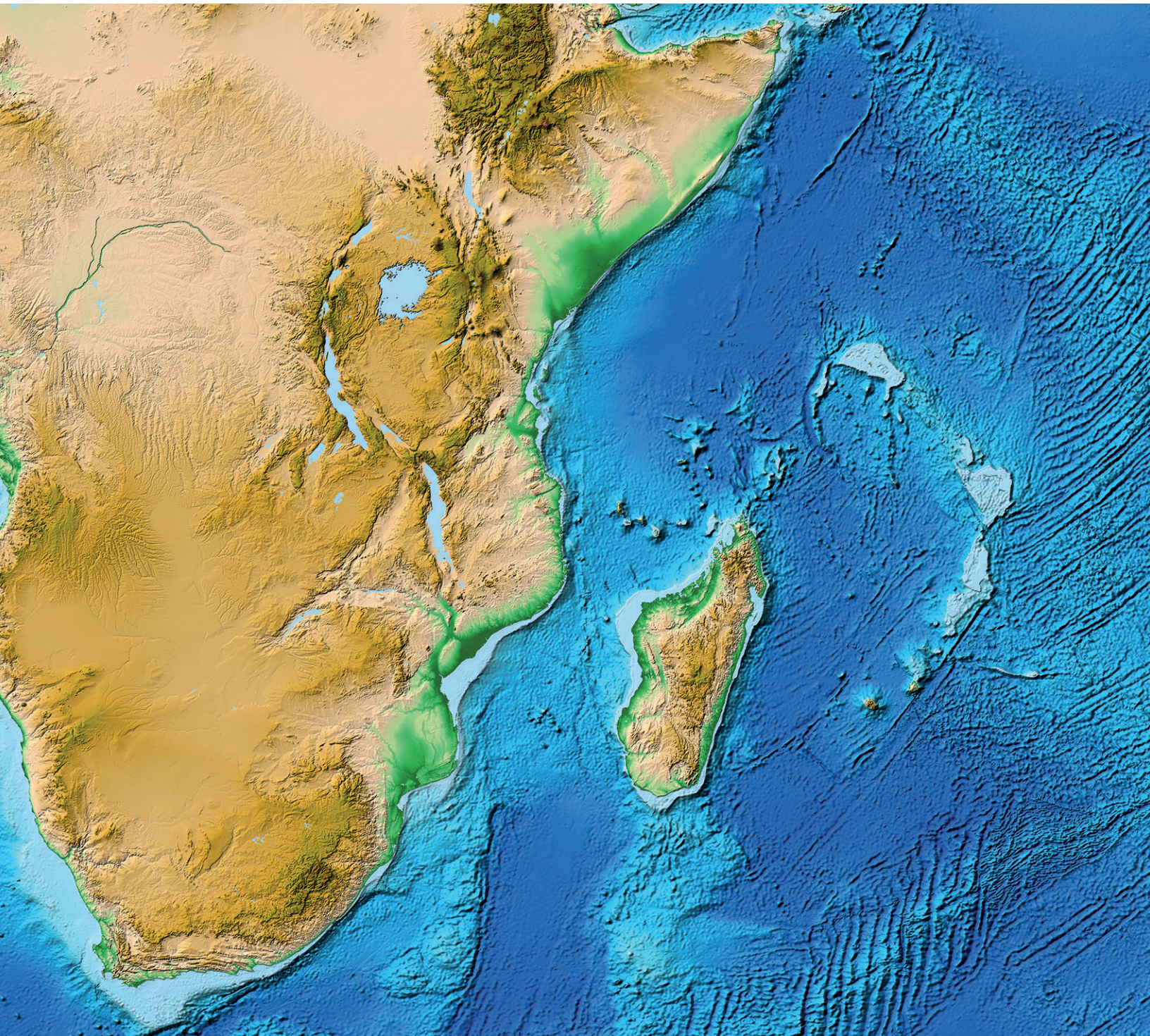
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Cover image: Relief model of the WIO surface that integrates land topography and ocean bathymetry. Amante and Eakins / National Geophysical Data Center, NOAA (2009)

Mechanisms of trophic partitioning within two fish communities associated with a tropical oceanic island

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Abstract

Understanding drivers of trophic partitioning at the community level is an essential prerequisite to the establishment of ecosystem-based management of fisheries. In this study, we identify drivers of trophic partitioning within a community of epipelagic fish and a community of deep-water fishes off Reunion Island. Effects of intrinsic (species identity, etc.) and environmental variables (fishing zone, month) on stomach content composition and stable isotope ratios were tested using regression trees and linear models respectively. Our results demonstrated firstly an independence of both communities, with very few common prey although they occurred in similar localities, and secondly, very different patterns of resources partitioning among each community. The community of epipelagic fish segregated into three trophic guilds composed of species foraging on a limited range of prey. This observation is not consistent with the general view that these high trophic level species are opportunistic and generalist. The habitat seems to be the main driver of deep-water fishes feeding partitioning, which is in accordance with the sound-scattering layer interception hypothesis. Deep-water fishes would distribute in the water column at different depths and all species would feed on the same resources at each depth. The results of this study suggest that fisheries management should be very different for epipelagic (more species-centred) and deep-water fish (more habitat-centred).

Keywords Trophic partitioning, Deep-sea, Epipelagic, Predator, Stable isotopes, Stomach contents

Introduction

In the context of increasing demand for marine-derived food (Msangi *et al.*, 2013), fisheries have extended both down the marine food web (decrease in the mean trophic level – TL – of catches of 0.1 TL.decade^{-1}; Pauly *et al.*, 1998) and into the depths (increase in the mean depth of fishing of 62.5 m.decade^{-1}; Watson and Morato, 2013). This rapid development of fisheries led to drastic declines of numerous fish stocks, with 58% of known stocks being overfished or already collapsed (Froese *et al.*, 2012). Moreover, fisheries can extend their effects beyond targeted species by affecting habitats or non-target species, and fish communities, thereby changing the structure and function of ecosystems (Jackson *et al.*, 2001; Hsieh *et al.*, 2006; Myers *et al.*, 2007). In order to understand the impacts of fisheries on ecosystems, it is nowadays acknowledged that the implementation of model-based ecosystem fisheries management is necessary (Garcia *et al.*, 2003; Pikitch *et al.*, 2004; Cury *et al.*, 2008). Such models are useful to evaluate and predict the impacts of resource overexploitation and climate change on ecosystems and to propose measures to make fisheries more sustainable.

Prior to the development of such models, information on biological interactions, energy transfer, consumption and production at the different trophic levels is required (Pauly *et al.*, 2002; Christensen and Walters, 2004), but such information is usually lacking. In particular, the influence of biotic and abiotic parameters on trophic habits still requires clarification. Predator species, ontogeny and distance to shore have been demonstrated to have significant influence

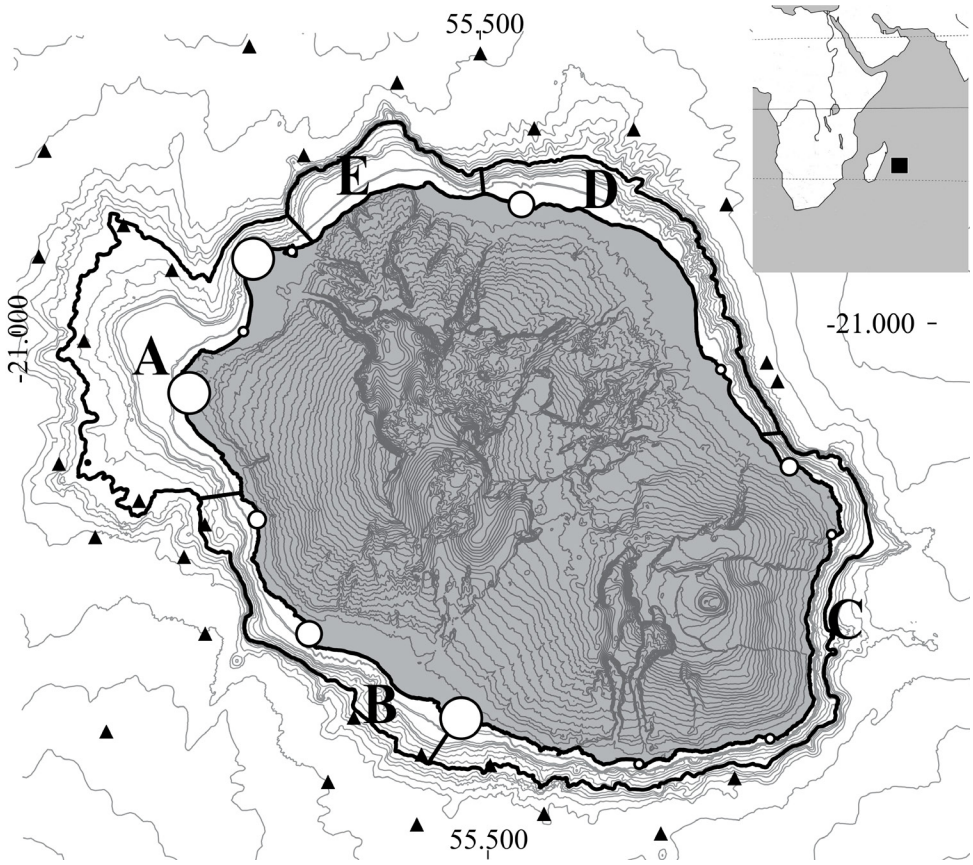


Figure 1. Map of Reunion Island representing deep-water fish fishing zones in bold letters, limited by the 600 m isobath, and anchored fishing aggregating devices in black triangles. White circles represent harbours with size proportional to the number of fishermen, from 2 (smallest circles) to 42 (largest circles).

on predator diet and community structure (Haight, 1993; Lowe *et al*., 1996; Jaquemet *et al*., 2011, Allain *et al*., 2012). Nevertheless, some regional or temporal diet variations suggest various degrees of dietary specialisation according to parameters that remain undetermined for many species, including both oceanic (eg *Coryphaena hippurus* and *Thunnus albacares*; Buckley and Miller, 1994; Taquet, 2004; Graham *et al*., 2007; Tripp-Valdez *et al*., 2010) and deep-water predators (eg *Beryx decadactylus* and *Etelis coruscans*; Haight, 1993; Dürr and González, 2002; Trystram *et al*., in revision).

The present study aims to investigate the drivers of diet variability in communities of predatory fish. For this purpose, we analysed the trophic ecology of several species in two exploited communities of fish around Reunion Island. This small volcanic island located in the Western Indian Ocean has a limited island shelf that naturally enhances the connectivity between coastal, oceanic and deep-sea ecosystems. In recent years a significant decrease in the landings of both epipelagic and deep-water predatory fishes exploited by the local artisanal fisheries was reported (Fleury *et al*., 2012; Guyomard *et al*., 2012; Le Manach *et al*., 2015). Although they are economically important for the artisanal fishing sector, knowledge of the ecology of these fish species remains very limited. Jaquemet *et al*. (2011) showed that yellowfin (*Thunnus albacares*) and skipjack (*Katsuwanus pelamis*) tuna feed upon diverse assemblages of coastal fish and crustacean larvae and juveniles off Reunion Island around anchored fish aggregating devices,. The trophic habits of eight deep-water species were very recently described around Reunion Island and recorded a surprising diversity of dietary patterns among species (Trystram *et al*., in revision). The factors driving these diet variations among deep-water fishes remain unclear, while individual length within each species appeared to affect dietary pattern, as both $\delta^{13}C$ and $\delta^{15}N$ increased with length (Trystram *et al*., in revision).

The present study investigated the effects of multiple exploratory variables (depth, fishing zone and month, species, length, sex and maturity) on stomach content composition and stable isotope ratios of the

two communities. Carbon and nitrogen stable isotope ratios measured in fish muscle give long-term information on the organic matter sources they depend upon, and their trophic level, respectively (Peterson and Fry, 1987).

Materials and Methods

Sampling

Study area

The study was conducted off Reunion Island, a small (60 km diameter) oceanic island of volcanic origin, situated in the southwestern Indian Ocean (Fig. 1). The mountainous central part of the island (3070 m maximum) creates a clear distinction between the wet windward east coast and the dry leeward west coast, where a small discontinuous fringing coral reef has developed. The island's volcanic cone topography results in steep slopes of up to 60° and a limited shallow island shelf (maximum 5 km wide) that leads to offshore ecosystems directly adjacent to coastal ecosystems. As such, physico-chemical gradients in the vicinity of the island are strong and most likely represent major structuring factors for ecological communities.

Biological models

The study focused on eight deep-water and eight epipelagic fish species. Deep-water species were sampled during a directed stock assessment effort, whereas six of the eight epipelagic species were caught by local fishermen in the vicinity of anchored fishing aggregative devices (aFAD), and two coastal shark species were caught during culling programmes coordinated by local authorities to control species involved in shark attacks along the shore. The deep-water species considered were the red bream (*Beryx decadactylus*), the oblique-banded grouper (*Epinephelus radiatus*), the deep-sea red snapper (*Etelis carbunculus*), the deep-sea long-tail red snapper (*E. coruscans*), the brilliant pomfret (*Eumegistus illustris*), the ornate jobfish (*Pristipomoides argyrogrammicus*), the goldbanded jobfish (*P. multidens*) and the shortnose spurdog (*Squalus megalops*), which represented 64% of the 2680 fishes collected during the sampling effort. Epipelagic species considered were the yellowfin tuna (*Thunnus albacares*), the skipjack tuna (*Katsuwonus pelamis*), the dolphinfish (*Coryphaena hippurus*), the wahoo (*Acanthocybium solandri*), the great barracuda (*Sphyraena barracuda*), and the giant trevally (*Caranx ignobilis*), which constitute ~90% of the artisanal fishery landings in Reunion (SIH, 2013). Tiger shark (*Galeocerdo cuvier*) and bull shark (*Carcharhinus leucas*) have not been targeted by artisanal fishermen for over 15 years (Le Manach *et al*., 2015) therefore samples were collected during specific culling programmes.

Sample collection

Epipelagic fishes were sampled between January 2012 and December 2014 off the west coast, whereas deep-water fishes were sampled all around the island between April and December 2014 at depth ranging from 100 m to 600 m. Each fresh fish was weighed and measured (total length) on board. Deep-water fishes were kept whole in a coolbox and then stored at -20°C in the laboratory. In the laboratory, each fish was dissected to collect the gut contents and to sample dorsal white muscle for stable isotopes analysis. In addition, the sex and sexual maturity of deep-water fishes were determined. The maturity was determined based on gonad dissection and translated into a qualitative variable with six stages (from 0 - juveniles, to 5 - spawning adult). Epipelagic fishes were gutted on board by the fishermen. Their stomachs were stored in coolboxes in labelled plastic bags and a sample of white dorsal muscle was collected for the stable isotopes ratio measurements. All samples were then stored in the laboratory at -20°C until further analysis. Finally, sharks were dissected in a cold room, the stomach contents and a sample of dorsal muscle were kept and stored at -20°C in the laboratory.

Laboratory processing

Prey identification

Stomach content samples were thawed and weighed in the laboratory. Prey items found were counted, weighted to an accuracy of 0.01 g and identified to the lowest possible taxonomic level using identification keys adapted to taxonomic groups and/or to anatomical parts (cephalopod beaks, teleosts, otoliths, etc) (Clarke, 1986; Smith and Heemstra, 1986; Smale *et al*., 1995) and then compared to Reunion species lists (Letourneur *et al*., 2004; Durville *et al*., 2009; Poupin, 2009) and to our own collection. Given the difficulties with identifying digested prey items, they were pooled into functional groups for some of the analyses (Table S1). Prey importance found in the stomach was expressed as the relative numerical abundance.

Stable isotope measurement

Frozen white dorsal muscle samples were freeze-dried at <0.5 mBar and <-40 °C for 48h using a Labconco freeze-drier coupled with a Vacuubrand 2.5 pump, then ground into a fine and homogeneous powder using an automated Retsch MM301 grinder.

Table 1. Description of observed and exploratory variables used in this study.

	Specificity	Name	Description	Unity	Type
Observed variables	All species	$\delta^{13}C$	Chemical tracer of organic matter sources	‰	quantitative
		$\delta^{15}N$	Chemical proxy of trophic level	‰	quantitative
		Stomach composition	Identity of each single prey	Ecological functioning group	qualitative
Exploratory variables	All species	Species	Identity of each predator	Species (16 modalities)	qualitative
		TL	Total length	cm	quantitative
		Month	Sampling month	Month (12 modalities)	qualitative
		Zone	Sampling zone		qualitative
	Deep-water	Depth	Sampling depth	m	quantitative
		Sex	Gender of predatory fishes	3 modalities (male, female, immature)	qualitative
		Maturity	Reproductive stage, from immature to spawning adult	6 modalities	qualitative
	Epipelagic	DistShore	Sampling distance from shore	m	quantitative

Low fish C/N ratio (<3.5, Table S2) suggested low lipid content, which reduces the need to perform lipid extraction or analytical corrections (Post *et al*., 2007). For tropical tuna, Sardenne *et al*. (2015) showed that the white muscle was low in lipids and consequently no lipid extraction was necessary. We assumed that the same was true for other large epipelagic species. For the deep-water shark *S. megalops*, which are enriched in urea, De Lecea and De Charmoy (2015) showed that chemical treatments did not modify muscle isotopic ratios, and that treatment was not required for this species. Prior to stable isotope measurements, all samples were weighed (0.5 mg) and packed into tin capsules in duplicate. Isotopic composition and %C and %N content were measured at the National Stable Isotope Laboratory, GNS Science, Lower Hutt, New Zealand, the IsoEnvironmental, Rhodes University, Grahamstown, South-Africa, or at the Stable Isotope Facility, LIENSs laboratory, La Rochelle, France, using an isotope ratio mass spectrometer, interfaced to an elemental analyser in continuous-flow mode (EA-IRMS). Standard reference materials were used to ensure accuracy and precision between laboratories. Results were expressed in conventional delta notation (δ), defined as parts per thousand (‰), according to Peterson and Fry (1987).

Factors driving diet composition

The potential effects of explanatory variables (described in Table 1) on prey composition (expressed in term of functional group, Table S1) in predator diet were investigated using the classification and regression tree (CART) approach (Breiman *et al*., 1984). This non-parametric method uses a partitioning algorithm to estimate a series of binary decision rules that divide the data into smaller homogeneous subgroups in an optimal way. All data are represented by a single node at the top of the tree. The tree is then built by repeatedly splitting the data. Each split is defined by a simple rule based on a single explanatory variable. Splits are chosen to maximize the homogeneity of the resulting two nodes. However, the splitting procedure grows an overlarge tree with a very low predictive power. To keep the tree reasonably small (i.e. keep the predictive power high), a prune back procedure is applied. Following Kuhnert *et al*. (2012), we predicted the composition of prey (expressed in term of functional group) consumed by the predators, given the explanatory variables. Unidentified prey were not taken into account in the analysis. Analyses were conducted using the 'rpart' package of the statistical open source R software.

Trophic structure of the communities

Epipelagic and deep-water community-wide aspects of the trophic structure were compared using Layman's metrics (Layman *et al*., 2007) based on carbon and nitrogen stable isotope ratios, and calculated using each species isotopic averages as measurement units.

The degree of trophic level diversity and basal resource diversity of the food web were assessed with the $\delta^{15}N$ (NR) and $\delta^{13}C$ (CR) range of values respectively. The isotopic niche occupied by each community was represented by the area of the smallest convex hull (TA) including all species of each community in the isotopic space ($\delta^{13}C$-$\delta^{15}N$ bi-plot). The mean distance to centroid (CD), calculated as the mean Euclidian distance between each species isotopic values and the mean $\delta^{15}N$ and $\delta^{13}C$ values of the community, was used as a proxy for the global degree of trophic diversity. Mean nearest neighbour distance (MNND) and its standard deviation (SDNND) among all species pairs are measures of species packing and its evenness within a trophic niche. Small MNND express a high trophic redundancy among species comprising each community.

Factors driving the isotopic composition of white muscle

The potential effects of explanatory variables on $\delta^{13}C$ and $\delta^{15}N$ (Table 1) were investigated using linear models followed by ANOVA. This procedure allowed the identification of explanatory variables that significantly affect $\delta^{13}C$ and $\delta^{15}N$ ratios. For these variables univariate procedures were used to explore the direction and amplitude of each effect.

Data were first tested for normality and homoscedasticity using a Jarque-Bera test (Thadewald and Bünin, 2007) and a Levene test, respectively. For qualitative variables statistical differences between two modalities were tested using either a Student t test or a Mann-Whitney U test, depending on the normality and homoscedasticity of the data. Statistical differences between more than two modalities were tested using a one-way variance analysis (ANOVA) test (followed by Tukey's multiple comparison), or a Kruskal-Wallis H test, followed by multiple pairwise comparison using the kruskalmc procedure, depending on the normality and homoscedasticity. Monotonic direction (increasing or decreasing) and amplitude effects of quantitative variables on stable isotopic ratios were tested using either the Pearson or Spearman ρ correlation test, depending on the normality and homoscedasticity of variables.

Statistical significance was established at 5% for all statistical tests. All statistics were performed using R.

Results

Factors driving diet composition

The classification tree applied to diet composition expressed in terms of prey functional groups presented very different pictures for deep-water and epipelagic fish (Fig. 2). Indeed, among all exploratory variables, depth, location (zone), and fish species, had a significant influence on the diet of deep-water fish only when the identity of the predator allowed separating the epipelagic community into 3 homogeneous groups (Fig. 2).

T. albacares and *K. pelamis* fed mostly on Stomotopoda (28%), Brachyoura (megalopa stage, 21%) and squid (21%), while *A. solandri* and *C. hippurus* fed on the juvenile stage of reef-associated species (46%), and the four other species (*G. cuvier, C. leucas, C. ignobilis* and *S. barracuda*) fed on demersal coastal fish (29%) and squid (20%, Fig. 2). For these species no effect of month, fishing zone, distance from shore, and predator length was detected on diet composition. This result suggests that epipelagic predators partitioned available prey between groups of specialised species, while their feeding habits appeared homogeneous within each species.

On the other hand, CART analysis emphasized the importance of predator species, depth and fishing area, on deep-water fish trophic habits, segregating the studied species in four groups. This analysis predicted a high dietary overlap between *B. decadactylus* and *E. radiatus* (feeding chiefly on Caridea, which composed 77% of their prey) on the one hand, and between the six remaining species on the other hand (Fig. 2). Only the fishing depth and area allowed prediction of the dietary habits of *S. megalops, E. illustris, E. carbunculus, E. coruscans, P. multidens* and *P. argyrogrammicus*. Thus, all predators present in a given area and at a given depth would consume the same prey, irrespective of the predator species. Above 345 m depth, all predators fed on shrimps (42%) all around Reunion Island, whereas there was a distinction between the East and West coasts in the feeding habits of predators caught below 345 m depth. Below 345m on the East coast, all predators seem to rely mainly on mesopelagic prey (lantern fish – Mytophiliformes, 64%), whereas on the West coast, they fed on a mix of Caridea (36%) and mesopelagic prey (30%). The month, fish length, sex and maturity had no significant effect on the deep-water fish diet composition.

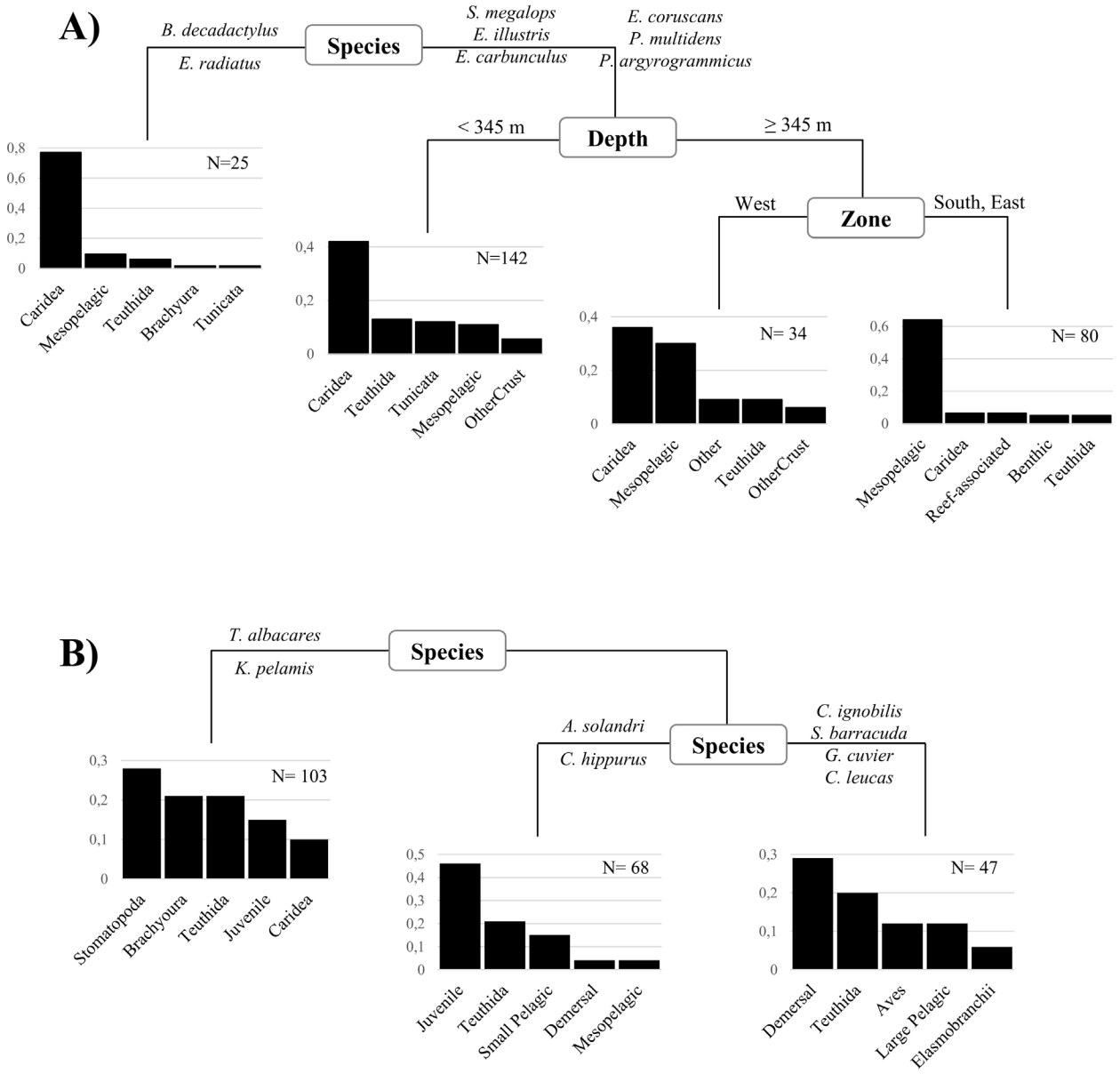


Figure 2. Pruned regression tree predicting diet composition of A) eight deep-water predators and B) eight epipelagic predators. The exploratory variables are represented in Table 1.

Structure of the community of deep-water and epipelagic fish

Stable isotope based metrics of trophic structure were very similar between demersal and epipelagic fish communities (Table 2). Both communities exhibited similar degrees of trophic level diversity, basal resource diversity and isotopic niche (assessed by NR, CR and TA respectively Table 2, Fig. 3). Their global degree of trophic diversity and species packing were not statistically different (assessed by CD and MNND respectively, Table 2). However, the epipelagic fish community exhibited a significantly lower species packing evenness (SDNND = 0.08) than the deep-water fish community (SDNND = 0.29, Fisher test: F^{7}_{7} =10,304, p=0.006) (Table 2). To sum up, the two communities presented similar isotopic niches but a different species distribution within each niche, with epipelagic species being more evenly distributed than deep-water species (Fig. 3).

Factors driving the isotopic composition of the species

While the models analysing the variance of the stable isotope ratios in fish were statistically significant for both communities (all models $p < 0.001$), it explained more of the variance for deep-water fish (explaining 74% of $\delta^{13}C$ variability and 70% of $\delta^{15}N$ variability,

Table 3) than for epipelagic fish (explaining 34% of $\delta^{13}C$ variability and 25% of $\delta^{15}N$ variability, Table 4). Among the five considered variables only species identity significantly affects the isotopic ratios for the epipelagic fishes (Table 4), while six and seven of the nine exploratory variables (seven main variables and two interaction terms) significantly influenced the $\delta^{13}C$ and $\delta^{15}N$ ratio in deep-water fishes (Table 3).

The average $\delta^{13}C$ values in epipelagic fishes ranged from -17.7 to -15.8 ‰ and $\delta^{15}N$ values ranged from 10.7 to 12.5 ‰ (Table S2). Both $\delta^{13}C$ and $\delta^{15}N$ were significantly different between species (Kruskal-Wallis: $H_{df=7}$ = 129, p < 0.001 and $H_{df=7}$ = 68, p < 0.001). The highest and the lowest carbon and nitrogen values were found in *C. leucas* (-15.8 ± 0.6 ‰) and *K. pelamis* (-17.7 ± 0.4 ‰) respectively. The isotopic values of *C. leucas* were not significantly different from those of *C. ignobilis* ($\delta^{15}N$= 12.5 ± 0.6 ‰ and 12.0 ± 0.3 ‰; $\delta^{13}C$= -15.8 ± 0.6 ‰ and -16.0 ± 0.5 ‰ respectively) and were isotopically enriched compared to all other species. *K. pelamis* and *T. albacares* fed at the lowest trophic level ($\delta^{13}N$ = 10.7 ± 0.5 ‰ and 11.0 ± 1.0 ‰ respectively) but seemed to depend on similar carbon sources as *C. hippurus* and *A. solandri* ($\delta^{13}C$ = -17.7 ± 0.4, -17.5 ± 0.5, -17.7 ± 0.9 and -17.7 ± 1.7 respectively). In fact, these four species were significantly ^{13}C-depleted compared to the four other epipelagic species. *G. cuvier* and *S. barracuda* had intermediate nitrogen and carbon isotope values ($\delta^{15}N$= 12.0 ± 0.7 ‰ and 11.6 ± 0.8 ‰; $\delta^{13}C$= -16.9 ± 0.7 ‰ and -16.6 ± 0.4 ‰ respectively).

For the deep-water species, the month had no effect on both $\delta^{13}C$ and $\delta^{15}N$, and in addition the sex of the predator had not effect on $\delta^{13}C$ (Table 3). The stage of maturity of fish affected both $\delta^{13}C$ (Kruskal-Wallis: $H_{df=5}$ = 52, p < 0.001) and $\delta^{15}N$ ($H_{df=5}$ = 99, p < 0.001). Both isotopic tracers significantly increased with the fish maturity, from an average $\delta^{13}C$ of -18.3 ± 0.2 ‰ and $\delta^{15}N$ of 11.4 ± 0.6 ‰ for juveniles, to an average $\delta^{13}C$ of -17.4 ± 0.6 ‰ and $\delta^{15}N$ of 12.7 ± 0.7 ‰ for spawning adults. The $\delta^{15}N$ significantly increased with depth (Spearman's rank correlation: S=17404130, p < 0.001, ρ = 23 %), from 11.1 ± 0.3 ‰ above 100 m, to 12.9 ± 0.3 ‰ below 500 m, whereas $\delta^{13}C$ values were not affected by depth (S = 22369470, p = 0.79, ρ = 1.2 %).

Finally, the fishing zone only significantly influenced the $\delta^{13}C$ and $\delta^{15}N$ values for *E. illustris* and *E. carbunculus* (Kruskal-Wallis tests, p < 0.05), with enrichment in heavy isotopes increasing from West (zone A) to East (zone D, Fig. 4).

Discussion

In a context of a global rise in concern about the sustainability of fishing activities and the need to adopt an ecosystem-based management approach to fisheries, improving our understanding of the factors driving variations in fish feeding habits is a crucial prerequisite. The novelty of the present study is that it combines both stable isotopes and stomach content analysis to identify the factors that structure two fish communities in the same location. Our results demonstrated firstly, an independence of both communities, with very few common prey items, although caught in similar localities, and secondly, a very different pattern of resource partitioning among each community, with the species feeding habits being the main driver for the epipelagic species, and the habitats for the deep-water fishes. Overall these results support our hypothesis that different factors structure the two communities, though they exist in similar localities. It should be noted however that epipelagic fishes were sampled over a two-year period whereas deep-water fishes were sampled during nine months only, potentially affecting interpretations.

Table 2. Layman's metric for the two studied fish communities

Metric	Demersal	Pelagic	Statistics
NR	1.85	1.8	
CR	1.31	2	
TA	1.5	1.7	
CD	0.63 ± 0.34	0.86 ± 0.38	U = 20, p = 0.23
MNND	0.48	0.49	U = 32, p=0.98
SDNND	0.29	0.08	F^7_7 = 10,304, p=0.006

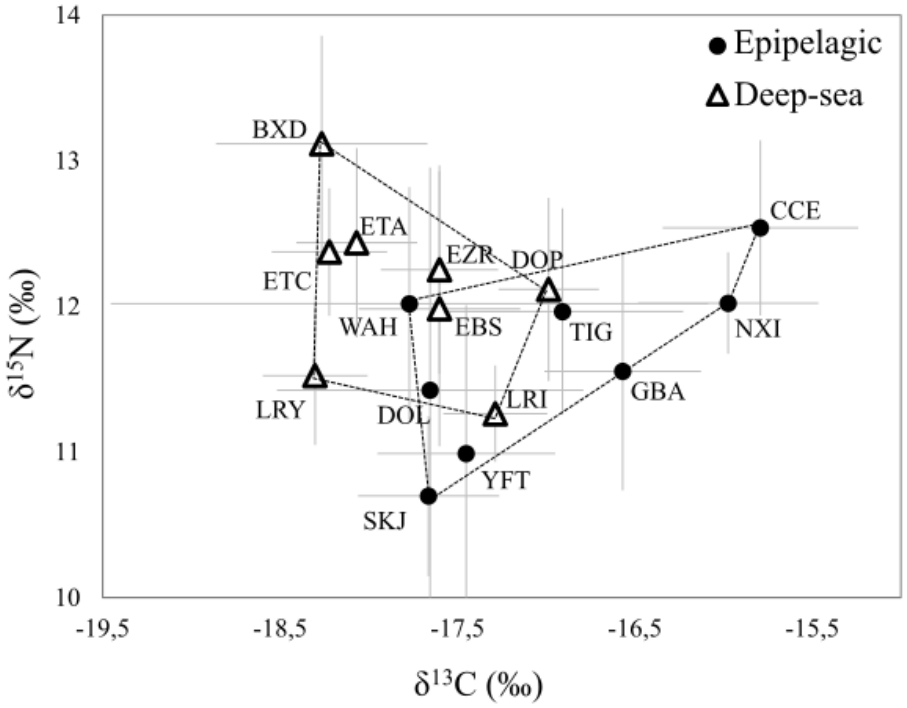


Figure 3. Isotopic structures of the deep-water and epipelagic studied fish communities. Deep-water species are: BXD, *Beryx decadactylus*; ETA, *Etelis coruscans*; ETC, *Etelis carbunculus*; LRY, *Pristipomoides argyrogrammicus*; LRI, *Pristipomoides multidens*; EBS, *Eumegistrus illustris*; EZR, *Epinephelus radiatus* and DOP, *Squalus megalops*. Epipelagic species are: YFT, *Thunnus albacares*; SKJ, *Katsuwonus pelamis*; WAH, *Acanthocybium solandri*; DOL, *Coryphaena hippurus*; GBA, *Sphyraena barracuda*; NXI, *Caranx ignobilis*; TIG, *Galeocerdo cuvier* and CCE, *Carcharhinus leucas*.

Trophic independence of epipelagic and deep-water fish communities

According to the analyses of the major functional groups of prey consumed by the studied species, the epipelagic and deep-water fish communities rely on different resources. Considering the geomorphology of the island, which results in close proximity between coastal and oceanic ecosystems, one could expect a greater trophic similarity between these two communities. It seems that even in similar localities, they remain independent in their functioning. Interestingly, for both communities, the analyses of the isotopic niche suggested that they exploit a limited number of carbon sources, probably because these sources are limited both in surface and deeper waters around Reunion Island.

The main prey found in surface predators were larval stage Stomatopoda, juveniles of reef-associated species, and coastal shallow benthic species, typical of surface waters, whereas the main prey found in deep-water predators were mesopelagic species such as Myctophids and large shrimps. Some studies previously reported a significant proportion of Myctophids consumed by surface predators such as *C. hippurus* (Castriota *et al*., 2007), *A. solandri* (Iversen and Yoshida, 1957), *T. albacares* and *K. pelamis* (Jaquemet *et al*., 2011) in different locations, including Reunion Island. Most Myctophid species belong to the sound-scattering layer community that engages in vertical migrations at night to access biomass produced in surface waters during the day. This migration can move horizontally in addition to vertically in areas close to seamounts or oceanic islands, becoming available to surface coastal predators during the night (Benoit-Bird and Au, 2006). In the present study, the high abundance of Myctophids in deep-water fishes and their absence in the stomach of surface predators could reflect local particularities such as a deep thermocline (Manola et al. 2015), which could limit the vertical movement of mesopelagic prey, or be a consequent of sampling bias (low sample size, sampling not heterogeneous through time for some species). The timing of the foraging activity of the surface predators might also prevent these species accessing the vertically migrating Myctophids. Further investigations on the distribution, abundance and movement of mesopelagic organisms in relation to the structure of the water masses are required to understand the local availability of such prey to surface predators.

Table 3. Results of an ANOVA applied on linear models assessing the effect of exploratory variables on the stable isotopic ratios of the deep-water fish species.

		$\delta^{13}C$				$\delta^{15}N$			
	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Depth	1	0.004	0.004	0.04	0.84	20.00	20.00	88.23	< **0.001*****
TL	1	57.49	57.49	597.77	< **0.001*****	12.44	12.44	54.87	< **0.001*****
Zone	4	5.99	1.50	15.56	< **0.001*****	38.05	9.51	41.97	< **0.001*****
Species	7	50.79	7.26	75.45	< **0.001*****	112.19	16.03	70.72	< **0.001*****
Month	1	0.09	0.09	0.95	0.33	0.02	0.02	0.075	0.78
Sex	2	0.17	0.08	0.86	0.42	3.90	1.95	8.60	< **0.001*****
Maturity	4	2.43	0.61	6.32	< **0.001*****	17.31	4.33	19.10	< **0.001*****
TL*species	7	4.32	0.62	7.29	< **0.001*****	19.92	2.85	15.42	< **0.001*****
Area*species	18	3.46	0.19	2.27	**0.002****	4.97	0.28	1.49	0.08
Residuals	467	39.54	0.08			86.61	0.19		
P-val model			< 0.001***				< 0.001***		
R^2			74%				70%		

The observed dietary difference between the two studied fish communities was result of a difference in the resource use among species. The surface community gathered in 3 homogeneous dietary groups based on predator species identity only, while within the deep-water community, the depth and the geographical location were also important factors explaining the trophic variability. In other words, for the epipelagic community, all individuals of a given species seem to have similar diets wherever and whenever they are caught, independent of their size. On the contrary, all deep-water predators caught in a given area and depth seem to consume the same prey, independent of species. The fact that such morphologically different species fed on the same prey in a given area likely reflects a low prey availability that would force fishes to exploit the same resources. This similarity in the diet is also observed in the isotopic space, where the

Table 4. Results of an ANOVA applied on linear models assessing the effect of exploratory variables on the stable isotopic ratios of the epipelagic fish species.

		$\delta^{13}C$				$\delta^{15}N$			
	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Species	7	67.168	9.5954	14.2740	<**0.001*****	46.446	6.6351	8.5721	<**0.001*****
TL	1	0.837	0.8375	1.2458	0.27	0.289	0.2894	0.3739	0.54
Month	1	0.109	0.1086	0.1615	0.69	4.550	4.5500	5.8783	**0.02***
Zone	19	10.992	0.5785	0.8606	0.63	13.615	0.7166	0.9257	0.55
DistShore	1	1.850	1.8498	2.7518	0.10	1.835	1.8346	2.3702	0.12
Residuals	141	94.784	0.6722			109.139	0.7740		
P-val model					< 0.001***				<0.001***
R^2					35%				25%

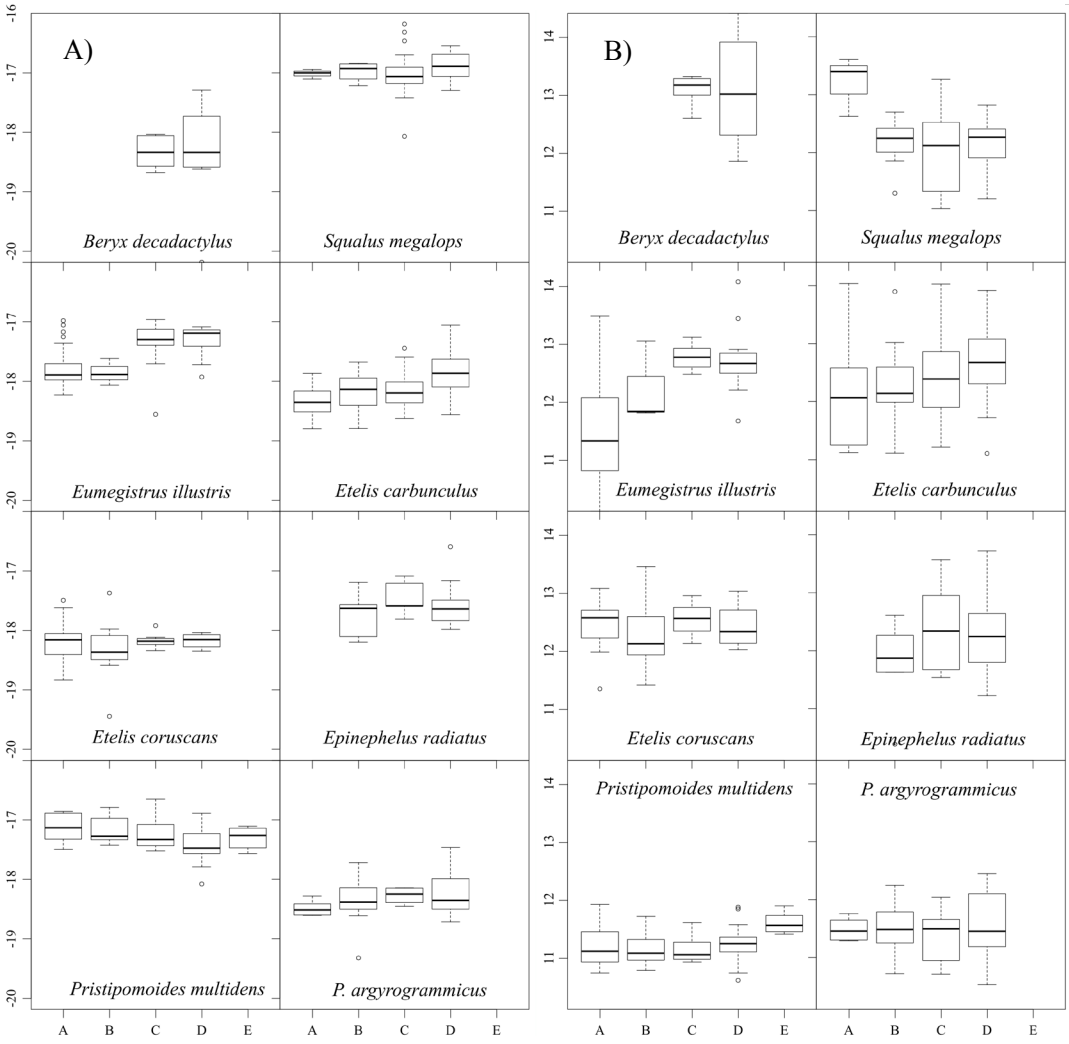


Figure 4. Variations of A) $\delta^{13}C$ and B) $\delta^{15}N$ with fishing zone (see Figure 1) of eight deep-water fish species.

distribution of the deep-water fishes is more packed than for the epipelagic species. Such an observation is in accordance with the fact that deep-water ecosystems are considered as highly food-limited (Iken *et al*., 2001). This segregation of the two communities can be related to the structure of the water masses. In tropical areas, surface waters are usually well stratified, exhibiting a deep thermocline (Manola *et al*., 2015), as observed around Reunion Island, where the temperature is homogeneous in the first 100 meters before decreasing gradually from 24°C to 12°C at 500 meter depth (Leroy and Barbaroux, 1980).

Factors structuring the surface and the deep-water fish communities

To explore the diet and stable isotope variability between species within the epipelagic community, five exploratory variables were considered: predator species, total length, month, fishing zone and distance from shore. Among these variables, only the species was identified to have a statistically significant effect. The absence of effect from the other exploratory variables is surprising given the information on their feeding ecology contained in the existing literature. Both size and distance from shore were demonstrated as important factors for tuna diet (Allain *et al*., 2012; Ménard *et al*., 2013), even in the Western Indian Ocean (Jaquemet *et al*., 2011). The studied species are highly mobile predators, meaning that the distance from the shore should not be a limiting factor in the context of the present study (most distant catch was ~15km offshore). In addition, some of the species caught at the same place during the same periods exhibited differences in their diet composition and stable isotope ratios. This suggests that the trophic segregation among species is mostly driven by intrinsic factors rather than environmental ones. The swimming characteristics, the diving capability, the prey detection

and catching ability are all likely major structuring factors for this community of epipelagic predators. In this community, the species seem rather specialized in their feeding habits, which could be a mechanism to reduce competition for resources, which are often considered in low abundant and patchy in tropical surface waters (Weimerskirch, 2007). The presence of the coastal ecosystems of the island also has to be considered in the foraging behaviour of the large pelagic fish. Indeed Jaquemet *et al.* (2011) in a comparison of the diet of tuna caught in the vicinity of the island and far offshore, showed clear differences in the diet composition, with offshore tuna feeding more on deep prey species whereas tuna in the vicinity of the island feed mostly on coastal species, as found in the present study. It seems that inshore-offshore transfers of organic matter is a key factor affecting the epipelagic fish around Reunion Island.

Deep-water demersal fish diet variability was explored in the light of seven exploratory variables. For this community, fishing zone and depth had significant effects on individual stomach contents in addition to the species identity. Moreover, both intrinsic (predator species, total length, sex and maturity) and environmental (fishing zone and depth) factors affected the deep-water fish isotopic ratio. Both carbon and nitrogen isotopic ratios increased with individual length for all deep-water demersal fish species (Trystram *et al.*, in revision). These results are in accordance with previous studies on the diet and distribution of deep-water fishes around oceanic islands and seamounts, which reported high habitat-dependence and trophic shifts associated with the length of the individuals (Fock *et al.*, 2002; Misa *et al.*, 2013). The feeding of these species is highly constrained by abiotic conditions, which limit prey availability. In these conditions, it is not surprising that variables characterising habitat determine the structure of the community of deep-water fishes. Their main feeding opportunity seems to be the interception of mesopelagic organisms that undertake diel migration to feed in the upper layers of the water column. These results support the sound scattering layer interception hypothesis for deep-water fish diet (Fock *et al.*, 2002; Trystram *et al.*, in revision). Depth and other abiotic conditions act on these migrating organisms, rendering them more or less available to the fish. The effects of sex and length on the stable isotope ratios suggest ontogenetic changes in trophic ecology and differences related to reproduction. All these mechanisms could reveal adaptations of the species to limited resources, with an overall strategy toward a reduction of the overlap between the diet of the different species and stages of development.

The difference observed in the stomach contents according to the depth of fish collection, and between the West and East coasts, could reflect differences in the distribution of mesopelagic organisms. Carid shrimps would be more abundant in the upper layer compared to Myctophids (see Fig. 2A). At first, this result seems surprising as it is in opposition with observations made in Hawaii, where Myctophids were more abundant in the upper layer. This difference can be explained by the fact that in this study fishes were caught mostly below 150m, a depth at which Myctophids are still abundant in Hawaii, but less so than in upper layers (Benoit-Bird and Au, 2006). In these conditions, feeding on large shrimps could be advantageous for the fish, as they could be easier to catch and could provide more energy. The difference between the West and East coasts follows the same pattern as with depth, suggesting that shrimps are more abundant on the West coast. This observation could be the consequence of an island effect as Reunion Island lies in the path of the south-equatorial current (Pous *et al.*, 2014). The obstruction of the island could create a sheltered zone behind the island, such as the situation described for Tome Island, where a complex flow pattern forms downstream of the island (Bakun, 2006). Upstream the island a local high in the sea surface topography is created, which would tend to accelerate the down-gradient flow skirting either side of the island obstruction, creating bands of swift flow downstream north and south of the island; these last features providing lateral torques that drive counter-rotating eddies behind the island, with upwelled waters in their core. As a consequence, on the West coast, the upwelled waters could raise deep waters and favour the presence of mesopelagic shrimps close to the surface, whereas the accumulation of water on the East coast would favour downwelling, which would lead to an increase of the upper layer the water column, which would render the Myctophids that migrate to the upper layers more accessible to the fishes (Benoit-Bird and Au, 2006).

Conclusion

In this study we propose that the factors underlying the trophic structure of two communities of fish that are spatially closely located and exploited by artisanal fishermen in Reunion Island are different. The community of surface predatory fishes exploits different functional groups of prey and this seems to be mostly related to intrinsic factors rather than being controlled

by the environment. This specialization of the different species might be a response to both a low biomass and a high diversity of resources that the predators can exploit. On the other hand, the community of deep-water fishes seems to be mostly structured by environmental factors, which control the distribution of the prey in the water column, though there seem to be within-species mechanisms to reduce the competition between sex and age classes. As a consequence, all species at a given depth exploit the same resources, while individuals of the same species do not necessary feed on the same prey in different habitats (i.e. depth). This situation is related to the fact that resources are rare below the euphotic zone and that the main feeding opportunity seems to be the deep scattering layer, composed of mesopelagic prey that undergo diel vertical migrations. Interestingly, the two communities seem to function independently from each other, although both have evolved in the vicinity of Reunion Island. This suggests that surface species do not dive deep to forage and deep-water species do not forage in the epipelagic zone, or that the species in each community do not forage at the same time. This apparent independence of each community is counterbalanced however by the fact that all species rely mostly on the pelagic primary production of the euphotic zone. More precisely, the epipelagic community may primarily depend on inshore-offshore transfer of biomass, with export of coastal material to the oceanic realm, and the deep-water community depending on the export of surface materiel to deeper waters; all these transfers depending on the movements of prey (passive drifting of fish larvae or active movement of mesopelagic micronektonic animals). Further investigations should be conducted to better understand the patterns of predator and prey distribution in space and time and the role of each species in the transfer of biomass and energy between ecosystems. The results presented in this study suggest that fisheries management should be very different for epipelagic and deep-water fishes. For epipelagic fisheries management should be more species-centred (restriction by size or season for example, for one particular species all around the island), whereas deep-water fisheries management should be more habitat-centred (with restricted zones, deep marine protected areas for example).

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Supplementary materials

Table S1. Correspondence between prey species or families and ecological functional group. NI: unidentified.

Predator	Functional Group	Family	Species
Deep-sea fish	Bathydemersal	Berycidae	
		Scorpaenidae	
		Serranidae	
		Trachichthyidae	
	Benthic	Bembridae	*Parabembras robinsoni*
		Bothidae	
		Congridae	
		Lophiidae	
		Muraenidae	*Muraenesox baggio*
		Peristediidae	*Satyrichthys sp*
	Brachyura	CrabNI	
		Majidae	
		Portunidae	*Chrybdis sp*
	Caridea	Caridea	*Heterocarpus laevigatus*
		Panaeoidea	*Aristaeomorpha foliacea*
		Peneidae	
		ShrimpNI	
	Epipelagic	Carangidae	
	Pelagic Tunicata		
	Mesopelagic	Bregmacerotidae	
		Carapidae	
		Epigonidae	*Sphyraenops bairdianus*
		Gempylidae	NI
			Thyrsitoides marleyi
		Gonostomatidae	
		Macroramphosidae	
		Myctophidae	*Benthosema sp*
			Ceratoscopelus warmingii
			Diaphus effulgens
			Diaphus lucidus
			Lampanyctus vadulus
			NI
			Pseudoscopelus sp
		Nemichthyidae	
		Sternoptychidae	*Argyropelecus aculeatus*
			NI
			Polyipnus indicus
		Stomiiformes	
	Octopoda	Octopoda	
	Other	Algae	
		Annelida	
		Bivalvia	
		Echinoidea	

Predator	Functional Group	Family	Species
		Gasteropoda	
		Gravel	
		Sipuncula	
		Taeniidae	
	OtherCeph	Sepiolidae	
	OtherCrust	Aegidae	
		Amphipoda	
		Cirripedia	
		Enoplometopidae	*Enoplometopus sp*
		Isopoda	
		Lysiosquillidae	*Lysiosquilla sp*
			Lysiosquilla tredecimdentata
		Munididae	*Munida shaula*
		Odontodactylidae	
		Palinura	
		Scyllaridae	
		Squillidae	
	Reef-associated	Acanthuridae	
		Chaetodontidae	
		Holocentridae	NI
			Sargocentron sp
		Menidae	*Mene maculata*
		Monacanthidae	
		Mullidae	NI
			Upeneus sp
		Ostraciidae	*Lactoria sp*
		Pomacentridae	
		Syngnathidae	
		Tetraodontidae	NI
			Sphoeroides pachygaster
	Teuthida	Bathyteuthidae	
		Histioteuthidae	*Histioteuthis sp*
		Lepidoteuthidae	*Lepidoteuthis sp*
		Loliginidae	
		Lycoteutidae	
		Onychoteutidae	
		OtherTeuthida	
Epipelagic fish	Aves	Phasianidae	*Gallus gallus*
		Sternidae	*Anous sp*
			NI
	Coastal.Fish	Acanthuridae	*Brachycentron sp*
			NI
		Balistidae	
		Batrachoïdidae	
		Diodontidae	
		Fistulariidae	
		Holocentridae	*Myripristis sp*

Predator	Functional Group	Family	Species
			Sargocentron sp
		Lutjanidae	*Aprion viriscens*
			Lutjanus sp
		Monacanthidae	
		Mullidae	*Parapeneus sp*
		Muraenidae	
		Ostraciidae	
		Polynemidae	*Polydactylus sp*
		Scaridae	
		Scorpaenidae	NI
			Scorpaena scrofa
		Tetraodontidae	
	Crust.Benthic	Paguroidea	
		Raninidae	*Ranina ranina*
	Crust.Epipelagic	Amphipoda	NI
			Phrosina semilunata
		Isopoda	
		Lysiosquillidae	*Lysiosquilla tredecimdentata*
		NI	
		Odontodactylidae	*Odontodactylus scyllarus*
		Ostracoda	
		Palinuridae	
		Squillidae	*Neoanchisquilla tuberculata*
	Elasmobranchii	NI	
		Sphyrnidae	
		Torpedinidae	
	Gaster.Meso	Cavoliniidae	*Cavolinia sp*
	Juvenile	Acanthuridae	*Acanthurus sp*
			Naso sp
			NI
		Antennaridae	*Histrio histrio*
		Balistidae	*Cantherhinus sp*
			NI
			Rhinecanthus sp
		Blennidae	
		Carangidae	
		Carapidae	
		Chaetodontidae	
		Dactylopteridae	*Dactyloptena orientalis*
		Diodontidae	
		Holocentridae	*Myripristis sp*
			NI
			Sargocentron sp
		Labridae	
		Monacanthidae	
		Mullidae	
		NI	

Predator	Functional Group	Family	Species
		Ostraciidae	
		Pomacentridae	
		Scorpaenidae	
		Serranidae	
		Sphyraenidae	
		Synodontidae	
		Tetraodontidae	*Lagocephalus sp*
			NI
		Zanclidae	*Zanclus canescens*
	Large.Pelagic.Fish	Carangidae	*Carangoïdes sp*
			Caranx ignobilis
			Caranx sexifaciatus
		Coryphaenidae	*Coryphaena hippurus*
		Istiophoridae	
		Scombridae	*Gymnocerda unicolor*
			Katsuwonus pelamis
			NI
			Thunnus albacares
	Mesopelagic	Bramidae	NI
			Pteraclis sp
		Gempylidae	*Nealotus tripes*
			NI
		Nomeidae	
		Paralepididae	*Lestrolepis sp*
		Trachichthyidae	*Gephyroberyx darwini*
	Octopoda	NI	
		Octopodidae	
	Shrimp.Epipelagic	Caridae	
		NI	
	Small.Pel.Fish	Carangidae	*Decapterus macarellus*
			Decapterus sp
			Selar crumenophtalmus
		Chanidae	*Chanos chanos*
		Clupeidae	*Sardinella gibbosa*
		Exocoetidae	*Exocoetus sp*
			Exocoetus volitans
			NI
		Nomeidae	*Cubiceps sp*
		Scombridae	
	Teuthida	Chirotheuthidae	
		Histioteuthidae	
		NI	
		Ommastrephidae	*Stenotheuthis oulaniensis*

Species	Stomach contents					Stable isotopes				
	Depth	Ndis	Nfood	%empt	Mean TL [min-max]	N	Mean TL [min-max]	Mean $\delta^{13}C$ ±SD	Mean $\delta^{15}N$ ±SD	C/N
Acanthocybium solandri	0	28	25	10.7	107 [64-142]	21	109 [97-142]	-17.7 ±1.7	12.0 ±0.8	3,4 ±0,4
Caranx ignobilis	0	13	9	30.8	104 [83-135]	15	99 [83-135]	-16.0 ±0.5	12.0 ±0.3	3,4 ±0,1
Carcharhinus leucas	0	24	16	33.3	227 [178-267]	27	224 [171-275]	-15.8 ±0.6	12.5 ±0.6	3.0 ±0.1
Coryphaena hippurus	0	53	49	7.5	96 [58-128]	34	96 [69-120]	-17.7 ±0.9	11.4 ±1.5	3,5 ±0,5
Galeocerdo cuvier	0	58	30	48.3	280 [206-336]	56	276 [206-336]	-16.9 ±0.7	12.0 ±0.7	2.9 ±0.1
Katsuwonus pelamis	0	23	16	30.4	61 [47-92]	18	60 [39-90]	-17.7 ±0.4	10.7 ±0.5	3,2 ±0,1
Sphyraena barracuda	0	14	8	42.9	116 [103-138]	10	110 [64-138]	-16.6 ±0.4	11.6 ±0.8	3,2 ±0,1
Thunnus albacares	0	97	91	6.2	72 [45-145]	34	77 [49-145]	-17.5 ±0.5	11.0 ±1.0	3,3 ±0,2
Beryx decadactylus	404 ±73	27	19	29.6	50 [39-58]	23	49 [35-60]	-18.3 ±0.6	13.1 ±0.7	3.3 ±0.6
Epinephelus radiatus	202 ±41	43	6	86.0	37 [30-46]	33	37 [12-62]	-17.6 ±0.3	12.3 ±0.7	3.1 ±0.1
Etelis carbunculus	298 ±49	791	60	92.4	28 [16-48]	158	29 [16-98]	-18.1 ±0.3	12.4 ±0.7	3.2 ±0.1
Etelis coruscans	314 ±27	94	15	84.0	43 [27-112]	47	52 [21-112]	-18.2 ±0.3	12.4 ±0.4	3.2 ±0.2
Eumegistrus illustris	432 ±65	89	18	79.8	67 [50-85]	73	67 [45-87]	-17.6 ±0.5	12.0 ±0.9	3.2 ±0.1
Pristipomoides argyrogrammicus	279 ±48	273	50	81.7	24 [16-29]	71	23 [16-29]	-18.3 ±0.3	11.5 ±0.5	3.2 ±0.1
Pristipomoides multidens	115 ±35	109	11	89.9	54 [35-70]	46	54 [34-86]	-17.3 ±0.3	11.3 ±0.3	3.2 ±0.1
Squalus megalops	384 ±40	289	107	63.0	57 [35-78]	63	57 [31-80]	-17.0 ±0.3	12.1 ±0.6	2.5 ±0.1

Table S2. Characteristics of data used to explore factors influencing stomach contents and stable isotope composition. Ndis: number of dissected stomachs; Nfood: number of stomachs containing food; %empt: percentage of empty stomachs; TL: total length (cm); N: number of samples; C/N: atomic ratio of carbon to nitrogen composition.