Deep-Sea Research II 95 (2013) 83–92

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Pelagic cephalopods in the western Indian Ocean: New information from diets of top predators

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ARTICLE INFO

Available online 28 August 2012

Keywords:
Beaks
Diet composition
Ommastrephidae
Octopod
Pelagic fish
Sooty tern
Squid
Trophic ecology

ABSTRACT

Using a combination of diverse large predatory fishes and one seabird, we collected information on the cephalopod fauna of the western Indian Ocean. We analyzed the stomach contents of 35 fishes representing ten families (Xiphiidae, Istiophoridae, Scombridae, Carangidae, Coryphaenidae, Alepisauridae, Dasyatidae, Carcharhinidae, Alopiidae and Sphyrnidae) and of the sooty tern *Onychoprion fuscata* of the Mozambique Channel from 2000 to 2010. Both fresh and accumulated beaks were used for identifying cephalopod prey. Cephalopods were important prey for twelve predators; swordfish *Xiphias gladius* had the highest cephalopod proportion; sooty tern (*O. fuscata*) and bigeye tuna (*Thunnus obesus*) had high proportions too. We recovered 23 cephalopod families and identified 38 species. Ten species from four Teuthida families (Ommastrephidae, Onychoteuthidae, Histioteuthidae and Ancistrocheiridae) and two Octopoda families (Argonautidae and Bolitaenidae) occurred very frequently in the stomach contents, while Sepiida were rare. Ommastrephidae were the most cephalopod food sources: the purpleback flying squid *Sthenoteuthis oualaniensis* was the most prevalent prey by far, *Ornithoteuthis volatilis* was important for eleven predators and few but large specimens of the neon flying squid *Ommastrephes bartramii* were recovered in the stomachs of swordfish in the Indian South Subtropical Gyre province only. Predators' groups were identified based on cephalopod prey composition, on depth in which they forage, and on prey size. Surface predators' diets were characterized by lower cephalopod diversity but greater average numbers of cephalopod prey, whereas the deep-dwelling predators (swordfish and bigeye tuna) preyed on larger specimens than surface predators (*O. fuscata* or yellowfin tunas *Thunnus albacares*). Our findings emphasized the usefulness of a community of marine predators to gain valuable information on the biology and the distribution of the cephalopod forage fauna that are discussed with regard to biogeographic province, marine predator, fishing gear to catch the large pelagic fishes, and size of the beaks recovered in the stomachs.

1. Introduction

Cephalopods are widely distributed in the open ecosystems of the world ocean: they are among the most abundant in number and biomass of nektonic organisms (Jereb and Roper, 2010), and are a dominant component in marine food webs both as predators and as food for top predators (Rodhouse and White, 1995; Clarke, 1996; Boyle and Rodhouse, 2005). In addition they are a valuable direct human resource and are heavily exploited for bait by fisheries. Several important families such as the Ommastrephidae family (e.g., *Illex argentinus*, *Dosidicus gigas*) support major fisheries in both neritic and oceanic waters around the world (Rodhouse, 1997; Hunsicker et al., 2010). This commercial importance has made the large ommastrephids the target of many scientific investigations and their biology is consequently reasonably well-known (Nigmatullin et al., 2001; Zuyev et al., 2002; Bower and Ichii, 2005; Markaida, 2006; Parry, 2006, 2008; Xinjun et al., 2007). However, the biology and ecological role of the unexploited squid species remain poorly known in many areas of the world ocean, including the tropical and equatorial ecosystems of the Indian Ocean. Much more investigations are needed on cephalopods in order to better understand their role in the marine

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http://dx.doi.org/10.1016/j.dsr2.2012.08.022

ecosystems. But research cruises devoted to the study of squids are very few, and in addition, cephalopods are difficult to collect by nets. Large predatory fishes (e.g., tunas, billfishes, swordfish, etc.), marine mammals and seabirds can be efficient biological samplers for collecting information on cephalopods, due to their opportunistic feeding behavior (Rodhouse, 1990; Cherel and Weimerskirch, 1999; Cherel et al., 2004, 2007; Potier et al., 2007). Indeed, cephalopod predators capture larger specimens and a greater diversity of species than does sampling gear. In stomach contents, cephalopod beaks are diagnostic hard part structures that resist digestion and that can accumulate over time (beaks without flesh attached and/or eroded). Therefore, both fresh and accumulated beaks in good condition are a helpful source of information for identifying cephalopod prey ingested by predators (Clarke, 1986). Investigations on the dietary habits of large marine predators can thus provide new information on species composition, abundance, and distribution of cephalopods occurring within the predator foraging range (Cherel et al., 2004).

In this study, our main objective was to collect information on the cephalopod community of the western Indian Ocean using a combination of several large fish predators and one seabird as biological samplers. We used an extensive dataset of stomach samples collected from a diverse community of large predatory fishes representing ten families (Xiphiidae, Istiophoridae, Scombridae, Carangidae, Coryphaenidae, Alepisauridae, Dasyatidae, Carcharhinidae, Alopiidae and Sphyrnidae). Fishes were caught in the area by fishery vessels from 2000 to 2010. In addition, we used an extra dataset from dietary habit of sooty tern *Onychoprion fuscata* investigated during the breeding seasons on three islands of the Mozambique Channel (Europa, Juan de Nova and Glorieuses). The sooty tern is the most abundant marine bird species in all tropical waters. The cephalopod diversity recovered in the stomach contents of these marine predators is constrained by local prey availability and the foraging behavior of predators, including vertical distribution for fishes arising from physiological abilities. These varying sources of information allowed us to investigate the usefulness of cephalopod eaters for describing the importance of cephalopods in the pelagic food webs of the western Indian Ocean.

2. Material and methods

2.1. Sample collection

From 2000 to 2010, 35 large predatory fishes (sharks, billfishes, scombrids, carangids and other osteichthyes) were sampled in the western Indian Ocean from longline and purse seine cruises, and from troll lines, in three biogeographic provinces of Longhurst (1998): the Indian Monsoon Gyres province (MONS), the Indian South Subtropical Gyre province (ISSG), the Eastern Africa Coastal province (EAFR) (Fig. 1 and Table 1). Longhurst's division is based on biogeochemical properties of the provinces according to primary production, nutrients dynamics and mixed layer depth. Purse seine sets and troll lines sampled surface waters, while the average maximum depth reached by the longline hooks was 200 m. Fish were measured (lower jaw-fork length for billfishes and fork length for other species) and stomachs were collected onboard for diet analysis. In addition, stomach contents of sooty terns (*O. fuscata*) were collected during two consecutive breeding seasons at the three main colonies located in the Mozambique Channel (Fig. 1): on Europa island (22°20S, 40°22E) in 2002 and 2003, and on Juan de Nova Island (17°03S, 42°44E) and Lys Island (Glorieuses Archipelago 11°31S, 47°22E) in 2003 and 2004. Food samples were primarily collected at dusk when adult terns return to the colonies to feed their

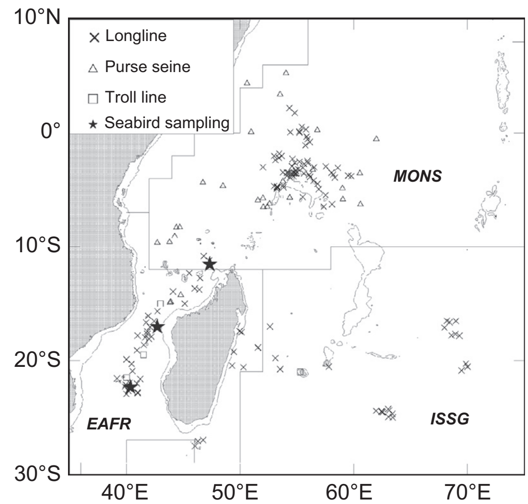

Fig. 1. Locations of the three types of fishing sets carried out during the study to collect stomach samples of predatory fishes. The sooty terns colonies located in the Mozambique Channel are shown.

Table 1
Number of stomachs with fresh remains only, collected for each predator in three biogeographic provinces of Longhurst (EAFR: the Eastern Africa Coastal province; ISSG: the Indian South Subtropical Gyre province; MONS: Indian Monsoon Gyres province).

Group	Species	Biogeographic province			Total
		EAFR	ISSG	MONS	
	Istiophorus platypterus	12		15	27
	Makaira indica		1	2	3
Istiophorids	*Makaira mazara*		3	1	4
	Tetrapturus angustirostris	9	2		11
	Tetrapturus audax	3	2	1	6
Xiphiid	*Xiphias gladius*	116	103	131	350
	Acanthocybium solandri	2	14	15	31
	Auxis thazard	2		1	3
	Euthynnus affinis			5	5
Scombrids	*Katsuwonus pelamis*	18	36	73	127
	Thunnus alalunga	5	4	4	13
	Thunnus albacares	73	31	284	383
	Thunnus obesus	40	2	56	98
	Caranx crysos			1	1
	Decapterus macarellus			6	6
Carangids	*Elagatis bipinnulata*	2		29	31
	Seriola rivoliana			7	7
	Uraspis secunda			2	2
	Alepisaurus ferox	122	1	139	262
	Canthidermis maculatus			5	5
	Coryphaena hippurus	34	35	31	100
Other osteichthyes	*Gempylus serpens*	1			1
	Kyphosus cinerascens			14	14
	Lobotes surinamensis			3	3
	Sphyraena barracuda	8	2	6	16
	Tarachtichthys steindachneri	1	1		2
	Alopias superciliosus	1		1	2
	Carcharhinus albimarginatus			1	1
	Carcharhinus falciformis	6		27	33
Sharks	*Carcharhinus longimanus*	2		1	3
	Carcharhinus plumbeus	1			1
	Galeocerdo cuvier			1	1
	Prionace glauca			1	1
	Sphyrna lewini			2	2
Rays	*Pteroplatytrygon violacea*	3		4	7
Seabirds	*Onychoprion fuscata*	325		108	433
Total		786	237	977	1995

chicks. They were mostly taken from randomly chicks by spontaneous regurgitation when handled, after a returning parent had completed feeding them. All samples were kept frozen at −20 °C. In the laboratory the same protocol was applied to each sample. Both accumulated (eroded fish otoliths; cephalopod broken beaks, beaks with no flesh attached, or beaks with damaged wings) and fresh items were sorted. Fresh remains were divided into broad prey classes (fishes, cephalopods, other molluscs, crustaceans and others) and weighed to calculate their proportion by wet mass in the diet. Identification of cephalopod prey relied on the external morphological features of either intact specimens or beaks (both lower and upper). Fresh cephalopod items without beaks were rarely recovered (≈1%). Beaks were identified by reference to features given by Clarke (1986) and by comparison with material held in our own reference collection. The World Register of Marine Species (WoRMS) was used to provide the names of the studied organisms (Appeltans et al., 2012). In this study 1562 and 433 stomach contents with prey remains were used for fishes and terns, respectively (Table 1).

2.2. Data analysis

Lower Rostral Length (LRL) of beaks was measured to 0.1 mm with a vernier caliper, and allowed us to estimate the size distributions of several cephalopod species in the predators' stomachs. In addition, the allometric equations given by Clarke (1986) were used to estimate dorsal mantle length (DML) of

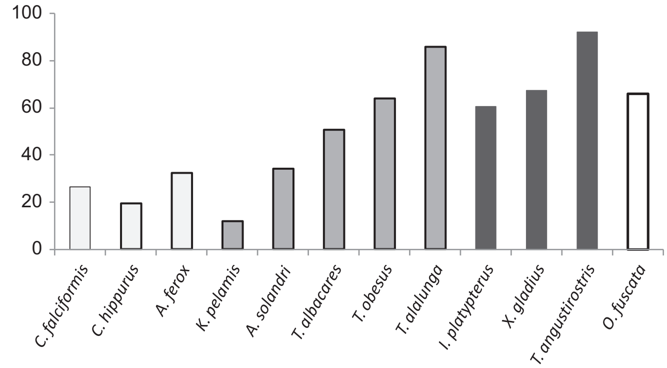

Fig. 2. Frequencies of occurrence of cephalopod prey in the diet of twelve predators (eleven predatory fishes and one seabird) in the western Indian Ocean. Occurrences were defined as the percentages of all the non-empty stomachs (including fresh and/or accumulated beaks). Different gray tones segregate the shark species *Carcharhinus falciformis*, from *Coryphaena hippurus* and *Alepisaurus ferox*, from scombrids (*Acanthocybium solandri*, *Thunnus albacares*, *T. obesus*, *T. alalunga*), from billfishes (*Istiophorus platypterus*, *Xiphias gladius*, *Tetrapturus angustirostris*), and from the sea bird *Onychoprion fuscata*.

Table 2
Frequency of occurrence (FO in number) and wet mass (in %) of prey types from fresh remains recovered in the stomachs of 35 large predatory fishes and one seabird from the western Indian Ocean. The mean length (in cm ± SD) is given for the predatory fishes in fork length (FL) or in lower jaw-fork length (LJFL).

Group	Species	Length measurement	Length ± SD (cm)	Cephalopods		Other molluscs		Crustaceans		Fish		Other	
				FO	Mass (%)	FO	Mass (%)	FO	Mass (%)	FO	Mass (%)	FO	Mass (%)
Istiophorids	*Istiophorus platypterus*	LJFL	187 ± 29	14	13.0	0	0.0	9	10.8	26	76.1	1	0.0
	Makaira indica	LJFL	224 ± 2	0	0.0	0	0.0	0	0.0	3	100.0	0	0.0
	Makaira mazara	LJFL	222 ± 11	0	0.0	0	0.0	0	0.0	4	100.0	0	0.0
	Tetrapturus angustirostris	LJFL	162 ± 15	8	20.0	0	0.0	2	0.4	11	79.6	0	0.0
	Tetrapturus audax	LJFL	204 ± 36	2	8.4	1	0.1	5	1.5	5	90.0	0	0.0
Xiphiid	*Xiphias gladius*	LJFL	136 ± 34	198	70.2	1	0.0	113	1.6	228	28.1	0	0.0
Scombrids	*Acanthocybium solandri*	FL	98 ± 22	7	1.9	0	0.0	1	0.5	29	97.5	0	0.0
	Auxis thazard	FL	40 ± 3	0	0.0	0	0.0	1	0.3	2	99.7	0	0.0
	Euthynnus affinis	FL	59 ± 6	0	0.0	0	0.0	3	16.5	4	83.5	0	0.0
	Katsuwonus pelamis	FL	63 ± 11	16	2.5	3	0.0	85	64.9	56	32.5	0	0.0
	Thunnus alalunga	FL	100 ± 6	9	13.4	0	0.0	7	79.3	10	7.4	0	0.0
	Thunnus albacares	FL	100 ± 32	144	7.1	7	0.0	256	59.3	251	33.5	15	0.0
	Thunnus obesus	FL	95 ± 33	53	23.2	0	0.0	45	48.0	52	28.8	1	0.0
Carangids	*Caranx crysos*	FL	43	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0
	Decapterus macarellus	FL	39 ± 2	0	0.0	0	9.2	1	84.9	0	5.9	0	0.0
	Elagatis bipinnulata	FL	62 ± 13	2	0.3	0	0.0	17	83.4	9	16.1	1	0.2
	Seriola rivoliana	FL	30 ± 1	0	0.0	0	0.0	2	72.6	1	27.4	0	0.0
	Uraspis secunda	FL	31	0	0.0	0	0.0	0	0.0	2	100.0	0	0.0
Other osteichthyes	*Alepisaurus ferox*	FL	115 ± 28	81	11.0	51	3.5	225	59.3	152	25.6	61	0.6
	Canthidermis maculatus	FL	33 ± 1	0	0.0	0	0.0	5	100.0	0	0.0	0	0.0
	Coryphaena hippurus	FL	92 ± 17	15	4.3	1	0.0	21	15.7	94	79.9	4	0.1
	Gempylus serpens	FL	86	1	15.0	0	0.0	1	64.5	1	20.6	0	0.0
	Kyphosus cinerascens	FL	25 ± 2	0	0.0	0	0.0	5	87.5	1	12.5	0	0.0
	Lobotes surinamensis	FL	44 ± 8	0	0.0	0	0.0	3	100.0	0	0.0	0	0.0
	Sphyraena barracuda	FL	98 ± 13	1	1.1	0	0.0	6	25.5	14	73.5	0	0.0
	Tarachtichthys steindachneri	FL	71	0	0.0	0	0.0	1	11.3	1	88.7	0	0.0
Sharks	*Alopias superciliosus*	FL	102 ± 16	2	13.7	0	0.0	0	0.0	0	86.3	0	0.0
	Carcharhinus albimarginatus	FL	86	0	0.0	0	0.0	0	0.0	1	100.0	0	0.0
	Carcharhinus falciformis	FL	114 ± 43	5	2.1	0	0.0	10	13.5	23	82.8	2	1.6
	Carcharhinus longimanus	FL	96 ± 29	1	0.1	0	0.0	2	64.7	2	10.1	1	25.1
	Carcharhinus plumbeus	FL	205	0	0.0	0	0.0	0	0.0	1	100.0	0	0.0
	Galeocerdo cuvier	FL	90	1	0.0	0	0.0	0	0.0	1	0.0	1	100.0
	Prionace glauca	FL	200	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0
	Sphyrna lewini	FL	182 ± 26	1	0.0	0	0.0	0	0.0	2	100.0	0	0.0
Rays	*Pteroplatytrygon violacea*	FL	46 ± 11	2	31.9	0	0.0	6	67.6	0	0.3	1	0.2
Seabirds	*Onychoprion fuscata*	[a]	[a]	286	41.1	0	0.0	17	0.7	381	58.2	9	0.0

[a] No data.

Table 3
Cephalopod prey in total number and percentage in the diet of eleven predatory fishes and one seabird from the western Indian Ocean.

Ordre	Family	Species	Istiophorids		Xiphiid			Scombrids			Osteichthyes		Sharks	Seabird
			Istiophorus platypterus	*Tetrapturus angustirostris*	*Xiphias gladius*	*Acanthocybium solandri*	*Katsuwonus pelamis*	*Thunnus alalunga*	*Thunnus albacares*	*Thunnus obesus*	*Coryphaena hippurus*	*Alepisaurus ferox*	*Carcharhinus falciformis*	*Onychoprion fuscata*
Octopoda	Amphitretidae	*Amphitretus pelagicus*	0	0	1 (0.2)	0	0	0	1 (0.1)	0	0	3 (2.3)	0	0
	Argonautidae	*Argonauta argo*	0	1 (1.5)	3 (0.5)	1 (4.3)	0	0	13 (0.9)	0	1 (4.3)	13 (10.0)	0	0
		Argonauta hians	0	0	0	0	1 (2.9)	0	5 (0.4)	0	0	0	0	0
	Alloposidae	*Haliphron atlanticus*	0	0	4 (0.7)	0	0	1 (2.1)	2 (0.1)	0	0	7 (5.4)	0	0
	Bolitaenidae	*Japetella diaphana*	0	0	3 (0.5)	0	0	1 (2.1)	10 (0.7)	20 (5.7)	0	9 (6.9)	0	0
	Tremoctopodidae	*Tremoctopus violaceus*	0	1 (1.5)	3 (0.5)	0	0	0	3 (0.2)	0	0	4 (3.1)	0	0
	Other octopoda		0	0	0	0	0	0	2 (0.1)	0	0	3 (2.3)	0	0
Sepiida	Spirulidae	*Spirula spirula*	0	0	2 (0.4)	0	0	0	1 (0.1)	2 (0.6)	1 (4.3)	1 (0.8)	0	1 (0.1)
	Sepiidae	*Sepia officinalis*	0	0	0	0	0	0	0	0	0	0	0	1 (0.1)
Teuthida	Ancistrocheiridae	*Ancistrocheirus lesueurii*	0	0	28 (5.0)	0	0	0	1 (0.1)	1 (0.3)	0	0	0	0
	Chiroteuthidae	*Chiroteuthis* sp.	0	0	1 (0.2)	0	0	0	1 (0.1)	0	0	0	0	0
		Grimalditeuthis bonplandi	0	0	0	0	0	0	2 (0.1)	1 (0.3)	0	0	0	0
	Cranchiidae	*Cranchia scabra*	0	0	2 (0.4)	0	0	0	1 (0.1)	0	0	0	0	0
		Taonius sp.	0	0	1 (0.2)	0	0	0	1 (0.1)	1 (0.3)	0	0	1 (3.4)	0
		Other Cranchiids	0	0	2 (0.4)	0	0	0	1 (0.1)	2 (0.6)	0	0	0	0
	Ctenopterygidae	*Chtenopteryx sicula*	0	0	0	0	0	0	2 (0.1)	2 (0.6)	0	0	0	0
	Cycloteuthidae	*Cycloteuthis akimushkini*	0	0	1 (0.2)	0	0	0	0	0	0	0	0	0
	Enoploteuthidae	*Abraliopsis gilchristi*	0	0	0	0	0	0	0	0	0	1 (0.8)	0	0
		Other Enoploteuthids	0	0	6 (1.1)	0	0	0	6 (0.4)	5 (1.4)	0	0	0	8 (1.1)
	Histioteuthidae	*Histioteuthis hoylei*	0	0	15 (2.7)	0	0	0	0	3 (0.9)	0	3 (2.3)	0	0
		Histioteuthis meleagroteuthis	0	0	1 (0.2)	0	0	0	0	0	0	0	0	0
		Histioteuthis sp.	0	0	6 (1.1)	0	0	0	0	0	0	0	0	0
	Mastigoteuthidae	*Mastigoteuthis* sp.	0	0	1 (0.2)	0	0	2 (4.2)	25 (1.8)	4 (1.1)	0	0	1 (3.4)	0
	Neoteuthidae		0	0	1 (0.2)	0	0	0	2 (0.1)	0	0	0	0	0
	Octopoteuthidae	*Octopoteuthis* sp.	0	2 (3.0)	0	0	0	0	1 (0.1)	0	0	0	0	0
		Taningia danae	0	0	0	0	0	0	2 (0.1)	1 (0.3)	0	2 (1.5)	0	0
	Onychoteuthidae	*Onychia loennbergii*	1 (0.8)	3 (4.5)	70 (12.5)	2 (8.7)	0	0	7 (0.5)	22 (6.3)	0	4 (3.1)	0	2 (0.3)
		Callimachus rancureli	0	0	0	0	0	0	24 (1.7)	17 (4.8)	0	9 (6.9)	1 (3.4)	0
		Onychoteuthis banksii	2 (1.6)	2 (3.0)	3 (0.5)	0	0	4 (8.3)	32 (2.3)	1 (0.3)	0	1 (0.8)	1 (3.4)	0
		Other Onychoteuthids	0	0	0	0	0	0	0	0	0	0	0	2 (0.3)
	Ommastrephidae	*Ommastrephes bartramii*	0	0	136 (24.4)	0	0	0	1 (0.1)	0	0	0	0	0
		Ornithoteuthis volatilis	2 (1.6)	6 (9.1)	43 (7.7)	1 (4.3)	4 (11.8)	12 (25.0)	281 (19.8)	31 (8.8)	0	8 (6.2)	1 (3.4)	42 (5.7)
		Sthenoteuthis oualaniensis	117 (91.4)	51 (77.3)	174 (31.2)	17 (73.9)	29 (85.3)	9 (18.8)	931 (65.7)	195 (55.4)	11 (47.9)	7 (5.4)	20 (69.0)	474 (64.8)

	Other Ommastrephids	0	0	3 (0.5)	0	0	0	0	0	0	0	0	164 (22.4)
Pholidoteuthidae	*Pholidoteuthis boschmai*	0	0	1 (0.2)	0	0	0	3 (0.2)	12 (3.4)	0	1 (0.8)	0	0
Pyroteuthidae	*Pterygioteuthis* sp.	0	0	0	0	0	1 (2.1)	0	1 (0.3)	0	0	0	0
Thysanoteuthidae	*Thysanoteuthis rhombus*	0	0	7 (1.3)	0	0	0	3 (0.2)	3 (0.9)	0	0	0	0
Undetermined fresh cephalopods		6 (4.6)	0	40 (7.2)	2 (8.7)	0	18 (37.5)	52 (3.7)	28 (8.0)	10 (43.5)	54 (41.5)	4 (13.8)	37 (5.1)
Total		128 (100.0)	66 (100.0)	558 (100.0)	23 (100.0)	34 (100.0)	48 (100.0)	1416 (100.0)	352 (100.0)	23 (100.0)	130 (100.0)	29 (100.0)	694 (100.0)

Sthenoteuthis oualaniensis and *Ornithoteuthis volatilis* from LRL, and then to compute predator–prey size ratios. The proportion of each identified cephalopod taxon was expressed in two ways, i.e.: frequency of occurrence (FO) and percentage of total number (%*N*).

The potential effects of explanatory variables (biogeographic provinces, predator species, and fishing gear) on the cephalopod prey composition in the predators' diet were investigated using Kruskal–Wallis (KW) non-parametric tests and the classification and regression tree (CART) approach proposed by 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 the data are represented by a single node at the top of the tree. Then the tree is 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. To keep the tree reasonably small, a prune back procedure is applied. Following Kuhnert et al. (2011), we predicted the composition of cephalopod prey consumed by the predators, given the explanatory variables. The proportion in number of a cephalopod prey is calculated as a case weight for the classification tree model. Undetermined cephalopods were not taken into account in the analysis. For a given predator, identified cephalopod items have observed weights (proportions in number). Each terminal node (or leaf) of the tree is characterized by a predicted cephalopod prey distribution. Analyses were conducted using the library *rpart* of the statistical open source R software (R Development Core Team, 2011).

3. Results

3.1. Cephalopods in the diet of the predators

Fish prey dominated by wet mass ($>50\%$) the diet of 18 predators among the 35 fish predators investigated in our study, and the diet of the sooty tern (Table 2). For seven species, fish were the only food source. Cephalopods constituted the majority of the mollusc prey by wet mass except for *Decapterus macarellus*. Twenty-one predators had fresh remains of cephalopods in their diet. No predator had only accumulated beaks. A total of 3684 lower beaks were recovered in predators' stomachs: 2360 beaks were fresh items and 1324 were accumulated. *Xiphias gladius* showed the highest cephalopod proportion by wet mass by far (70%; Table 2), and sooty tern (*O. fuscata*) and bigeye tuna (*Thunnus obesus*) had high proportions too (41% and 23%, respectively). Cephalopods (both fresh and accumulated items) were an important prey class for twelve predators that were properly sampled in our study: stomach number with fresh cephalopod remains (plus accumulated beaks) ranged from 5 (9) for *Carcharhinus falciformis* to 286 (286) for *O. fuscata*. Fig. 2 illustrates the occurrence (in %) of cephalopods in their diets. For the three billfishes more than 60% of the stomachs contained cephalopods, and *Tetrapturus angustirostris* had the highest occurrence (92%). For scombrids, the frequency of occurrence ranged from 12% (*Katsuwonus pelamis*) to 86% (*Thunnus alalunga*). Dolphinfish (*Coryphaena hippurus*) and lancetfish (*Alepisaurus ferox*) showed an occurrence of 20% and 32%, respectively, while cephalopods occurred in 26% of the silky shark. Lastly, 66% of the stomach contents of sooty terns contained cephalopod remains.

Kruskal–Wallis tests showed that fishing gear ($H=18.8$, df$=2$, $P<0.001$), biogeographic province ($H=36.6$, df$=2$, $P<0.001$) and predator species ($H=175.7$, df$=19$, $P<0.001$) influenced the cephalopod number recovered in the stomachs of predatory fishes. Overall, purse seiners (surface gear) caught predators that feed more on cephalopods than longliners; the MONS province ranked first in terms of frequency by number; and the average number of cephalopods ranged from 2 (*Elagatis bipinnulata*, *Gempylus serpens*, *Pteroplatytrygon violacea*) to 43 (*Alopias superciliosus*). Note that 124 *S. oualaniensis* were recovered in the stomach of one yellowfin tuna (*Thunnus albacares*) caught by troll line in the EAFR province. For sooty terns, the average number of cephalopods was low compared with fish stomach contents and differed by province: 2.2 ± 1.57 and 3.6 ± 2.95 in EAFR and MONS provinces, respectively (Wilcoxon rank sum test, $W = 4963$, $P < 0.001$).

3.2. Cephalopod diversity

Among the twelve selected predators, the ommastrephid *S. oualaniensis* was the most important identified cephalopod prey by far, contributing to more than 50% of the total number of cephalopods for six predators, and up to 91% for *Istiophorus platypterus* (Table 3). *S. oualaniensis* ranked first for ten predators, second for *T. alalunga*, and five for *A. ferox*. Two other Ommastrephidae were important cephalopod food sources: *O. volatilis* was frequently recovered in the diet of eleven predators, and *Ommastrephes bartramii* contributed significantly to the total number of identified cephalopod prey of *X. gladius*. The Onychoteuthidae *Onykia loennbergii*, *Callimachus rancureli* and *Onychoteuthis banksii* were other important cephalopod prey. The argonautid *Argonauta argo* was abundant in the diet of the lancetfish *A. ferox*, as the pelagic octopus *Japetella diaphana* for lancetfish and for the bigeye tuna *T. obesus* too. Other important cephalopod prey included *Ancistrocheirus lesueurii*, *Histioteuthis hoylei* and *Haliphron atlanticus* (Table 3). Table 4 displays the occurrence of cephalopod prey for eight extra predators with a low number of sampled stomachs (cephalopod remains were not identified for *Gempylus serpens*).

Fig. 3 displayed the species richness of the cephalopod prey identified in the stomach contents of the twelve predators. Contributions of the three known orders of cephalopods (Sepiida, Octopoda and Teuthida) are indicated. Two tuna species (*T. albacares*, *T. obesus*), the swordfish (*X. gladius*) and the lancetfish (*A. ferox*) had the highest diversity (from 16 to 28 identified taxa in their diets). In this study, Octopoda grouped five families including six identified species, but they did not contribute significantly to the total number of cephalopod prey except for lancetfish and to a less extent for bigeye tuna (Table 3). Sepiida are represented by two species rarely recovered in the diet of our predators: *Sepia officinalis* (one specimen in the stomach of a sooty tern only) and *Spirula spirula*. Teuthida dominated the cephalopod prey by far, with 16 families including 24 species. The most significant families were Ommastrephidae, Onychoteuthidae, Histioteuthidae and Ancistrocheiridae (one species only).

3.3. Classification tree for diet data

To investigate the structure of the diet data and assess the influence of explanatory variables, we conducted a classification tree analysis on the proportions in number of the identified cephalopod prey consumed by the predators, using fishing gear, biogeographical province and predator species as covariates. Four groups were identified by the pruned tree (Fig. 4). The first split separated predator species: one group clustered a great number of predators (930) including all the istiophorids, four scombrids, two sharks, two other osteichthyes and the sooty terns. The diet of these predators was dominated by *S. oualaniensis* and to a less extent by *O. volatilis*. Further splits separated the MONS province from ISSG and EAFR provinces. The EAFR and ISSG group mixed 217 fish predators from six species whose diet was dominated by *O. bartramii*, *O. loennbergii* and *S. oualaniensis*. Then the "MONS"

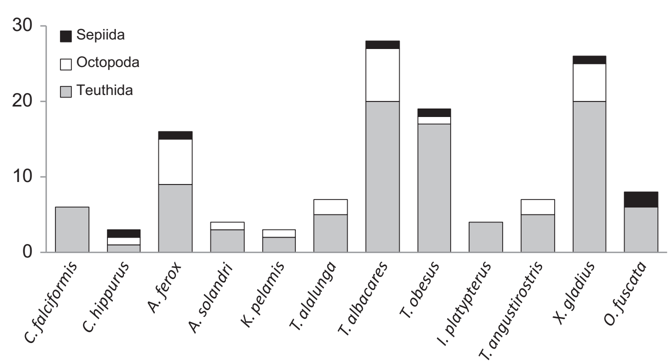

Fig. 3. Species richness of cephalopod prey recovered in the diet of twelve predators (eleven predatory fishes and one seabird) in the western Indian Ocean, and contribution of the three orders Sepiida, Octopoda and Teuthida of cephalopods.

Table 4
Occurrence of the cephalopod prey in the diet of one billfish, two predatory fishes, four sharks and one ray from the western Indian Ocean. The low number of sampled stomachs for that species did not allow us to estimate proportions by number.

Ordre	Family	Species	Istiophorids	Osteichthyes		Sharks				Rays
			Tetrapturus audax	*Elagatis bipinnulata*	*Sphyraena barracuda*	*Carcharhinus longimanus*	*Alopias superciliosus*	*Galeocerdo cuvier*	*Sphyrna lewini*	*Pteroplatytrygon violacea*
Octopoda	Argonautidae	*Argonauta argo*		X						
	Alloposidae	*Haliphron atlanticus*						X		
Sepiida	Spirulidae	*Spirula spirula*		X						
Teuthida	Ancistrocheiridae	*Ancistrocheirus lesueurii*						X		
	Cycloteuthidae	*Cycloteuthis akimushkini*						X		
	Gonatidae	*Gonatus antarcticus*						X		
	Histioteuthidae	*Histioteuthis hoylei*				X		X		
		Histioteuthis sp.							X	
	Octopoteuthidae	*Taningia danae*				X			X	
	Ommastrephidae	*Ornithoteuthis volatilis*	X							X
		Sthenoteuthis oualaniensis	X		X		X			

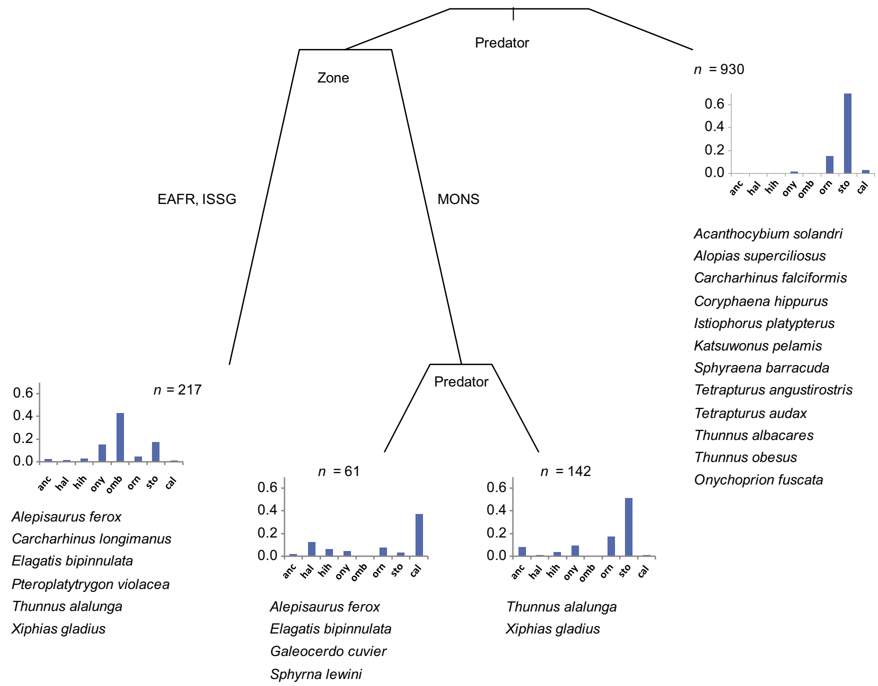

Fig. 4. Pruned classification tree that predicts the composition of cephalopod prey consumed by the predators. Each terminal node of the tree is characterized by a predator number, a predicted prey distribution for the main cephalopod species (anc: *Ancistrocheirus lesueuri*, hal: *Haliphron atlanticus*, hih: *Histioteuthis hoylei*, ony: *Onykia loennbergii*, omb: *Ommastrephes bartramii*, orn: *Ornithoteuthis volatilis*, sto: *Sthenoteuthis oualaniensis*, cal: *Callimachus rancureli*), and a subset of predators. Explanatory variables used to develop the tree are predator species and biogeographic provinces of Longhurst (EAFR: the Eastern Africa Coastal province; ISSG: the Indian South Subtropical Gyre province; MONS: Indian Monsoon Gyres province).

branch of the tree separated two groups of predators: one grouped *T. alalunga* and *X. gladius* with a predicted cephalopod prey distribution dominated by *S. oualaniensis*, and then by *O. volatilis*, *O. loennbergii* and *A. lesueurii*; the second group clustered 62 fish predators from 4 species with *C. rancureli* the most dominant predicted cephalopod prey, and with *H. atlanticus* and *H. hoylei* as other important cephalopod prey. Fishing gear was never retained as an influenced explanatory variable in the pruned tree.

3.4. Prey size

The size distribution of six cephalopod species for which more than 30 measures of lower rostral length (LRL) were carried out, was examined (Fig. 5). The modes of the size distributions were similar for *C. rancureli*, *S. oualaniensis*, *O. volatilis* and *O. banksii*, but two species (*O. bartramii* and *O. loennbergii*) showed greater LRL and flat distributions. Overall, these six species were segregated by their LRL ($H=547.3$, df=5, $P<0.001$). Pairwise comparisons indicated that *O. banksii* and *S. oualaniensis* did not differ significantly, such as *O. volatilis* and *C. rancureli*. Then we statistically analyzed the differences in LRL of the same cephalopod species eaten by different predators. Fig. 6 displays the cases for *S. oualaniensis* and *O. volatilis* and Table 5 shows the estimated prey:predator size ratios from DML and predator body length averages. Predator species, for which more than 24 measures of LRL were carried out, were selected. Differences were significant for *S. oualaniensis* ($H=590.2$, df=5, $P<0.001$) (Fig. 6a). Pairwise comparisons indicated that mean size was identical for *I. platypterus*, *T. angustirostris* and *T. obesus*, only. Swordfish consumed the largest *S. oualaniensis*, while the yellowfin tuna *T. albacares* and especially the sooty terns preyed on the smallest specimen. For *O. volatilis*, the three predator species did not eat on the same size classes ($H=110.1$, df=2, $P<0.001$): the yellowfin tuna consumed the smallest individuals, while swordfish preyed on the biggest (Fig. 6b). Prey:predator size ratios ranged from 3.5% to 14.8% (swordfish).

4. Discussion

Overall the micronekton fauna of the western Indian Ocean is poorly documented. To our knowledge this study is the first in the western Indian Ocean that investigates the importance of pelagic cephalopods using an extensive number of marine predators as biological samplers of the cephalopod fauna. Potier et al. (2007) analyzed the prey composition and the resource partitioning among three large pelagic fish predators caught by longline in the waters surrounding the Seychelles Islands. These authors showed that fish prey was the group with the highest number of taxa (31 families and 40 species), and they recovered 19 cephalopod families and identified 25 species. Our data put together the dataset of Potier et al. (2007) and new data from additional areas, from surface fishing gears (purse seine and troll line), and from stomach contents of the sooty tern collected from three colonies in the Mozambique Channel (Jaquemet et al., 2008). In our study, we recovered 23 cephalopod families and we identified 38 species, i.e. 34% more than Potier et al. (2007). Among them, ten species from four Teuthida families (Ommastrephidae, Onychoteuthidae, Histioteuthidae and Ancistrocheiridae) and two Octopoda families (Argonautidae and Bolitaenidae) occurred frequently in the stomach contents of our predators (Table 3). Ommastrephidae strongly dominated the cephalopod forage fauna and the purpleback flying squid *S. oualaniensis* was the most prevalent prey by far. Previous soviet investigations carried out in the same area showed that *S. oualaniensis* represented 26.7% and 15.1% of the total index of relative importance (IRI) in the diet of yellowfin and bigeye tunas caught by longliners (non-published data). Our findings corroborate studies on the diet of two other tropical seabirds breeding on Europa Island in the Mozambique Channel. *S. oualaniensis* contributed 19% by number in the diet of great frigatebirds *Fregata minor* (Weimerskirch et al., 2004) and 15.4% by reconstituted weight in the diet of the red-tailed tropicbird *Phaethon rubricauda* (Le Corre et al., 2003).

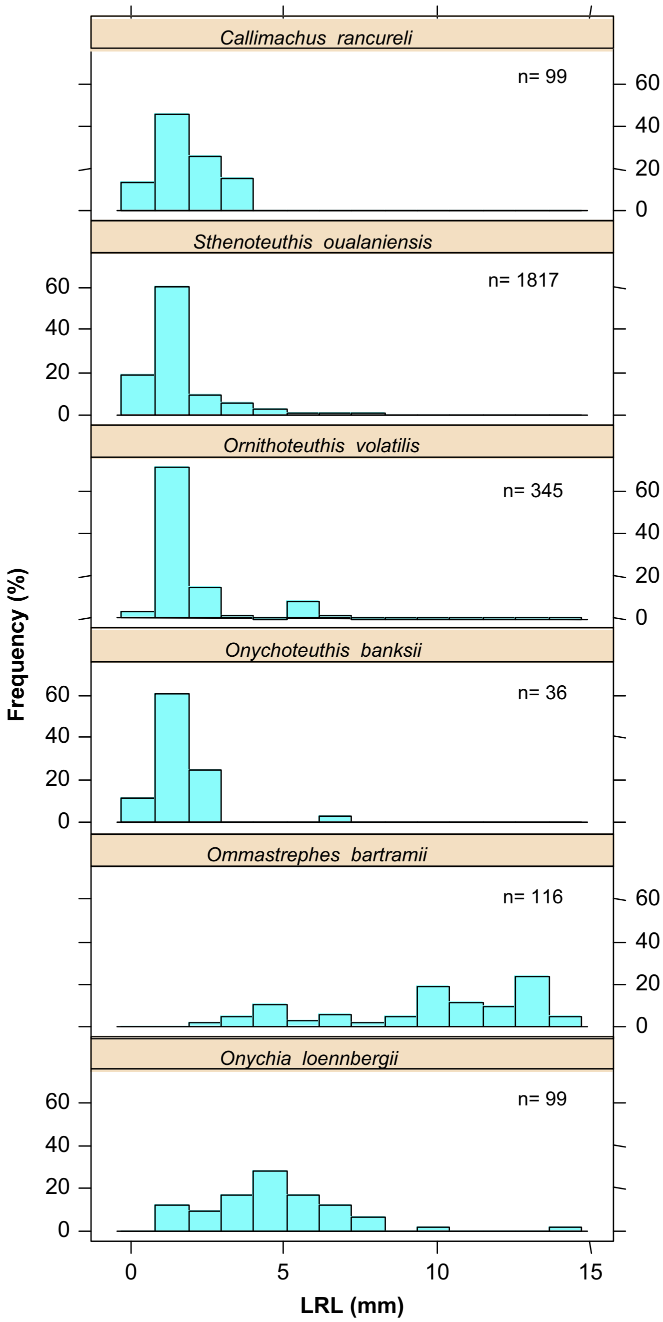

Fig. 5. Frequency distribution of lower rostral lengths (LRL in mm) of six cephalopod species eaten by twelve predators in the western Indian Ocean.

In addition red-footed boobies *Sula sula* at Tromelin Island consumed mostly squid of the family Ommastrephidae (Kappes et al., 2011), and squids (most likely ommastrephids) figured prominently in the diet of two other seabird species (brown noddy *Anous stolidus* and white-tailed tropicbird *Phaethon lepturus*) in the Seychelles archipelago (Catry et al., 2009).

S. oualaniensis is widely distributed and abundant in the oceanic tropical Indo-Pacific zone (Jereb and Roper, 2010). In the Indian Ocean, the biomass of this truly pelagic species has been roughly estimated about two million tons (Zuyev et al., 1985). In the Northern part of the Arabian Sea, its density could reach up to 4–8 tons km^{-2} (Gutsal, 1989). But the structure of *S. oualaniensis* populations remains poorly known. In addition, the species is most likely in a process of adaptive radiation. Nesis (1993) described three different forms, which differ by anatomy, geographic distribution and period of spawning: (1) the giant form is found exclusively in the Red and Arabian Seas; (2) the dwarf form, with no photophore, inhabits the equatorial waters of the Indian Ocean, and spends most of its life in the upper mixed layers; (3) the middle-sized form, characterized by a dorsal photophore, is the most abundant and has a wider geographic repartition with a much deeper vertical distribution than the dwarf form. However, two extra forms have been segregated on the basis of gladius morphology and presence or absence of dorsal photophore (Jereb and Roper, 2010; Young and Vecchione, 2011).

According to Potier et al. (2011), the twelve main predators of this study can be grouped in three classes on the basis of prey size and prey taxonomy. *K. pelamis*, *C. hippurus*, *I. platypterus*, *A. solandri* and *C. falciformis* foraged in the surface layer. *T. albacares*, *T. alalunga*, *T. angustirostris*, and *A. ferox* fed primarily in the mixed layer, while *T. obesus* and *X. gladius* were deep-dwelling fish predators. Surface predators were characterized by a lower diversity of cephalopod forage fauna than predators of the two other categories. Indeed these last predators can forage deeper and then can have access to a more diverse prey community in the water column. However stomach contents of surface fish predators caught by purse seiners (mainly tunas) had a greater average number of cephalopods than sub-surface predators caught by longliners. Tunas caught by purse seiners occur generally in dense schools at the surface and these tunas usually seek out and feed on large concentrations of monospecific prey (Bard et al., 2002; Ménard and Marchal, 2003). In our case, we thus believe that some surface predators caught by purse seiners or troll lines with fresh remains of cephalopods feed sometimes on concentrations of juveniles squids that usually live in the homogeneous surface layer. The highest numbers of *S. oualaniensis* were indeed recovered in stomachs of yellowfin tunas caught by surface fishing gears. Large schools with huge number of individuals are common for squids, and it has been shown for the purpleback flying squid that diurnal vertical migrations by juveniles were absent or very short in distance (Zuyev et al., 1985, 2002).

The neon flying squid *O. bartramii* was a dominant cephalopod prey in the diet of swordfish caught in the ISSG biogeographical province, whereas swordfish preyed on *S. oulaniensis* in the MONS province. *O. bartramii* is another widely distributed ommastrephid species, but it is indeed absent in the equatorial waters of the three oceans (Jereb and Roper, 2010). Soviet studies already showed that the importance of the purpleback squid in the diet of tunas decreased in the tropical waters around Mauritius (6.2% of the IRI for yellowfin tuna; non-published data). The distribution of both species overlapped in the samples collected in the ISSG and EAFR (i.e., in the Mozambique Channel) provinces. However frequency distributions of LRL of *O. bartramii* and *S. oualaniensis* showed great size differences (Fig. 5). *O. bartramii* obviously reached the greatest sizes in our samples. In the North Pacific the mean size of *S. oualaniensis* was about 40% of the mantle length of the smallest *O. bartramii* (Young and Hirota, 1998) and both squid species have clearly different trophic ecology (Parry, 2006). Few *O. bartrami* were indeed recovered in the stomachs of swordfish in ISSG province but their big size compensated obviously a great number of small *S. oualaniensis* (or any small prey).

The size distribution of the beaks of the purpleback squid recovered in the stomachs differed among predators (Fig. 6A): swordfish caught the largest specimens, bigeye tunas ranked second, while sooty terns fed on the smallest specimens. The same trend was observed for *O. volatilis* (Fig. 6B). Swordfish and bigeye tunas are known to undertake large vertical migrations. They can prey actively at greater depths and catch larger specimens than other predators such as yellowfin tuna

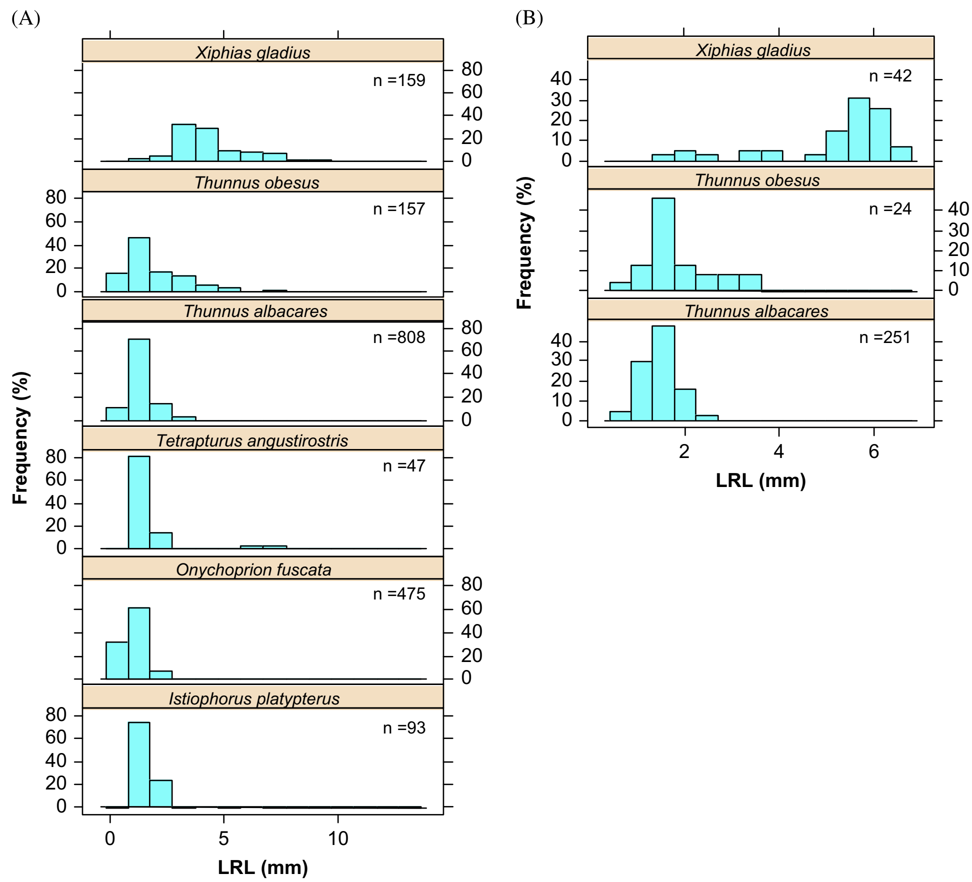

Fig. 6. Frequency distribution of lower rostral lengths (LRL in mm) of (A) *Sthenoteuthis oualaniensis* eaten by five predatory fishes and the sooty tern *O. fuscata*, and (B) *Ornithoteuthis volatilis* eaten by three predatory fishes.

Table 5
Estimated prey:predator size ratios (in %) from averages of dorsal mantle length (DML in mm) of *Sthenoteuthis oualaniensis* and *Ornithoteuthis volatilis*, and body length of five predators.

Cephalopod species	Predator species	DML (mm)	Predator body length (cm)	Ratio (%)
Ornithoteuthis volatilis	*Thunnus albacares*	40.3	115	3.5
	Thunnus obesus	56.4	101	5.6
	Xiphias gladius	185.6	137	13.5
Sthenoteuthis oualaniensis	*Istiophorus platypterus*	68.3	189	3.6
	Tetrapturus angustirostris	72.8	161	4.5
	Thunnus albacares	60.3	108	5.6
	Thunnus obesus	83.7	103	8.1
	Xiphias gladius	182.0	123	14.8

(Ménard et al., 2006; Potier et al., 2007). On the other hand, our predators could feed on different forms of *S. oualaniensis*, each having different size and bathymetric distributions (Nesis, 1993).

O. loennbergii is another oceanic medium-large sized squid that was important in fish diet in the present study, both as juveniles and adults (large size distribution of LRL; Fig. 5). The squids *A. lesueuri*, *H. hoylei*, *H. atlanticus*, the argonautid *Argonauta argo*, and the pelagic octopus *Japetella diaphana* were also commonly found as cephalopod prey of large predatory fishes, while they were rarely reported in significant numbers in the diet of cephalopod eaters (e.g., Okutani and Tsukada, 1988). Our study emphasized the usefulness of a community of marine predators to gain valuable information on the biology and the distribution of the cephalopod forage fauna. In addition, our findings reinforced the understanding of the trophic role of cephalopods that constitute a link in the transfer of energy from lower trophic levels (most likely zooplankton and micronekton) to higher trophic levels (tunas, billfishes, swordfish, sharks, and seabirds). Further investigations are needed and should combine new tools such as trophic indicators or tracers in food chain pathway, and genetic barcoding for taxonomy (Jackson et al., 2007).

Acknowledgment

We wish to thank the institutions and projects which provided vessels for the different cruises and contributed financially to the lease of those platforms: IRD, the Paul Emile Victor Institute (IPEV), the Agulhas Somali Currents Large Marine Ecosystem (ASCLME) project, the South West Indian Ocean Fisheries Project (SWIOFP), and the Fonds Français pour l'Environnement Mondial (FFEM). Funding was also provided by the IOSSS project (European Fisheries

Funds UE-FEP 2007–2013 No. 31122/DRAM/2009 and La Réunion Régional Council No. DAE4/20090164). We wish to thank the crew of the research and fishing vessels who participated actively to this research program and hosted us on board. This work was partly supported by the BIOPS project funded by la Fondation pour la Recherche sur la Biodiversité (No. CD-AOOI-07-013). In addition, this paper represents research conducted as part of the CLIOTOP program. We thank Chingis Nigmatullin and Uwe Piatkowski for their wise comments and helpful suggestions. This paper is a contribution to a CLIOTOP initiative to develop understanding of squid in pelagic ecosystems.

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