African Journal of Marine Science 2007, 29(1): 113–122
Printed in South Africa — All rights reserved

AFRICAN JOURNAL OF MARINE SCIENCE
ISSN 1874–232X
doi: 10.2989/AJMS.2007.29.1.10.75

Role of pelagic crustaceans in the diet of the longnose lancetfish *Alepisaurus ferox* in the Seychelles waters

M Potier[1]*, F Ménard[2], Y Cherel[3], A Lorrain[2], R Sabatié[4] and F Marsac[2]

[1] *Institut de Recherche pour le Développement (IRD), BP 172, 97492 Ste Clotilde Cedex, La Réunion*
[2] *IRD, Centre de Recherche Halieutique Méditerranéenne et Tropicale, BP 171, 34203 Sète Cedex, France*
[3] *Centre d'Etudes Biologiques de Chizé, UPR 1034 du Centre National de la Recherche Scientifique, BP 14, 79360 Villiers en Bois, France*
[4] *Pôle Halieutique, Laboratoire d'Ecologie Halieutique, Agrocampus-Rennes, 65 rue de St Brieuc, 35042 Rennes Cedex, France*
* *Corresponding author, e-mail: michel.potier@univ-reunion.fr*

The role of pelagic crustaceans in the diet of the longnose lancetfish *Alepisaurus ferox* was investigated from stomach content analysis of fish collected in the waters surrounding the Seychelles Archipelago in the western Indian Ocean. Crustaceans accounted for 88.4% by prey number and 73.7% by reconstituted mass during the South-West monsoon season. During the North-East monsoon season, crustaceans remained the main prey group and accounted for 63.7% by prey number and 46% by reconstituted mass. There was a clear seasonal pattern with the portunid crab *Charybdis smithii* predominating during the South-West monsoon season and the pelagic stomatopod *Natosquilla investigatoris* during the North-East monsoon season. This pattern likely reflects variations in prey availability linked to current movements around the Seychelles Archipelago. Most of the prey consisted of slow-swimming and small individuals, which occur in dense swarms during the pelagic phase of their life history. The dietary trends of lancetfish are consistent with opportunistic feeding on the most abundant prey. They exploit short food chains based on carnivorous crustaceans, and play an important role in the pelagic trophic functioning of the western Indian Ocean.

Keywords: crustaceans, feeding habits, lancetfish, seasonality, Seychelles

Introduction

There is a large gap in our knowledge of trophic pathways in open-sea pelagic ecosystems regarding the intermediate trophic levels, i.e. the small fish, cephalopods and crustaceans that are consumed by commercially important top predators such as tuna, swordfish and billfish. Therefore, the prey composition of the stomach contents of pelagic top predators provide unique information on the forage fauna of these poorly known ecosystems. The longnose lancetfish *Alepisaurus ferox* is a predator that could provide this important insight into the intermediate trophic levels of the pelagic food-webs (Legand and Wauthy 1961, Parin 1988). The species has a worldwide distribution, from 45°N to 45°S, in the open-sea pelagic ecosystems of the world ocean (Orlov and Ulíchenko 2002). *A. ferox* is a common bycatch species on tuna longlines (Bartram and Kaneko 2004). Their stomach contents are often well preserved because of their digestive characteristics: food is stored in the stomach and digestion takes place in the intestine (Rofen 1966). As such, identification of prey items from the stomachs of *A. ferox* is easier than for other predators such as tuna, swordfish and billfish (Potier *et al.* 2007). Thus, the lancetfish could be considered a useful biological sampler of the pelagic ecosystems.

The feeding habits of the lancetfish have been studied in the Atlantic Ocean (Haedrich 1964, Matthews *et al.* 1977) and the Pacific Ocean (Haedrich and Nielsen 1966, Grandperrin and Legand 1970, Okutani and Tsukada 1988). They have been described as daytime feeders, hunting epipelagic and mesopelagic prey (Haedrich 1964, Haedrich and Nielsen 1966). In the Indian Ocean, most studies have been carried out in the eastern sector (Fujita and Hattori 1976, Okutani and Tsukada 1988, Parin 1988). However, in the western Indian Ocean, Romanov and Zamorov (1998) recorded a juvenile yellowfin tuna *Thunnus albacares*; those authors also observed a high rate of cannibalism in large lancetfish (EV Romanov, IRD, pers. comm.).

The objective of the present study is to explore the role of the pelagic crustaceans in the trophic functioning in Seychelles waters, a poorly known high-sea ecosystem. Seasonal changes of the crustacean species in the diet composition of lancetfish were also investigated.

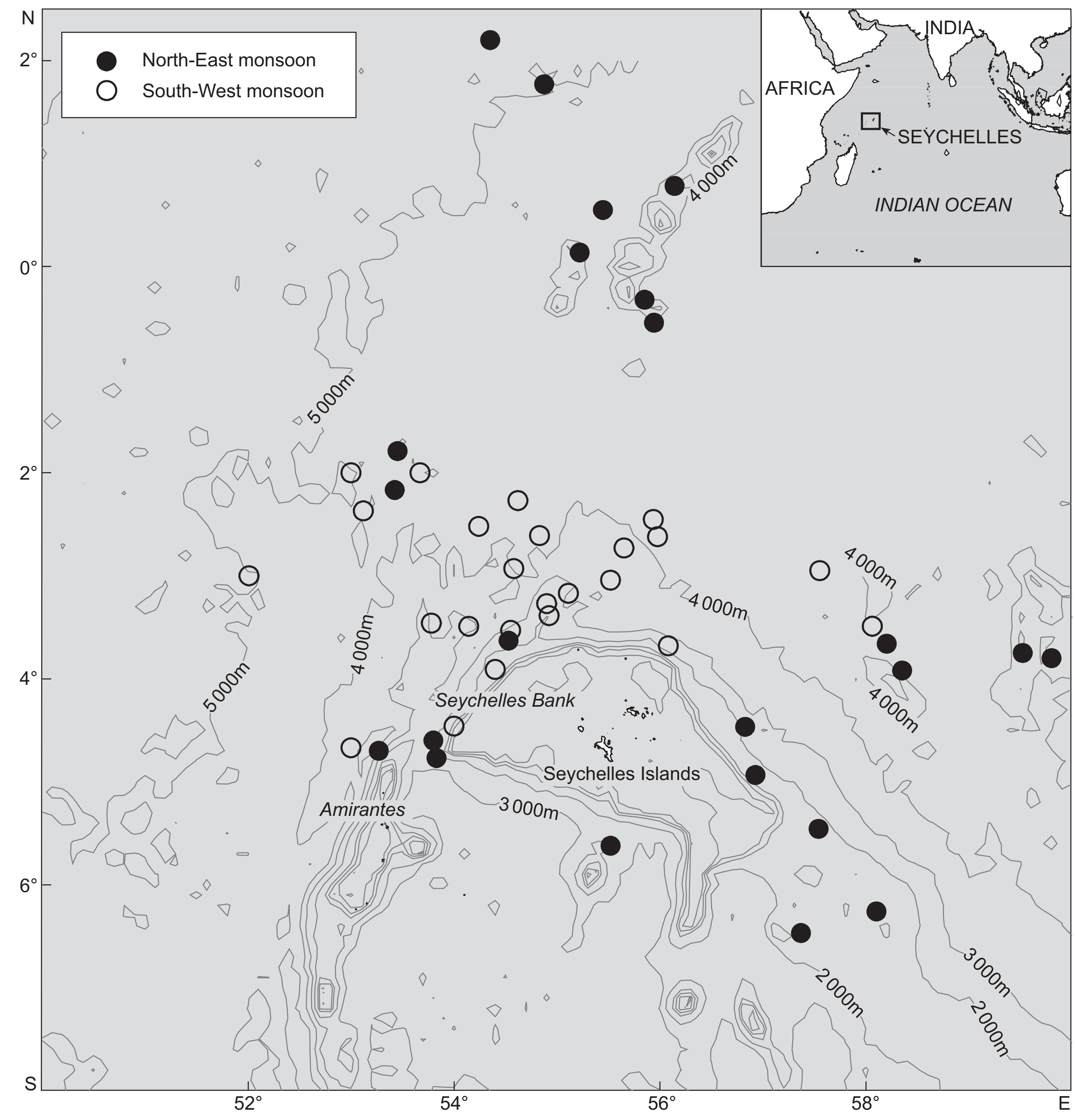

Figure 1: Locations of the longline sets carried out during the South-West monsoon and the North-East monsoon seasons around the Seychelles shelf in 2001, 2002 and 2003

Table 1: Number and catch rate of lancetfish and other species according to monsoon season during the scientific cruises carried out around the Seychelles shelf

Catch	South-West monsoon n	South-West monsoon Catch rate (number 100 hooks^{-1})	North-East monsoon n	North-East monsoon Catch rate (number 100 hooks^{-1})	Total n	Total Catch rate (number 100 hooks^{-1})
Lancetfish	271	2.4	224	1.2	495	1.7
Other species	139	1.3	476	2.6	615	2.1
Total	410	3.7	700	3.8		

Material and Methods

Study site

The study area was located within the Economic Exclusive Zone of the Seychelles (0°–7°S; 52°–59°E). Sampling took place during the North-East monsoon (November–April) and the South-West monsoon (May–October) seasons between 2001 and 2003. During the former, the Equatorial Counter Current flow is predominant in the study area, whereas a clockwise gyre occurs in the area during the South-West monsoon season. Longnose lancetfish were caught during nine scientific cruises conducted in 2001, 2002 and 2003 on board the longliner *Amitié* of the Seychelles Fishing Authority (Figure 1, Table 1). Field operations during the cruises are detailed in Potier *et al.* (2007).

Stomach analysis

A total of 150 stomachs were randomly sampled from the 495 longnose lancetfish stomachs of fish caught during the nine surveys. They were removed from freshly caught fish by cutting at the last gill and after the pyloric valve. The fork length (FL, cm) was measured for individual fish. Stomachs were put in a sealed bag and immediately frozen at –20°C.

In the laboratory, the stomachs were thawed and drained for 24 hours. The contents of each stomach were weighed and divided into main prey classes (crustaceans, fish, squid and others), which were each weighed to provide the proportion of wet mass in the diet. Fresh remains always made up by far the largest proportion of the stomach contents. 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 excluded from the analysis, because they would overemphasise the importance of some prey in the diet. For each main class, the different identifiable items were sorted and counted. The identifiable organs were used to determine the number of prey items. For fish, the number of lower jaws (dentary bones), parasphenoids or the maximum number of either left or right otoliths was assumed to reflect the total number of fish prey in the stomach. Similarly, the greatest number of either upper or lower beaks was used to estimate the number of cephalopods. For crustaceans, telsons or parts of pereopods (propod or dactylopod) were counted. The sorted items were determined to the lowest possible taxon.

The reconstituted mass was estimated using allometric equations that relate dimensions of identifiable organs to the mass of the species. Allometric equations by Smale *et al.* (1995) and Clarke (1986), as well as our own equations, were used. Standard length (SL) of fish, dorsal mantle length (DML) of cephalopods and total length (TL) of crustaceans were measured. However, the size of the pelagic crab *Charybdis smithii* was expressed as the carapace width (CW). When prey items were partly digested, equations relating hard parts (otolith, telson and beak) to size were used to estimate the prey size. Size dimensions were expressed in mm.

Data analysis

Diet composition was investigated using three diet indices for each identified prey item i: the frequency of occurrence in stomachs (O_i = the number of stomachs including prey species or category i divided by the total number of non-empty stomachs); the numerical importance (N_i = the total number of prey species or category i divided by the total number of prey items); and the reconstituted mass (RM_i = the total reconstituted mass of prey species or category i divided by the total reconstituted mass of prey items). Because the aim of the study was to explore the predation impact and the role of crustaceans in the diet, N_i and RM_i were computed with the data pooled across all the stomachs.

However, to investigate year and seasonal effects in the stomach contents, individual food samples were taken into account. Kruskal-Wallis rank-sum tests were performed on the prey numbers, wet mass, the index of stomach fullness (ISF — computed as the percentage of mass of the stomach content over the mass of the predator), and on the size distribution of the different prey species or categories. In addition, the degree of trophic overlap between both monsoon seasons was estimated by computing two indices of niche overlap: the Morisita's original index C*,* which is the appropriate overlap index for prey numbers (Smith and Zaret 1982); and the simplified Morisita index C_{mh} proposed by Horn (1966), and usually called the Morisita-Horn index (see Krebs 1998), which is the appropriate overlap index for prey mass. They were calculated as follows:

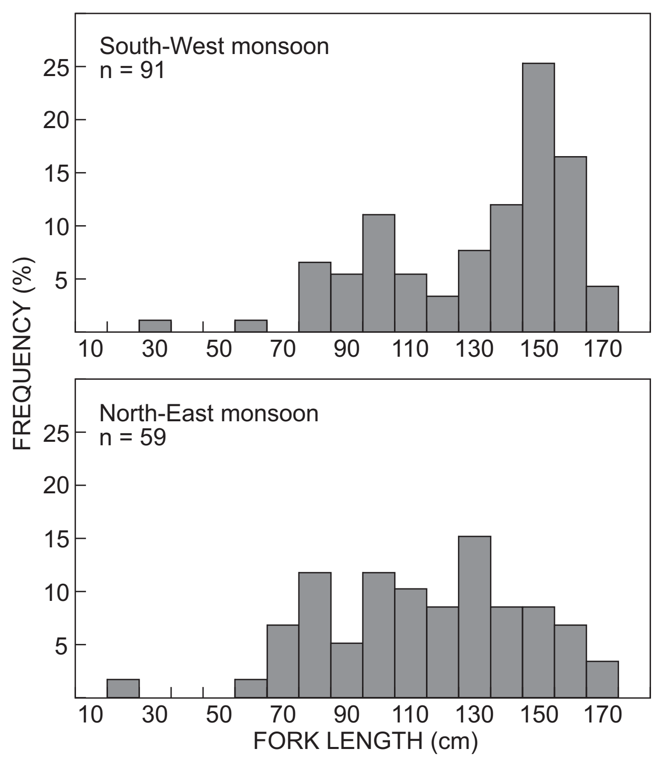

Figure 2: Size distribution of the lancetfish examined for stomach content during the South-West and North-East monsoon seasons

Table 2: Frequency of occurrence (FO), numbers (N) and reconstituted mass (RM) of prey items identified from stomach contents of *Alepisaurus ferox* (total for all 139 samples pooled)

		FO		N		RM	
Prey item	Species	n	%	n	%	g	%
CEPHALOPODS		42	30.2	66	2.9	838.1	6.8
Enoploteuthidae	*Abraliopsis* sp.	1	0.7	1	<0.1	2.6	<0.1
Histioteuthidae	*Histioteuthis hoylei*	1	0.7	1	<0.1	285.6	2.3
Ommastrephidae	*Ornithoteuthis volatilis*	4	2.9	5	0.2	18.2	0.1
	Sthenoteuthis oualaniensis	3	2.2	4	0.2	13.3	0.1
Onychoteuthidae	*Moroteuthis lonnbergii*	3	2.2	3	0.1	9.7	0.1
	Walvisteuthis rancureli	9	6.5	10	0.4	216.9	1.8
Octopoteuthidae	*Taningia danae*	1	0.7	1	<0.1	2.1	<0.1
Pholidoteuthidae	*Pholidoteuthis boschmai*	1	0.7	1	<0.1	3.0	<0.1
Alloposidae	*Haliphron atlanticus*	4	2.9	7	0.3	19.4	0.2
Amphitretidae	*Amphitretus pelagicus*	3	2.2	3	0.1	35.1	0.3
Argonautidae	*Argonauta argo*	3	2.2	3	0.1	74.3	0.6
Bolitaenidae	*Japetella diaphana*	14	10.1	16	0.7	123.9	1.0
Tremoctopodidae	*Tremoctopus violaceus*	2	1.4	2	0.1	9.7	0.1
	Octopodid larvae	4	2.9	6	0.3	9.4	0.1
	Pteroctopus sp.	1	0.7	1	<0.1	14.8	0.1
Unident. octopods		1	0.7	1	<0.1	0.2	<0.1
Spirulidae	*Spirula spirula*	1	0.7	1	<0.1	0.0	<0.1
CRUSTACEA		115	82.7	1 891	81.8	8 605.5	70.2
Portunidae	*Charybdis smithii*	60	43.2	512	22.2	6 394.7	52.1
Crab larvae		5	3.6	6	0.3	0.9	<0.1
Enoplometopidae	*Enoplometopus* sp.	3	2.2	13	0.6	7.1	0.1
Oplophoridae	*Oplophorus typus*	7	5.0	22	1.0	4.8	<0.1
Odontodactylidae	*Odontodactylus scyllarus*	1	0.7	1	0.0	0.2	<0.1
Squillidae	*Natosquilla investigatoris*	42	30.2	912	39.5	2 089.5	17.0
Phrosinidae	*Phrosina semilunata*	23	16.5	250	10.8	36.3	0.3
Platyscelidae	*Platyscelus ovoides*	46	33.1	163	7.1	68.0	0.6
Pronoidae	*Parapronoe crustulum*	4	2.9	4	0.2	0.6	<0.1
Phronimidae	*Phronima sedentaria*	1	0.7	1	<0.1	0.2	<0.1
Brachyscelidae	*Brachyscelus crusculum*	3	2.2	7	0.3	3.1	<0.1
FISH		77	55.4	195	8.4	2 618.5	21.4
Acanthuridae	*Naso* sp.	1	0.7	1	<0.1	2.2	<0.1
Alepisauridae	*Alepisaurus ferox*	17	12.2	21	0.9	1 572.9	12.8
Anoplogasteridae	*Anoplogaster cornuta*	1	0.7	3	0.1	31.6	0.3
Balistidae	*Canthidermis maculatus*	2	1.4	2	0.1	34.9	0.3
Bramidae	*Brama brama*	1	0.7	2	0.1	6.3	0.1
Carangidae	*Decapterus* sp.	1	0.7	1	<0.1	3.1	<0.1
Chiasmodontidae	*Chiasmodon niger*	3	2.2	3	0.1	9.1	0.1
Diodontidae	*Diodon* sp.	1	0.7	1	<0.1	79.5	0.6
Exocoetidae	*Exocoetus volitans*	1	0.7	1	<0.1	44.9	0.4
Myctophidae	*Diaphus* spp.	2	1.4	2	0.1	11.5	0.1
Nomeidae	*Cubiceps pauciradiatus*	3	2.2	4	0.2	4.4	<0.1
Omosudidae	*Omosudis lowei*	23	16.5	33	1.4	298.6	2.4
Ostraciidae	*Ostracion cubicus*	1	0.7	1	<0.1	0.5	<0.1
Paralepididae	*Paralepis* sp.	22	15.8	31	1.3	186.3	1.5
Phosichthyidae	*Vinciguerria nimbaria*	2	1.4	2	0.1	1.5	<0.1
Scombridae	*Auxis* sp.	1	0.7	1	<0.1	146.5	1.2
	Other scombrids	1	0.7	1	<0.1	1.9	<0.1
Scorpaenidae		1	0.7	1	<0.1	0.6	<0.1
Sternopthychidae	*Argyropelecus gigas*	4	2.9	5	0.2	12.7	0.1
	Argyropelecus sladeni	1	0.7	1	<0.1	3.3	<0.1
	Pterycombus petersii	1	0.7	1	<0.1	21.5	0.2
	Sternoptyx diaphana	2	1.4	2	0.1	12.2	0.1
Tetraodontidae	*Lagocephalus lagocephalus*	1	0.7	1	<0.1	0.9	<0.1
Trachichthyidae	*Hoplostethus* sp.	2	1.4	2	0.1	1.6	<0.1
Unident. fish		11	7.9	15	0.6	114.1	0.9
Fish larvae		11	7.9	57	2.5	16.1	0.1

Table 2 (cont.)

Prey item	Species	FO		N		RM	
		n	%	n	%	g	%
OTHER PREY		38	27.3	159	6.9	200.7	1.6
Alciopidae	*Rhynchonerella angelini*	23	16.5	72	3.1	16.6	0.1
Heteropods	*Carinaria* sp.	17	12.2	75	3.2	166.7	1.4
Pteropods		2	1.4	3	0.1	0.3	<0.1
Plants		2	1.4	3	0.1	13.0	0.1
Salpidae		2	1.4	6	0.3	4.1	<0.1
Total		139		2 311		12 262.7	

$$C = \frac{2\sum_{i=1}^{S} p_{A,i} \times p_{B,i}}{\sum_{i=1}^{S} p_{A,i}\left[\left(n_{A,i}-1\right)/\left(N_A-1\right)\right] + \sum_{i=1}^{S} p_{B,i}\left[\left(n_{B,i}-1\right)/\left(N_B-1\right)\right]}$$

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

where C is the Morisita index of overlap between Season A and Season B, C_{mh} the Morisita-Horn index, S the total number of identified prey species (or category) in the feeding habits of lancetfish in both seasons, $p_{A,i}$ and $p_{B,i}$ the proportion resource i of the total resources in Season A and in Season B respectively, $n_{A,i}$ and $n_{B,i}$ the number of individuals that use resource i in Season A and in Season B respectively, and N_A and N_B the total number of individuals in both seasons. C and C_{mh} range from 0 (no prey in common) to 1 (complete overlap). Bootstrapping techniques based on 500 replications allowed estimation of the 95% confidence intervals for the two overlap indexes. All the computations and tests were performed on S-Plus (Insightful 2005).

Results

Diet composition

A total of 150 stomachs (including 11 empty stomachs) of lancetfish, ranging in length from 15cm to 170cm, were analysed (Figure 2). Kruskal-Wallis tests showed no year effect on the number of prey ($H = 2.271$, $p = 0.321$), the wet mass ($H = 0.846$, $p = 0.655$) and the ISF ($H = 2.131$, $p = 0.344$). For the 139 samples pooled, crustaceans accounted for 65.8% of the diet by fresh mass. Crustaceans were present in 115 stomachs (82.7%) and ranked first by number (81.8%) and by reconstituted mass (70.2%; Table 2). The swimming crab *Charybdis smithii* and the pelagic stomatopod *Natosquilla investigatoris* were the main crustacean prey. *C. smithii* contributed 52% of the reconstituted mass and was found in 43% of the stomachs, and *N. investigatoris* was the most numerous prey (39.5%) and occurred in 30% of the stomach contents. Hyperiid amphipods *Platyscelus ovoides* and *Phrosina* sp. were found in appreciable numbers and occurred frequently in the stomachs. Other decapods occurred in small amounts: the oplophorid *Oplophorus typus*, the enoplometopid *Enoplometopus* sp. and the stomatopod *Odontodactylus scyllarus*. Crab larvae in megalop stage were also present in several stomach contents (Table 2).

Fish prey, with 21 identified items, ranked second in the diet, occurring in 55% of the samples and accounting for 8% of the diet by number and 21% by reconstituted mass. Among them, *Omosudis lowei*, *Paralepis* sp. and *A. ferox* (i.e. cannibalism) formed the bulk of the fish prey. Conspecific prey represented 13% of the diet by reconstituted mass. Other fish species were rarely observed and were of minor importance in the diet. Most of them were mesopelagics, such as *Chiasmodon niger* and several species of sternoptychids. Some juvenile epipelagic fish species were recorded, the balistid *Canthidermis maculatus* and several juveniles of coral fish (e.g. acanthurids, ostraciids and scorpaenids).

A total of 66 fresh cephalopods, from 17 prey species or categories, were found in 42 stomachs. The onychoteuthid *Onykia rancureli* and the bolitaenid *Japetella diaphana* were the main prey species. However, cephalopod prey contributed only 3% by number and 7% by reconstituted mass to the overall diet and played a minor dietary role.

Seasonality in the diet

The size distributions of lancetfish did not differ much between seasons (i.e. 15–165cm in the North-East monsoon and 29–170cm in the South-West monsoon, Figure 2). In all, 1 694 fresh prey items from 41 prey species or categories were found in 85 stomachs collected during the South-West monsoon season, and 617 fresh prey items from 43 prey species or categories were found in the 54 stomachs during the North-East monsoon season. Plots of the cumulative number of stomachs analysed versus the cumulative number of prey species or categories found in the stomachs for each season (plots not shown) had similar asymptotes. This indicated that a sufficient number of stomachs were analysed to produce an accurate description of diet in terms of prey diversity during both seasons. Kruskal-Wallis tests showed significant differences in seasons for the number of prey ($H = 6.50$, $p = 0.011$), wet mass ($H = 21.28$, $p < 0.001$) and ISF ($H = 6.66$, $p < 0.01$). In terms of individual diet, these indices were higher during the South-West monsoon season. The median of the prey number increased from 4 in the North-East monsoon season to 10 in

Table 3: Frequency of occurrence (FO), numbers (N) and reconstituted mass (RM) of the main prey categories identified from stomach contents of *Alepisaurus ferox* during the North-East monsoon (total for all 54 samples pooled) and South-West monsoon (total for all 85 samples pooled) seasons

		North-East monsoon			South-West monsoon		
Prey category	Species	%FO	%N	%RM	%O	%N	%RM
Cephalopods		44	7.0	17.0	21.2	1.4	5.4
	Walvisteuthis rancureli	7.4	0.8	1.6	5.9	0.3	1.8
	Japetella diaphana	16.7	1.8	5.7	5.9	0.3	0.3
Crustacea		68.5	63.7	46.0	91.8	88.4	73.7
	Charybdis smithii	9.3	1.0	12.9	64.7	29.9	57.8
	Natosquilla investigatoris	40.7	39.4	30.3	23.5	39.5	15.1
	Phrosina semilunata	16.7	9.2	0.7	16.5	11.4	0.2
	Platyscelus ovoides	35.2	8.9	1.5	31.8	6.4	0.4
Fish		70.4	13.3	29.8	45.9	6.7	20.1
	Alepisaurus ferox	16.7	1.8	10.3	9.4	0.6	13.2
	Omosudis lowei	20.4	2.3	6.9	14.1	1.1	1.8
	Paralepis sp.	20.4	2.4	5.5	12.9	0.9	0.9
Other prey		37.0	16.0	7.2	2.2	3.6	0.8
	Carinaria sp.	18.5	10.5	6.2	9.4	0.6	0.7
	Rhynchonorella angelini	18.5	3.7	0.7	15.3	2.9	0.1

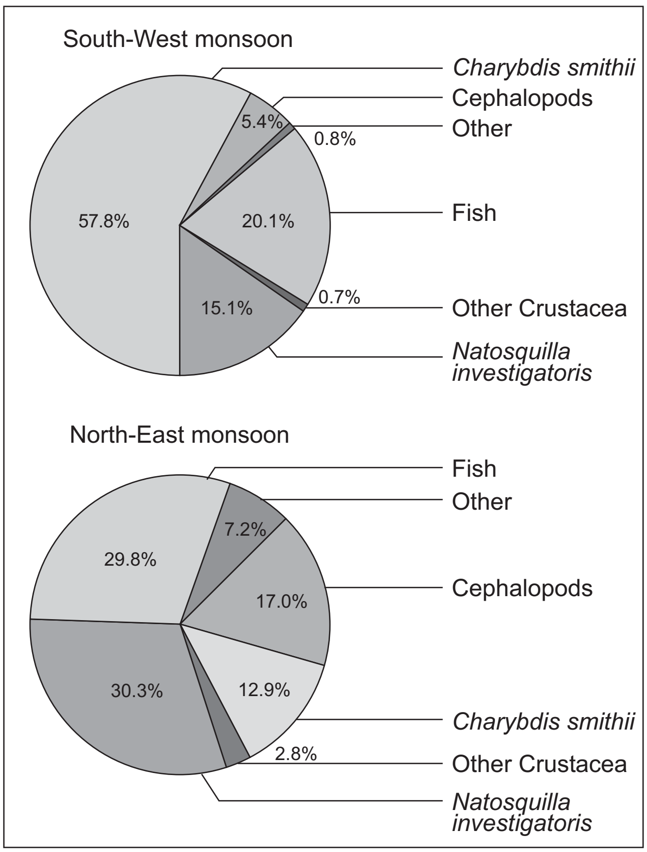

Figure 3: Proportions by reconstituted mass of the two main crustacean species (*C. smithii* and *N. investigatoris*), other crustaceans, fish, cephalopods and the other prey during the South-West monsoon and North-East monsoon seasons

the South-West monsoon season, and the median of the wet mass increased from 19.6g to 63.1g and the ISF median from 1.24% to 2.22% respectively.

The Morisita's and Morisita-Horn's indices were similar: C = 0.443 (95% confidence interval = [0.302; 0.673]) and C_{mh} = 0.432 (95% confidence interval = [0.292; 0.719]). A significant overlap is assumed for index values >0.6 (Zaret and Rand 1971, Keast 1978). This threshold is included in the upper confidence intervals owing to several prey species, which accounted for significant values by number (*N. investigatoris*, *Phrosina semilunata* and *Platyscelus ovoides*) and by reconstituted mass (*N. investigatoris*, *C. smithii* and *A. ferox*) during both North-East and South-West monsoon seasons (Table 3). However, diets are different during the South-West and North-East monsoon seasons, with 25 prey species or categories common to both seasons only (46% of the recorded species).

Kruskal-Wallis tests were also performed by main prey class on the number, wet mass and reconstituted mass. Seasonal effects were significant for crustaceans (H = 15.62, $p < 0.001$; H = 36.16 $p < 0.001$; H = 35.70, $p < 0.001$ respectively) and cephalopods (H = 9.18, $p < 0.01$; H = 7.82 $p < 0.01$; H = 7.09, $p < 0.01$ respectively). A significant difference was found for fish with prey number only (H = 5.94, p = 0.015).

Crustaceans dominated the diet in both seasons, occurring in 91.8% and 68.5% of the stomachs during the South-West and North-East monsoon seasons respectively (Table 3). *C. smithii* was found in 64.7% of the stomachs and contributed to 57.8% by reconstituted mass and to 29.9% by prey number during the South-West monsoon season (Table 3, Figure 3). However, during the North-East monsoon season, *C. smithii* was very scarce in the diet, being replaced by *N. investigatoris* which was the most important prey item by number (39.4%) and by reconstituted mass (30.3%; Table 3).

Contrary to crustaceans, fish prey occurred more frequently, in higher numbers and greater reconstituted mass in the North-East monsoon season. This trend was fairly consistent in all three years of sampling, except for the reconstituted mass of the *A. ferox* prey, because larger sizes were consumed during the South-West monsoon season (mean size increased from 157mm to 301mm SL). Cephalopod prey showed a similar decreasing trend between the seasons (Table 3), but their contribution to the diet was relatively minor.

Table 4: Mean size, standard deviation and range of the main prey items according to monsoon season. Results of the Kruskal-Wallis tests comparing the mean size and predator:prey (P:p) size ratio between seasons are given

	North-East monsoon				South-West monsoon				Kruskal-Wallis	
Prey item	n	Mean ± SD (mm)	Range (mm)	Mean ± SD P:p ratio	Range n	P:p (mm)	(mm)	ratio	H	P
Cephalopods (DML)	24	36.5 ± 17.8	14–71	29.4	10	47.7 ± 39.6	9.8–136	26.5	0.09	ns
Amphipods (TL)	77	18.9 ± 2.9	13.3–27.7	56.5	109	15.8 ± 3.2	8.8–21.9	80.1	60.13	<0.01
N. investigatoris (TL)	227	51.4 ± 13.6	33.8–83.9	15.3–25.5	276	61.1 ± 6.7	18.7–83.0	20.7	38.25	<0.01
C. smithii (CW)	5	49.7 ± 11.4	39.5–69.2	28.9	229	38.2 ± 6.4	26.0–60.5	25.3	7.45	<0.01
Fish (SL)	68	86.5 ± 66.8	14–310	12.4	87	91.6 ± 111.7	11–630	13.8	1.16	ns

DML = Dorsal mantle length
TL = Total length
CW = Carapace width
SL = Standard length
ns = Not significant

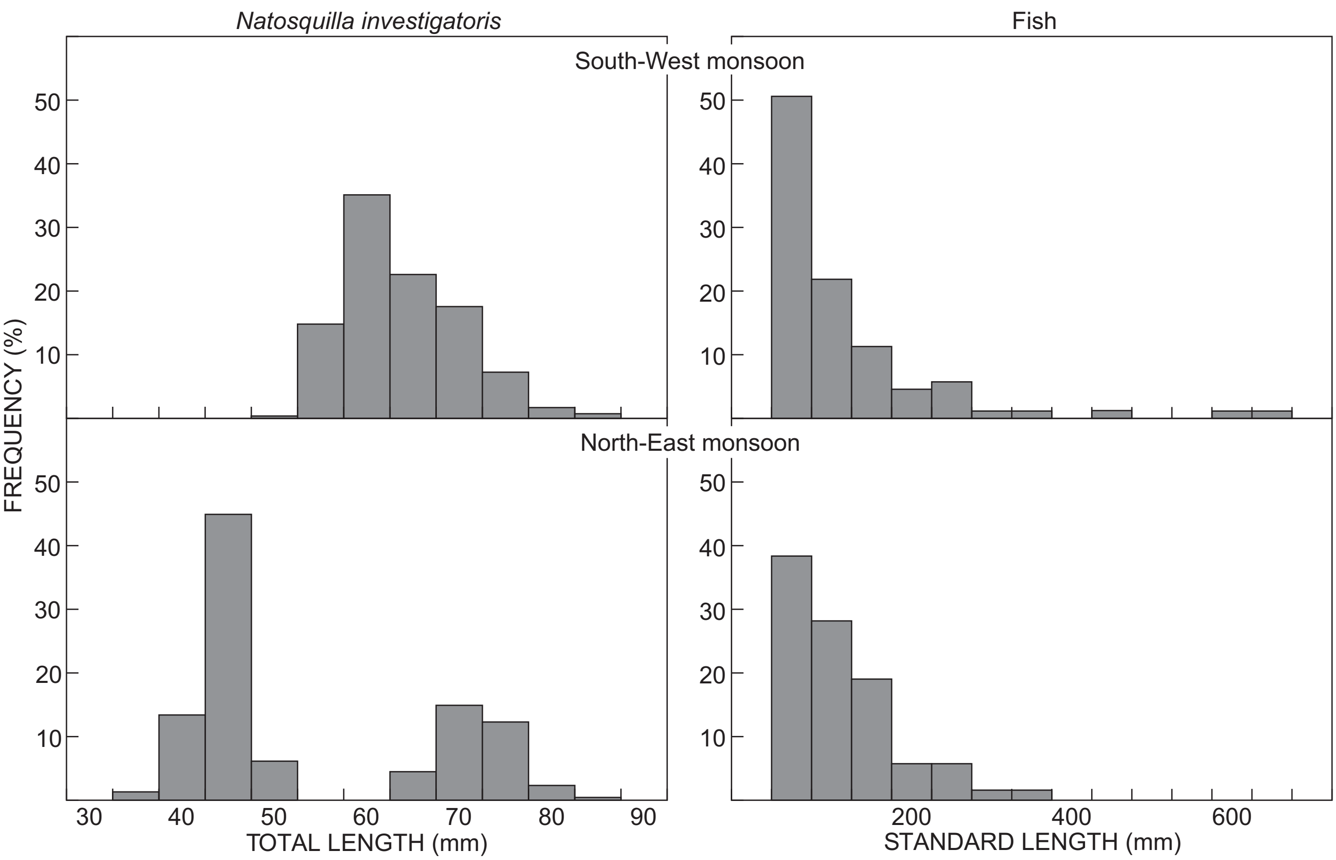

Figure 4: Prey size distributions of *N. investigatoris* and of the fish prey category during the South-West monsoon and North-East monsoon seasons

Seasonality of the prey size

The mean sizes of *C. smithii* and amphipods were smallest during the North-East monsoon season (Table 4). The size frequency distribution of *N. investigatoris* was bimodal during that season, precluding a reliable estimate their mean size (Figure 4). The two modes likely corresponded to two different cohorts, with mean sizes of 42mm and 70mm. The mean size of *N. investigatoris* during the South-West monsoon was 61mm. Although the mean sizes of cephalopod and fish prey were not significantly different between seasons (Table 4), a few large conspecific prey were found in the stomachs of lancetfish during the South-West monsoon season.

Predator:prey size ratios were estimated using the mean sizes of lancetfish and that of the different prey groups or items (Table 4). Generally, the seasonal variations of the size ratios were low for fish and cephalopod prey and

Table 5: Stomach content analysis of lancetfish from different areas including the present study percentages by number (N) and by wet mass (M). Stomach number and total number of prey items are indicated

	Hawaiian waters		Central Pacific		Present study	
Prey items	%N	%M	%N	%M	%N	%M
Cephalopods	5.1	19.2	4.8	22.9	3.4	10.7
Crustacea: amphipods	54.2	18.1	0.8	–	21.6	1.2
decapods	0.5	0.6	–	–	56.4	60.2
Fish	16	52.2	93.3	75.6	10.1	26
Polychaete worms	7.3	1.5	0.4	0.5	3.8	0.2
Heteropods	15.4	8.1	–	–	4	1.6
Pteropods	0.8	0.1	–	–	0.2	–
Other	1.7	0.2	0.7	0.1	0.5	0.1
Total preys	1 178	–	252	–	2 315	–
Number of stomachs	40	–	24	–	139	–

greater for amphipods. For *N. investigatoris*, size ratios varied from 20.7 during the South-West monsoon to 15.3 and 25.5 during the North-East monsoon, depending on the cohort.

Discussion

In this study, 59 prey species or categories, including 11 crustaceans were found in the stomachs of lancetfish caught in the western Indian Ocean. Such prey diversity is reported for this species elsewhere in the world oceans. In the western Pacific (Fourmanoir 1969, Grandperrin and Legand 1970), central Pacific (Moteki *et al.* 1993), eastern Pacific (Haedrich and Nielsen 1966) and the Atlantic Ocean (Haedrich 1964), fish (mainly mesopelagics) formed the bulk of the lancetfish diet (Table 5). Juvenile coral fish have been found in the diet of lancetfish near the coast of the western Pacific (Fourmanoir 1969), as was the case in lancetfish caught in this study near the Seychelles shelf. Crustacean prey dominated the diet of lancetfish under study, with *C. smithii* and *N. investigatoris* being the main prey species both numerically and in reconstituted mass. *C. smithii* is common in the western Indian Ocean (Thomas and Kurup 2001), and it was the dominant prey item during the South-West monsoon season. This portunid crab was also found in large quantities in the stomachs of yellowfin tuna *Thunnus albacares* caught by longlines in that region (Zamorov *et al.* 1992, Potier *et al.* 2007). *C. smithii* is an epipelagic species and its vertical distribution has been found to be is associated with position of the thermocline and oxycline (van Couwelaar *et al.* 1997). It feeds on crustaceans, gastropods, and fish (Losse 1969, Balabsurbramanian and Suseelan 1998) and forms between 50% and 90% of the micronekton fauna in the upper 200m in the north-western Indian Ocean (van Couwelaar *et al.* 1997). *C. smithii* may thus play an important role, both as a predator and as prey, in the pelagic foodweb of the western Indian Ocean.

During the North-East monsoon season, *C. smithii* was very scarce in the diet of lancetfish. This period corresponds to the breeding phase of the crab, during which time they become benthic dwellers (van Couwelaar *et al.* 1997). During the North-East monsoon season, *N. investigatoris* replaced *C. smithii* as the major crustacean prey. *N. investigatoris* occurs in very dense and extensive swarms in the surface waters of the western Indian Ocean (Losse and Merrett 1971, Potier *et al.* 2002), and these swarms are targeted by both lancetfish and surface-feeding tuna (Potier *et al.* 2002). Two cohorts *N. investigatoris* were found in the stomachs of lancetfish during the North-East monsoon season, whereas only one cohort occurred in the diet during the South-West monsoon season. This pattern shows the possible occurrence of a new cohort during the North-East monsoon, which grows during the South-West monsoon and is consumed by lancetfish one year later. Most stomatopods are bottom dwellers, but *N. investigatoris* appears to be the only pelagic species (S Ah-Yong, Australian Museum, Sydney, pers. comm.). The species has large eyes, which may be an adaptation for their swarming behaviour at the surface. The diet of *N. investigatoris* is similar to that of *C. smithii*. It is likely a detritivore but seems able to feed on small surface fish (Losse and Merrett 1971). The occurrence of large swarms of this stomatopod in the western Indian Ocean is not as common as those of *C. smithii,* which appear regularly on an annual basis (Losse and Merrett 1971).

Most of the prey found in the lancetfish stomachs were small slow-swimming species. More motile marine organisms — such as large cephalopods, fish of the Exocaetidae family and other large epipelagic fish — were absent in the diet. The lancetfish is more an ambush-style hunter than an active predator (Romanov and Zamorov 2002). Haedrich (1964) and Haedrich and Nielsen (1966) suggested that the lancetfish is a diurnal feeder with a foraging activity that is limited to the upper 300m of the water column, based on the lack of myctophids in the diet composition. In the present study, myctophids were very scarce in the stomach (occurring only twice). Furthermore, most of the lancetfish were caught during daytime. Our results therefore lend support to the belief that lancetfish are daytime feeders.

This study and those of Zamorov *et al.* (1992) and Potier *et al.* (2002) highlight the importance of crustaceans in the trophic ecosystem of the western Indian Ocean. Therefore, changes in the abundance of crustaceans would have a strong impact on the pelagic fisheries in that region. High abundances of crustaceans observed in that area may affect the catchability of large predators by competing with longline baits (Suzuki 1964, Merrett 1968) and may increase their vulnerability to surface fishing gear such as purse-seines

(Potier *et al.* 2002). The results here are comparable to the eastern Pacific region where the swimming crab *Pleuroncodes planipes* contributes considerably to the trophic ecology of top predators (Alverson 1963, Longhurst 1967a, 1967b). The annual distribution of this crab, which is found up to 1 000 km off the coast of Baja California, is strongly associated with the upwelling intensity in that region. In the western Indian Ocean, the strength of the monsoon currents may affect the distribution of *C. smithii* and *N. investigatoris*. The larvae and sub-adults of *P. planipes* are found in pelagic waters (Longhurst 1967a), whereas all life phases of *C. smithii* and *N. investigatoris* can be found in pelagic waters.

The present work shows the value of lancetfish in sampling unstudied or poorly-known forage marine fauna. The shift observed from *C. smithii* to *N. investigatoris* highlights the opportunistic feeding behaviour of this predator. Clearly, more information is needed on the feeding habits of top predators, as well the biology of their prey, to understand the trophic relationships in open-sea pelagic ecosystems.

Acknowledgements — The authors thank the Seychelles Fishing Authority (SFA) and the crew of the longliner *Amitié* for helping us to undertake this research programme. We are grateful to two anonymous referees and to Elise Bradbury for their wise comments and helpful suggestions. This work is a contribution of the Research Unit 'THETIS' UR109 of the Institut de Recherche pour le Développement.

References

Alverson FG (1963) The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean*. Inter-American Tropical Tuna Commission Bulletin* **7**: 293–396

Balasubramanian CP, Suseelan C (1998) Natural diet of the deep water crab *Charybdis smithii* McLeay (Brachyura: Portunidae) of the seas around India. *Indian Journal of Fisheries* **45**(4): 407–411

Bartram PK, Kaneko JJ (2004) Catch to bycatch ratios: comparing Hawaii's longline fisheries with others. *SOEST 04-05, JIMAR Contribution 04-352*: 40pp

Clarke MR (1986) *A Handbook for the Identification of Cephalopod Beaks*. Clarendon Press, Oxford

Fourmanoir P (1969) Contenus stomacaux d'*Alepisaurus* (Poissons) dans le sud-ouest Pacifique. *Cahier ORSTOM, série Océanographie* **8**(4): 51–60

Fujita K, Hattori J (1976) Stomach content analysis of longnose lancetfish *Alepisaurus ferox* in the Eastern Indian Ocean and the Coral Sea. *Japanese Journal of Ichthyology* **23**(3): 133–142

Grandperrin R, Legand M (1970) Contribution á la connaissance des *Alepisaurus* (Pisces) dans le pacifique équatorial et sud-tropical. *Cahier ORSTOM, série Océanographie* **8**(3): 13–34

Haedrich RL (1964) Food habits and young stages of North Atlantic *Alepisaurus* (Pisces, Iniomi). *Breviora* **201**: 1–15

Haedrich RL, Nielsen JG (1966) Fishes eaten by *Alepisaurus* (Pisces, Iniomi) in the southeastern Pacific Ocean. *Deep-Sea Research* **13**: 909–919

Horn HS (1966) Measurement of overlap in comparative ecological studies. *The American Naturalist* **100**(914): 419–424

Insightful (2005) *S-Plus 7*. Insightful Corporation, Seattle, Washington

Keast A (1978) Trophic and spatial interrelationships in the fish species of an Ontario lake. *Environmental Biology of Fishes* **3**(1): 7–31

Krebs CJ (1998) *Ecological Methodology* (2nd edn). Addison-Welsey Publishers, Inc., Menlo Park, California

Legand M, Wauthy B (1961) Importance présumée d'*Alepisaurus* sp. dans le cycle biologique de thons de longue ligne au large de la Nouvelle-Calédonie. Internal Report, Centre díocéanographie Noumea, ORSTOM

Longhurst AR (1967a) The pelagic phase of *Pleurocondes planipes* Stimpson (Crustacea, Galatheidae) in the California current. *California Cooperative Oceanic Fisheries Investigations Reports* **XI**: 142–154

Longhurst AR (1967b) The role of pelagic crabs in the grazing of phytoplankton off Baja California. *Ecology* **48**(2): 190–200

Losse GF (1969) Notes on the portunid crab *Charybdis edwardsi* Leene and Buitendijk 1949 from the western Indian Ocean. *Journal Natural History* **3**: 145–152

Losse GF, Merrett NR (1971) The occurrence of *Oratosquilla investigatoris* (Crustacea: Stomatopoda) in the pelagic zone of the Gulf of Aden and the equatorial western Indian Ocean. *Marine Biology* **10**: 244–273

Matthews FD, Damkaer DM, Knapp LW, Collette BB (1977) Food of western North Atlantic tunas (*Thunnus*) and lancetfishes (*Alepisaurus*). *NOAA Technical Report NMFS SSRF* **706**: 1–19

Merrett NR (1968) Tuna longline survey in the equatorial western Indian Ocean. *East African Agricultural and Forestry Journal* **34**: 17–65

Moteki M, Fujita K, Kohno H (1993) Stomach contents of longnose lancetfish, *Alepisaurus ferox*, in Hawaiian and central equatorial Pacific waters. *Journal of Tokyo University of Fisheries* **80**(1): 121–137

Okutani T, Tsukada S (1988) Squids eaten by lancetfish and tunas in the Tropical Indo-Pacific oceans. *Journal of Tokyo University of Fisheries* **75**(1): 1–44

Orlov MA, Ulíchenko VA (2002) A hypothesis to explain onshore records of long nose lancetfish *Alepisaurus ferox* (Alepisauridae, Teleostei) in the North Pacific Ocean. *Marine and Freshwater Research* **53**: 303–306

Parin NV (1988) *Fishes of the High Seas*. Nauka, Moscow (in Russian)

Potier M, Lucas V, Marsac F, Sabatié R, Ménard F (2002) On-going research activities on trophic ecology of tuna in equatorial ecosystems of the Indian Ocean. Fourth session of the IOTC working party on tropical tunas, Shangaï, Chine, 3–11/06/2002. *WPTT/02/24 IOTC Proceedings* **5**: 368–374

Potier M, Marsac F, Cherel Y, Lucas V, Sabatié R, Maury O, Ménard F (2007) Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fisheries Research* **83**: 60–72

Rofen RR (1966) Family Omosudidae. Fishes of the Western North Atlantic. Memoires Sears FN. *Marine Research* **1**(5): 462–481

Romanov EV, Zamorov VV (1998) Some biological features of longnose lancetfish *Alepisaurus ferox* (Alepisauridae) from the western Indian Ocean. In: Coetzee L, Gon J, Kulongowski C (eds) *African Fishes and Fisheries: Diversity and Utilisation. Book of Abstracts*. International Conference for the PARADI Association and the Fisheries Society of Africa, Grahamstown, South Africa, 13–18 Sept 1998. FISA and PARADI, South Africa, p 326

Romanov EV, Zamorov VV (2002) First record of a yellowfin tuna (*Thunnus albacares*) from the stomach of a longnose lancetfish (*Alepisaurus ferox*). *Fishery Bulletin* **100**(2): 386–389

Smale MJ, Watson G, Hecht T (1995) *Otolith Atlas of Southern African Marine Fishes*. Ichthyological Monographs. JLB Smith Institute of Ichthyology, South Africa

Smith EP, Zaret TM (1982) Bias in estimating niche overlap. *Ecology* **63**(5): 1248–1253

Suzuki T (1964) Tuna longlining in the Gulf of Aden. *Report FAO/EPTA (Food and Agriculture Organization/Expanded Programme of Technical Assistance)* **1844**: 26pp

Thomas JV, Kurup BM (2001) On the emergence of a non-edible swarming crab *Charybdis* (*Goniohellenus*) *smithii* McLeay in the trawl fishing grounds of Kerala: a case of ecosystem overfishing. In: Claereboudt M, Goddard S, Al-Oufi H, McIlwain J (eds) *Proceedings 1st International Conference on Fisheries, Aquaculture and Environment in the NW Indian Ocean*. Sultan Qaboos University, Muscat, Sultanate of Oman, pp 68–74

van Couwelaar M, Angel MV, Madin LP (1997) The distribution and biology of the swimming crab *Charybdis smithii* McLeay, 1838 (Crustacea: Brachyura: Portunidae) in the NW Indian Ocean. *Deep-Sea Research II* **44**: 1251–1280

Zamorov VV, Spiridinov VA, Napadovsky GV (1992) On the role of the swimming crab *Charybdis smithii* (McLeay 1838) in the feeding habit of yellowfin tuna *Thunnus albacares* (Bonnaterre). *Workshop on Stock Assessment of Yellowfin Tuna in the Indian Ocean, Colombo, Sri Lanka, 7–12/10/91. IPTP Collection Volume Working Document* **6**: 70–75

Zaret MR, Rand AS (1971) Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* **52**(2): 336–342

Manuscript received August 2006; accepted January 2007