate and dynamics.

Our results firstly show that the required food conditions for ML outbursts, which involve combinations of food quality and quantity, should mainly be found in the most productive Mediterranean coastal areas, and more rarely in the open sea, and that variations in food concentrations may induce rapid outbursts or collapse of ML populations. Results also indicate that food concentrations directly impact reproduction, and that for a given fixed available prey biomass, ML abundance is maximum for the prey of richest nutritional value. As our model considers two levels of ecological integration, individual and population, it has been shown that the response to starvation or to recovery from starvation after food replenishment occurs at

\textsuperscript{*} Corresponding author
Email address: lena.alekseenko@gmail.com (E. Alekseenko)
different time scales depending on the integration level. Then, different scenarios of global change have been simulated in order to analyze the inter-annual variability in ML population dynamics. Our model could reproduce typical 3 months ML blooms, which is also observed in nature, and it suggests that this is the result of a combination of species properties and environmental forcings. Our simulations also reveal that an increase in temperature promotes the occurrence of jellyfish outbreaks. Finally, the strongest forcing influence on ML dynamics is the reduction of fish competitors for food due to an increase in fishing pressure. This forcing significantly impacts not only the frequency of the outbreaks, but also ML accumulated population growth over a ten-year period. Finally, our simulations call for long-term (over at least a ten-year period) observations with a temporal resolution of one month or less.

Keywords: *Mnemiopsis leidyi*, mechanistic biogeochemical model Eco3M, flexible-stoichiometry, prey quality, environmental window for ML outbursts;

1. Introduction

The introduction of invasive aquatic species into new habitats has been identified as one of the four greatest threats for the world oceans (Werschkun et al, 2014). Aquatic invasions are virtually irreversible and, once the newcomers are established, their impact may also increase in severity over time. During the last decades, a dramatic increase in the number of alien species has been observed in different marine ecosystems. Many of these species became successfully adapted to their new habitats, thereby leading to serious ecosystem changes, disruptions of ecosystem services and the associated economic consequences (Vila et al., 2010). The transfer of invasive species does not only occur over larger distances, between continents, but also locally, over regional seas (David et al., 2013).

One recent example of a drastically impacting invasive species is the gelatinous zooplankton – ctenophora *Mnemiopsis leidyi*, referred to as ML hereafter (Pitt & Lucas, 2013). The species ML originates from the east coast of the USA and the Caribbean Sea and was introduced in the early 1980s in the Black Sea and the Azov Sea, where it could spread, and sometimes dominate the local food webs due to its high adaptation capacity in combination with increasing shipping traffic, global warming, eutrophication, pollution
and overfishing. This led to a devastating reduction in fish catch levels in these seas (Shiganova & Bulgakova, 2000; Mills, 2001; Byers, 2002; Salihoglu, 2011). Since then, ML has spread further and it is also found today in a wide range of habitats in Eurasian seas: from the brackish closed and semi-closed seas and lagoons to the Mediterranean Sea and Atlantic coastal areas, from temperate to subtropical regions, from high productive to oligotrophic environments (Pitois & Shiganova, CIESM, 2015). ML is a highly opportunistic species: a simultaneous hermaphrodite with direct development, capable of self-fertilization; what means that viable offspring can be produced from a single adult (Purcell et al., 2001). When food is abundant, each organism can ingest up to ten times its own body weight during a single day, which is far more than it is able to digest. Inversely, an organism can survive for up to three weeks without food (Finenko et al., 2010). ML is found in an extremely wide range of environmental conditions, from cold (0°C) to warm (32°C) waters, with salinities ranging from <2 to 45‰ (Purcell et al., 2001, Pitt & Lucas, 2014, Kremer 1994, Colin et al., 2010, Shiganova et al., 2001, 2011). Consequently, ML presents a tremendous potential for growth, survival and reproduction that enables this species to be a predominant zooplanktivore in a wide variety of habitats. Especially in estuarine and coastal waters, ctenophores can reach very high abundance, since it feeds on prey ranging from microplankton (50 microns) to fish larvae (> 3 mm) by clearing large volumes of water (Colin et al. 2010).

The high number of ML recorded during the last years along the Mediterranean coastlines (Fig. 1), especially along the northern coast (Galil et al., 2009; Boero et al., 2009; Fuentes et al., 2010; Kylie and Lucas, 2014), strongly suggest that ML is now well established in the Mediterranean Sea. From an ecosystem perspective, the apparent increase and synchrony in jellyfish outbreaks in both the western and eastern Mediterranean basins are sending warning signals of a potential phase shift from a fish to a "gelatinous sea" (Boero, 2013).

Climate warming, eutrophication, coastal habitat degradation and overfishing are among the most probable drivers of ML development, though the invasion pathways of this species and the reasons for its successful colonization of new habitats are not well identified yet, and the lack of data makes any further investigation difficult. The recent knowledge on the impact of climate warming, eutrophication, coastal habitat degradation and overfishing on ML development has led to the following conclusion:

— Field observations of ML species revealed that its physiology is tempe-
nature dependent (Javidpour et al., 2009) and global warming is likely to affect the timing and distribution of ML in those areas (Pitois & Shiganova, CIESM, 2015).

— It was observed that ML was very abundant in coastal and lagoon waters, which are highly affected by eutrophication. Eutrophication has become a major component of coastal habitat degradation in the Mediterranean during the last decades (MerMex group, 2011). Ludwig et al. (2009) report increasingly high loads of dissolved inorganic nitrogen associated with an increase in the \( \text{NO}_3 : \text{PO}_4 \) ratio of the Mediterranean river outputs. This ratio determines which nutrient will limit biological productivity at the base of the food web and may select plankton communities with distinct biogeochemical functions (Deutsch & Weber, 2012).

— Overfishing may also play a crucial role in the development of ML. One of the well-known cases is the Black Sea in 1989 where ML has strongly developed by emptying the ecological niche occupied by small pelagic fishes, thereby allowing gelatinous competitors to rehabit (Gucu, 2002).

Modelling can provide an additional understanding of mechanisms through the characterization of environmental conditions that could support and/or favor the gelatinous zooplankton ML and the description of the associated changes in the planktonic community structure.

Several models describing ML behavior have already been used for various specific studies. Among them are individual-growth models constructed by Kremer (1976), Kremer & Reeve (1989) for the study of ML development in Narragansett Bay. Salihoglu et al. (2011) and Shiganova et al. (2018) have developed a zero-dimensional population-based model considering four stages, namely: egg, juvenile, transitional and adult stages, and the associated processes. In the two latter studies, the model used could represent consistent development patterns in the Black Sea. All the above-mentioned models offer a basis for the study of ML behavior within different size or age classes. Food concentration and temperature were the main forcings considered in these models, which do not consider the other trophic levels of the planktonic food web. Also, these 0D models are designed to simulate ML dynamics in a given region of interest. Oguz et al. (2008) developed a model including the lower trophic levels of the planktonic food web by considering three phytoplankton groups, three zooplankton groups (as we do in our model), and a simplified particulate and dissolved nitrogen cycle. This model
was used in a two-layer configuration (i.e. the 0-50m euphotic zone and the sub-thermocline layer) in the Black Sea. Another group of models considers ML dynamics in a three-dimensional configuration. Among them are statistical models based on the estimation of the probability of ML occurrence, which depends on different key factors measured in situ (Collingridge et al., 2014 and Siapatis et al., 2008). One of these models is used to study the North Sea and Baltic Sea (Collingridge et al., 2014), and the other, - the Aegean and Mediterranean seas (Siapatis et al., 2008). The limits of the statistical approach lie in the fact that it does not take into account the key processes of ML population growth, reproduction, metabolic demands and mortality. Mechanistic three-dimensional models are designed for this purpose. Van der Molen et al. (2015) and David et al. (2015) have performed an extensive study using a multi-model approach with different types of models, namely a high-resolution particle tracking model with passive particles, a low-resolution particle tracking model with a reproduction model coupled to a biogeochemical model, and a dynamic energy budget (DEB) model. The aim of these works was to investigate the reasons for ML dispersal in the region of the Scheldt estuaries and the southern North Sea. Analysis of the influence of temperature and food variability on ML reproduction and outbursts have been performed in these works.

We propose here another mechanistic model, based on the Eco3M-MED biogeochemical model (Alekseenko et al., 2014), in which we have added a new compartment for ML. This model has several advantages in that (i) it considers seven plankton functional types (PFTs) from bacteria to ML, (ii) C, N and P biogeochemical cycles are described in the model; (iii) organisms are represented in terms of abundance (ind.l$^{-1}$) and in terms of C, N and P concentrations (mol.l$^{-1}$), thereby offering the possibility to handle intracellular ratios and also intracellular quotas that influence the kinetics of most of the physiological processes undertaken by each PFT.

The aim of this paper is to investigate through a theoretical study, the impact of several external factors (namely temperature, food availability and quality (stoichiometry)) on ML physiology and population dynamics and to define environmental windows leading to ML blooms. Though theoretical, this study also aims at providing “realistic” results, in the sense that they could help in understanding some aspects of ML dynamics in the Mediterranean Sea.
2. Materials and methods

2.1. Terminology

In this paper, the terms abundance and concentration will respectively refer to a number of individuals per unit volume and to a C (or N, P) biomass in mol per unit volume. Internal quota term (in mol.ind\(^{-1}\)) will correspond to the X biomass per individual, and internal ratio (in molX.molY\(^{-1}\) where X and Y stand either for C, N or P) to the proportion of biomasses C :N, C :P, N :P. Relative quotas (varying in the range 0-100 %, see eq. 1) will also be used in this work.

\[
\tilde{Q}_X = \frac{Q_X - Q_{X \text{min}}}{Q_{X \text{max}} - Q_{X \text{min}}} \cdot 100\%.
\]

2.2. General features of Eco3M-MED model

The Eco3M (Ecological Mechanistic and Modular) modelling tool (Baklouti et al. 2006a, b) is used in this work. Several configurations (i.e. several flexible-stoichiometry models representing the low levels of the marine food web) have already been embedded in this tool featuring a modular structure (e.g., Baklouti et al. 2006b; 2011; Eisenhauer et al., 2009; Fontana et al. 2009; Auger et al. 2011, Alekseenko et al. 2014; Guyennon et al., 2015).

In a recent configuration of Eco3M (referred to as Eco3M-MED, Alekseenko et al., 2014; Guyennon et al., 2015), organisms are represented both in terms of elemental concentrations (in mol C, N or P per liter) and abundances (in cells or individuals per liter), thereby enabling the delivery of internal quotas (in mol C, N or P per cells) in addition to internal ratios (in mol X per mol Y). These internal quotas and ratios are calculated dynamically for each organism and contribute to the kinetics of regulation of most of the physiological processes included in the model. The introduction of abundances has several other advantages: it enables a direct comparison (i.e., without using a conversion factor from biomasses, as is usually done) of the model outputs with the growing data set of bacteria, phytoplankton or zooplankton abundances that are provided by recent techniques such as flow cytometry and plankton counts. It also makes it possible to differentiate in the modeled population biomass growth the respective contributions of organism recruitment (production of new organisms) and biomass synthesis.

The conceptual scheme of the biogeochemical model Eco3M-MED used in this study accounts for the complex food-web of the NW Mediterranean...
Sea (Fig. 2). Compared to the previous version of Eco3M-MED described in Alekseenko et al. (2014), a new functional type has been introduced in the planktonic food web, namely the gelatinous carnivorous zooplankton represented by the species ML. Therefore, the Eco3M-MED model developed in this work includes the following 40 state variables:

- Three nutrients: nitrate ($\text{NO}_3$), phosphate ($\text{PO}_4$), and ammonium ($\text{NH}_4$). Silicate is not considered here since it is assumed that, in the Mediterranean Sea, it does not limit diatom growth.
- Dissolved organic matter ($\text{DOM}$) constituted by labile and semi-labile organic carbon ($\text{LDOC}$, $\text{SLDOC}$), labile organic phosphorus ($\text{LDOP}$), and labile organic nitrogen ($\text{LDON}$).
- Particulate organic detrital matter ($\text{POM}$) constituted by: carbon, phosphorus and nitrogen ($\text{POC}$, $\text{POP}$, $\text{PON}$).
- Bacterial cells with their carbon, nitrogen and phosphorus content ($\text{BAC}$, $\text{BAC}_C$, $\text{BAC}_N$, $\text{BAC}_P$).
- Two size classes of phytoplankton cells (<10 $\mu$m and >10 $\mu$m; referred to as 'small' and 'large' in the model) with their carbon, nitrogen, phosphorus and chlorophyll content ($\text{PHYS}$, $\text{PHYS}_C$, $\text{PHYS}_N$, $\text{PHYS}_P$, $\text{PHYS}_{\text{Chl}}$ and $\text{PHYL}$, $\text{PHYL}_C$, $\text{PHYL}_N$, $\text{PHYL}_P$, $\text{PHYL}_{\text{Chl}}$).
- Four compartments of zooplankton organisms with their carbon, nitrogen, and phosphorus contents: nano-, micro-, meso- and gelatinous zooplankton represented respectively by heterotrophic nano-flagellates ($\text{HNF}$, $\text{HNF}_C$, $\text{HNF}_N$, $\text{HNF}_P$), ciliates ($\text{CIL}$, $\text{CIL}_C$, $\text{CIL}_N$, $\text{CIL}_P$), copepods ($Z$, $Z_C$, $Z_N$, $Z_P$) and ML ($\text{ML}$, $\text{ML}_C$, $\text{ML}_N$, $\text{ML}_P$).

2.3. ML population model and terminology

ML adult life stage is explicitly represented in the model. ML adults are able to reproduce under certain conditions of their physiological state. The reproduction rate and most of the physiological processes undertaken by these adults are indeed regulated by their internal quotas of carbon, nitrogen and phosphorus ($Q_C$, $Q_N$ and $Q_P$). The minimum and maximum quota values are given in Table 1.

The ML life phase between egg and adult stages, hereafter called the “juvenile phase”, is not explicitly represented. This phase actually includes both larval and juvenile individuals and lasts between 16 and 40 days depending on the food density and water temperature (Collingridge et al., 2014, Salihoglu et al., 2011). We also assume that juveniles have not yet reached the
minimum nutritional state necessary to achieve reproduction. Thus, recruited adults from juveniles are not yet sexually mature and they will be referred to as immature adults. $T_{rep}$ stands for the time necessary for immature adults to reach the mature stage for reproduction (i.e. the time to become mature adults). For mature adults, as spawning occurs, the entire amount of material required to grow from egg stage to adult stage is instantly and explicitly transferred from the prey biomass pools (copepods and ciliates) to the ML adult pool. In other words, the lag time between the egg and adult stages is not accounted for by the model, but the accumulated ingested food needed for the juvenile growth is explicitly taken into account through implicit ML juvenile grazing on ML prey.

In the following sections, we will use the term specific population growth rate (SPGR in h$^{-1}$) to express the number of new individuals per individual and unit time. The population growth rate (PGR in ind.l$^{-1}$.h$^{-1}$) will refer to the increase in the number of individuals per unit volume and unit time. The specific growth rate (SGR in molC.molC$^{-1}$.h$^{-1}$ or in h$^{-1}$) to express the biomass change of an individual per mean biomass and unit time.

2.4. ML activities

This section describes the model formulation of ML physiological and demographic processes. The processes and the assumptions used to establish the associated formulations are presented in a specific subsection. Fig. 3 shows a schematic representation of ML physiological processes that have been incorporated in the Eco3M-MED biogeochemical model. Table 2 contains the list of model functions.

2.4.1. Feeding

Dietary flexibility allows ML to exploit a wide range of planktonic food sources, such as microplankton, mesozooplankton, and fish eggs (Costello et al., 2012, Purcell et al., 1994, 2001), thereby revealing an essential trait associated with the invasive success of ML.

A review of the nature of the prey ingested by ML is presented in Costello et al. (2012, their Table 2), based on in situ gut content from various geographical locations, including ML native and invaded ecosystems. According to this review, the dominant prey found in ML gut is copepod for most ecosystems. In another survey, Purcell et al (2012) suggest that direct predation on eggs and fish larvae appears to be of a secondary order compared to the
predation on zooplankton. Hamer et al. (2010) corroborate this by investigating the potential link between ML and fish populations, performing ML feeding experiments on both eggs and larvae. They found no significant correlation could be detected between ML abundance and the abundance of fish eggs. In the same study, C and N stable isotope signatures of three potential prey groups (fish eggs, small plankton and larger plankton) showed that ML primarily feeds on plankton, while fish eggs are of minor importance. In addition, a feeding selection experiment, with fish eggs and copepods offered in the same proportion, corroborated these findings: ML ingested significantly more copepods, and feeding on fish eggs was not significantly different from zero. Finally, Hamer et al. (2010) showed that ML has no serious potential as a direct predator of fish eggs, but individuals of this species might compete for food with larval fish. In the Mediterranean and Black seas, the contribution of ichthyoplankton to M. leidyi diet seems to be negligible according to a large number of studies (CIESM, 2011, Finenko et al., 2013). On the basis of these observations, ML prey were restricted to zooplankton in our model.

The abundance and composition of zooplanktonic prey are likely to influence ML population dynamics differently depending on the life stage (McNamara et al., 2013). Whereas laboratory measurements of ML clearance rates showed a preference of ML adults for copepods (Madsen & Røisgard, 2010), ML juveniles exert significant predatory control over planktonic ciliates and other microzooplanktonic compartments, including copepod nauplii (Stoecker et al., 1987; Sullivan & Gifford, 2004, 2007). Despite the fact that only the ML adult stage is explicitly represented in the present version of the model, an implicit representation of the ML juvenile grazing impact on different food sources is included. That means that C, N and P quotas which are affected to each new adult organism in the model come from a small part (the egg weight) from their mother’s C, N and P pool, but the rest come from the C, N and P pools of the ML juvenile’s prey, namely copepods (arbitrarily representing 80% of the food) and ciliates (20%). This implicit specific feeding rate during the juvenile stage is represented in the model through the function:

\[
f^{gjuv} = \sigma Q^{min}_X f^\mu, \tag{2}
\]

where \(Q^{min}_X\) is the minimum internal quota in element X for an ML adult, \(\sigma\) is the proportion of \(Q^{min}_X\) which is taken by ML from their preys during their implicit juvenile stages, \(f^\mu\) is the function describing the specific rate
of ML growth (described in the next subsection).

The specific feeding rate of adult ML is represented by a Holling II formulation revisited by Koojman (2010):

\[
f_{\text{ML}}^{\text{gz}} = \frac{I_m[Z]}{F + [Z]},
\]

where \(I_m\) is the maximum ingestion rate of ML, \(F\) the clearance rate, and \([Z]\) the mesozooplankton abundance.

As already done in Baklouti et al. (2011), a feedback regulation of the gross grazing flux is operated through the \(h^{Q_X}\) quota function representing the feedback of the internal individual status on ML feeding. The mathematical expression of this quota function is given by Eq. (4) which has already been used in Geider et al. (1998) to regulate net uptake of nutrient by phytoplankton:

\[
h^{Q_X} = \left( \frac{Q_{X}^{\text{max}} - Q_X}{Q_{X}^{\text{max}} - Q_{X}^{\text{min}}} \right)^{0.06}.
\]

The excess of a given element \(X\) among C, N, and P goes to particulate organic matter (POM).

2.4.2. Population growth and reproduction

The classical Droop formulation (Eq. 5) combined with Leibig’s law of the minimum are used to describe the specific growth rate \(f^\mu\) in the model:

\[
f^\mu = \bar{\mu} \cdot \text{min}_X \left[ 1 - \frac{Q_X^{\text{min}}}{Q_X} \right].
\]

In this formulation, \(Q_X\) represents the actual intracellular quota in a given element \(X\) among C, N, and P, and \(\bar{\mu}\) the maximum theoretical growth rate of ML.

\(Q_X^{\text{min}}\) is the amount of element \(X\) used in ML organism structure and metabolism and exceeding amount can be used as storage for growth and reproduction. In the model, it is assumed that all ML adults, in which \(Q_X\) exceeds \(Q_X^{\text{min}}\), are mature (i.e. able to reproduce).

2.4.3. Mortality

The natural mortality specific rate \(f^m\) is represented through a kinetic rate depending on the following relative carbon internal quota \(Q_C\):

10
\[ f^m = \begin{cases} k_m, & \text{if } Q_C \geq Q_{C_{\text{min}}} \\ k_m + A(2\tilde{Q}_C)^2, & \text{if } Q_C < Q_{C_{\text{min}}} \end{cases} \quad (6) \]

where \( k_m \) is the minimum specific mortality rate and \( A \) is a constant.

Equations (6) suggest that when ML adults have deficient nutritional states (i.e. \( Q_C < Q_{C_{\text{min}}} \)), their natural mortality rate is enhanced. In substance, we assume that the specific natural mortality increases quadratically with \( \tilde{Q}_C \).

A quadratic mortality function is also applied to ML to implicitly represent its predation by higher trophic levels:

\[ f^{mq} = k_{mq}, \quad (7) \]

where \( k_{mq} \) is the specific quadratic mortality rate.

### 2.4.4. Metabolic requirements

In several models describing ML activities (Kremer & Reeve, 1989; Salihoglu et al., 2011), it is assumed that ML individual mass reduction is mainly due to respiration and to excretion losses exceeding assimilated inputs. Furthermore, laboratory experiments show a linear relationship between the ML respiration rate and food availability (Kremer 1982, Finenko et al. 1995, Anninsky et al. 1998).

In the present model, ML respiration formulation is split into two terms: the first represents the energetic costs associated with the basal maintenance (which is related to carbon biomass), while the second term expresses the costs induced by the ingestion process (active metabolism).

\[ f^{\text{resp}} = \begin{cases} r_m \cdot \left(1 + \frac{Q_C - Q_{C_{\text{min}}}}{Q_{C_{\text{min}}}}\right) + r_i \cdot f_{ML}^{22}, & \text{if } Q_C \geq Q_{C_{\text{min}}} \\ r_m + r_i \cdot f_{ML}^{22}, & \text{if } Q_C < Q_{C_{\text{min}}} \end{cases} \quad (8) \]

where \( r_m \) is the metabolic respiration-excretion rate and \( r_i \) the respiration cost due to ingestion requirements.

This formulation suggests that when the carbon reserve pool is not empty (i.e. \( Q_C > Q_{C_{\text{min}}} \)), the respiration associated with the individual maintenance is taken into account in addition to the basal respiration and to respiration costs for ingestion. The excretion formulation taken into account in the model is:
\[ f_{\text{exc}}^X = f^{g^2}Q_X^Z \left(1 - h^{Q_X}\right) + r_m. \] (9)

Only the equations relative to the new features of the model are presented here (Appendix A). The remaining equations can be found in Alekseenko et al. (2014).

3. Simulations and scenarios

Different modelling scenarios have been considered in this study (Table 3):

— TS1 : Analysis of the effective functional response and comparison with the theoretical one; in this scenario, the level of ML adult’s food (i.e. copepods) is set to constant;

— TS2 : experiments on the impact of the diet quantity and quality on the time necessary for just-recruited ML to reach sexual maturity; only ML immature adults are present at the beginning of the simulation; in TS2a scenario, the impact of several food levels is investigated while in TS2b, the quality of prey on the dynamics is investigated through simulations using different prey abundances corresponding to the same food concentration in terms of carbon biomass; in TS2c scenario the impact of temperature and \( Q_{10} \) on SGR of mature and immature ML individual is investigated;

— TS3 : Starvation experiments; in this scenario, ML adults are starved for more or less long periods and then food is reintroduced at different fixed levels;

— TS4 : 0D microcosm experiments; in this scenario, the whole of the trophic web is explicitly represented and forced by dynamic light and temperature conditions;

— TS5 : Nutrient ratio experiments; this scenario investigates the impact of varying inorganic \( NO_3 \) and \( PO_4 \) concentrations and \( NO_3 : PO_4 \) ratios;

— TS6 : Competitive pressure on ML prey; this scenario investigates the impact of different competition pressures exerted on ML prey, namely copepods.

In scenarios TS1 to TS3, temperature is fixed while it varies according to the function plotted in Fig.10 (\( Q_{10} \) function) in the remaining scenarios.

In scenarios TS4 to TS6, copepod abundance and biomass are not constant, but derived from the biogeochemical model forced by a light seasonal cycle.
in the NW Mediterranean Sea. However, results will not be interpreted in terms of seasonality but in terms of variation with time expressed in weeks or years (for long-term simulations), since the seasonality of hydrodynamic features cannot be reproduced with a 0D model.

3.1. Effective functional response experiment (TS1)

Scenario TS1 was designed to mimic ML-copepods laboratory experiments in chemostat. It consisted in several numerical experiments in which the abundance of ML’s food (i.e. copepods) was set at a given value, while the lower trophic levels were not considered. Eleven copepod abundance levels ranging between 2.5 ind.l$^{-1}$ and 250 ind.l$^{-1}$ have been tested. The duration of each simulation was 10 days. For these numerical experiments, copepods were the only food source for ML juveniles and adults. Copepods were characterized by a constant internal content in N and P equal to: $\tilde{Q}_N = \tilde{Q}_P = 50\%$. In 9 experiments out of 11, copepods’ relative internal carbon content was set to 50%. Two experiments were run just for $Z$ abundance of 250 ind.l$^{-1}$ in which $\tilde{Q}_C$ was not equal to 50%: one using $\tilde{Q}_C = 0\%$ and the other in which $\tilde{Q}_C = 100\%$.

3.2. Impact of diet quality and quantity on ML growth (TS2)

Scenario TS2a was performed to assess the necessary time for ML immature adults to reach the nutritional status allowing their sexual maturity (and thereby their reproduction) as a function of food availability (copepods). For this, only ML immature adults (characterized by an internal quotas $Q_C = \sigma Q_{C}^{\min}$, $Q_N = \sigma Q_{N}^{\min}$, $Q_P = \sigma Q_{P}^{\min}$, which are listed in the Table 1) are introduced at the beginning of the simulation. Since $\sigma$ is a proportion of C, N and P taken by juvenile ML from its predators and it is below 1. So, in this case $\tilde{Q}_C$, $\tilde{Q}_N$, $\tilde{Q}_P$ are below zero. They fed on copepods for which abundance and internal quotas are set to constant ($\tilde{Q}_N = \tilde{Q}_P = 100\%$ and $\tilde{Q}_C = 50\%$, in order to simplify the interpretation of the experiment, N and P are not limiting copepod growth). As for TS1, this scenario also mimics chemostat-like laboratory experiments with copepod abundance set at the desired level during the experiment.

Several abundances of copepod were used: 2.5, 5, 10, 25, 100 and 250 ind.l$^{-1}$. As for scenario TS1, food abundance and biomass were maintained constant during the whole of the simulated period. The duration of each simulation equals 12 weeks.
TS2b is a complimentary scenario, which is analogous to TS2a, but the duration of this scenario is much longer (1 year), and the number of tested copepod abundances is limited to three values. The main idea of such a scenario is to study the impact of food quality (for a given food quantity) on ML dynamics. The food quantity (i.e. copepod biomass) is set to $7.5 \cdot 10^{-5}$ molC.l$^{-1}$, corresponding to three different combinations of the copepod abundance and internal carbon content: (a) 250 ind.l$^{-1}$ with $Q_C$=0%, (b) 150 ind.l$^{-1}$ with $Q_C$=50%, and (c) 107.14 ind.l$^{-1}$ with $Q_C$=100%.

Another complementary scenario TS2c has been performed in order to investigate the impact of temperature on individual specific growth rate (SGR) of mature (adult, able to reproduce) and immature (juvenile, unable to reproduce) ML. This scenario was designed so as to reproduce laboratory experiments. The goal was to compare modeled SGR values with laboratory measurements available in literature. It is worth noting that the laboratory experiments on ML’s SGR were held under different temperature conditions. For a better comparison with the different available data, four levels of imposed constant copepod abundance (20, 50, 100 and 200 ind.l$^{-1}$, the same numbers as in Reeve et al., 1989 and in Purcell et al., 2001) with $Q_C$=100% have been given to a juvenile ML under different temperature conditions (11, 14, 20 and 26 °C).

Another important temperature-related parameter which impacts SGR values is $Q_{10}$. For all experiments in this work, the $Q_{10}$ of 1.5 has been taken from Salihoglu et al. (2013), for ML in the Black Sea. However other observations from the native environment showed that $Q_{10}$ was varying, depending on ML biomass (Kremer, 1979, typically from 1.4 to 1.8). Thus four additional modelling experiments have been designed with four different values of $Q_{10}$ (1.5, 2, 2.5, and 3), a constant copepod abundance of 200 ind.l$^{-1}$, $Q_C$=100%, and T=26°C. The duration of TS2c scenario was of two weeks.

3.3. Starvation experiment (TS3)

A 52 week scenario (TS3) has been built in order to study the survival ability of ML when submitted to scarce food conditions. Carbon-limited ML adults ($Q_C = 50\%$ and $Q_N = Q_P = 100\%$ ), at an abundance of $1 \cdot 10^{-3}$ ind.l$^{-1}$, were initially considered in the system without any food source. After different starvation periods (1, 4, 6, 8 and 12 weeks), a constant abundance of prey (copepods) was introduced. These prey were characterized by a carbon relative quota equal to 50% ($Q_C = 50\%$ ) and N and P relative quotas of 100% ($Q_N = Q_P = 100\%$). Three values of copepod abundance have been
considered (within the range of the Mediterranean Sea), namely 2.5, 5 and 10 ind.l\(^{-1}\).

3.4. 0D microcosm experiments (TS4)

After three theoretical scenarios (TS1-TS3), we aimed to investigate ML long-term population dynamics and individual responses under dynamic environmental conditions (0D microcosm experiments) using three different temperature forcings. As for light forcing, a typical seasonal temperature cycle of NW Mediterranean Sea was used to force the 0D biogeochemical model:

\[
T_{\text{ref}} = \max\left(13; \left| 25 \cdot \cos \left(0.45\pi \left(\frac{t/3600 - 5000}{4380}\right)\right) \right|\right), \quad (10)
\]

\[
Irr = \max\left(1; \max\left(50; \left| 800 \cdot \cos \left(0.45\pi \left(\frac{t/3600 - 400}{3942}\right)\right) \right|\right)\right) \sin \left(\frac{\pi t}{12 \cdot 3600}\right) \quad (11)
\]

where \(t\) stands for the elapsed time since the beginning of the simulation. In this scenario and in the following, the whole planktonic food-web is now considered (see Fig.2) and behaves dynamically. The model state variables have initial values in the same ranges as those observed in the NW-Mediterranean Sea.

The impact of temperature on ML physiology was investigated in three test cases: (a) test case CT: the physiological rates do not vary with temperature \(f_{Q_{10}} = 1\), considered as the reference scenario; (b) test case VT: ML grazing and growth rates vary with temperature \(T_{\text{ref}}\) according to the \(f_{Q_{10}}\)-function given by Eq.12; (c) test case VT-HT: the same test case as (b) but with an ambient temperature increased by 2\(^{\circ}\)C (i.e. equal to \(T_{\text{ref}} + 2^{\circ}\)C).

\[
f_{Q_{10}} = Q10^{\frac{T_{\text{ref}}-15}{10}}, \quad (12)
\]

All TS4 experiments were run for 10 years.

3.5. Nutrient ratio experiments (TS5)

Scenario TS5 has been designed to investigate the impact of the NO\(_3\) : PO\(_4\) ratio over the Mediterranean planktonic web in the interannual time scale. Different values of PO\(_4\) and NO\(_3\) were considered in these experiments which correspond to three different environmental condition that could be
encountered in the Mediterranean ecosystems, namely: (a) the Rhône region of freshwater influence (ROFI) conditions in which both nutrient concentrations are high \((\text{NO}_3 = 5 \mu M, \text{PO}_4 = 0.25 \mu M)\) and the \(\text{NO}_3 : \text{PO}_4\) ratio equals 20 (test case HN-LNP); (b) ROFI conditions in which \(\text{NO}_3\) concentration is still high \((\text{NO}_3 = 5 \mu M)\) but that of phosphate is lower than in the previous case \((\text{PO}_4 = 0.125 \mu M)\), leading to a \(\text{NO}_3 : \text{PO}_4\) ratio of 40 (test case HN-HNP); (c) oligotrophic conditions as encountered in most of the Mediterranean Sea \((\text{NO}_3 = 1.25 \mu M, \text{PO}_4 = 0.0625 \mu M, \text{and} \ \text{NO}_3 : \text{PO}_4 = 20, \text{test case LN-LNP})\) (d) oligotrophic conditions with a strong phosphorous depletion \((\text{NO}_3 = 1.25 \mu M, \text{PO}_4 = 0.0313 \mu M, \text{and} \ \text{NO}_3 : \text{PO}_4 = 40, \text{test case LN-HNP})\).

Water buckets of 2.5 l were considered in this scenario. The chemostat was characterized by an inflow of water of 0.025 l.d\(^{-1}\) with constant nutrient concentrations. Nutrient inflow was temporarily stopped when the level of \(\text{NO}_3\) in the chemostat was higher than 10 \(\mu M\). The duration of each experiment was 10 years.

3.6. Experiments on competitive pressure on ML food (TS6)

The invasive ctenophore ML has a strong reputation as a threat to fish stocks. Negative consequences for zooplanktivorous fish due to ML predation impact on the zooplankton have been observed in various ecosystems (Waggett and Costello 1999 Shiganova & Bulgakova, 2000; Kideys & Romanova 2001; Purcell et al. 2001; Shiganova et al. 2001, Madesen & Røisgard, 2010, Gucu et al., 2002).

Scenario TS6 aims to identify the competitive impact on copepods by ML competitors, including a small pelagic fish, on the food-web dynamics, and specifically on that of ML. This is done through the specific quadratic mortality rate \(f_{mq}^Z\) (Appendix B, Table 2 in Alekseenko et al, 2014), which implicitly represents in the model the level of competitive pressure exerted on copepods. Three different values of \(f_{mq}^Z\) of copepods have been used, namely 3\(\cdot\)10\(^{-8}\), 6\(\cdot\)10\(^{-8}\) and 9\(\cdot\)10\(^{-8}\) l.ind\(^{-1}\).s\(^{-1}\), which respectively correspond to the test cases referred to as LFP (same as VT case), MFP and HFP test cases. Higher \(f_{mq}^Z\) values correspond to higher competitive pressure on copepods, thus to stronger competition between other organisms and ML for the available food. This could also be seen as higher fish recruitment or lower fishing catchment. Here we do not take into account a case when ML itself exerts a pressure on fish eggs and larvae, which could happen in nature under some special conditions, as discussed by Cowan & Houde (1993). This
scenario again mimics a microcosm experiment for which temperature and light forcings describe the same seasonal cycles as those given by eq. 10 and 11 respectively. The duration of each experiment was 36 months.

4. Results

Results obtained from the scenarios described in section 3 are presented in this section in separate subsections for each scenario.

4.1. Effective functional response experiment (TS1 results)

Eleven numerical experiments were run to calculate the effective (i.e. simulated) functional responses at steady state and compare them to the theoretical one (Fig.4). These experiments enable us to verify that the simulated feeding rates produce a functional response which is similar to the theoretical one used in the model. The model also delivers the functional response expressed in terms of biomass (molC.ind$^{-1}$.h$^{-1}$), which is a function of the prey carbon content. Red dotted lines in Fig. 4 show the envelope of possible functional responses when the prey carbon relative quota varies from 0% to 100%. For instance, the model predicts a feeding rate of 2.7 ind.ind$^{-1}$.h$^{-1}$ when the copepod abundance equals 50 ind.l$^{-1}$. This corresponds to a feeding rate expressed in carbon biomass varying from $0.7 \times 10^{-6}$ to $1.8 \times 10^{-6}$ molC.ind$^{-1}$.h$^{-1}$, depending on the nutritional status of copepods.

In Fig. 4b, the nutrition rate at Z=250 ind.l$^{-1}$ with $Q_{C}^{min}$ (which approximately reaches the saturation rate for $Q_{C}^{min}$) is equivalent to the nutrition rate at Z=25 ind.l$^{-1}$ with the $Q_{C}^{mean}$ (slightly above half-saturation rate for $Q_{C}^{mean}$) and at Z=12 ind.l$^{-1}$ with $Q_{C}^{max}$ (slightly below the half-saturation rate for $Q_{C}^{max}$).

Fig.4c shows the functional response for different prey biomasses (i.e. for different combinations of prey abundance times internal C quota). From this figure, it is seen that ML feeding depends on the quality of the encountered prey. For example, for a given prey biomass of $7.5 \times 10^{-5}$ molC.l$^{-1}$ and a given ML ingestion rate (in ind.ind$^{-1}$.h$^{-1}$), a variety of ML feeding rates (in molC.ind$^{-1}$.h$^{-1}$) could be calculated, ranging from $1.05 \times 10^{-6}$ molC.ind$^{-1}$.h$^{-1}$ when preys have an internal carbon quota of 0%, to $2.4 \times 10^{-6}$ molC.ind$^{-1}$.h$^{-1}$ for preys with a carbon internal content equal to 100%. Thus, the richer are the prey (i.e. when their internal quota is high), the higher is the ingestion rate in molC.ind$^{-1}$.h$^{-1}$.
4.2. Impact of diet on ML population growth and dynamics (TS2 results)

TS2a numerical experiments consider ML predation on copepod prey fixed at a given abundance level. Corresponding results are summarized in Fig. 5 and Table 4. Time evolution in ML abundance and carbon relative quota ($\bar{Q}_C$) delivered by TS2a simulations are shown in Fig. 5. Starting with an initial cohort of immature ML adults fed with different copepod prey levels, ML individuals reach the mature adult stage (i.e. when $\bar{Q}_C \geq 0\%$, cf section 2.4.2) after periods of time ($t_{rep}$ in Table 4) varying from 12.2 hours (for the prey level of 250 ind.l$^{-1}$) to 129 h (for the prey level of 5 ind.l$^{-1}$). The abundance of the ML cohorts over the simulation initially decreases (Fig.5d) as long as the individual $\bar{Q}_C$ is negative, which lasts for a longer or shorter time depending on the food level, and then increases as soon as reproduction occurs and exceeds the mortality rate.

The prey level of 2.5 ind.l$^{-1}$ does not allow any positive population growth. In this case, reproduction never occurs, since ML’s $\bar{Q}_C$ remains negative until the end of simulation ($\bar{Q}_C$ decreases down to -8.5%). This means that its internal quota $Q_C$ is below $Q_C^{\min}$ due to higher carbon losses (associated with respiration, excretion and mortality) than carbon gains obtained through grazing.

The abundance of the ML population reached at the end of the simulation (i.e. when steady state is reached) increases with copepod prey abundance through an asymptotic law, reaching after 12 weeks a maximum value near 1.4 ind.l$^{-1}$ with a carbon internal quota of 41% (Fig.6).

Table4 summarizes model results of TS2a through the three indicators, namely $t_{rep}$ and SGR, previously defined (see section 2.3), and $Fl_Q$. The term $Fl_Q = (1 - \sigma) Q_C^{\min}/t_{rep}$ corresponds to the carbon quantity accumulated in immature ML adults before reaching the mature adult stage. It is equivalent to the time-integrated balance of all simulated carbon fluxes (feeding - respiration - excretion - mortality - quadratic mortality) of ML. $Fl_Q$ is positive beyond a food prey level of 5 ind.l$^{-1}$, and increases with food abundance. The SGR, which can also be interpreted as the number of new (immature) ML individuals per adult and per hour, increases with prey level and reaches 18.3 % per hour when food availability is 250 ind.l$^{-1}$. According to the model, in the Mediterranean where copepod abundance ranges from 2.5 to 10 ind.l$^{-1}$, ML SGR is up to 0.0105 per hour, i.e. 25.2 % per day.

Fig. 7 shows the temporal dynamics over one year of ML carbon quota and abundance for a constant carbon biomass of copepods equal to $7.5 \cdot 10^{-5}$ molC.l$^{-1}$. From this figure, it can be seen that, for the same food biomass,
different dynamics of ML abundance and ML quotas can be calculated according to the carbon quota of copepods. The test with the lowest copepod abundance (but the richest carbon quota) leads to the highest ML abundance as well as the highest carbon quota (Fig.7).

Conversely, the test with the highest copepod abundance (but with the lowest quota) leads to the lowest ML abundances and lowest ML quotas. The difference between these two extreme cases is significant: ML abundances at steady state differ by around 42% and ML internal carbon quota by 25%.

The time necessary to reach steady state also varies according to the quality of the food, from about 6 months for the carbon-poorest copepods to about 4 months for the carbon-richest copepods.

From Fig.8 it can be seen how the SGR of mature and immature ML vary with temperature and food concentration (Figs.8a-b) and with $Q_{10}$ (Fig.8c), thereby allowing to estimate an envelope where SGR varies depending on these conditions. Figs.8a-b show estimations of SGR depending on the temperature conditions. It can be seen that for a given temperature, SGR of immature ML is always 20-40% higher than SGR of mature ML. This difference between SGR of mature and immature ML is decreasing with temperature increase. In both cases (for mature and immature ML, Fig.8a and Fig.8b) SGR is increasing with temperature. For mature ML, SGR varies from 0.1 $d^{-1}$ (at $11^\circ C$) to 0.39 $d^{-1}$ (at $26^\circ C$), for the immature ML - it is from 0.16 $d^{-1}$ (at $11^\circ C$) to 0.55 $d^{-1}$ (at $26^\circ C$). SGR increases with food increase.

Another temperature-related parameter impacting ML physiology is $Q_{10}$.

For the experiment TS2c with the highest temperature and food concentration (green triangles on Figs.8a-b), we studied the impact of $Q_{10}$ among values within the range 1.5-3: for the food concentration of 200 ind.l$^{-1}$ with $Q_{C}$=100% and a temperature of $26^\circ C$. This figure shows that there is a correlation between $Q_{10}$ and SGR. SGR of immature ML is higher than SGR of mature ML.

4.3. Starvation experiment (TS3 results)

In scenario TS3 (Fig. 8), we analyze ML individual and population responses to different starvation periods (from 1 to 12 weeks), followed by food replenishment at three different constant abundances: 10 ind.l$^{-1}$, 5 ind.l$^{-1}$ and 2.5 ind.l$^{-1}$ (the internal carbon quota of copepods is the same in all experiments $Q_{C} = 50\%$). For the three food levels, ML carbon relative quota ($Q_{C}$) decreases as long as starvation lasts (Fig. 8a, c and e). From food replenishment time, $Q_{C}$ increases up to a stationary value, similar for a given food
level whatever the starvation duration, but which varies with this food level: 13.5% for Z=10 ind.l\(^{-1}\), 5.2% for Z=5 ind.l\(^{-1}\) and -8.5% for Z=2.5 ind.l\(^{-1}\) (respectively Fig. 8a, 8c and 8e). It is worth noting that the increase in ML’s \(\tilde{Q}_C\) after food reintroduction is all the more rapid in that food level is high (Fig. 8a, c and e). During the first week of starvation, the initial reserves of ML individuals allows the maintenance of a positive \(\tilde{Q}_C\), and ML population abundance still increases. Beyond this period, \(\tilde{Q}_C\) becomes negative and reproduction stops. Consequently, ML population abundance decreases as long as starvation continues, and even after (Fig. 8b, d and f). When food is reintroduced (at time \(t_1\)) after the starvation period, the ML population does not respond immediately and ML abundance still decreases as long as \(\tilde{Q}_C\) is negative. As soon as \(\tilde{Q}_C\) becomes positive (at time \(t_2\)), ML reproduction restarts, and ML population abundance increases again. Table 5 summarizes the time delays \((t_2 - t_1)\) between food introduction and the beginning of ML population reproduction, for the two highest levels of food abundance for which \(\tilde{Q}_C\) reach positive values after food reintroduction. This time delay non-linearly increases with the starvation duration following a saturation curve and decreases with the level of food (results not shown).

For the starvation experiments with the highest food levels (10 and 5 ind.l\(^{-1}\) in Fig. 8b, and d), the time to recover the initial conditions of population abundance is much longer than the starvation duration, whatever this duration. Moreover, the slope of the population increase after food replenishment is rather constant whatever the starvation history, but increases with the food level. For the highest food abundance (i.e. 10 ind.l\(^{-1}\), Fig.9b), the increase in ML population reaches more or less rapidly a plateau (10 ind.l\(^{-1}\), depending on the starvation duration. In the experiment with the lowest food level (2.5 ind.l\(^{-1}\)), the population continues to decrease even after food reintroduction (Fig.9f).

**4.4. 0D microcosm experiments (TS4 results)**

Results relative to the temperature impact on the modeled food-web (see Fig.2), and especially on ML and copepods, are shown in Fig.10. During the simulation, the lower trophic levels (from bacteria to microzooplankton) were abundant throughout the simulated period and biomass concentrations were not significantly affected by the higher trophic levels (results not shown). The carbon relative quota (\(\tilde{Q}_C\)) of copepod was always close to 100%, thereby revealing the absence of C-limitation during the simulation (results not
shown). Hence it can be considered that during these experiments, copepod and ML were in rich carbon conditions.

Fig. 10 shows the 10-year dynamics of copepod and ML abundances and of ML $\bar{Q}_C$, for the three cases presented in section 3.4 (i.e. CT, VT, and VT-HT). When temperature has no impact on ML process rates (case CT), the dynamics of copepods and ML are quasi-periodic, with a period that seems to increase with time. For this experiment, the copepod abundance varies in the range 0.5-5.5 ind.l$^{-1}$ (this also corresponds to the NW Mediterranean copepod range). For ML, its $\bar{Q}_C$ is in the range -35 – 15% and its abundance varies between $5 \cdot 10^{-7}$ and 16 ind.l$^{-1}$.

During the first three years, the dynamics simulated by the two experiments in which temperature impacts ML process rates (i.e. VT and VT-HT cases) are quite similar, but they significantly differ from the CT case. These dynamics do not reveal any periodicity and seem to be chaotic. After three years of simulation, the patterns provided by VT and VT-HT cases begin to differentiate. From year 5, the difference in terms of amplitude and frequency of the abundance signals becomes very significant.

According to Fig. 10b, when copepod abundance drops below $\sim 2$ ind.l$^{-1}$ (we recall that the copepod carbon content is maximum throughout the simulation), ML $\bar{Q}_C$ becomes negative, thereby increasing ML mortality (see for example, the second half of the first year). This phenomenon is more or less pronounced over the course of the 10 years of simulation (see for example the very strong decrease in ML observed during the second half of the 7th year for the VT case).

For the three cases, the lower the abundance of copepods, the lower ML $\bar{Q}_C$ is. It can also be seen that the higher ML mortality, the stronger ML abundance decline is, and the longer the period of ML recovery is after copepod stock replenishment. The period of ML recovery can last from 1 to 2 years (see for example, between years 1 and 2 for VT and VT-HT cases, or between years 7 and 9 for VT case, where ML abundance is below 10-20 ind.l$^{-1}$, which can be considered as if ML was absent from the ecosystem).

Such successions of ML presence/absence induce shifts between food-webs-with-ML to food-webs-without-ML, thereby impacting copepod dynamics. In these cases, top down pressure dominates bottom up pressure. As an example, the strong increase in ML abundance between years 6 and 7 for the VT case emptied the copepod stock (Fig. 10), leading, in turn, to the decline in ML abundance down to $1 \cdot 10^{-37}$ ind.l$^{-1}$. After such a predator-prey cycle, it took almost two years for copepods to recover their initial abundance value.
and almost three years for ML.

In order to see whether these different abundance dynamics lead to effective differences in terms of ML productivity, accumulated fluxes corresponding to the number of new individuals per liter (population growth) produced during the simulated period have been calculated. The temporal variations of these fluxes (i.e. accumulated abundances) as well as those of ML instantaneous abundance are presented in Fig.10e for the three experiments. During the simulation, the three tests produce quite similar accumulated fluxes, characterized by stepping curves. The three curves remain interlaced over the whole simulation, without any noticeable difference between them.

4.5. Nutrient ratio experiments (TS5 results)

Four different combinations of $NO_3$ and $PO_4$ concentrations (HN-LNP, HN-HNP, LN-LNP and LN-HNP, cf section 3.5) in nutrient inflow have been used in these experiments, that mimic a laboratory test in chemostat (Fig.11). Note that HN-LNP and VT (see Fig.10) simulations are performed with the same initial conditions and parameter values, except that VT simulation is not in "chemostat mode" (no nutrient inflow occurs during the simulation).

Fig. 10 shows that the ML population peaks systematically following copepod peaks in all cases except LN-HNP (see below). However, the intensities of copepod and ML peaks are not correlated (see, for example, the quite similar ML peaks in years 3 and 4 which follow copepod peaks of different intensities). The delay between the maximum values of successive copepod and ML peaks ranges between 40-150 days, depending on ML $Q_C$ (see starvation test TS2).

In the two cases of high nitrate (HN-LNP and HN-HNP where $NO_3 = 5\mu M$), relatively small differences between results are observed during the first 4.5 years of simulation (Fig.11). Afterwards, these two simulations behave differently, showing shifted oscillations.

By contrast, for low $NO_3$ level (1.25$\mu M$), the experiments with low and high $NO_3 : PO_4$ ratios (i.e. LN-LNP and LN-HNP) reveal strong differences from the beginning of the simulation. In the condition LN-HNP, copepod population first decreases and takes about 4 years to recover its initial abundance, while ML takes about 9 years to recover. For the LN-LNP condition, copepod and ML abundances deliver a quasi-periodic dynamic (around 3-year period).

Fig.11a and b also show that ML decrease is stronger when copepod levels are below 2 ind.l$^{-1}$. The highest ML blooms (0.25-0.3 ind.l$^{-1}$) are observed
for the highest copepod levels (closer to 5.5 ind.l\(^{-1}\)), followed by a rapid decline of copepod stocks. When copepod levels are close to 0 ind.l\(^{-1}\), ML rapidly decline in all the TS5 test cases. Accumulated abundances calculated for the HN cases are very similar (interlaced curves). By contrast, LN cases provide very different curves. For the LN-LNP case, accumulated abundance is always lower than that of HN cases while it is nearly zero until year 9 in the LN-HNP case.

4.6. Competitive predation experiments (TS6 results)

The impact of competitive predation in the modeled food-web is shown in Fig.12. In these experiments, we investigate the impact of competitive predation (implicitly represented in the model, see section 3.6) on copepods and ML dynamics. The copepod abundance dynamics is highly impacted by this parameter.

The lowest competitive predation rate case (LFP test case) induces high fluctuations in the dynamics of copepods, allowing abundance values to be reached as high as 5.5-6 ind.l\(^{-1}\) and as low as nearly 0 ind.l\(^{-1}\). By contrast, the copepod abundance remains nearly constant (around 2 ind.l\(^{-1}\)) for the highest predation rate case (HFP test case) and fluctuate between 1 and 3 ind.l\(^{-1}\) for the intermediate case (MFP test case).

Competitive predation rate also impacts ML dynamics. In all experiments ML survives, but shows more fluctuating abundances (including stronger blooms) when competitive predation rate is low. The more predation by other organisms and fish on copepods increases, the weaker are amplitudes of ML abundance fluctuations, thereby reducing outbreak occurrences.

5. Discussion

Model skill assessment

To be helpful for the understanding of various characteristics of ML population dynamics observed in nature, under specific conditions, the model had first to be assessed. These characteristics include the duration and the frequency of ML outbursts, the orders of magnitude and the maximum amplitude of ML abundances, and the rate of ML population increase. It was first found both for observations (from various ecosystems including ML native and non-native) and in our model simulations that ML outbursts do not last more than 2-3 months (Shiganova et al, 2011, Boero et al., 2013, Lukas et al., 2011, Purcell et al., 2001). Moreover, as a first approximation,
model outputs from the 3-month long experiments with imposed constant food for ML (test series TS2) can be compared to ML observations from various ecosystems where ML is established.

In the ML native ecosystem of Narragansett Bay, over 2.5 months per year, ML blooms with average abundances reaching about $10^{-2} - 10^{-1}$ ind.l$^{-1}$ can be observed, associated with average zooplankton concentrations in this area in the range 10-100 ind.l$^{-1}$ (Costello et al., 2012). For such food levels, the model calculates ML abundances in a consistent but wider range ($10^{-3} - 1$ ind.l$^{-1}$, see Fig.5c). According to the model, in ML non-native ecosystems with average copepod concentrations below 3 ind.l$^{-1}$, characterizing oligotrophic offshore waters of the Mediterranean Sea, ML has no possibility of blooming, since its physiological demands are much higher than the available food (see light blue curve on the Fig.5c). This is in agreement with several in situ studies (Ghabooli et al., 2013, CIESM, 2014, Fuentes et al., 2010), showing that ML was not found in such areas. If we consider the Mediterranean coastal areas, which are much richer in zooplankton, with concentrations higher than 10 ind.l$^{-1}$, the simulated ML abundance is in the order of $10^{-3}$ ind.l$^{-1}$ (see magenta curve in Fig.5c and lines for higher food concentration). This order of magnitude of ML abundance can also be found, for example, in the Black Sea in recent years (Shiganova et al., 2018) and in the Sea of Marmara (Isinibilir et al., 2004). For the highest food concentration of 25-250 ind.l$^{-1}$, simulated ML abundance is in the range $5 \cdot 10^{-2} - 1$ ind.l$^{-1}$ (Fig.5c); this is in agreement with ML abundances measured in the Black Sea, Azov Sea and Caspian Sea (Shiganova, personal communication). In conclusion, our model could reproduce the orders of magnitude of ML abundances observed in various ecosystems differing by their eutrophisation and zooplankton levels.

Modeled SGR values can also be compared to the measured ones in different studies (Reeve et al., 1989, Purcell et al., 2001, Finenko et al., 2000, 2006, Larson, 1985). The values of SGR found by these authors are quite different, mainly due to the specific experimental conditions, such as (i) imposed copepod levels (in Reeve et al., 1989 and Purcell et al., 2001, the levels are the same: 20, 50, 100 and 200 ind.l$^{-1}$; in Finenko et al., 1995, the levels are in the range 60-100 ind.l$^{-1}$), (ii) temperature conditions (in Reeve et al., 1989 and Purcell et al., 2001, it is 26°C; in Finenko et al., 2006 11°C and 14°C.), (iii) ML age/size chosen for the experiment (in Reeve et al., 1989, it corresponds to mature ML, in Purcell et al., 2001 - to immature ML; in Finenko et al., 2006 - to mature and immature ML), (iv) ML taken from
different locations (from Narragansett Bay in Reeve et al., 1989 and Purcell et al., 2001, from the Black Sea in Finenko et al., 2000, and from the Caspian Sea in Finenko et al., 2006), and also (v) water container sizes chosen for experiment and conversion parameters (from carbon biomass, wet weight, dry weight, etc).

The values of SGR estimated in these experiments are within the range of 0.43-0.87 d\(^{-1}\) for immature ML at the highest temperature (at 26\(^\circ\)C) (Purcell et al., 2001, corresponding to copepod abundance range 20-200 ind.l\(^{-1}\)) and in the range of 0.23-0.34 d\(^{-1}\) for the same food quantities for mature ML (Reeve et al., 1989, Purcell et al., 2001); for the lower temperatures (11-14\(^\circ\)C), values of SGR are around 0.07 d\(^{-1}\) (Finenko et al., 2006, in the Caspian Sea). Larson (1985) estimated SGR of ML in natural waters (in different waters of U.S.) in the range 0.1-0.3 d\(^{-1}\) (see his Table 4).

TS2c numerical experiments were designed to take into account all these conditions, not only for model skill assessment through comparison with data, but for a better understanding of the impact of each of these factors on ML SGR. Food and temperature are known to have the greatest impact on ML dynamics (Costello et al., 2012). Temperature impacts ML exponentially (through the Q\(_{10}\)-function), where the Q\(_{10}\)-function is a function of temperature and Q\(_{10}\) parameter, which is estimated in situ.

Modeled SGR shown in Figs.8a-b with Q\(_{10}\)=1.5 gave an SGR range of 0.1-0.39 d\(^{-1}\) for mature ML and of 0.16-0.55 d\(^{-1}\) for immature SGR, both increasing with temperature and food concentration. These values are within the same order of magnitude as the measured SGR, but slightly underestimated for the highest temperature when compared to the measured temperatures given in Reeve et al. (1989) and Purcell et al. (2001). In order to go further, we performed additional numerical experiments for the highest food concentration and temperature with varying Q\(_{10}\) values (Fig.8c). Fig.8c shows that the modelled SGR is highly dependent on Q\(_{10}\). SGR is increased from 0.39 d\(^{-1}\) to 0.92 d\(^{-1}\) for mature ML, and from 0.55 d\(^{-1}\) to 1.1 d\(^{-1}\) for immature ML when Q\(_{10}\) varies from 1.5 to 3. The range of modeled SGR with varying Q\(_{10}\) is wider, and it now includes the values found by Reeve et al. (1989) and Purcell et al. (2001).

Few long term observations of ML exist (Purcell et al. 2001), mainly along the East coast of North America, in the Narragansett Bay (Beaulieu et al., 2013) and in the Chesapeake Bay (Miller, 1974; Purcell et al. 2001), and in the Black sea (Shiganova, 2001; Kideys et al., 2000, Finenko et al., 2013).
vations in coastal or oceanic areas show irregular peaks of abundances both in frequency and intensity. CIESM (2015) mentions that the winter biology of ML is a key parameter to understand population dynamics, as it does not present benthic resting stages (Rapoza et al., 2005; Boero et al. 2008). Its survivability is due to its good resistance to long term starvation combined with an ability to restore growth and reproduction as soon as conditions are favorable. As ML is able to self-fertilize (Baker & Reeve 1974; Sasson & Ryan, 2016), extremely low densities of individuals may not affect reproduction capabilities, whereas small-sized individuals are able to mobilize matter for reproduction (Finenko et al., 2006; Jaspers et al., 2011). Therefore, a population reserve with extremely low-density of small individuals might be the seed of later new population outbreaks; probably in successive phases of population growth, when water temperature and resource abundances allow out-crossing reproduction and large-sized spawning individuals (Costelo et al. 2006; Sasson and Ryan, 2016). Several features of our long term simulations (see our Fig. 10) reproduce observed biological patterns of ML dynamics. One property of our model is its capacity to reproduce such population dynamics variations (outbreaks and disappearance) without changing the parametrization of physiological and demographic processes. Although our seasonal pattern of temperature was a regular forcing function, the interactions between plankton dynamics and ML population induced chaotic-like dynamics of outbreaks. Moreover, our model seems able to reproduce the general properties characterizing ML peaks of abundances as observed in various ecosystems, such as the 2-3 months duration of such peaks, the order of magnitude of ML abundances found in native and non-native ML ecosystems. Our simulations suggest that the match or mismatch with the prey, and the high SGR and reproduction rates, increased at high temperatures, are the main factors inducing ML outbreaks. Conversely, long phases of near-absence of simulated ML individuals are due to a collapse of ML population followed by several years needed to recover a sufficient stock to make possible new outbreaks when matching with a planktonic prey production phase.

Finally, other factors liable to strongly modify ML outbreaks that are not taken into account in our study are coastal hydrographic retention of individuals, mainly during winter time (Kremer & Nixon, 1976; Beaulieu et al., 2013; Costello et al, 2012), and the presence of ML predators such as Beroe ovata (Shiganova et al., 2001).

**Functional response and reproduction function**

The functional response is an essential specific life trait conditioning many
aspects of the species survival and prosperity. ML functional response is the first factor that has been investigated in this paper aiming at improving our understanding of the conditions favoring ML development and outbreaks. First, it must be noted that there is a general confusion in the definition and use of the concept of functional response (which can be expressed either in abundance or in biomass). The initial concept (ref: Holling cf paper Capparoy & Carlotti, 1996) deals with numbers of ingested prey vs individual prey concentrations, but biogeochemical models usually use a mass currency, i.e. ingested mass of prey vs prey biomass concentrations (Carlotti & Poggiale, 2010). An interesting property of the model used in this study is that it allows to delivery of the functional response in all possible combinations of units with prey density expressed either in individual abundance or biomass concentration per liter, and feeding rate in abundance or biomass of consumed prey per predator per unit time (see Fig 4).

Generally, the variations in the functional response types are attributed to (i) the prey species composition, (ii) the range of size (or stage) of prey and predators and the associated swimming behavior, (iii) the patchiness and/or the relative densities of prey and predators and any environmental parameter affecting patchiness, since these factors are considered to modify the different parameters of the functional responses (i.e. attack rate, handling time, satiation, see for instance Capparoy & Carlotti, 1996 for details). In addition to all these factors, this study highlights the importance of the nutritional status of prey when handling functional responses where relatively lower concentrations of prey can be compensated by high nutritional values, as shown in Fig. 4.

Fig. 4 also shows that to a given functional response expressed in abundance (available prey and consumed prey) corresponds an infinity of functional responses in biomass located in an envelope that is generated by all the possible nutritional states of prey. The same conclusion could be drawn for a given functional response expressed in biomass, which can correspond to a variety of functional responses expressed in terms of prey abundances, according to the nutritional quality of the prey (up to a tenfold increase or decrease in the present example).

Furthermore, the shape of the functional response expressed in biomass (here type 2, Fig. 4b) is identical to that of the functional response expressed in abundances (Fig. 4a) because a constant quota of carbon has been consided for each simulation. When the prey quota varies in addition to abundance (which is a realistic situation), the shape of the functional response expressed...
in biomass can be of any other type because the values of ingestion rate may fall anywhere between the two envelopes. All this suggests that a full characterization of the functional response requires the experimental determination of two functional responses: one expressed in terms of individual abundances and the other in terms of biomass.

In the NW Mediterranean, the average copepod abundance range is generally below 10 ind. l\(^{-1}\), more often in the range 1-2 ind. l\(^{-1}\) in the open sea (e.g. Nowaczyk et al., 2011; Donoso et al., 2017 both using 120 µm mesh size nets), with generally higher values on shelves and coastal zones (Espinasse et al., 2014, 2017). In this range of prey abundance, ML functional response is almost linear (type I), varying from 0 to 1 ind. ind\(^{-1}\). h\(^{-1}\) and from 0 to 0.6 molC. ind\(^{-1}\). h\(^{-1}\) (Fig. 4b). This suggests that ML generally starves in the NW Mediterranean Sea due to low food concentrations in oceanic waters. However, ML ingestion rate increases rapidly in the food range 10-50 ind. l\(^{-1}\).

This could explain ML’s establishment in more productive Mediterranean littoral regions and coastal lagoons (Fuentes et al. 2010; Delpy et al, 2016, Shiganova et al, 2014, Pitois & Shiganova, CIESM, 2015). In the first part of the curve (Fig. 4), the functional response slope is steep, and therefore predation on copepods is very strong relative to their abundance: the percentage of ingested copepods per hour correspond to 10% of the population when the abundance of copepods is low, while this percentage drops to 1.7% when the abundance of copepods is high. This may explain sudden switchovers (stiff dynamics) between populations of copepods and ML obtained at low copepod concentrations obtained in experiments TS3-TS5 (Figs. 9-11).

**Impact of the prey quality on ML ingestion rate and ML dynamics**

Fig. 4c shows that for a given prey biomass (i.e. for different combinations of prey abundance times prey internal C quota), the richer the prey (i.e. the higher the internal quota), the higher the ingestion rate (in molC. ind\(^{-1}\). h\(^{-1}\)) is. This suggests that ML feeding highly depends on the quality of the encountered prey. As a consequence, ML dynamics also depends on the nutritional quality of prey. An important result is that for a given fixed available prey biomass, ML abundance is maximum for the prey of richest nutritional values (see Fig. 7). In the TS2 scenario, we tested the ability of immature ML adults to reach the sexual maturity for different fixed food levels. We have found that for high level of copepods (5 ind. l\(^{-1}\) and more), ML juveniles take less than 1 week to reach their sexual maturity. The food level of 2.5 ind. l\(^{-1}\) is critical, since in this case and for lower food concentrations, ML never reach
sexual maturity. This is due to the predominance of biomass losses compared
to gains by predation. Therefore, according to these model results, it could be
supposed that, in ecosystems with low food conditions (i.e. below 5 ind.l$^{-1}$),
ML reproduction is very unlikely to occur. This result is also consistent with
experimental data showing that at natural prey densities below 4 copepods
per liter, ML is not satiated (Reeve et al., 1989).

The model considers two levels of ecological integration : individual and
population. For a given food level (in TS2 only prey abundance varies but
not their internal quota), surviving ML individuals reach the same internal
quota whatever the starvation duration (Fig.9a, c, e), and this quota value
depends on the food level. In the same way, for a given food level, the ML
population will reach the same abundance whatever the starvation duration
(reached beyond the time period presented in Fig.9). However, it can be seen
that the response to starvation occurs at different time scales depending on
the integration level : the stationary quota of ML individuals is reached by
survivors after a few weeks, while it takes several months or even years for the
ML population to “forget” the starvation period and recover its initial abun-
dance value. Finally, the period necessary to reach steady state conditions
will increase with the starvation duration.

Moreover, for short starvation periods (one week), ML individual and
population growths were barely affected by starvation in the case where food
recovery is sufficient (i.e. Z equal or higher than 5 ind.l$^{-1}$, see Fig.9a, c, e). The same phenomenon for short starvation periods have been observed in the
laboratory-controlled experiments performed by Jaspers et al. (2015). These
authors found that starved ML continue to reproduce for up to 12 days after
cessation of feeding, with high overall hatching success of 65–90%.

For longer periods of starvation, ML population abundance will be af-
affected. This impact is however likely overestimated by the model since, in
natural conditions, population response to long term starvation induces new
forms of resistance (latency stage, dormancy, etc) which will potentially limit
the population mortality.

Characteristics of ML dynamics impacting population blooms

TS3 scenarios at the scale of one year illustrate that, even under stable
environmental (i.e. light and temperature) conditions, depending on the star-
vation duration, the ML population will bloom or not in the current year (see
Fig.9). This is a supplementary source of irregularity in ML dynamics and
in the occurrence of ML outbreaks.

In the case of varying environmental conditions through the introduction
of light and temperature seasonal variations (TS4), model results showed that, the more the ML population drop is important, the longer the delay is before it restores (see Fig.10 and the following). The nature of this relationship between the minimum value reached by the abundance and the restoring time is worth understanding. As seen in Fig. 9e, near zero values of ML abundance can be interpreted as a total disappearance of ML with the linear scale. Only a logarithmic representation (Fig. 9d) offers a means to highlight differences between those different near zero ML abundances. These low concentrations of ML (below 0.1 ind.m$^{-3}$) are spread over several orders of magnitude (from $10^{-1}$ to $10^{-35}$ ind.m$^{-3}$). Although these very low abundances are all considered as an absence of ML for any observer, it turns out that they have a major impact on the timing of the reappearance of ML when food conditions become again favorable. In our tests TS4, TS5 and TS6, the duration between two ML ourbreaks can typically vary between 1 and 3 years (Fig.10d).

**Forcings impacting ML population growth**

In this work, three major conditions impacting ML dynamics through the predation pressure on copepods were studied: light irradiance, water temperature, nutrient availability. In the model, only water temperature directly impacts ML physiology, when all forcing conditions impact ML resources (lower trophic levels and/or copepod).

Regarding the effect of water temperature, the conclusions are not straightforward (Fig.10) and depend on the criteria selected for analysis. If the criterion is the number of ML bloom occurrences, it is higher in the VT-HT case (9 outbreaks in 10 years) than in the CT (8 outbreak events) and VT (6 outbreaks) cases. This means that an increase in the mean temperature may promote the occurrence of jellyfish outbreaks. Now, if we consider the integrated amounts of jellyfish produced over 10 years (Fig.10), the impact of temperature seems less clear since occurrences of jellyfish in the VT and CT simulations are rare but are compensated by higher amplitudes of the different peaks.

The impact of $NO_3 : PO_4$ ratio is noticeable at low $NO_3$ concentration since in the corresponding simulations, ML abundance decreases from the beginning of the simulation and for several years (Fig.11b). This long period with lower predation on copepods enables them to grow and reach an abundance level sufficient for the re-occurrence of an ML bloom. Depending on the levels of $NO_3$ and $PO_4$ concentrations, different numbers of blooms occurred: six outbreaks for HN-HNP case, six for the HN-LNP case, three
for the LN-LNP case and only one for the LN-HNP case. For the highest NO$_3$ concentration, the same number of outbreaks is simulated whatever the NO$_3$ : PO$_4$ ratio, while for the lowest NO$_3$ concentration, there are more outbreaks for the low NO$_3$ : PO$_4$ ratio (three outbreaks for LNP against only one for HNP). This could be explained by the fact that in the former case, copepods dynamics are quite similar for HNP and LNP cases (Fig.11a), while in the latter case major changes in the low trophic levels (not shown) significantly impact the dynamics of copepods and thereby that of ML.

Competitive implicit grazing pressure exerted on copepods by other organisms than ML, including small pelagic fishes, plays an important role in ML population dynamics: the lowest competitive predation pressure leads to the highest integrated ML population growth over the ten simulated years, and to the alternates of periods with ML disappearance followed by strong blooms over the simulated period. By contrast, for the highest competitive predation, ML abundance remains quite low and constant though with a slight tendency to increase during the ten-year simulation. In short, according to our model, the lowest grazing pressure on copepods (which could correspond to a situation of intensive fishing) produce the highest occurrence and intensity of ML blooms. By contrast, the highest grazing pressure (which could be found for low fishing activity), ML is always present but at very low concentrations.

Unlike for previous experiments (TS4 and TS5), ML accumulated abundances are clearly different in the three simulations of experiment TS6. This is due to the fact that the total pressure (ML + other organisms) exerted on copepods is approximately constant, and that an increase in one of these two pressures necessarily reduces the other pressure. Copepod grazing by ML is indeed higher when the pressure exerted by other organisms is lower, resulting in higher ML abundances. According to our simulations, the forcing with the greatest influence on ML dynamics is that of competitive grazing pressure on copepods (which could be a proxy of fishing pressure), since it significantly impacts not only the frequency of ML outbreaks, but the accumulated population growth of ML over 10 years.

Similar conclusions have been drawn by Gucu et al. (2002) using different sources of observations from the Black Sea. They conclude that overfishing plays a crucial role in the successful development of ML, by emptying the ecological niche occupied by small pelagic fishes, and allowing gelatinous competitors to re-inhabit. The zooplankton fish pathway was blocked by heavy fishing pressure in the 1980s in the Black Sea, so the flow of excess biological material was diverted, to a large extent, in favor of gelatinous organisms,
including ML. As a consequence, the fish compartments were remarkably reduced. Based on field data and the relevant literature in the Black Sea, Shiganova & Bulgakova (2000) also discussed the dramatic effect of ML on fish eggs and larvae, in terms of feeding and stocks. These authors indeed found noticeable changes in fish diet composition in absence of copepods. Moreover, when copepods were not found at all in fish stomachs, fish average length, weight, and fat content were lower, and mortality increased during winter.

**Observation period : short vs long-term observation periods**

In Fig. 10, during the first 3-4 years, the effects of the ratio of nutrients are barely perceptible in the cases high $NO_3$ cases (HN). These effects become significant after 4 years, not in terms of integrated quantities over the long term, but in terms of short-term amounts and number of bloom events. Shorter simulations could lead us to the conclusion that the $NO_3 : PO_4$ ratio has no impact on the food web structure at high $NO_3$, while here it highlights the fact that the impact of this ratio is significant at medium- and long-term only (for example, there is a peak in ML abundance for the low $NO_3 : PO_4$ ratio (LNP) in the 7th year, while there is none for the high $NO_3 : PO_4$ ratio (HNP). This example (and others in this study) shows that long-term simulations are required to study and understand ML population dynamics and successions. This study suggests that the same long-term acquisition is required for in situ observations, and that the frequency of observations should not exceed one month since bloom durations do not last more than 2-3 months, as suggested both by in situ observations and our model simulations (Shiganova et al., 2011, Boero et al., 2013, Lukas et al., 2011, Purcell et al., 2001). Moreover, it is not only the frequency of occurrence of jellyfish which needs to be observed, but also the amplitude of these occurrences since, according to this study, the amplitude seems to partly condition the time of the occurrence of the next bloom.

**Model properties and results compared to previous modelling studies**

The model presented in this study differs from previous Mnemiopsis models in many aspects: (i) Mnemiopsis population is simply represented through a single variable; (ii) it is an enhanced flexible-stoichiometry model, since organisms are also represented through individual abundances in addition to their representation through C, N and P concentrations. As a consequence, internal quotas can be calculated, thereby providing a proxy of mean individual weight for ML and other populations; (iii) a two-way
coupling has been developed with the lower trophic levels from bacteria to mesozooplankton (copepods).

Though our model does not include a detailed stage-structured representation of ML as in Salihoglu et al., (2011) or Shiganova et al. (2018) for example, it has proved to provide a realistic description of the main individual and population properties (SGR, abundances, SPGR, etc.) and to restitute to a certain extent the development of cohort and the rapid population outbreaks or long-duration disappearance. Moreover, our model allows representation of the dynamics of Mnemiopsis population from seasonal to decanal scales in a variable trophic environment. Most of the parameters for ingestion and metabolic processes are taken from Salihoglu et al. (2011), which itself extensively used information from historical references on Mnemiopsis data and modeling (Kremer, 1976, Kremer & Reeve, 1989). However, the new feature of our model is that it represents the predator-prey functional responses on the basis of densities and not biomass. Thanks to this model capacity, it has been shown, as far as we know for the first time, that for a given prey biomass, ML population growth will be higher with a lower number of C-rich prey than for a higher number of C-poor prey.

Some previous modelling studies have been undertaken in a 3D configuration, combining a lagrangian transport of Mnemiopsis at regional scale with food and temperature conditions, forcing a detailed DEB model (van der Molen et al., 2015; David et al., 2015). These simulations at regional and seasonal scales are interesting, as they highlight the capability of ML to maintain low population through winter due to low temperature tolerance and starvation. However, such detailed structured population models are not suitable (accounting for computational costs) to explore the long-term dynamics along with the interactions with lower trophic levels through a two-way coupling with LTL. Even if the results are not shown in the present paper, the present model has already been run in a 3D regional context in versions including (Alekseenko et al., pers. comm.) or not (Alekseenko et al., 2014; Guyennon et al., 2015) the ML compartment.

6. Conclusions

In the present work, Mnemiopsis leidyi (ML) have been added in the trophic web described by the biogeochemical model Eco3M-MED. With this model, we investigated, through different numerical experiments and scenarios, the impact of starvation, food availability and quality, temperature,
nutrient availability and ratios and competitive pressure on ML physiology and population growth. After a thorough study of the model properties at the individual and population levels, different scenarios of climate change have been simulated in order to analyze inter-annual variability of this species and the role of environmental parameters impacting these variations.

Though academic, the simulated scenarios are indeed helpful in understanding the role of ML physiology and external factors on ML dynamics, and in drawing some hypotheses concerning the environmental windows leading to ML establishment and outbreaks in the natural environments, especially along the coasts of the Mediterranean Sea.

Our results firstly show that the required food conditions for ML outbursts, which involves a combination of food quality and quantity, should mainly be found in the most productive Mediterranean coastal areas and more rarely in the open sea, and that variations in food concentration may induce rapid outburst or collapse of ML populations. Results also indicate that food concentration directly impact reproduction, and that for a given fixed available prey biomass, ML abundance is maximum for the prey with the richest nutritional value.

As our model considers two levels of ecological integration, individual and population, it has been shown that the response to starvation or to recovery from starvation after food replenishment occurs at different time scales, depending on the integration level: individuals react immediately to food replenishment, whereas the population’s response depends on the demographic structure, mainly the presence of mature adults.

Different global change scenarios have been run in order to analyze inter-annual variability in ML population dynamics (i.e. mainly the intensity and frequency of ML outbreaks), and to identify how key environmental parameters impact this variability. When varying some environmental factors (temperature, food availability and quality issued from different nutrient ratios, and competitive pressure on ML’s food), ML population dynamics turns out to be rather chaotic, with the strongest ML blooms followed by the deepest population drops. The intensity of the ML population drops during starvation periods determines the time lapse before the reappearance of ML when food conditions become favorable again. This could explain the absence of ML during several years in the natural environment. These simulations also highlight that (i) an increase in the mean temperature promotes the occurrence of jellyfish outbreaks, (ii) through its effect on prey quality, the nutrient ratio at the basis of the primary production modifies the outbreaks frequency, mainly
at low nitrate concentrations, and (iii) changes in top-down pressure on ML prey (implicitly representing changes in fishing pressure) impact not only the frequency of the outbreaks, but also the accumulated population growth of ML over a ten-year period, and seems to be the forcing most influencing ML dynamics. Since the conclusions of this work (mainly those relative to ML development in rich coastal areas, to the low frequency and non-periodicity of presence-absence cycles, etc.) were derived from an academic study using a 0D model, it would be worth checking whether these results would be confirmed in a three-dimensional model accounting for the presence of physical forcings generating spacial patchy prey and predator distributions as well as temporal variations at different scales (day, season, inter-annual, multi-decade, etc.).

In addition to these results, this work gives rise to two recommendations: (i) since, according to the nutritional states of prey, a given functional response expressed in abundance corresponds to an infinity of functional responses in biomass, and conversely, a full characterization of the functional response for modelers would require the experimental determination of the functional response in two units: individual abundances and biomass, (ii) due to the low frequency of the ML presence-absence fluctuations, our simulations call for long-term (over at least a ten-year periods) observations with a temporal resolution of one month or less.

Acknowledgements

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References


The MerMex Group: Durrieu deMadron X., Guieu C., Sempéré R., Connan P., Cossa D., D’Ortenzio F., Estournel C., Gazeau F., Rabouille C.,


Table 1: Model symbols and parameters for ML. Parameter values have been taken or estimated from measured data from Salihoglou et al., 2011[1], 2013[2]; Kylie et al., 2009[3], Madsen & Riisgard, 2010[4]; Lucas et al., 2011[5].

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Units</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>ML</td>
<td>ML abundance</td>
<td>ind.l</td>
<td>1.5</td>
<td>[2]</td>
</tr>
<tr>
<td>$\bar{\mu}$</td>
<td>maximum specific growth rate</td>
<td>s$^{-1}$</td>
<td>4.62 $10^{-6}$</td>
<td>[2]</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>proportion of the minimum internal quota in immature adult (see Section 3.2)</td>
<td></td>
<td>0.85</td>
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<tr>
<td>$Q_{\text{max}}$</td>
<td>maximum carbon content</td>
<td>mol.ind$^{-1}$</td>
<td>2.58 $10^{-4}$</td>
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<tr>
<td>$Q_{\text{mean}}$</td>
<td>mean carbon content</td>
<td>mol.ind$^{-1}$</td>
<td></td>
<td></td>
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<tr>
<td>$Q_{\text{min}}$</td>
<td>minimum carbon content</td>
<td>mol.ind$^{-1}$</td>
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<td></td>
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<tr>
<td>$Q_{\text{maxC}}$</td>
<td>maximum nitrogen content</td>
<td>mol.ind$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Q_{\text{meanN}}$</td>
<td>mean nitrogen content</td>
<td>mol.ind$^{-1}$</td>
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<td></td>
</tr>
<tr>
<td>$Q_{\text{minN}}$</td>
<td>minimum nitrogen content</td>
<td>mol.ind$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Q_{\text{maxP}}$</td>
<td>maximum phosphate content</td>
<td>mol.ind$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Q_{\text{meanP}}$</td>
<td>mean phosphate content</td>
<td>mol.ind$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Q_{\text{minP}}$</td>
<td>minimum phosphate content</td>
<td>mol.ind$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Q_{\text{meanCN}}$</td>
<td>mean C :N ratio in ML</td>
<td>mol.mol$^{-1}$</td>
<td>4.13</td>
<td>[3, 5]</td>
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<td>$Q_{\text{minCN}}$</td>
<td>minimum C :N ratio in ML</td>
<td>mol.mol$^{-1}$</td>
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<td>$Q_{\text{maxCN}}$</td>
<td>maximum C :N ratio in ML</td>
<td>mol.mol$^{-1}$</td>
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<td>$Q_{\text{meanCP}}$</td>
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<tr>
<td>$Q_{\text{maxCP}}$</td>
<td>maximum C :P ratio in ML</td>
<td>mol.mol$^{-1}$</td>
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<td></td>
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**Feeding**

<table>
<thead>
<tr>
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<th>Unit</th>
</tr>
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<tbody>
<tr>
<td>$F$</td>
<td>clearance rate (prey1)</td>
<td>ind.l$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>$I_{\text{max}}$</td>
<td>max. ingestion rate (prey1)</td>
<td>ind.ind$^{-1}$ s$^{-1}$</td>
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<tr>
<td>$\alpha_1$</td>
<td>proportion of Z ingested by ML juveniles</td>
<td>0.8</td>
</tr>
<tr>
<td>$\alpha_2$</td>
<td>proportion of CIL ingested by ML juveniles</td>
<td>0.2</td>
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**Mortality**

<table>
<thead>
<tr>
<th>Symbol</th>
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<th>Unit</th>
</tr>
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<tbody>
<tr>
<td>$k_{\text{m}}$</td>
<td>specific natural mortality rate</td>
<td>s$^{-1}$</td>
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<tr>
<td>$A$</td>
<td>constant in mortality function</td>
<td></td>
</tr>
<tr>
<td>$k_{\text{mq}}$</td>
<td>specific quadratic mortality rate</td>
<td>l.ind$^{-1}$ s$^{-1}$</td>
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</table>

**Respiration and excretion**

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<th>Definition</th>
<th>Unit</th>
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<tr>
<td>$r_{\text{res}}$</td>
<td>respiration-excretion rate</td>
<td>s$^{-1}$</td>
</tr>
<tr>
<td>$r_{\text{i}}$</td>
<td>respiration rate for ingestion demands</td>
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Table 2: List of functions used to describe ML physiology in the model.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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<td>$f^\mu$</td>
<td>Specific growth rate</td>
<td>s$^{-1}$</td>
</tr>
<tr>
<td>$f^{\text{fe}}$</td>
<td>Specific feeding rate of Z by ML</td>
<td>s$^{-1}$</td>
</tr>
<tr>
<td>$f^{\text{fjuv}}$</td>
<td>Specific feeding rate during juvenile stages</td>
<td>s$^{-1}$</td>
</tr>
<tr>
<td>$f^m$</td>
<td>Specific natural mortality rate</td>
<td>s$^{-1}$</td>
</tr>
<tr>
<td>$f^{\text{mq}}$</td>
<td>Specific quadratic mortality rate (implicit feeding)</td>
<td>l.ind$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>$f^{\text{res}}$</td>
<td>Specific respiration rate</td>
<td>s$^{-1}$</td>
</tr>
<tr>
<td>$f_X$</td>
<td>Specific excretion rate</td>
<td>s$^{-1}$</td>
</tr>
<tr>
<td>$kQ_X$</td>
<td>Quota function for element X among C, N and P</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 2: In grey – conceptual scheme of the biogeochemical model for the NW Mediterranean Sea (Eco3M-MED, Alekseenko et al. 2014) implemented in the Eco3M tool; in red - additional variables and processes: namely one functional group of carnivorous gelatinous plankton and associated processes, and two new variables expressing N and P contents in mesozooplankton.

Table 3: Forcings taken into account in the modelling scenarios. *calc - means dynamically calculated by the biogeochemical model including the low trophic levels.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>day/night</th>
<th>seasonal</th>
<th>seasonal</th>
<th>copepod</th>
<th>batch (B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TS1</td>
<td>YES</td>
<td>NO</td>
<td>NO</td>
<td>fixed</td>
<td>B</td>
</tr>
<tr>
<td>TS2</td>
<td>YES</td>
<td>NO</td>
<td>NO</td>
<td>fixed</td>
<td>B</td>
</tr>
<tr>
<td>TS3</td>
<td>YES</td>
<td>NO</td>
<td>NO</td>
<td>fixed</td>
<td>B</td>
</tr>
<tr>
<td>TS4</td>
<td>YES</td>
<td>YES</td>
<td>YES</td>
<td>*calc</td>
<td>B</td>
</tr>
<tr>
<td>TS5</td>
<td>YES</td>
<td>YES</td>
<td>YES</td>
<td>calc</td>
<td>C</td>
</tr>
<tr>
<td>TS6</td>
<td>YES</td>
<td>YES</td>
<td>YES</td>
<td>calc</td>
<td>B</td>
</tr>
</tbody>
</table>
Figure 3: Physiological processes undertaken by ML and taken into account in the model.

Table 4: Test series TS2a. Synthesis of simulated experiments with final values of three indicators: $t_{rep}$, $F_IQ$ and SPGR. $t_{rep}$: time necessary to reach the adult stage mature for reproduction; $F_IQ$: mean ML carbon accumulation rate over $t_{rep}$; SPGR: specific population growth rate (in $h^{-1}$) between the 8th and the 12th week depending on the available copepod abundance ($Z$ in ind.l$^{-1}$) of 2.5, 5, 10, 25, 100 and 250 ind.l$^{-1}$ with copepod $Q_C$ equal to 50% and $Q_N = Q_P = 100%$.

<table>
<thead>
<tr>
<th>Copepod abundance (Z) with $Q_C = 50%$(ind.l$^{-1}$)</th>
<th>Copepod Carbon biomass (molC.l$^{-1}$)</th>
<th>$t_{rep}$ (h)</th>
<th>$F_IQ$ (molC.ind$^{-1}$h$^{-1}$)</th>
<th>SPGR (h$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.5</td>
<td>1.25 $10^{-6}$</td>
<td>-</td>
<td>-</td>
<td>$-4.77\ 10^{-4}$</td>
</tr>
<tr>
<td>5</td>
<td>2.5 $10^{-6}$</td>
<td>129</td>
<td>$1\ 10^{-7}$</td>
<td>0.0022</td>
</tr>
<tr>
<td>10</td>
<td>5 $10^{-6}$</td>
<td>47</td>
<td>$2.75\ 10^{-7}$</td>
<td>0.0105</td>
</tr>
<tr>
<td>25</td>
<td>1.25 $10^{-5}$</td>
<td>23</td>
<td>$5.61\ 10^{-7}$</td>
<td>0.0505</td>
</tr>
<tr>
<td>100</td>
<td>5 $10^{-5}$</td>
<td>14.4</td>
<td>$8.96\ 10^{-7}$</td>
<td>0.1431</td>
</tr>
<tr>
<td>250</td>
<td>1.25 $10^{-4}$</td>
<td>12.2</td>
<td>$1.06\ 10^{-6}$</td>
<td>0.1830</td>
</tr>
</tbody>
</table>
Figure 4: Test series TS1. Functional response for ML depending on the prey (i.e. copepod, Z) abundance and biomass. (a) Magenta crosses: values of simulated ingestion rate (in ind.ind\(^{-1}\).h\(^{-1}\)) at steady state for the 9 food level experiments (in ind.l\(^{-1}\)) for copepods with $\tilde{Q}_C$ equal to 50%. Dotted blue line corresponds to the theoretical functional response for ML predation (Eq.2). (b and c) Magenta crosses: values of ingestion rate (in molC.ind\(^{-1}\).h\(^{-1}\)) at steady state for the 9 food level experiments (in ind.l\(^{-1}\)) for copepod with $\tilde{Q}_C$ equals to 50%. Brown diamonds: values of ingestion rate (in molC.ind\(^{-1}\).h\(^{-1}\)) at steady state for the highest food level experiment (in ind.l\(^{-1}\)) for copepod with $\tilde{Q}_C$ equals to 0 and 100% (respectively lower and upper diamonds). Dotted lines: theoretical functional responses expressed in molC.ind\(^{-1}\).h\(^{-1}\) for different copepod $\tilde{Q}_C$ values. Dotted blue line: same as in (a) with copepod $\tilde{Q}_C$ equal to 50%, but with ingestion rate expressed in molC.ind\(^{-1}\).h\(^{-1}\). Dotted red lines: with copepod $\tilde{Q}_C$ equal to 0% (lower dotted red line) and to 100% (upper dotted red line). Grey vertical line represent three values of copepod abundance with three different internal Quotas of Carbon chosen in the TS2b test series.

Table 5: Test series TS3. Time delays between the recovery of ML individual feeding activity and the restart of ML population growth ($t_2 - t_1$) for the starvation/replenishment tests with food abundance at 10 ind.l\(^{-1}\) and 5 ind.l\(^{-1}\) presented in Fig.7.

<table>
<thead>
<tr>
<th>Feeding start $t_1$(weeks)</th>
<th>$t_2 - t_1$ (days) for two copepod levels</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$Z=5$ ind.l(^{-1})</td>
</tr>
<tr>
<td>4</td>
<td>17.8</td>
</tr>
<tr>
<td>6</td>
<td>19.3</td>
</tr>
<tr>
<td>8</td>
<td>21.1</td>
</tr>
<tr>
<td>12</td>
<td>22.5</td>
</tr>
</tbody>
</table>
Figure 5: Test series TS2a. Temporal dynamics of ML individual carbon relative $\bar{Q}_C$ (a and b) and ML population abundance (c and d) for different constant food levels. Simulation over 12 weeks (a and c) and zoom during the two first days (b and d). ML population starts with $1 \times 10^{-6}$ ind.$\cdot l^{-1}$ and with individual quotas $\bar{Q}_C = 50\%$ and $\bar{Q}_N = \bar{Q}_P = 100\%$; Levels of food abundances ($Z$) : 2.5 (light blue line), 5 (black line), 10 (magenta line), 25 (red line), 100 (blue dotted line) and 250 (blue line) ind.$\cdot l^{-1}$, with copepod $\bar{Q}_C$ equal to 50% and $\bar{Q}_N = \bar{Q}_P = 100\%$. T=15°C.

Figure 6: Test series TS2a. Synthesis of simulated experiments in constant food conditions : ML abundance (ind.$\cdot l^{-1}$) and $\bar{Q}_C$ (%) 12 weeks after the start of simulation depending on the available copepod abundance ($Z$ in ind.$\cdot l^{-1}$) of 2.5, 5, 10, 25, 100 and 250 ind.$\cdot l^{-1}$ with copepod $\bar{Q}_C$ equal to 50% and $\bar{Q}_N = \bar{Q}_P = 100\%$. T=15°C.
Figure 7: Test series TS2b. Temporal dynamics of ML individual carbon relative $\tilde{Q}_C$ and ML population abundance for constant copepod Carbon biomass conditions of $7.5 \times 10^{-5}$ molC.l$^{-1}$ depending on the available copepod quantity and quality (ind.l$^{-1}$) of 250 ind.l$^{-1}$ with $\tilde{Q}_C=0\%$ (red line), 150 ind.l$^{-1}$ with $\tilde{Q}_C=50\%$ (green line), and 107.14 ind.l$^{-1}$ with $\tilde{Q}_C=100\%$ (blue line). For ML and copepods we consider $\tilde{Q}_N=\tilde{Q}_P = 100\%$; $T=15^\circ$. 

Figure 8: Test series TS2c. Estimation of SGR (d$^{-1}$) values for mature ML (a) and immature ML (b) depending on the constant copepod abundance in different temperature conditions, at $Q_{10} = 1.5$; (c) SGR values for mature and immature ML at constant copepod abundance of 200 ind.l$^{-1}$ with $\tilde{Q}_C=100\%$ and at the temperature of $26^\circ$C depending on the choice of $Q_{10}$. Dotted lines show estimated trends for each experiment.
Figure 9: Test series TS3. Tests on starvation durations followed by food recovery at different food levels. Temporal dynamics of ML individual carbon relative $\tilde{Q}_C$ (left column) and ML population abundance (right column) for different food replenishment levels (a and b : $Z=10$ ind.$l^{-1}$, c and d : $Z=5$ ind.$l^{-1}$, e and f : $Z=2.5$ ind.$l^{-1}$) and for different starvation durations (blue line : 1 week, green line : 4 weeks, black line : 6 weeks, magenta line : 8 weeks and red line : 12 weeks). Copepod $\tilde{Q}_C$ equal to 50% and $\tilde{Q}_N = \tilde{Q}_P = 100\%$. T=$15^\circ$C. As an example, for the 12 weeks starvation experiment : $t_1$ corresponds to the starting date of food recovering and ML individual growth recovery and $t_2$ - to the ML reproduction starting date ($Q_C=0\%$).
Figure 10: Test series TS4. Temperature impact on: a) $Q_{10}$ variation, b) copepod abundance (Z in ind.l$^{-1}$), c) ML relative quota of carbon (%), d) ML abundance (ind.l$^{-1}$) in log scale and e) ML abundance: instantaneous and accumulated values (ind.l$^{-1}$). Black line - no temperature taken into account (CT case), blue line - $T_{\text{ref}}$ temperature taken into account in the physiology of ML (VT case), red line - $T_{\text{ref}} +2^\circ\text{C}$ temperature taken into account in the physiology of ML (VT-HT case).
Figure 11: Test series TS5. Nutrient ratio impact on a) copepod abundance (Z in ind. l⁻¹), b) ML abundance in log scale in ind. l⁻¹ and c) ML abundance: instantaneous and accumulated values (ind. l⁻¹). Blue line - NO₃=5 µM and NO₃ : PO₄=20 (HN-LNP case), black line - NO₃=5 µM and NO₃ : PO₄=40 (HN-HNP case), green line - NO₃=1.25 µM and NO₃ : PO₄=20 (LN-LNP case), red line - NO₃=1.25 µM and NO₃ : PO₄=40 (LN-HNP case).
Figure 12: Test series TS6. Impact of competitive pressure on ML prey: a) copepod abundance (Z in ind.l$^{-1}$), b) ML relative quota of carbon (%) and c) ML abundance in log scale in ind.l$^{-1}$ and d) ML abundance: instantaneous and accumulated values (ind.l$^{-1}$). Blue line - reference test with $f_Z^{mq} = \lambda \, s^{-1}$ (LFP case), green line - $f_Z^{mq} = 2\lambda \, s^{-1}$ (MFP case), red line - $f_Z^{mq} = 3\lambda \, s^{-1}$, where $\lambda = 3 \cdot 10^{-8} \, s^{-1}$ (HFP case).