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

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ABSTRACT

The role of the pelagic crustaceans in the diet of the longnose lancetfish (*Alepisaurus ferox*) was investigated through the analysis of stomach contents collected in the waters surrounding the Seychelles Archipelago. Crustaceans accounted for 88.4% by prey number and for 73.7% by reconstituted mass during the South-West monsoon. During the North-East monsoon, they remained the main prey group and accounted for 63.7 % by prey number and for 46% by reconstituted mass. A clear seasonal pattern was apparent, with the portunid crab *Charybdis smithii* predominating during the South-West monsoon and the stomatopod *Natosquilla investigatoris* during the North-East monsoon. The observed changes probably reflect variations in prey availability linked to current movements occurring in this part of the western Indian Ocean. Most of the prey consisted of slow swimming and small individuals, known to live in dense swarms during their pelagic phase. In pelagic Seychelles waters, the trends observed in the diet of lancetfish are consistent with opportunistic feeding on the most abundant prey. It exploits short food chains based on carnivorous crustaceans. Such results emphasise the role of pelagic crustaceans in the trophic chain of the western part of the Indian Ocean.

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

INTRODUCTION

The largest gap in our knowledge of trophic pathways in open-sea pelagic ecosystems concerns the intermediate trophic levels, i.e. the small fishes, cephalopods and crustaceans that are consumed by commercially important top predators such as tunas, swordfish and billfishes. Therefore, the prey compositions 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 very important predator species that permits us to study this crucial compartment of the pelagic food webs (Legand and Wauthy 1961, Parin 1988). *A. ferox* has a worldwide distribution from 45°N to 45°S in the open-sea pelagic ecosystems of the world ocean (Orlov and Ul'chenko 2002). This predatory fish is a regular by-catch 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 occurs in the intestine (Rofen 1966). Therefore, the taxonomic identification of the prey items from the stomach contents is easier than for other predators such as tunas, swordfish and billfishes. Hence, the use of lancetfish as biological samplers is of great interest for studying the food chains in the pelagic ecosystems.

Studies on the feeding habits of the lancetfish have been carried out in the Atlantic Ocean (Haedrich 1964, Matthews *et al.* 1977), and in the Pacific Ocean (Haedrich and Nielsen 1966, Grandperrin et Legand 1970, Okutani and Tsukada 1988). Lancetfish has been described as a daily feeder, hunting epipelagic and mesopelagic prey (Haedrich 1964, Haedrich and Nielsen 1966). In the Indian Ocean, most studies have been carried out in the eastern part (Fujita and Hattori 1976, Okutani and Tsukada 1988, Parin 1988). However, in the western Indian Ocean, Romanov and Zamorov (1998) reported the peculiar event of a juvenile yellowfin tuna preyed on by a lancetfish, and these authors have observed a high rate of cannibalism for large lancetfish (Romanov, comm. pers.).

During nine oceanographic cruises carried out from 2001 to 2003 with a longliner, 139 non-empty stomachs of lancetfish have been sampled in the pelagic waters surrounding the Seychelles Archipelago (western Indian Ocean). The description of the dietary habits of lancetfish is beyond the scope of this paper. The detailed food composition is investigated in another study, which explores the ways in which the food resources are partitioned among three predators: yellowfin tuna, swordfish and lancetfish (Potier *et al.*, 2007). The objective of the present study is to explore the role of the pelagic crustaceans in the trophic functioning of this poorly known high sea ecosystem. To this end, we have reanalysed the stomach content of lancetfish. Seasonal changes of the crustacean species in the diet composition of lancetfish were also investigated.

MATERIAL AND METHODS

Stomach sampling

The study area was located in the EEZ of the Seychelles (0-7°S and 52°-59°E), and was surveyed twice during the North-East and South-West monsoons from 2001 to 2003. During the North-East monsoon (November-April), the Equatorial Counter Current flows across the area, and during the South-West monsoon (May-October), a clockwise gyre occurs in the area.

A total of 150 stomachs were randomly sampled from the 495 longnose lancetfishes caught during the nine scientific cruises carried out on board the longliner l'"*Amitié*" of the Seychelles Fishing Authority (SFA) (Fig. 1 and Tab. 1). The stomachs were collected when fish were hauled on board. They were removed from the abdominal cavity by cutting at the last gill and after the pyloric valve. Each fish was measured in Fork length (FL in cm). Stomachs were put in a sealed bag and immediately frozen.

Stomach content analysis

At the laboratory, the stomachs were thawed and drained during 24 hours. The contents of each stomach were weighed and divided into main prey classes (crustaceans, fish, squids, others), which were weighed in order to provide the proportion by wet mass in the diet. Fresh remains always made up by far the largest proportion of our stomach content samples. 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. 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 weight of the species. Published allometric equations (Smale *et al.* 1995, Clarke 1986) and our own equations were used. Standard length (SL) of fishes, 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 (W). When prey items were partly digested, equations relating hard parts (otolith, telson, and beak) to size were used to estimate the prey size. Size dimension was expressed in mm.

Data analysis

To investigate the diet composition of lancetfish, we used 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 (W_i = the total reconstituted weight of prey species or category *i* divided by the total reconstituted weight of prey items). Because our goal was to explore the predation impact and the role of crustaceans in the diet, N_i and W_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, on the wet mass, on the index of stomach fullness (ISF – computed as the weight of the stomach content over the weight of the predator, in %), and on the size distribution of the different prey species or categories. In addition, the degree of trophic overlap between both monsoons 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 weight. They are calculated from the following formula:

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

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

where *C* = the Morisita index of overlap between season *A* and season *B*, C_{mh} = the Morisita-Horn index, *S* = total number of identified prey species (or category) in the feeding habits of lancetfish in both seasons, $p_{A,i}$ and $p_{B,i}$ = proportion resource i is of the total resources in season A and in season B, respectively, $n_{A,i}$ and $n_{B,i}$ = number of individuals that use resource i in season A and in season B, respectively, N_A and N_B = 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 us to estimate 95% confidence intervals for the two overlap indexes. All the computations and tests were performed on S-Plus (Insightful 2005).

RESULTS

Importance of crustaceans in the diet

A total of 150 stomachs (including 11 empty stomachs) of lancetfish whose fork lengths ranged from 15 to 170 cm (Fig. 2) were analysed. Kruskal-Wallis tests were performed on the number of prey ($H = 2.271$, $p = 0.321$), on the wet mass ($H = 0.846$, $p = 0.655$) and on the ISF ($H = 2.131$, $p = 0.344$), and showed no year effect. In the 139 samples pooled, prey was dominated by crustaceans, which accounted for 65.8% of the diet by fresh mass. Crustaceans occurred in 115 samples (82.7%) and ranked first by number (81.8%) and by reconstituted weight (70.1%) (Table 2). The swimming crab *Charybdis smithii* and the stomatopod *Natosquilla investigatoris* were the main prey: *C. smithii* contributed to more than 52% of the reconstituted mass and was found in 43% of the stomachs. *N. investigatoris* was the most numerous prey (39.5%) and occurred in 30% of the contents. Amphipods of the hyperiid group (*Platyscelus ovoides* and *Phrosina* sp.) were found in significant 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 observed in several stomach contents.

Fish prey, with 21 identified items, ranked second, occurring in 55% of the samples, accounting for 8% of the diet by number, and for 21% by reconstituted mass. Among them, *Omosudis lowei*, *Paralepis sp.* and *Alepisaurus ferox* (i.e., cannibalism) formed the bulk of the fish prey. In fact, 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 mesopelagic, such as *Chiasmodon niger* and several species of the sternoptychid family. Some juvenile epipelagic fish species were recorded: the balistid *Canthidermis maculata*, which is frequently associated with Fish Aggregating Devices, and several juveniles of coral fish families (e.g., acanthurids, ostraciids and scorpaenids).

A total of 66 fresh cephalopods from 17 prey species or categories were recovered in 42 stomach samples. The onychoteuthid *Onykia rancureli* and the Bolitaenid *Japetella diaphana* were the main species. However, cephalopod prey contributed only 3% by number and 7% by reconstituted mass to the overall diet: their importance in the lancetfish diet was low.

The polychaet *Rhynchonerella angelini* of the Alciopidae family, the heteropod *Carinaria* sp., the pteropods *Cavolinia* sp. and *Diacavolinia* sp., and several salps were also recovered in the stomach contents. Heteropods and polychaets accounted for 3% by number and 1% by reconstituted mass. Some plant remains were also observed in very small amount.

Seasonality of the lancetfish's diet

The size distributions of lancetfish did not differ greatly between seasons (from 15 to 165cm in the North-East monsoon and from 29 to 170cm in the South-West monsoon; Fig. 2). A total of 1694 fresh prey items from 41 prey species or categories were recovered from the 85 non-empty stomachs during the South-West monsoon, and 617 fresh prey items from 43 prey species or categories were recovered from the 54 non-empty stomachs during the North-East monsoon. We plotted the cumulative number of stomachs analyzed in random order along the x-axis, versus the cumulative number of prey species or categories encountered in the stomachs along the y-axis. The curves (not shown) approached almost the same asymptote, indicating that a sufficient number of stomachs have been analysed to produce an accurate description of diet in terms of prey diversity during both seasons. Kruskal-Wallis tests showed significant differences in South-West and North-East monsoons 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 food samples, these diet indices per stomach were indeed higher during the South-West monsoon: the median of the prey number increased from four in the North-East monsoon to ten in the South-West monsoon, the median of the wet mass from 19.6 to 63.1g, and the ISF median from 1.24 to 2.22%.

The Morisita's and Morisita-Horn's indexes were very close: $C = 0.443$ (95% confidence interval = [0.302; 0.673]) and $C_{mh} = 0.432$ (95% confidence interval = [0.292; 0.719]). A significant overlap is traditionally assumed for index values greater than 0.6 (e.g. Zaret and Rand, 1971; Keast 1978). This threshold is included in the upper parts of the confidence intervals. This is due to several prey species, which accounted for significant values by number (*Natosquilla investigatoris*, *Phrosina semilunata* and *Platyscelus ovoides*) and by reconstituted weight (*N. investigatoris*, *Charybdis smithii* and *Alepisaurus ferox*) during North-East and South-West monsoons (Table 3). However, diets appear to be quite different during the South-West and North-East monsoons, with 25 prey species or categories common to both seasons, only.

Kruskal–Wallis tests were also performed by main prey class (crustaceans, cephalopods and fishes) on the number, the wet mass and the 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). For fishes, a significant difference was observed with prey number only (H = 5.94, p = 0.015).

Fig. 3 displays by season the proportion by reconstituted weight of the two main crustacean species (*C. smithii* and *N. investigatoris*), as well as the other crustaceans, fishes, cephalopods and other prey. Crustaceans dominated the diet in both seasons, occurring in 91.8 and 68.5% of the stomachs during the South-West and North-East monsoons, respectively (Table 3). During the South-West monsoon, the swimming crab *Charybdis smithii* was recovered in 64.7% of the stomachs, and contributed to 57.8% by reconstituted mass and to 29.9% by prey number (Table 3). During the North-East monsoon, *C. smithii* disappeared almost totally from the lancetfish diet, and was replaced by the stomatopod *Natosquilla investigatoris*, which ranked first by number (39.4%) and by reconstituted mass (30.3%).

Contrary to the crustacean, frequency of occurrence, number of prey, and reconstituted mass were always larger in the North-East monsoon for the fish category including the main prey fish species *Omosudis lowei* and *Paralepis atlantica* (Table 3). This main trend between North-East and South-West monsoons occurred in 2001, 2002 and 2003. However, this pattern was not observed with the reconstituted weight of the *A. ferox* prey, because larger sizes were consumed during the South-West monsoon (mean size increased from 157 to 301mm SL). Cephalopod prey showed roughly the same decreasing trend as fish prey between North-East and South-West monsoons (Table 3) but their contribution to the lancetfish diet was always minor.

Seasonality of the prey size

The mean sizes of *Charybdis smithii* and of the amphipods were smaller during the North-East monsoon than during the South-West monsoon (Table 4). The size frequency distribution of the stomatopod *Natosquilla investigatoris* was bimodal during the North-East monsoon, precluding the calculation of a reliable global mean for that season (Fig. 4). These two modes probably correspond to two different cohorts, with mean sizes of 42 and 70mm, respectively, while the mean size during the South-West monsoon was 61mm. Although the mean sizes of cephalopod and fish prey were not significantly different between North-East and South-west monsoons (Table 4), we did recover a few large conspecific prey in the stomachs of lancetfish during the South-West monsoon.

Predator-prey size ratios were estimated using the mean sizes of lancetfish and of the different prey groups or items. Prey consumed by lancetfish was small, and therefore, size ratios were always high (Table 4). Overall, the seasonal variations of the size ratios were low for fish and cephalopod prey, but greater for amphipods. With *N. investigatoris*, size ratios varied from 20.7 during the South-West monsoon to 15.3 or 25.5 during the North-East monsoon, depending on the cohort.

DISCUSSION

In this study, 59 prey species or categories including 11 crustaceans were recovered in 139 non-empty stomachs of lancetfish caught in the western Indian Ocean. This prey diversity is of the same order of magnitude to that described in different areas of the world ocean. However, in the western Pacific (Fourmanoir 1969, Grandperrin et Legand 1970), central Pacific (Moteki *et al.* 1993), eastern Pacific (Haedrich and Nielsen 1966) and the Atlantic Ocean (Haedrich 1964), fish prey was always dominant (Table 5), and mesopelagic fish of the Omosudidae, Alepisauridae and Paralepididae families formed the bulk of the lancetfish diet (Fourmanoir 1969, Haedrich 1964). Fourmanoir (1969) observed juveniles of coral fish in the stomach contents of lancetfish caught near the coasts of the western Pacific. We also recovered coral fish juveniles in lancetfish caught near the Seychelles shelf, which is evidence that lancetfish are opportunistic feeders. However, crustacean prey strongly dominated the diet of lancetfish in our data, whichever diet indices were taken into account. Amphipods were dominant in number in the Hawaiian waters (Moteki *et al.* 1993), but they represented 18% of the wet mass only (Table 5). In the western Indian Ocean during the investigated period, the swimming crab *Charybdis smithii* and the pelagic stomatopod *Natosquilla investigatoris* formed the main prey species in number and in reconstituted mass. *C. smithii*, which is very common in the western Indian Ocean (Thomas and Kurup 2001), was dominant during the South-West monsoon only. This portunid crab was also found in great quantities in the stomachs of yellowfin tunas (*Thunnus albacares*) caught by longlines in the same area (Zamorov *et al.* 1992; Potier *et al.* 2007). *C. smithii* inhabits the epipelagic zone, and its vertical distribution is linked to the respective position of the thermocline and oxycline (Van Couwelaar *et al.* 1997). This portunid crab feeds on crustaceans, gastropods, and fish (Losse 1969, Balabsurbramanian and Suseelan 1998) and forms from 50-90% of the micronekton fauna caught in the upper 200m (Van Couwelaar *et al.* 1997). *C. smithii* may thus play a dominant role, both as a predator and as prey, in the pelagic food chains of the western Indian Ocean.

We observed that during the North-East monsoon, *C. smithii* disappeared almost completely in the diet of the lancetfish. Indeed, this time period corresponds to the breeding phase of the crab, during which this species becomes benthic and is no longer observed in its pelagic phase (Van Couwelaar *et al.* 1997). During the North-East monsoon, the stomatopod *Natosquilla investigatoris* replaced *C. smithii* in the diet of lancetfish. *N. investigatoris* has a more superficial distribution, and occurs in very dense and extensive surface concentrations (Losse and Merrett 1971, Potier *et al.* 2002). These oceanic swarms constitute an important target for various predators, from lancetfish to surface tunas (Potier *et al.* 2002). Two cohorts were recovered in the stomachs of lancetfish during the North-East monsoon, while one cohort (one mode in the size distribution) was observed during the South-West monsoon. This pattern shows the possible occurrence of a new cohort during the North-East monsoon that grows during the South-West monsoon and is consumed by lancetfish one year later. However, the biology and ecology of *N. investigatoris* is still poorly known. Most stomatopods are bottom dwellers but *N. investigatoris* seems to be the only pelagic species characterized by enlarged eyes, which may be an adaptation for their swarming behaviour at the surface of very deep water. The diet of *N. investigatoris* is similar to the diet of *C. smithii*: this stomatopod is likely to be a detritivore but seems able to feed on small surface fishes (Losse and Merrett 1971). The occurrence of huge biomass of this stomatopod in the western Indian Ocean does not seem as regular as the occurrence of *C. smithii*, which has a well known annual cycle. Losse and Merrett (1971) previously reported a similar event during the period 1965-1967 in the Gulf of Aden and in the equatorial western Indian Ocean.

Most of the prey recovered in the lancetfish stomachs were small individuals of slow swimming species. Fast swimming marine organisms such as large cephalopods, fishes of the Exocaetidae family, and other large epipelagic fish were absent. This type of forage fauna is actively chased by a predator, while the lancetfish is more an ambush-style hunter than an active chaser (Romanov and Zamorov 2002). Such foraging behaviour explains the prey composition in the lancetfish diet. Haedrich (1964) and Haedrich and Nielsen (1966) suggested that the lancetfish is a diurnal feeder with a foraging activity limited to the first 300m of the water column. They justified their assumption by the lack of myctophids in the diet composition. In our observations as well, this prey family was almost totally absent in the stomach contents (two occurrences only). Furthermore, most of the lancetfish were caught during daytime. Therefore, our results tend to confirm Haedrich and Nielsen's hypothesis.

To the best of our knowledge, this study is the first investigation of the seasonality of the lancetfish diet in the western Indian Ocean. A strong seasonal pattern was evidenced by changes in the mean stomach content (which was higher during the South-West monsoon), in the number of prey items consumed, and in the prey species composition. The prey composition in the stomachs of lancetfish is constrained by local prey availability and foraging behaviour. We thus believe that our results reflect temporal changes in the composition of the forage fauna around the Seychelles. However, precise information on the prey composition and on the relative biomasses in the environment is required to study the potential selection of prey by a top predator. Further investigations will be needed to combine diet analysis with acoustic data and pelagic trawling which may give further independent information.

Our study highlights the existence of food chains based on crustaceans in this part of the Indian Ocean. The dominance of crustaceans in the diet of top predators (Zamorov *et al.* 1992, Potier *et al.* 2002) may be, at least in certain situations, a strong characteristic of the pelagic ecosystem in the western Indian Ocean and could have a strong impact on the pelagic fisheries. The demographic explosions 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 (purse seine) (Potier *et al.* 2002). The results observed in our study area can be compared to the eastern Pacific region where the swimming crab *Pleuroncodes planipes* (Alverson 1963, Longhurst 1967a, 1967b) contributes significantly to the food chain of top predators. The annual geographic distribution of this crab (which is found up to 1 000 km off the coast of Baja California) is strongly related to the upwelling intensity. In the western Indian Ocean, the intensity 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 emphasizes the usefulness of lancetfish to sample 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, not only on the feeding habits of top predators, but also on the biology of their prey to understand the trophic relationships in open-sea pelagic ecosystems.

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Legend of figures

Figure 1. Locations of the longline sets carried out during the South-West monsoon (○) and during the North-East monsoon (●) around the Seychelles shelf in 2001, 2002 and 2003.

Figure 2. Size distribution of the lancetfish individuals used in the diet study during South-West and North-East monsoons.

Figure 3. Proportions by reconstituted weight of the two main crustacean species (*C. smithii* and *N. investigatoris*), and of the other crustaceans, the fishes, the cephalopods and the other prey during the South-West (top) and North-East monsoons (bottom).

Figure 4. Prey size distributions of *Natosquilla investigatoris* (total length in mm) and of the fish species or categories (standard length in mm) during the South-West (top) and North-East monsoons (bottom).

List of Tables

Monsoon	South-West		North-East		total	
	N	N*100hooks^{-1}	N	N*100hooks^{-1}	N	N*100hooks^{-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		

Table 1

	Species prey	Occ		Nb		Recons	Mass
		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
Und. 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**	**1891**	**81.8**	**8605.5**	**70.2**
Portunidae	*Charybdis smithii*	60	43.2	512	22.2	6394.7	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	2089.5	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**	**2618.5**	**21.4**
Acanthuridae	*Naso* sp.	1	0.7	1	<0.1	2.2	<0.1
Alepisauridae	*Alepisaurus ferox*	17	12.2	21	0.9	1572.9	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
Und. Fish		11	7.9	15	0.6	114.1	0.9
Fish larvae		11	7.9	57	2.5	16.1	0.1
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
Plant		2	1.4	3	0.1	13.0	0.1
Salpidae		2	1.4	6	0.3	4.1	<0.1
Total		**139**		**2311**		**12262.7**	

Occc: Occurrence Nb: Number Recons Mass: Reconstituted Mass

Table 2

	Prey item	North-East monsoon			South-West monsoon		
		O%	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

Table 3

	North-East monsoon				South-West monsoon				Kruskal-Wallis	
	N	Mean±SD	Range	P/p ratio	N	Mean±SD	Range	P/p ratio	H	P
Cephalopods (DML)	24	36.5±17.8	14-71	29.4	10	47.7±39.6	9.8-136	26.5	.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 (W)	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 (mm)
TL: Total Length (mm)
W: Carapace width (mm)
SL: Standard Length (mm)

Table 4

	Hawaiian waters		Central Pacific		Present study	
	%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
Polychaet 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	1178	(…)	252	(…)	2315	(…)
N. stomachs	40	(…)	24	(…)	139	(…)

Table 5

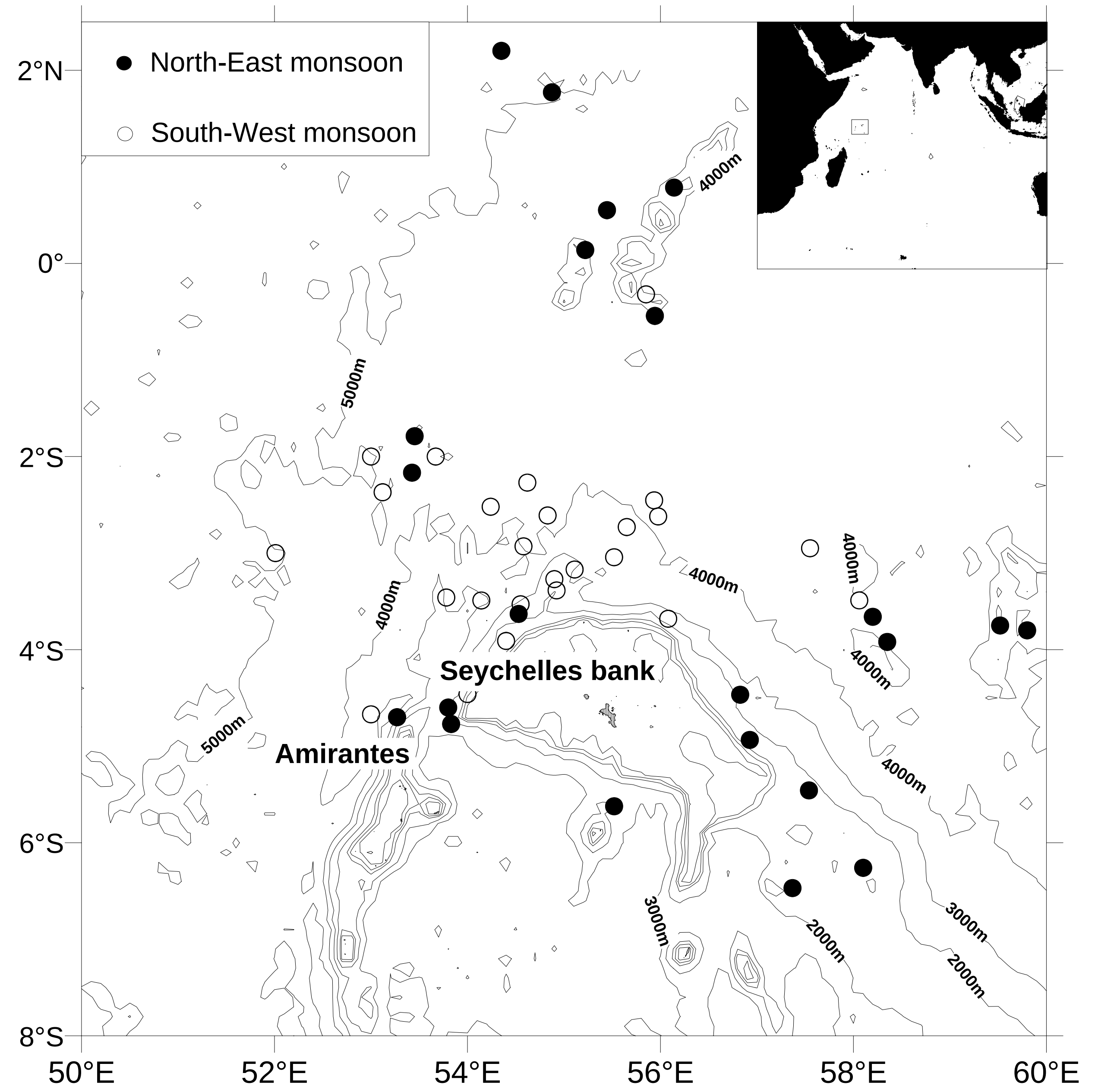
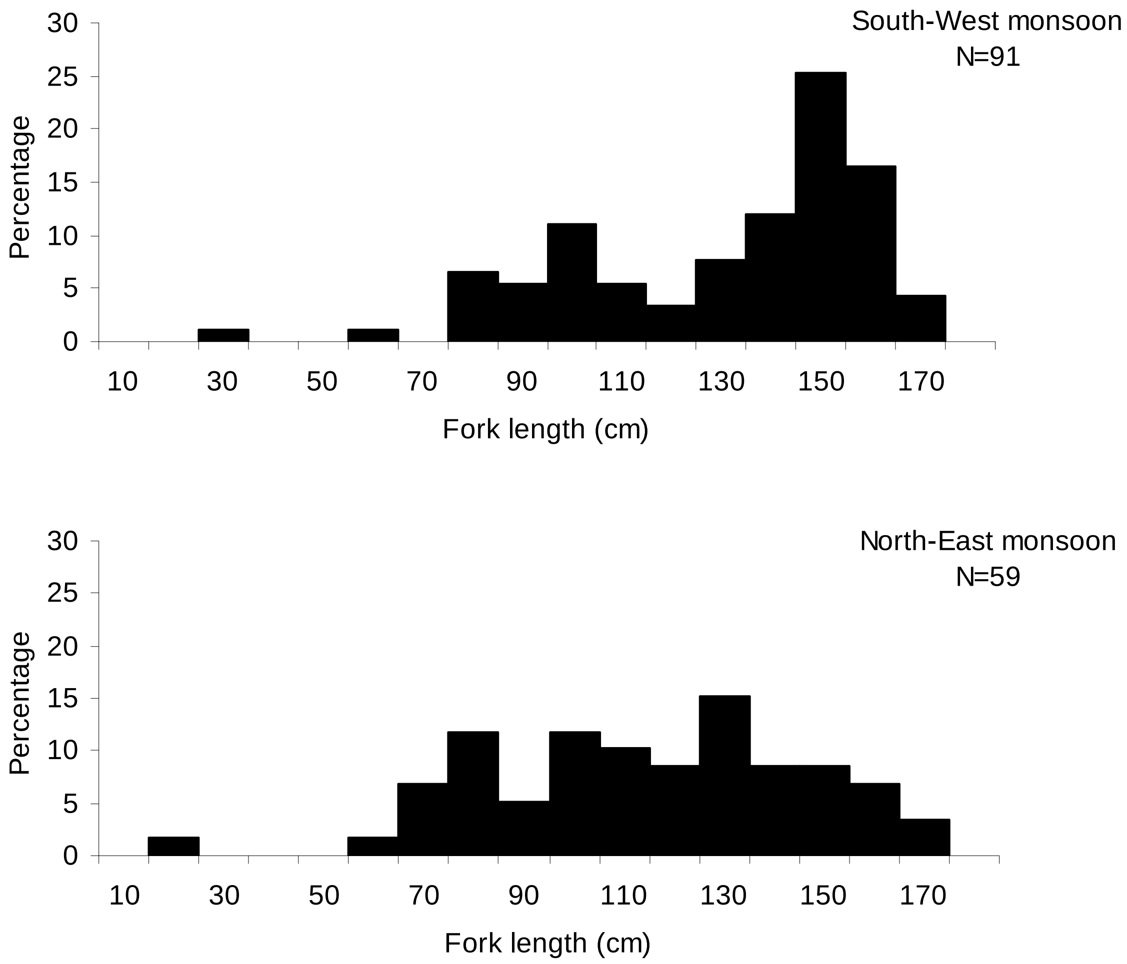

North-East monsoon
South-West monsoon
2°N
0°
2°S
4°S
6°S
8°S
50°E
52°E
54°E
56°E
58°E
60°E
4000m
5000m
3000m
2000m
Seychelles bank
Amirantes

figure1


South-West monsoon
N=91
Percentage
30
25
20
15
10
5
0
10
30
50
70
90
110
130
150
170
Fork length (cm)
North-East monsoon
N=59
Percentage
30
25
20
15
10
5
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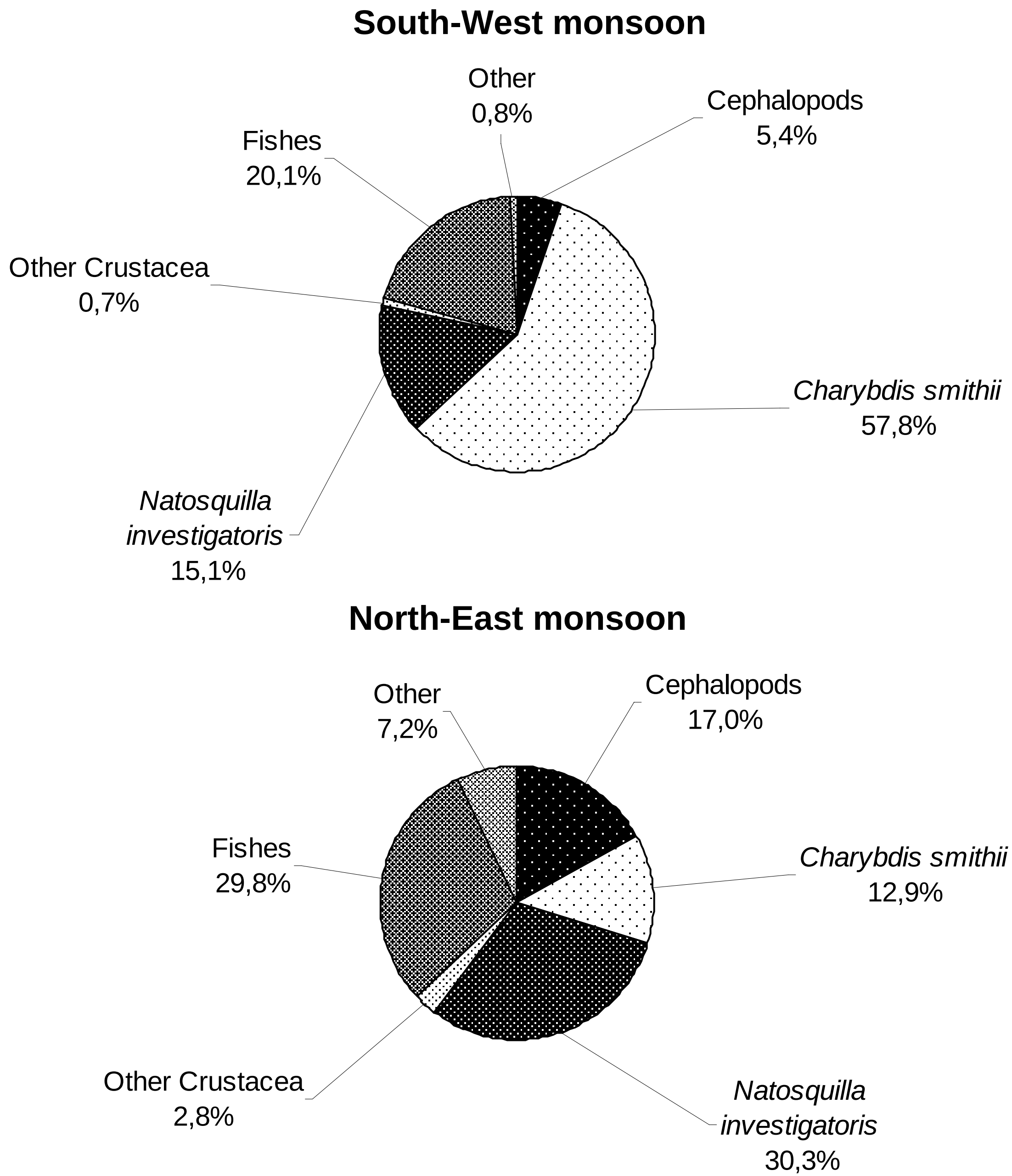
10
30
50
70
90
110
130
150
170
Fork length (cm)

figure2



Reconstituted weight

Figure 3

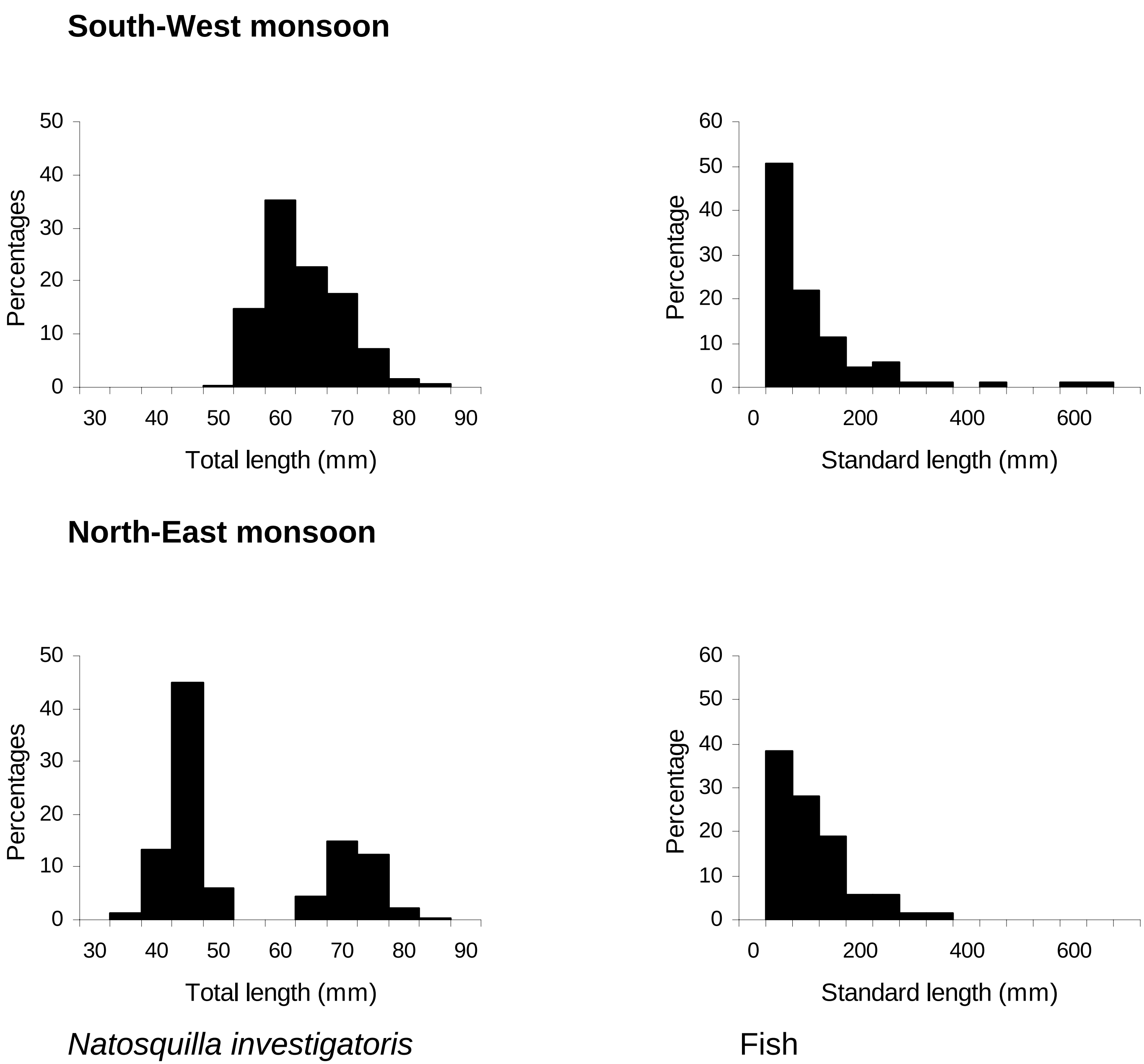

South-West monsoon
Percentages
Total length (mm)
Percentage
Standard length (mm)
North-East monsoon
Percentages
Total length (mm)
Percentage
Standard length (mm)
Natosquilla investigatoris
Fish

figure4