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Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean

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Abstract

Prey composition and resource partitioning were investigated among three large pelagic fish predators, yellowfin tuna (*Thunnus albacares*), swordfish (*Xiphias gladius*) and lancetfish (*Alepisaurus ferox*), in a poorly known oceanic area, the western Indian Ocean. The contents of 380 non-empty stomachs were analysed from specimens caught with longlines during scientific cruises carried out from 2001 to 2003. Diet data were processed by occurrence, mean proportion by number, wet weight, and mean proportion by reconstituted weight. Crustaceans, dominated by the swimming crab *Charybdis smithii* and the stomatopod *Natosquilla investigatoris*, were the major food source of lancetfish. Cannibalism was also significant for that species. Yellowfin tunas preyed upon a large diversity of mesopelagic fishes, crustaceans (*C. smithii* and crab larvae) and cephalopods (the ommastrephid *Sthenoteuthis oualaniensis*). Mesopelagic fishes (*Cubiceps pauciradiatus* and *Diretmoides parini*) and cephalopods (mainly *S. oualaniensis*) were the main prey of swordfish. Diet overlap between swordfish and yellowfin tuna was evidenced by high Morisita–Horn index. But the feeding habits of these three predators differed by foraging depth and prey size, with swordfish feeding at deeper depths and on larger prey than the more epipelagic lancetfish and yellowfin tuna. Using these three predators as biological samplers, the present study provides novel data on micronekton fauna that is poorly documented in the western Indian Ocean: 67 families and 84 species of prey were recovered in the stomach contents, and our results indicate the presence of large resources of pelagic crustaceans that play a primary role in the epipelagic food chain.

Keywords: Diet composition; Feeding; Food web; Lancetfish; Swordfish; Yellowfin tuna; Indian Ocean; Trophic overlap

1. Introduction

Catches of tunas and billfishes by longline and surface tuna fisheries have dramatically increased during the two last decades in the western Indian Ocean (from 130,000 tonnes in 1980 to 800,000 tonnes in 2002; FAO, 2004) whereas our knowledge of the biological components and the predator–prey interactions in this ocean is still scarce. Such a removal of top predators could have repercussions on the food web structure through top-down, trophic cascades (Kitchell et al., 1999; Essington et al., 2002). Therefore, it is necessary to assess the impact of the tuna fisheries on the pelagic ecosystems. Comparative studies of the food habits of top predators and the implications for resource partitioning will provide basic elements for an ecosystem approach to tuna fisheries management.

Many studies have investigated the diet of large pelagic fishes such as tunas and swordfish, due to their commercial value. Most of these studies took place in the Pacific and Atlantic Oceans (e.g. Alverson, 1963; Dragovich and Potthoff, 1972; Matthews et al., 1977; Borodulina, 1982; Stillwell and Kohler, 1985; Hernández-Garcia, 1995; Moteki et al., 2001; Bertrand et al., 2002). Very few studies have investigated the diet of large pelagic fish predators in the Indian Ocean. Watanabe (1960) has analysed the food composition of 35 bigeye tunas (*Thunnus obesus*) and 91 yellowfin tunas (*Thunnus albacares*) caught in the eastern Indian Ocean during the 1956–1957 period. Kornilova (1981) studied

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the detailed food composition of yellowfin tuna and of bigeye tuna in the equatorial Indian Ocean from 1969 to 1973, and she provided an advanced taxonomic identification of the prey. Other studies have analysed the main prey groups eaten by yellowfin tuna and skipjack tuna (*Katsuwonus pelamis*) in the Seychelles and in the Mozambique area (Roger, 1994), and around India (Maldeniya, 1996). Potier et al. (2004) investigated the feeding partitioning among yellowfin and bigeye tunas in the western Indian Ocean using preliminary data from longline and purse seine caught fish. In the present study, we detail the prey composition of the diets of lancetfish *Alepisaurus ferox*, yellowfin tuna *T. albacares* and swordfish *Xiphias gladius* in the waters surrounding the Seychelles Islands. Fishes were caught by longline during nine scientific cruises carried out between 2001 and 2003. Our main goals are to describe the dietary habits of these predators in relation to their habitat, and to explore the ways in which food resources are partitioned among them. We did not study seasonal variations in the feeding regimes because this goal was out of the scope of this paper. The pelagic forage fauna of the western Indian Ocean has seldom been studied before now. The diets of tunas and tuna-like species are characterized by a great diversity of prey species (e.g. Sund et al., 1981), and predation by these pelagic predators is often described as an opportunistic process (i.e. non-selective) constrained by local prey availability. Therefore, using top predators as biological samplers of the micronekton organisms, the prey composition of the stomach contents provides unique information on the diversity of the forage fauna of this poorly known ecosystem.

2. Materials and methods

2.1. Field operations

Yellowfin tuna, swordfish and lancetfish were caught by a 20-m longliner, *Amitié*, from the Seychelles Fishing Authority (SFA). Nine cruises (105 days at sea) were conducted from 2001 to 2003 in the area 2°N–7°S and 52°E–60°E surrounding the Seychelles, West Indian Ocean (Fig. 1 and Table 1). Overall, 78 longline sets were performed (6–14 longline sets per cruise). The depth of the longline gear was measured by time depth recorders (VEMCO 8-bit Minilog TDR) for 41 sets: the average hook depth was 85 m ± 40 m (2 standard deviations) and the average maximum depth reached by the hooks was 108 m ± 52 m. The maximum depth of the sets was relatively shallow (no greater than 185 m) compared to commercial longliners. A total of 47 vertical profiles of temperature and dissolved oxygen (DO) were made from 0 to 250 m with a SeaBird SBE 19 before setting the longline. According to the averaged profiles (Fig. 2), the fishing gear primarily sampled the mixed layer below 40 m, and also the thermocline to the oxygen-minimum zone. The former was characterized by temperatures ranging from 20 to 26 °C,

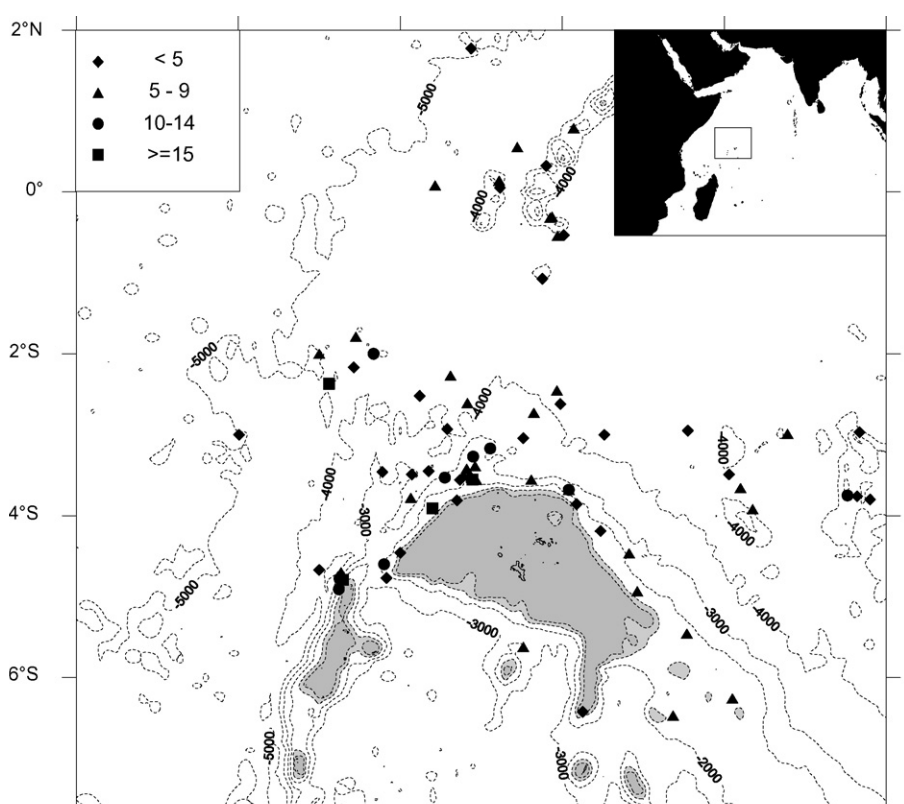

Fig. 1. Locations of longline sets carried out during the study. The number of stomachs collected by longline set is divided into four classes. The Seychelles and Amirantes banks (dark grey) are indicated by the 200 m isobath.

Table 1
Number of non-empty stomachs recovered during the nine longline cruises carried out in the Seychelles region from August 2001 to July 2003

Trip	Date	No. of days	Sets	Lancetfish	Yellowfin tuna	Swordfish	Total
AM1	August 2001	12	8	38	18	23	79
AM2	October 2001	8	7	19	4	7	30
AM3	November 2001	11	8	4	14	18	36
AM4	January–February 2002	10	6	18	5	5	28
AM5	February–March 2002	15	9	3	5	16	24
AM6	July 2002	16	14	17	1	9	27
AM7	December 2002	11	9	17	4	23	44
AM8	January–February 2003	14	10	12	59	21	92
AM9	July 2003	8	7	11	1	8	20
Total		105	78	139	111	130	380

and DO concentration of 2.6–3.6 ml l^{-1}. The deeper layer was characterized by temperatures ranging from 13 to 20 °C and encompassed the oxygen minimum (as low as 2.3 ml l^{-1} on the average).

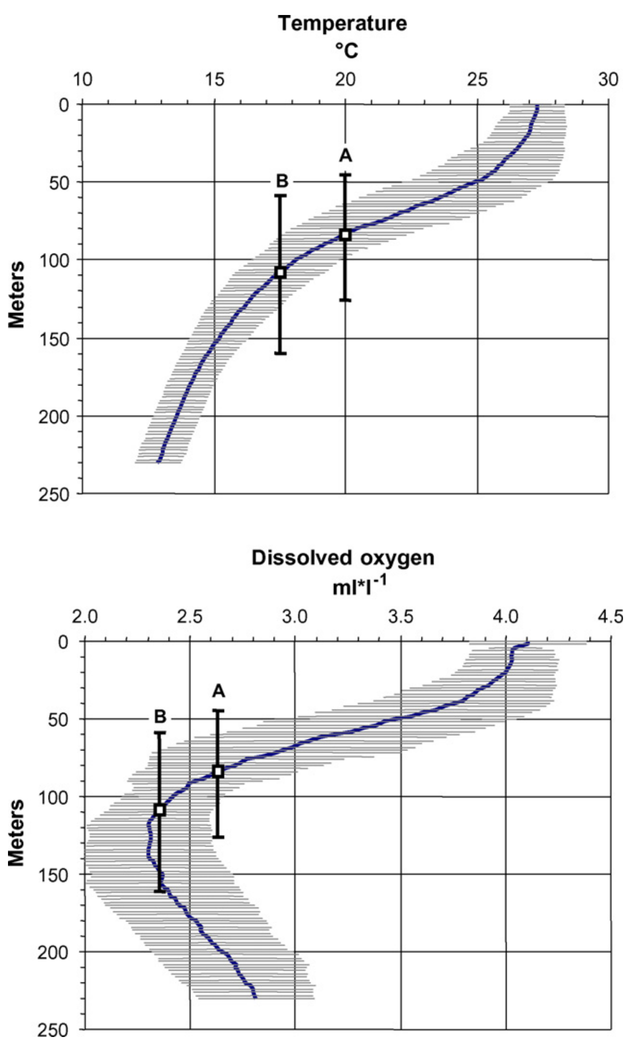

Fig. 2. Average distributions of temperature and dissolved oxygen vs. depth from 47 CTD casts made during the longline sets. The horizontal bars denote 1 standard deviation. The average (A) and maximum (B) depth of the longline hooks, and their respective standard deviation (vertical bar) are superimposed. These statistics were calculated from 72 records of depth-recorders along 41 longline sets.

2.2. Stomach content analysis

Stomach contents from freshly caught fishes were removed at sea. Length (fork length for tunas and lancetfish, and post-orbital fork length for swordfish) and sex were recorded for each individual. Stomachs were kept frozen at −20 °C. In the laboratory, each sample was thawed, drained and a four-step protocol was applied:

(1) The total weight of each stomach content was measured. Accumulated items, i.e. indigestible hard parts of prey items that accumulated over time (e.g. cephalopod beaks without flesh attached and eroded fish otoliths), were sorted and excluded from the analysis because they overemphasize the importance of some prey in fish diets. Fresh remains always made up by far the largest proportion of our stomach-content samples. The contents were divided into broad prey classes (crustaceans, fishes, squids, others), which were weighed to calculate their proportions by wet mass in the diet.
(2) The different items constituting a single class were sorted, counted and weighed. Identifiable fresh remains were used to determine the number of each prey item. For fishes, the number of mandibles, parasphenoids or the maximum number of left or right otoliths was assumed to reflect the total number of fishes that had been ingested. Similarly, the greatest number of either upper or lower beaks was used to estimate the number of cephalopods. For crustaceans, telsons or cephalo-thorax were counted.
(3) Prey were identified to the lowest possible taxon using keys and descriptions found in Clarke (1986), Nesis (1987), Smith and Heemstra (1986), Smale et al. (1995), Tregouboff and Rose (1978) and Crosnier and Forest (1973) and by comparison with the material held in our own reference collection.
(4) Prey items were measured using standard length (SL in cm) for fishes, the lower rostral length (LRL in mm) for cephalopods, and length of the propods (in cm) for pelagic crabs. When fish prey was partly digested, sizes were estimated from regression equations relating hard parts (otoliths, parasphenoids, dentary length) to SL.

We reconstituted the weight of each fresh prey items, using published allometric equations (Smale et al., 1995; Clarke, 1986) and our own relationships. When equations for a given species were not available, estimates were made from equations established for closely related species or for species with a similar morphology.

2.3. Data analysis

The study area is relatively small compared to the Indian Ocean basin (Fig. 1), and is not directly influenced by large landmasses. Therefore, all samples collected by the longline sets were pooled. Micronekton organisms exhibit different vertical behaviours in the water column; most of them undertake large vertical migrations during the twilight phases, but some organisms stay in the shallow layers day and night. Therefore, we divide the prey into two communities according to published information on their position in the water column: the epipelagic prey consisted of organisms which are found day and night within the upper 200 m, and mesopelagic prey consisted of organisms which remain between 200 and 1000 m during daytime. Cephalopods were classified between these communities according to Nesis (1987) and Sweeney et al. (1992). However, we classified Ommastrephids according to beak size: individuals with LRL less than 4.0 mm were considered as epipelagic juveniles, while individuals with LRL greater than 4.0 mm were classified as mesopelagic adults (Zuyev et al., 2002). For Octopoteuthids, Pholidoteuthids and Alloposids, the partition between epipelagic juveniles and mesopelagic adults was based on the chitinization of the beak: partially chitinized beaks were considered to belong to juveniles, while totally chitinized beaks were considered to belong to adults.

For a given predator, we used three diet indices for each identified prey item: the frequency of occurrence in stomachs (O defined as the percentage of all the non-emty stomachs examined), the mean proportion by number (MN), and the mean proportion by reconstituted weight (MRW). MN and MRW were calculated by taking the proportions of each prey species (or category) found in the individual stomachs, and then calculating the average of the proportions found in all the stomachs. We thus treated individual fish as the sampling unit, allowing us to compute standard deviations. The three diet indices were also calculated by broad prey classes (cephalopods, crustaceans, and fishes).

The diet overlap between the three predator species was assessed using the simplified Morisita index proposed by Horn (1966), and usually called the Morisita–Horn index (see Krebs, 1998). This overlap index was calculated from the reconstituted weight data using the following formula:

$$C_{\mathrm{mh}} = \frac{2\sum_{i=1}^{S} p_{A,i} \times p_{B,i}}{\sum_{i=1}^{S} p_{A,i}^2 + \sum_{i=1}^{S} p_{B,i}^2},$$

where C_{mh} is the Morisita–Horn index of overlap between predator species A and B; S the total number of identified prey items in the feeding regime of both predators, $p_{A,i}$ the MRW of prey item i consumed by predator species A, $p_{B,i}$ the MRW of prey item i consumed by predator species B. C_{mh} ranges from 0 (no prey in common) to 1 (complete overlap), and a significant overlap is traditionally assumed for index values greater than 0.6 (e.g. Zaret and Rand, 1971; Keast, 1978). To assess the effect of the taxonomic identification level on C_{mh}, we computed the overlap index using all prey categories (i.e., mixing different taxonomic levels of identification), and using prey categories identified at the genus level only. Bootstrapping techniques based on 500 replications allowed us to estimate 95% confidence intervals for the overlap indices.

Kruskal–Wallis rank sum tests were used to assess wether there is a predator size effect or year effect on the wet weight, the relative masses (stomach content wet weight divided by the fish weight), and the prey numbers. A modified form of the Kruskal–Wallis test (available from the S-News forum http://www.biostat.wustl.edu/archives/html/s-news/1999-03/msg00245.html) allowed us to perform post-hoc multiple comparison tests. All the computations and tests were performed on S-Plus (Insightful, 2005).

3. Results

The fork lengths of lancetfish and yellowfin tuna ranged from 15 to 170 cm (median = 127 cm) and from 32 to 161 cm (median = 95 cm), respectively. Post-orbital fork length of swordfish ranged from 56 to 192 cm (median = 98 cm) (Fig. 3).

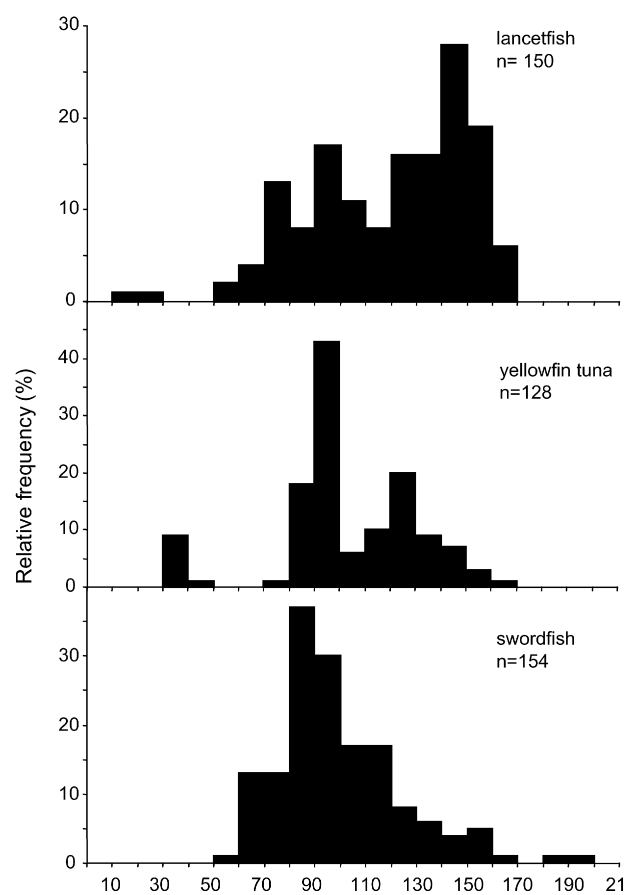

Fig. 3. Length frequency distributions of the lancetfish, yellowfin tuna and swordfish examined for stomach contents during the *Amitié* cruises from 2001 to 2003.

Size effects were tested on the total wet weight and on the number of prey. Depending on the number of fishes sampled, lancetfish individuals were split into 10 size classes, and yellowfin tunas and swordfish were split into eight classes. No size effect on the number of prey was significant for the three predators (Kruskal–Wallis test, $H = 9.48$, $p = 0.39$; $H = 13.75$, $p = 0.17$; $H = 10.05$, $p = 0.19$ for lancetfish, yellowfin tuna and swordfish, respectively). Conversely, a size effect was significant on the wet weight for the lancetfish and the yellowfin tuna ($H = 22.29$, $p < 0.01$; $H = 16.8$, $p < 0.05$) but not for the swordfish ($H = 10.06$, $p = 0.18$). The size did not have a significant effect on the relative masses (stomach content wet weight divided by the body weight estimated from length-weight allometric equations). Year effects were also assessed in the data. No significant differences were observed for swordfish and lancetfish ($p > 0.05$). Conversely, the year effect was significant for yellowfin on the number of prey ($H = 24.2$, $p < 0.01$) only. A post-hoc multiple comparison test showed that the year 2003 was significantly different from 2001 and 2002. Indeed, a very large number of crab larvae were consumed by 45 yellowfin tunas caught in a restricted area at the slope of African Island, Amirantes, and Seychelles Bank during the cruise AM8 in 2003. However, in this study we did not stratify the data by year and by size.

3.1. Overall diets

A total of 433 stomachs were collected during the nine longline trips, including 53 empty stomachs and 380 that contained food remains. The proportion of empty stomachs was 7% for lancetfish, 13% for yellowfin tuna and 16% for swordfish. The average wet weight of the 139 food samples of lancetfish was 87.2 g (range from 0.3 to 626.5 g). Crustaceans were the most important food source for that predator by wet weight (mean proportions of 55.0% versus 28.5% for fishes and 11.3% for cephalopods) and by reconstituted weight (MRW of 55.3% versus 27.4% for fishes and 11.5% for cephalopods; Table 2). Food samples of yellowfin tuna ($n = 111$) weighed on average 81.2 g (range from <0.1 to 1048.4 g). Fishes were the most important food source for that predator by wet weight (mean proportion of 46.4%) and by reconstituted weight (MRW of 48.4%). By wet weight, crustaceans (28.2%) ranked second in the diet of yellowfin tuna and cephalopods (25.4%) ranked third, while by reconstituted weight the reverse was observed. The average wet weight of swordfish food samples ($n = 130$) was 145.5 g (range from 0.2 to 1359.5 g). Fishes and cephalopods prevailed in the diet of swordfish by wet weight (mean proportions of 63.2% and 26.9%, respectively), and by MRW (59% and 35.5%, respectively; Table 4), while crustaceans were a minor part of the diet (9.9% by wet weight and 5.5% by MRW). In terms of mean proportions by number (MN), crustaceans formed the bulk of the diet of lancetfish (64%), ranked first for yellowfin tuna (53%), and were minor for swordfish (17%). Conversely, the proportions of fishes and cephalopods increased from lancetfish, to yellowfin tuna and then to swordfish: 19.3%, 30.5% and 58.6% for fishes, and 7.9%, 16%, and 24.8% for cephalopods, respectively.

3.2. Taxonomic analysis of the prey

- Lancetfish, *A. ferox* (Table 2 and Fig. 4a).

  Forty-five families and 2311 prey items were found in the stomachs of the 139 lancetfish sampled. On average, 16.6 prey were found per stomach. Crustaceans were the dominant food source regardless of the diet index. Fishes ranked second, whereas cephalopods played a minor role. The dominant items were the swimming crab *Charybdis smithii* (25.7% of the MN and 32.5% of the MRW) and the stomatopod *Natosquilla investigatoris* (19.0% of the MN and 16.3% of the MRW). Together they contributed 45% and 49% by MN and MRW, respectively. Among the 20 families of fish prey, Alepisauridae (including *A. ferox,* which indicate cannibalism) was the main component (2.1% by MN and 7% by MRW). We noted that *Omosudis lowei* and fishes from the Paralepididae family occurred frequently in the stomach contents (16.5% and 15.8%, respectively). Among the 12 cephalopod families, the Bolitaenid *Japetella diaphana* (2.7% by MN) and the Onychiteuthid *Walvisteuthis rancureli* (1.5% by MN) were the most frequent species.
- Yellowfin tuna, *T. albacares* (Table 3 and Fig. 4b).

  Forty-two families and 4791 prey items were counted in the stomachs of the 111 yellowfin tunas sampled. On average, 43.2 prey were found per stomach. Crustaceans occurred in 79 samples (71.2%) and contributed 53% by MN and 25% by MRW. Crab larvae (megalop stage) dominated the yellowfin's diet by MN (25.9%) but, owing to their small size, ranked second by MRW (8.5%). The other dominant crustacean prey were the portunid *C. smithii* (7.7% by MRW and 6.7% by MN), the hyperiid *Phrosina semilunata* (2.2% by MRW and 7.1% by MN), and the stomatopoda *Odontodactylus scyllarus* (1.7% by MRW and 3.6% by MN). The ommastrephids, known as flying squids (*Sthenoteuthis oualaniensis* and *Ornithoteuthis volatilis*) formed the main cephalopod prey by MN (9% and 4.7%, respectively) and by MRW (19.1% and 4.4%, respectively). The most frequent fish families were the Paralepididae, the Myctophidae and the Scombridae. They did not contribute significantly to the total number of prey (11.9% together), but the scombrids and the nomeid *Cubiceps pauciradiatus* (5%) were the main components of the fish prey by MRW (12.0% and 5%, respectively).
- Swordfish, *X. gladius* (Table 4, Fig. 4c).

  A total of 726 prey items belonging to 30 families was recorded in the stomachs of the 130 sworfish sampled. On average, 5.6 prey were found per stomach. Fishes occurred in 78% of the stomachs and dominated the diet by MN (58.6%) and by MRW (59%). The nomeid *C. pauciradiatus* (26.3% by MN and 24.8% by MRW) and the diretmid *Diretmoides parini* (8.7% by MN and 9% by MRW) were the dominant fish prey, while other fish species were less present. Cephalopods ranked second by MN and MRW. The most significant was *S. oualaniensis* (13.3% by MN and 15.9% by MRW) first, and then to a lesser extend the onychoteuthid *Moroteuthis lonnbergii* (3.4% by MN and 6.6% by MRW), the ommastrephid *O. volatilis* (3.0% by MN and 3.8 % by MRW), and the enoploteuthid *Ancistrocheirus lesueuri* (0.9% by MN and

Table 2
Frequency of occurrence, mean proportion by number (MN) and mean proportion by reconstituted weight (MRW) of prey species or categories recovered from stomach contents (139 samples) (*Alepisaurus ferox*)

	Species prey	Occ. *n*	Occ. %	MN ± S.D.	MRW ± S.D.
Cephalopods		42	30.2	7.85 ± 20.43	11.52 ± 25.62
Enoploteuthidae	*Abraliopsis* sp.	1	0.7	0.06 ± 0.71	0.00 ± 0.06
Histioteuthidae	*Histioteuthis hoylei*	1	0.7	0.03 ± 0.33	0.38 ± 4.46
Ommastrephidae	*Ornithoteuthis volatilis*	4	2.9	0.24 ± 1.84	0.36 ± 3.12
	Sthenoteuthis oualaniensis	3	2.2	0.40 ± 4.26	0.66 ± 6.37
Onychoteuthidae	*Moroteuthis lonnbergii*	3	2.2	0.20 ± 2.13	0.49 ± 5.04
	Walvisteuthis rancureli	9	6.5	1.49 ± 9.73	2.33 ± 12.68
Octopoteuthidae	*Taningia danae*	1	0.7	0.03 ± 0.33	0.00 ± 0.06
Pholidoteuthidae	*Pholidoteuthis boschmai*	1	0.7	0.03 ± 0.35	0.04 ± 0.43
Alloposidae	*Haliphron atlanticus*	4	2.9	1.30 ± 8.79	1.22 ± 7.52
Amphitretidae	*Amphitretus pelagicus*	3	2.2	0.28 ± 2.86	0.93 ± 8.46
Argonautidae	*Argonauta argo*	3	2.2	0.49 ± 4.36	1.00 ± 7.27
Bolitaenidae	*Japetella diaphana*	14	10.1	2.73 ± 11.74	3.28 ± 14.11
Tremoctopodidae	*Tremoctopus violaceus*	2	1.4	0.08 ± 0.56	0.21 ± 2.07
Octopodids larvae		4	2.9	0.34 ± 1.90	0.68 ± 6.16
Octopodidae	*Pteroctopus* sp.	1	0.7	0.06 ± 0.53	0.02 ± 0.23
Und. octopods		1	0.7	0.22 ± 2.16	0.03 ± 0.30
Spirulidae	*Spirula spirula*	1	0.7	0.02 ± 0.25	0.00 ± 0.05
Crustacea		115	82.7	64.02 ± 38.36	55.28 ± 41.48
Portunidae	*Charybdis smithii*	60	43.2	25.73 ± 37.17	32.49 ± 41.57
Crab larvae		5	3.6	0.30 ± 1.90	0.03 ± 0.17
Enoplometopidae	*Enoplometopus* sp.	3	2.2	0.56 ± 4.73	0.12 ± 1.05
Oplophoridae	*Oplophorus typus*	7	5.0	2.03 ± 10.17	0.49 ± 3.94
Odontodactylidae	*Odontodactylus scyllarus*	1	0.7	0.01 ± 0.14	0.01 ± 0.08
Squillidae	*Natosquilla investigatoris*	42	30.2	18.95 ± 33.57	16.28 ± 31.71
Phrosinidae	*Phrosina semilunata*	23	16.5	6.50 ± 18.34	1.62 ± 8.38
Pronoidae	*Parapronoe crustulum*	4	2.9	0.29 ± 2.25	0.02 ± 0.14
Phronimidae	*Phronima sedentaria*	1	0.7	0.03 ± 0.33	0.01 ± 0.12
Platyscelidae	*Platyscelus ovoides*	46	33.1	8.46 ± 18.84	4.09 ± 15.70
Brachyscelidae	*Brachyscelus crusculum*	3	2.2	1.05 ± 7.65	0.24 ± 1.94
Fishes		77	55.4	19.32 ± 30.30	27.44 ± 35.74
Acanthuridae	*Naso* sp.	1	0.7	0.04 ± 0.47	0.17 ± 2.02
Alepisauridae	*A. ferox*	17	12.2	2.07 ± 9.67	6.98 ± 21.29
Anoplogasteridae	*Anoplogaster cornuta*	1	0.7	0.18 ± 2.12	0.32 ± 3.81
Balistidae	*Canthidermis maculatus*	2	1.4	0.03 ± 0.33	0.05 ± 0.55
Bramidae	*Brama brama*	1	0.7	0.06 ± 0.65	0.33 ± 3.83
Carangidae	*Decapterus* sp.	1	0.7	0.78 ± 8.51	0.88 ± 8.67
Chiasmodontidae	*Chiasmodon niger*	3	2.2	0.68 ± 5.16	1.26 ± 10.25
Diodontidae	*Diodon* sp.	1	0.7	0.02 ± 0.20	0.22 ± 2.64
Exocoetidae	*Exocoetus volitans*	1	0.7	0.03 ± 0.39	0.18 ± 2.07
Myctophidae	*Diaphus* spp.	2	1.4	0.28 ± 2.43	0.99 ± 8.19
Nomeidae	*Cubiceps pauciradiatus*	3	2.2	0.15 ± 1.11	0.09 ± 0.90
Omosudidae	*Omosudis lowei*	23	16.5	4.91 ± 17.30	6.21 ± 19.52
Ostraciidae	*Ostracion cubicus*	1	0.7	0.05 ± 0.61	0.00 ± 0.04
Paralepididae		22	15.8	3.08 ± 13.28	3.86 ± 15.30
Phosichthyidae	*Vinciguerria nimbaria*	2	1.4	0.76 ± 8.49	0.74 ± 8.48
Scombridae	*Auxis* sp.	1	0.7	0.01 ± 0.07	0.01 ± 0.12
	Other scombrids	1	0.7	0.09 ± 1.06	0.01 ± 0.13
Scorpaenidae		1	0.7	0.02 ± 0.21	0.02 ± 0.23
Sternopthychidae	*Argyropelecus gigas*	4	2.9	0.51 ± 4.37	0.41 ± 2.74
	Argyropelecus sladeni	1	0.7	0.14 ± 1.70	0.04 ± 0.49
	Pterycombus petersii	1	0.7	0.18 ± 2.12	0.22 ± 2.59
	Sternoptyx diaphana	2	1.4	0.73 ± 8.48	0.84 ± 8.59
Tetraodontidae	*Lagocephalus lagocephalus*	1	0.7	0.06 ± 0.71	0.37 ± 4.36
Trachichthyidae	*Hoplostethus* sp.	2	1.4	0.14 ± 1.30	0.12 ± 1.35
Und. fishes		11	7.9	1.77 ± 9.87	1.89 ± 12.19
Fish larvae		11	7.9	2.54 ± 11.60	1.08 ± 7.23
Other prey		38	27.3	8.82 ± 19.82	5.76 ± 17.44
Alciopidae	*Rhynchonerella angelini*	23	16.5	2.96 ± 9.67	0.35 ± 1.30
Heteropods	*Carinaria* sp.	17	12.2	4.57 ± 14.66	4.28 ± 15.11
Pteropods		2	1.4	0.06 ± 0.51	0.01 ± 0.10
Plant		2	1.4	0.28 ± 2.12	0.25 ± 2.05
Salpidae		2	1.4	0.90 ± 8.73	0.79 ± 8.51

Occ.: occurrence, MN: mean proportion by number, MRW: mean proportion by reconstituted weight.

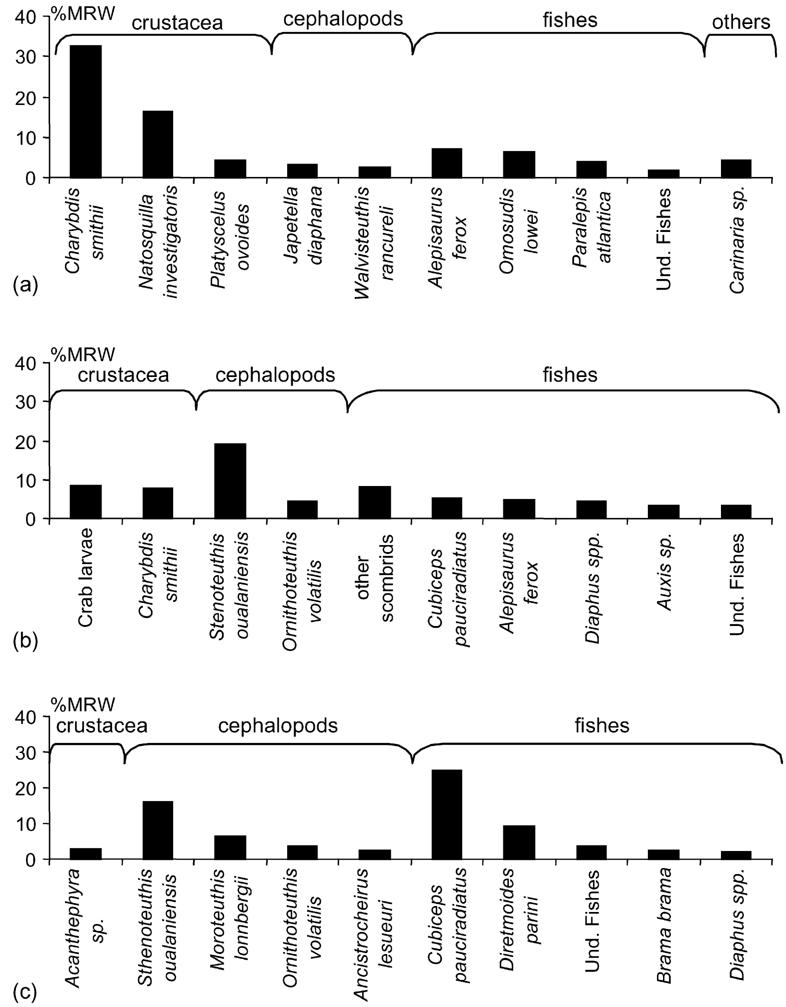

Fig. 4. Contribution of the main prey to the mean proportion by reconstituted weight (MRW) in the diet of (a) lancetfish, (b) yellowfin tuna, and (c) swordfish.

2.33% by MRW). Other cephalopod species did not exceed 0.6% each by MN. Crustaceans were rarely observed, except the oplophorid of the genus *Acanthephyra* (9.7% by MN and 2.7% by MRW).

3.3. Comparison of feeding regimes

For each pair of predators, the results of the Morisita–Horn index calculated using all the prey species or categories and the result calculated using only prey identified to the genus level were very close (Table 5). The confidence intervals estimated by bootstrap confirmed that yellowfin tuna and swordfish have the highest overlap indices (0.436–0.721) among all predator pairs. In fact, yellowfin tuna and swordfish share two similar prey that dominated the reconstituted weight: the ommastrephid *S. oualaniensis* and the nomeid *C. pauciradiatus* (Tables 3 and 4). At the other extreme, the swordfish-lancetfish pair exhibited very low overlap indices, while lancetfish and yellowfin tuna showed an intermediate level of trophic overlap.

The size distribution of different prey was also examined. Swordfish consumed larger fishes than lancetfish (Fig. 5a). The yellowfin tuna fish prey exhibited two modes that correspond to those of lancetfish and swordfish, respectively. The size distribution of *C. smithii* found in the stomachs of yellowfin tuna and lancetfish were identical (Fig. 5b). Among the cephalopod prey (Fig. 5c), the size distributions of the cephalopods found in the stomachs of yellowfin tuna and swordfish were clearly different: adults dominated in the swordfish's diet, whereas yellowfin tunas fed on juveniles.

3.4. Prey classification according to vertical habitat

Fig. 6 illustrates the occurrence of prey categorised by community (epipelagic versus mesopelagic organisms). Epipelagic prey dominated the diet of lancetfish and yellowfin tuna, whereas mesopelagic prey dominated the diet of swordfish.

Considering the main prey groups, mesopelagic fishes were more frequent than epipelagic in the diet of the three predators. Most of the crustacea prey were epipelagic species. They were preyed upon essentially by lancetfish and yellowfin tuna, and represented 94% and 100% of their crustacean prey, respectively. The shrimps of the oplophorid family were the single mesopelagic family observed in the stomachs. They were more frequent in the swordfish diet (28% of the content) than in any other predator. Epipelagic cephalopod prey were dominant in the lancetfish and yellowfin tuna diets: mainly octopods for

Table 3
Frequency of occurrence, mean proportion by number (MN) and mean proportion by reconstituted weight (MRW) of prey species or categories recovered from stomach contents (111 samples) (*Thunnus albacares*)

	Species prey	Occ.		MN ± S.D.	MRW ± S.D.
		n	%		
Cephalopods		65	58.6	15.99 ± 23.79	27.13 ± 34.57
Cranchiidae	*Cranchia scabre*	1	0.9	0.18 ± 1.92	0.41 ± 4.26
	Taonius sp.	1	0.9	0.10 ± 1.06	0.04 ± 0.42
Ctenopterygidae	*Ctenopteryx sicula*	1	0.9	0.09 ± 0.96	0.33 ± 3.46
Grimalditeuthidae	*Grimalditeuthis bonplandi*	2	1.8	0.22 ± 1.94	0.14 ± 1.06
Mastigoteuthidae	*Mastigoteuthis* sp	4	3.6	0.36 ± 2.51	0.23 ± 1.51
Ommastrephidae	*Ommastrephidae* spp.	1	0.9	0.46 ± 4.79	0.92 ± 9.58
	O. volatilis	28	25.2	4.73 ± 11.96	4.39 ± 13.75
	S. oualaniensis	50	45.0	9.01 ± 15.94	19.10 ± 29.85
Onychoteuthidae	*M. lonnbergii*	3	2.7	0.25 ± 1.51	0.30 ± 1.91
	Onychoteuthis banksi	2	1.8	0.07 ± 0.54	0.07 ± 0.58
	W. rancureli	3	2.7	0.28 ± 1.64	0.46 ± 3.68
Und. Oegopsida		1	0.9	0.04 ± 0.40	0.08 ± 0.86
Alloposidae	*H. atlanticus*	1	0.9	0.05 ± 0.48	0.03 ± 0.36
Bolitaenidae	*J. diaphana*	1	0.9	0.02 ± 0.23	0.06 ± 0.65
Tremoctopodidae	*T. violaceus*	1	0.9	0.04 ± 0.44	0.24 ± 1.61
Octopodids post larvae		1	0.9	0.09 ± 0.96	0.04 ± 0.36
Spirulidae	*S. spirula*	1	0.9	0.09 ± 0.96	0.00 ± 0.02
Crustacea		79	71.2	53.07 ± 40.12	24.47 ± 35.93
Portunidae	*C. smithii*	11	9.9	6.67 ± 21.81	7.71 ± 24.92
Crab larvae		45	40.5	25.85 ± 36.09	8.49 ± 21.64
Enoplometopidae	*Enoplometopus* sp.	3	2.7	0.70 ± 5.49	0.04 ± 0.30
Oplophoridae	*Acanthephyra* sp.	4	3.6	0.60 ± 4.89	0.19 ± 1.95
	O. typus	4	3.6	1.35 ± 9.54	1.43 ± 10.56
Lysiosquillidae	*Lysiosquilla tredecimdentata*	21	18.9	1.92 ± 6.60	0.91 ± 5.07
Odontodactylidae	*O. scyllarus*	30	27.0	3.59 ± 10.45	1.70 ± 5.20
Squillidae	*N. investigatoris*	4	3.6	1.71 ± 10.83	1.33 ± 9.67
	Neoanchisquilla tuberculata	2	1.8	0.89 ± 6.91	0.31 ± 2.77
Phrosinidae	*P. semilunata*	30	27.0	7.05 ± 17.27	2.20 ± 11.70
Brachyscelidae	*B. crusculum*	7	6.3	0.44 ± 3.25	0.29 ± 2.81
Platyscelidae	*P. ovoides*	15	13.5	2.27 ± 10.96	1.28 ± 10.02
Fishes		91	82.0	30.53 ± 35.41	48.39 ± 39.04
Alepisauridae	*A. ferox*	10	9.0	1.36 ± 6.99	4.64 ± 17.11
Argentinidae	*Nansenia macrolepis*	2	1.8	0.07 ± 0.54	0.29 ± 2.61
	Other argentinids	2	1.8	0.48 ± 4.79	0.84 ± 8.11
Balistidae	*C. maculatus*	4	3.6	0.42 ± 3.00	0.46 ± 2.82
Bramidae	*B. brama*	2	1.8	0.07 ± 0.55	0.55 ± 4.32
Carangidae	*Decapterus macrosoma*	8	7.2	1.42 ± 8.00	0.90 ± 4.30
Carapidae	*Echiodon* sp.	1	0.9	0.04 ± 0.47	0.05 ± 0.54
Chiasmodontidae	*C. niger*	1	0.9	0.13 ± 1.37	0.10 ± 1.03
Coryphaenidae	*Coryphaena equiselis*	2	1.8	0.03 ± 0.25	1.47 ± 10.93
Dactylopteridae	*Dactyloptena orientalis*	2	1.8	0.05 ± 0.45	0.04 ± 0.36
Exocoetidae	*E. volitans*	3	2.7	0.10 ± 0.60	1.14 ± 8.68
Gempylidae	*Gempylus serpens*	2	1.8	0.22 ± 1.66	2.07 ± 12.35
	Nealotus tripes	2	1.8	0.05 ± 0.33	0.17 ± 1.27
Hemiramphidae	*Hyporhamphus* sp.	1	0.9	0.31 ± 3.19	0.37 ± 3.85
Holocentridae	*Myripristis* sp.	4	3.6	0.14 ± 0.81	0.31 ± 2.10
Monacanthidae		3	2.7	0.10 ± 0.88	0.44 ± 2.67
Myctophidae	*Diaphus* spp.	16	14.4	2.47 ± 10.27	4.48 ± 14.19
Nomeidae	*C. pauciradiatus*	12	10.8	6.00 ± 21.65	5.04 ± 19.15
Omosudidae	*O. lowei*	10	9.0	0.50 ± 2.28	0.81 ± 3.01
Paralepididae	*Lestrolepis intermedia*	8	7.2	0.76 ± 4.92	1.06 ± 4.46
	Paralepis atlantica	18	16.2	2.40 ± 8.76	2.09 ± 6.55
Phosichthyidae	*V. nimbaria*	5	4.5	0.86 ± 5.49	0.14 ± 1.08
Scombridae	*Auxis* sp.	6	5.4	2.31 ± 12.54	3.18 ± 14.41
	Sarda orientalis	1	0.9	0.92 ± 9.58	0.92 ± 9.58
	Other scombrids	16	14.4	3.15 ± 10.39	7.93 ± 21.64
Scopelarchidae	*Scopelarchus analis*	2	1.8	0.23 ± 1.75	1.70 ± 12.14
Und. fishes		13	11.7	4.13 ± 15.98	3.18 ± 15.59
Fish larvae		11	9.9	1.83 ± 8.56	2.90 ± 13.30
Other prey		5	4.5	0.41 ± 2.17	0.01 ± 0.04
Heteropods	*Carinaria* sp.	2	1.8	0.14 ± 1.03	0.00 ± 0.02
Pteropods		1	0.9	0.16 ± 1.67	0.00 ± 0.02
Plant		2	1.8	0.05 ± 0.35	0.01 ± 0.05

Occ.: occurrence, MN: mean proportion by number, MRW: mean proportion by reconstituted weight.

Table 4
Frequency of occurrence, mean proportion by number (MN) and mean proportion by reconstituted weight (MRW) of prey species or categories recovered from stomach contents (130 samples) (*Xiphias gladius*)

	Species prey	Occ.		MN ± S.D.	MRW ± S.D.
		n	%		
Cephalopods		66	50.8	24.76 ± 33.53	35.53 ± 40.31
Chiroteuthidae	*Chiroteuthis* sp1	1	0.8	0.39 ± 4.40	0.35 ± 4.03
Cranchiidae	*Taonius* sp.	1	0.8	0.39 ± 4.40	0.22 ± 2.47
Enoploteuthidae	*Ancistrocheirus lesueuri*	6	4.6	0.89 ± 5.28	2.33 ± 11.91
	Enoploteuthidae sp1	2	1.5	0.42 ± 4.42	1.19 ± 9.54
Histioteuthidae	*H. hoylei*	3	2.3	0.54 ± 4.57	1.08 ± 7.67
	Histioteuthis meleagroteuthis	1	0.8	0.19 ± 2.20	0.06 ± 0.73
	Histioteuthidae sp1	1	0.8	0.11 ± 1.26	0.05 ± 0.53
Ommastrephidae	Ommastrephidae spp.	4	3.1	1.38 ± 9.97	1.73 ± 11.86
	O. volatilis	13	10.0	2.97 ± 11.68	3.76 ± 13.68
	S. oualaniensis	35	26.9	13.31 ± 27.70	15.93 ± 31.36
Onychoteuthidae	*M. lonnbergii*	12	9.2	3.41 ± 12.76	6.57 ± 21.42
Pholidoteuthidae	*P. boschmai*	1	0.8	0.16 ± 1.76	0.57 ± 6.43
Thysanoteuthidae	*Thysanoteuthis rhombus*	1	0.8	0.05 ± 0.55	0.66 ± 7.52
Und. Oegopsida		2	1.5	0.52 ± 4.63	1.21 ± 10.08
Crustacea		51	39.2	16.66 ± 26.28	5.49 ± 19.40
Portunidae	*C. smithii*	2	1.5	0.42 ± 3.49	0.03 ± 0.31
Peneidae	*Funchalia taaningi*	14	10.8	3.23 ± 12.07	1.26 ± 9.51
Oplophoridae	*Acanthephyra* sp.	35	26.9	9.66 ± 20.01	2.70 ± 13.50
	Acanthephyra sanguineus	2	1.5	0.32 ± 3.02	0.01 ± 0.06
	O. typus	1	0.8	0.13 ± 1.47	0.01 ± 0.09
Und. Shrimps		1	0.8	0.47 ± 5.28	0.12 ± 1.33
Squillidae	*N. investigatoris*	6	4.6	2.30 ± 12.60	1.36 ± 9.11
Fishes		107	82.3	58.58 ± 36.59	58.98 ± 40.92
Alepisauridae	*A. ferox*	2	1.5	1.12 ± 9.30	1.28 ± 9.71
Balistidae	*C. maculatus*	4	3.1	1.51 ± 10.17	1.85 ± 12.32
Bramidae	*B. brama*	7	5.4	2.13 ± 11.57	2.52 ± 13.34
Carangidae	*Decapterus* spp.	3	2.3	1.42 ± 10.21	0.87 ± 8.84
Coryphaenidae	*C. equiselis*	1	0.8	0.39 ± 4.40	0.70 ± 7.95
Diodontidae	*Diodon* sp.	1	0.8	0.16 ± 1.76	0.14 ± 1.54
Diretmidae	*Diretmus argenteus*	6	4.6	1.26 ± 9.11	1.56 ± 10.13
	Diretmoides parini	27	20.8	8.72 ± 20.58	9.02 ± 23.02
Exocoetidae	*E. volitans*	1	0.8	0.39 ± 4.40	0.29 ± 3.34
Gempylidae	*G. serpens*	6	4.6	1.10 ± 6.02	1.54 ± 7.53
	Thyrsitoides marleyi	1	0.8	0.19 ± 2.20	0.67 ± 7.60
Myctophidae	*Diaphus* spp.	7	5.4	2.14 ± 10.50	2.01 ± 10.57
	Lampadena luminosa	6	4.6	1.61 ± 9.37	1.16 ± 7.60
Nomeidae	*C. pauciradiatus*	58	44.6	26.32 ± 35.43	24.78 ± 36.08
Omosudidae	*O. lowei*	1	0.8	0.09 ± 0.98	0.04 ± 0.40
Paralepididae	*P. atlantica*	5	3.8	1.32 ± 9.39	1.30 ± 9.39
Scombridae	*Auxis* sp.	1	0.8	0.05 ± 0.52	0.05 ± 0.56
	Other scombrids	4	3.1	1.20 ± 9.24	1.22 ± 9.67
Scopelarchidae	*S. analis*	9	6.9	2.12 ± 8.24	1.54 ± 6.22
Stromateidae		2	1.5	0.22 ± 1.90	1.27 ± 10.24
Tetraodontidae	*L. lagocephalus*	2	1.5	0.45 ± 3.65	1.38 ± 11.06
Und. fishes		17	13.1	4.84 ± 16.39	3.59 ± 14.82

Occ.: occurrence, MN: mean proportion by number, MRW: mean proportion by reconstituted weight.

Table 5
Diet overlap estimated by the Morisita–Horn index and calculated by pair of predators using the proportions by reconstituted weight (MRW)

Predator	Lancetfish	Yellowfin tuna	Swordfish
Lancetfish	1	*0.326 (0.212–0.505)*	*0.048 (0.027–0.099)*
Yellowfin tuna	**0.321 (0.220–0.531)**	1	*0.540 (0.429–0.697)*
Swordfish	**0.043 (0.021–0.085)**	**0.572 (0.436–0.721)**	1

The values of the index computed with all the prey species or categories are in italics. The values computed with the prey identified to the genus level only are in bold. 95% confidence intervals generated by bootstrap are in parenthesis (500 replicates).

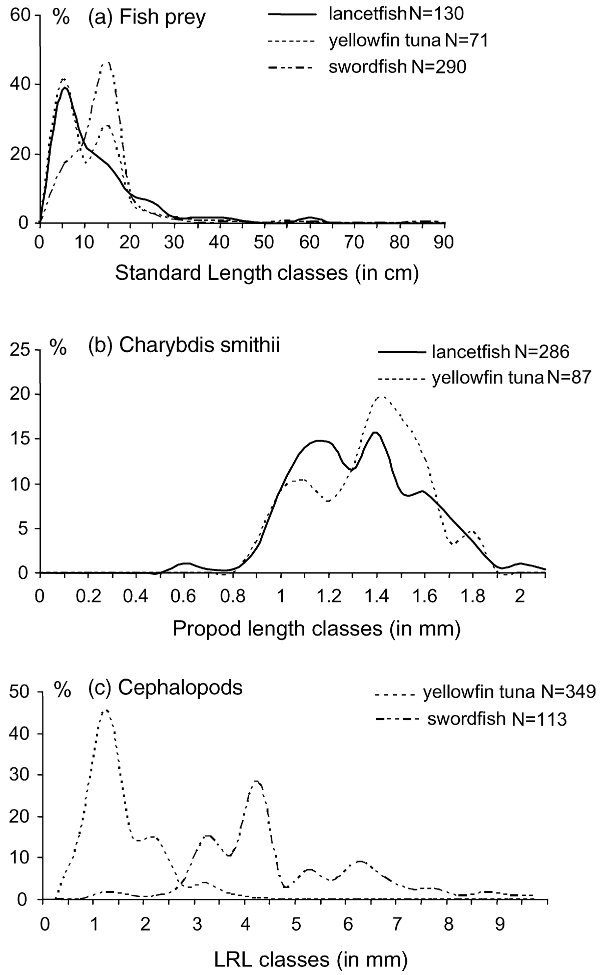

Fig. 5. Size spectra estimated from the size of fish prey, of *Charybdis smithii* and of ommastrephid prey recovered from the stomachs of the three predators.

lancetfish and juvenile ommastrephids (*S. oualaniensis*) for yellowfin tuna. Swordfish preyed essentially on the mesopelagic component of the cephalopod fauna: mainly adults of the ommastrephid and onychoteuthid families.

4. Discussion

4.1. Diet composition

This study is the first comparison of the diet composition of lancetfish, yellowfin tuna and swordfish in the western Indian Ocean based on an advanced taxonomic identification of the prey. For each predator, three to five prey items dominated the diet both by MN and by MRW: the most important items were *C. smithii* and *N. investigatoris* for lancetfish, juveniles of *S. oualaniensis*, *C. smithii* and *crab larvae* for yellowfin tuna, and *C. pauciradiatus* and adults of *S. oualaniensis* for swordfish.

The diet composition of lancetfish has been investigated in various areas of the world ocean (see Moteki et al., 1993), showing that its food composition can differ geographically. Haedrich and Nielsen (1966) and Fourmanoir (1969) noted a high degree of cannibalism among lancetfish in the Pacific. In our study, cannibalism was also observed (7% by MRW), but the overall diet is dominated by crustaceans (55.8% by MRW), a prey group already identified as dominant in previous studies (Fujita and Hattori, 1976; Moteki et al., 1993).

The pelagic crab *C. smithii* was also of importance (7.7% by MRW) in the diet of yellowfin tuna. Zamorov et al. (1992) were the first to report the importance of *C. smithii* for yellowfin tuna in the western tropical Indian Ocean. Predation on crabs has also been observed in the eastern tropical Pacific Ocean, where the red crab *Pleuroncodes planipes* and swimming crabs of the family Portunidae formed the main part of the yellowfin diet in certain areas (Alverson, 1963). Crab larvae were the most numerous prey items in numbers (25.9% by MN) in our analyses and their contribution by MRW was also significant (8.5%). In the study, the yellowfin tuna had the most balanced feeding regime of crustaceans, fishes and cephalopods among the three predators. Crustaceans dominate the yellowfin's diet by MN (53%), and fishes by MRW (48.4%). In the tropical eastern Pacific Ocean (Alverson, 1963) and in the tropical eastern Atlantic Ocean (Dragovich and Potthoff, 1972), the diet of the yellowfin tuna, analysed by volume and occurrence, exhibited the same global pattern. In the equatorial zone of the Indian Ocean, Kornilova (1981) showed that fishes prey were the most important prey by weight for yellowfin tuna.

Our findings showed that the diet composition of swordfish was dominated by mesopelagic fishes (Nomeidae and Diretmidae) and by mesopelagic cephalopods (Ommastrephidae and to a lesser extend Onychoteuthidae), contrary to other studies in the Atlantic and Pacific Oceans that cite cephalopods as the unique predominant component in the diet of swordfish (Toll and Hess, 1981; Stillwell and Kohler, 1985; Hernández-Garcia, 1995; Markaida and Hochberg, 2005).

Our stomach content analyses were performed on individuals caught by longlines set at relatively shallow depths compared to commercial longliners. Swordfish is a major target species of longline fisheries, and the lancetfish is a by-catch species, while yellowfin tuna is a target species of both purse-seine and longline fisheries. The diet composition of surface dwelling yellowfin tunas caught by purse-seine might give different results. In fact, several authors have shown that yellowfin tunas caught by purse seiners fed on monospecific concentrations of schooling prey in the surface layers of the equatorial Atlantic (Bard et al., 2002; Ménard and Marchal, 2003) and of the western Indian Ocean (Roger, 1994). In addition, Potier et al. (2004) found a lower diversity in the diet composition of yellowfin tunas caught by purse-seiners in the western tropical Indian Ocean. Maturity state may also influence the diet, however this effect was not considered here, because the maturity of each sampled adult predator was not recorded. Furthermore, our results are based on the analysis of a small number of stomach contents per predator species (from 111 to 139) collected during all the cruises. Extra samples would have enabled us to reinforce our analyses of diet composition—particularly to take into account spatio-temporal effects, which are evidenced by the high standard deviations of the diet indices calculated for each identified prey category (Tables 2–4). Indeed, feeding variability among individuals was probably due to the pooling of fish predators caught during nine scientific cruises carried out from 2001 to 2003 (Table 1).

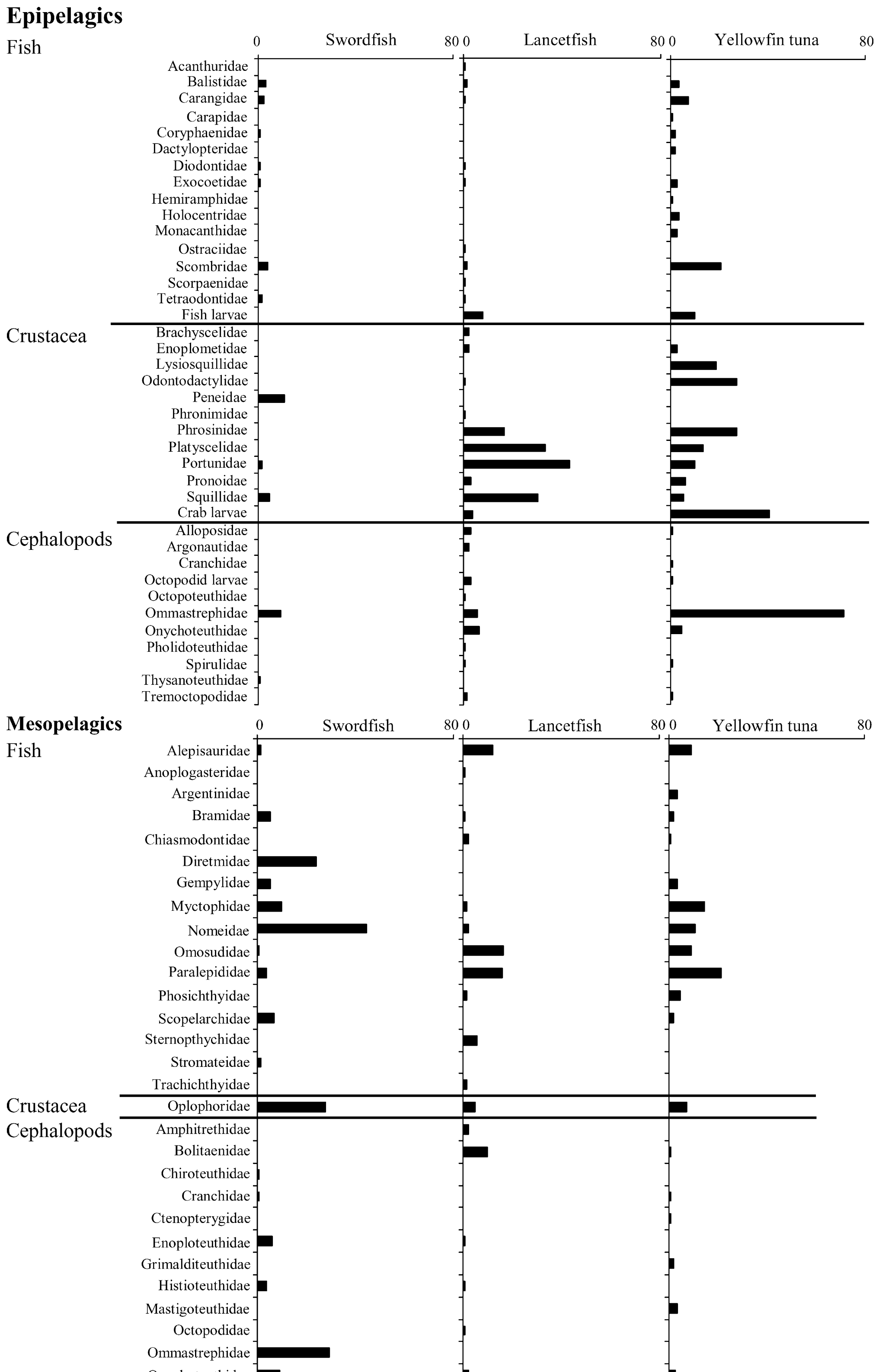

Fig. 6. Occurrence of the epipelagic and mesopelagic prey in the diet of lancetfish, yellowfin tuna and swordfish.

4.2. Resource partitioning

Diet indices for each prey species (or category), overlap index and prey size distributions give complementary information about the diet overlap and resource partitioning among the three predators. For example, the similarity in the diet of yellowfin tuna and swordfish, based on the Morisita–Horn index, is less valid once we consider the size of the cephalopod prey, because swordfish catch larger specimens than yellowfin tuna. And when we take into account the diet indices, the relatively high value of the Morisita–Horn index calculated between yellowfin tuna and lancetfish is due to the fact that they both feed on the same crustacean prey, while swordfish and lancetfish exhibit clear resource partitioning.

Dominance of the stomatopod *N. investigatoris* in the diet of lancetfish suggests that in the Seychelles area they feed primarily in the mixed layer. However, the proportion of mesopelagic fish prey (Omosudidae, Paralepididae and Alepisauridae) illustrated excursions of this predator to deeper layers during the day, and/or feeding activity at twilight on migrating fauna (Fig. 6). *N. investigatoris* was seldom found in the stomachs of yellowfin tuna, whereas Potier et al. (2004) found this Stomatopod was more dominant in the diet of yellowfin tuna caught by purse seiners. Among fish prey of the yellowfin tuna, the mesopelagic portion (66%) was greater than the epipelagic (33%), similar to the lancetfish. These two predators ingested 90% of the epipelagic fish prey identified in this study, and thus fed on animals that were available in shallower layers of the water column (Kornilova, 1981; Borodulina, 1982; Moteki et al., 1993, 2001; Bertrand et al., 2002). For swordfish, epipelagic species form only 9% of the total fish prey, and almost all cephalopod prey belong to the mesopelagic group. Swordfish are indeed known to undertake large vertical migrations (Carey and Robinson, 1981; Toll and Hess, 1981). In the study area, dissolved oxygen (DO) was less than 2.6 ml l^{-1} between 100 and 150 m. Such a concentration can limit the vertical movements of yellowfin (and probably lancetfish), but not those of swordfish, which have a higher tolerance to low oxygen levels (Carey and Robinson, 1981). Thus swordfish can prey actively at great depth.

4.3. Pelagic predators as biological samplers of micronekton organisms

The micronekton fauna of the western Indian Ocean is poorly documented. Hence, large pelagic predators such as lancetfish, tuna and swordfish can be efficient biological samplers for collecting information on micronektonic organisms, due to their opportunistic feeding behavior. The prey diversity in the stomach contents of top predators is constrained by local prey availability and the foraging behaviour of predators. To our knowledge, the only similar study in the area was performed by Kornilova (1981) on yellowfin and bigeye tunas. Therefore our study adds new information on the micronektonic organisms in the western Indian Ocean. We recorded a total of 67 families and 84 species of prey in the stomach contents of the three predators. Among them, eight species occurred in more than 10% of the stomach contents. The ommastrephid *S. oualaniensis* (23.2%), the nomeid *C. pauciradiatus* (19%) and the portunid *C. smithii* (19%) are the most prevalent prey species. The group with the highest number of taxa was fish prey (31 families and 40 species). The number of fish families found in stomach samples was 20 for lancetfish, 21 for yellowfin and 17 for swordfish.

Among crustaceans, the stomatopod *N. investigatoris* was a main prey of lancetfish. Since 1999, huge swarms of *N. investigatoris* have been observed in the surface waters of the western Indian Ocean, a sign of a recurrent demographic explosion previously reported in 1933, 1944 and 1965–1967 (Losse and Merrett, 1971). During this ongoing event, *N. investigatoris* has become the almost exclusive food of yellowfin tuna caught in surface schools by purse seiners in the Somali region (Potier et al., 2004). It is likely that this prey species has made up the bulk of the diet of the surface and sub-surface predators during the previous events. For instance, stomatopods (Squillidae) represented 44% (in weight) of the crustacean prey in the diet of the bigeye tuna caught in the western part of the Indian Ocean from 1969 to 1973 (Kornilova, 1981). If we assume that the dominance of a given prey in the diet of top predators reflects roughly its relative importance in the ecosystem, our results would suggest that pelagic crustaceans, juvenile ommastrephids and nomeids might play a key role in the food chain of large top predators such as yellowfin tuna and lancetfish in the western Indian Ocean during the period of 2001–2003.

Our results for yellowfin tuna can be compared with previous studies in the same area. At the family level, the diversity of the fish prey is similar to that estimated by Kornilova (1981). The higher number of fish families (34) found in Sri Lanka (Maldeniya, 1996) was related to the location of the surveys in coastal regions, while our study and Kornilova's study cover high sea ecosystems. Kornilova's work (1981) together with the present study offer the opportunity to compare the richness (number of species) in the yellowfin tuna diet for two distinct periods (1969–1973 versus 2001–2003). We extracted the results from Kornilova's study for the sub-area 10°N–10°S/40°E–60°E. In our study, the richness is 60% higher (54 species versus 33 species). The number of species recorded for crustaceans (12) and cephalopods (15) in the 2001–2003 period is twice the number found in the 1969–1973 period. Similarly, the number of fish species is higher (24 versus 19). For cephalopods and crustaceans, the same main prey species or categories were recovered during both time periods. The ommastrephid *S. oualaniensis*, the crab larvae, and the pelagic crab *C. smithii* represented the bulk of the cephalopod and crustacean prey. In contrast, the main fish prey differed between the studies. In Kornilova's study, the yellowfin tuna fed mainly on epipelagic fishes such as Exocoetids and the scombrid *Auxis thazard*, while mesopelagic fishes such as Alepisaurids, Nomeids and Bramids dominated the fish prey in the present study.

Precise information on the composition of prey available in the environment is required to study the potential selection of prey by different large pelagic top predators. Further investigations on forage fauna of top predators should then combine diet analysis with acoustic data and pelagic trawling, which may give independent information on the micronekton distribution and its behaviour.

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