Aquat. Living Resour. 21, 123–134 (2008)

DOI: 10.1051/alr:2008026
www.alr-journal.org

Aquatic
Living
Resources

Spatial distribution of *Cubiceps pauciradiatus* (Perciformes: Nomeidae) in the tropical Indian Ocean and its importance in the diet of large pelagic fishes

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Received 19 September 2007; Accepted 11 April 2008

Abstract – The bigeye cigarfish (*Cubiceps pauciradiatus*) is a small pelagic nomeid of the tropical world ocean, often recovered in the stomach contents of top predators such as tunas, billfishes and marine mammals. In the Indian Ocean, a few studies have investigated the biology and the ecology of this species that is one of the most abundant fish of the intermediate trophic levels. In this paper, we investigated the spatial distribution of *C. pauciradiatus* in the Indian Ocean using pelagic trawl catches carried out between 20°N and 45°S, and the importance of bigeye cigarfish in the diet of 9 piscivorous fishes sampled by different fishing gears in the western part of the Indian Ocean. The highest densities were observed along the eastern coast of Africa and in the Arabian Sea (87 000 individuals per square nautical mile) during the South-West Monsoon and in the eastern part of the Seychelles archipelago (62 200 ind. square nmi) during the North-East Monsoon. Small sized bigeye cigarfish (20–80 mm SL) was a regular and abundant prey (20 to 200 ind. per stomach) for schooling predators exploited by purse seine fishery such as large yellowfin and bigeye tunas chasing prey near the sea surface. Large sized bigeye cigarfish (61–150 mm SL) occurred in small numbers (3 to 20 ind. per stomach) in the stomach contents of swordfish and of large yellowfin and bigeye tunas caught by longline sets at great depths. Large concentrations of bigeye cigarfish occurred in zones of high productivity, and that species constituted seasonally a strong link in the transfer of energy from low to high trophic levels in this part of the Indian Ocean.

Key words: Diet / Feeding ecology / Bigeye cigarfish / Abundance / Trophic role / Tuna / Sailfish / Swordfish / Indian Ocean

Résumé – Distribution géographique de *Cubiceps pauciradiatus* (Perciformes : Nomeidae) dans l'océan Indien tropical et son rôle dans l'alimentation des grands pélagiques. Ce poisson pélagique, *Cubiceps pauciradiatus*, à répartition circum-tropicale, est fréquemment observé dans les contenus stomacaux des grands prédateurs tels les thons, les poissons à rostre et les mammifères marins. Dans l'océan Indien, très peu d'études ont été menées sur la biologie et l'écologie de cette espèce qui est l'une des plus abondantes des niveaux trophiques intermédiaires. Dans cet article, nous décrivons, à partir des résultats de chalutages pélagiques réalisés entre 20°N et 45°S, la répartition géographique de *C. pauciradiatus* dans l'océan Indien et son rôle dans l'alimentation de 9 grands prédateurs capturés à la senne et à la palangre dans l'ouest de l'océan Indien. En mousson de sud-ouest, les plus fortes densités sont observées le long de la côte est-africaine et en mer d'Arabie (87 000 par mille^2 de surface), et en mousson de nord-ouest, dans l'est du plateau des Seychelles (62 200 par mille^2). Les individus de petite taille (20–80 mm, longueur standard) sont trouvés en nombre (20 à 200 ind. par estomac) et régulièrement dans les estomacs des albacores et thons obèses pourchassant en bancs leurs proies à la surface. Les individus de grande taille (61–150 mm LS) sont rencontrés, toujours en petit nombre (3 à 20 ind. par estomac), dans les estomacs de l'espadon, des grands albacores et thons obèses capturés au moyen de palangres, en profondeur. De grandes concentrations de *C. pauciradiatus* sont observées dans les zones de fortes productions thonières, et, dans cette partie de l'océan Indien, cette espèce constitue, saisonnièrement, un relais important dans le transfert d'énergie du bas vers le haut de la chaîne trophique.

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Article published by EDP Sciences

1 Introduction

Fishes of the family Nomeidae are important components of the marine food webs in the open-sea pelagic ecosystems. They are not exploited by commercial fisheries but incidental catches of large specimens have been already reported by longliners (Abe 1955) and tuna purse seiners (Romanov 2002). Species of the genus *Cubiceps* are often recovered in the stomachs of top predators such as tunas (Alverson 1963; Legand et al. 1972; Bashmakov et al. 1991; Ménard et al. 2000; Bard et al. 2002; Potier et al. 2007c), swordfish (Young et al. 2006; Potier et al. 2007c), seabirds (Pinaud et al. 2005), fur seals (Beauplet et al. 2004), dolphins (Perrin et al. 1973; Dollar et al. 2003), and balaenopterid whales (Romanov 2002). The genus comprises 10 species (Agafonova 1994). Most of them are small (maximum body length around 200 mm) except *Cubiceps paradoxus* and *C. capensis* that can reach 750 mm and 1000 mm, respectively (Agafonova 1994).

The bigeye cigarfish (*Cubiceps pauciradiatus*) is one of the smallest nomeid fish, reaching a maximum length of 200 mm (Butler 1979). Described as an pelagic species, the bigeye cigarfish is distributed in all equatorial and tropical ecosystems of the world ocean (Agafonova 1994). Juveniles remain in the top 100 m of the sea (Salekhov 1990). They feed on a broad spectrum of mesozooplankton species living in the epipelagic zone, including copepods, decapods, chaetognaths, heteropods, polychaets and hyperiids (Gorelova et al. 1994). Adults are known to perform diel vertical migrations between the mesopelagic and epipelagic zones (Salekhov 1990; Agafonova 1994). At night, they are found in the upper layers, and they move to depth of 200–300 m during daytime. Adult fish prey on macrozooplanktonic and micronektonic organisms: large copepods, larval decapods, euphausiids, hyperiids, siphonophores, salps and small fish (myctophids and genus *Vinciguerria*) (Salekhov 1990; Gorelova 1994).

C. pauciradiatus is a major prey for several top predators in the pelagic ecosystem. In the eastern tropical Pacific, bigeye cigarfish was recovered in 24% of the stomachs of the pantropical spotted dolphin, *Stenella attenuata*, and was the third main fish prey by number (6% of the total prey items) (Robertson and Chivers 1997). In the equatorial Atlantic (0°–5°N, 10°–20°W), and from November to March, the species was the most important prey by number (>300 individuals per stomach) of large-sized yellowfin tunas of free schools exploited by surface purse seine fishery (Ménard et al. 2000; Bard et al. 2002). In the eastern part of the Seychelles archipelago (western Indian Ocean), Bashmakov (1991) noted that the bigeye cigarfish was the dominant prey of schooling tunas during the North-East Monsoon. Bigeye cigarfish was recovered in stomach contents of several top predators caught with longlines and purse seines during French research cruises carried out by IRD[1] from 2000 to 2006. Scientific observers on board Soviet purse seiners (Romanov 2002), which operated in the Indian Ocean during 1980–1990s, recorded frequently this species in tuna stomachs. In addition, dense schools of juveniles were also observed at sea surface in areas of high aggregations of tuna schools (Bashmakov 1990, pers. comm.).

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In this paper, we combined for the first time past data from the YugNIRO[2] databases reporting observations from purse seine, longline and pelagic trawl scientific expeditions (Romanov et al. 2006) with recent data collected during the 2000s by IRD cruises. Our main goal is to investigate the spatial distribution of bigeye cigarfish and to describe the importance in fish diets of this poorly known species in the tropical pelagic ecosystem of the western Indian Ocean.

2 Material and methods

2.1 Data source

YugNIRO pelagic trawlings started in the 1970s and were carried out regularly from 1980 till 1990. They covered the whole Indian Ocean from 20°N to 40°S and from 20°E to 120°E. In 2002, two cruises with pelagic trawlings were performed by IRD in the Seychelles area and in the Mozambique Channel. A total of 6737 tows from 60 cruises were used here for mapping the seasonal distribution and abundance of bigeye cigarfish (Table 1).

Stomach samples were collected by IRD from 2000 to 2006 on board longliners and large industrial purse seiners: six purse seiner cruises and nine longliner cruise took place around the Seychelles Islands (2°30N-6°30S, 52°E-62°E); one purse seine cruise and three longliner cruises were performed in the Mozambique Channel (9°30S-23°S, 40°E-47°E) (Table 1).

From 1984 to 1992, stomach samples were collected by YugNIRO during nineteen cruises carried out on board Soviet tuna purse seiners in the Seychelles area (Romanov 2002). In addition, YugNIRO longline research cruises were carried out from 1961 till 1989 and covered almost all the tropical and temperate waters of the Indian Ocean (Romanov et al. 2006). However, during these cruises, bigeye cigarfish were rarely recorded because most of the stomachs were processed on board and prey species were not identified accurately.

2.2 Data analysis

Trawl data. To investigate the spatial distribution and to estimate the abundance of the bigeye cigarfish, trawl catches were adjusted according to the swept area method. Let a be the area swept by the trawl:

$$a = DH_rX^2$$

and

$$D = 60\sqrt{(Lat_1 - Lat_2)^2 + (Lon_1 - Lon_2)^2\cos^2(0.5(Lat_1 + Lat_2))}$$

where D is the distance covered by the trawl estimated from exact positions of the start and the end of the haul, H_r is the length of the head-rope and X^2 is a constant estimated to 0.5 (Pauly 1980).

[2] YugNIRO – Southern Scientific Research Institute of Marine Fisheries & Oceanography, Crimea, Ukraine.

Table 1. Data sources used in this study. Some cruises were carried out during the two seasons.

Fishing gear	Institute	Season	Dates	Cruises	Nb. Sets	Depth range (m)	Trawls with *Cubiceps*	Trawls without *Cubiceps*
Trawls	YugNIRO	NE Monsoon	1977–2001	55	2939	10–1670	258	2681
		SW Monsoon	1976–2001	58	3757	10–1750	205	3552
	IRD	SW Monsoon	2002	2	41	25–255	15	26
							Stomachs with *Cubiceps*	Stomachs without *Cubiceps*
Longline	YugNIRO	NE Monsoon	1961–1989	74	2311	50–350	**	13 260
		SW Monsoon	1962–1989	84	2471	50–350	**	15 991
	IRD	NE Monsoon	2001–2004	5	40	50–125	53 (19.9%)	267
		SW Monsoon	2001–2004	7	61	50–125	56 (14.2%)	393
Purse seines	YugNIRO	NE Monsoon	1984–1992	19	405	0–50	171 (27.6%)	620
		SW Monsoon	1984–1991	13	207	0–50	5 (1.2%)	412
	IRD	NE Monsoon	2000–2006	5	32	0–50	101 (41.4%)	244
		SW Monsoon	2000–2006	4	37	0–50	30 (9.0%)	335

** No information was available on the genus of the fish prey regarding YugNiro longline cruises.

The abundance was expressed in number of individuals per square nautical mile (ind. nmi^{-2}). Daytime trawls were excluded from the analysis. Every trawl was classified according to the season on which it was made, i.e. NE Monsoon (from November to April), and SW Monsoon (from May to October). Comparisons between seasons and spatial distribution were analysed through non-parametric statistics.

2.3 Predator classification

Tuna schools at sea surface are exploited by purse seine fishery, while longliners target individual fish at greater depths. The estimated depth of longline hooks ranged from 50 to 125 m, and from 50 to 350 m for IRD and YugNIRO cruises, respectively. Hereafter, surface predators refer to fishes that are caught by industrial purse seiners: they usually seek out concentrations of favoured prey near the surface (0–50 m) and they have a schooling feeding behaviour. Subsurface predators refer to fishes that are caught by longliners and that usually exhibit an individual feeding behaviour. Individuals of three tuna species (albacore *Thunnus alalunga*, yellowfin *T. albacares*, and bigeye *T. obesus* tunas) can be grouped as surface or subsurface caught predatory fishes, according to the fishing gear. The other predator fish species owned to one group only: skipjack tuna (*Katsuwonus pelamis*), frigate mackerel (*Auxis thazard*) and barracuda (*Sphyraena barracuda*) were assigned to surface predators, while swordfish (*Xiphias gladius*), the sailfish (*Istiophorus platypterus*), the striped marlin (*Tetrapturus audax*), and the longnose lancetfish (*Alepisaurus ferox*) were assigned to subsurface predators. Specimens of *C. pauciradiatus* were assumed to be adults at 80 mm onward (Agafonova and Poluyaktov 1992).

Predatory fish were measured: eye-fork length for billfishes and swordfish (EOFL), and fork length (FL) for other species), weighed and dissected on board.

2.4 Stomach content analysis

Stomachs were usually frozen at –20 °C and transported to laboratory for further analysis. For YugNiro samples, either stomachs were processed on board or stored in the formaldehyde. In the laboratory, each stomach was thawed, and both accumulated (eroded otoliths) and fresh items subsequently sorted. Accumulated items were excluded from the analysis because they overemphasize the importance of some prey in fish diets. Fresh remains were divided into broad prey classes (fish, cephalopods, crustaceans and others), which were weighed to calculate their proportion by mass in the diet. Identification of fish prey relied on the external morphology of either intact specimens or fresh otoliths. Otoliths were identified by reference to features given by Smale et al. (1995) and Rivaton and Bourret (1999), and by comparison with material held in our own reference collection. The length of the sagitta of bigeye cigarfish (L_o) was measured to 0.1 mm with a vernier calliper. We used our own allometric equations to estimate standard length (mm):

$$SL = 1.7844L_o + 0.8797,\ n = 150,\ R^2 = 0.954.$$

2.5 Data and statistical analyses

The contribution of *C. pauciradiatus* to the diet of a given predator was investigated using three indices: the frequency of occurrence (O_i = the number of stomachs including *C. pauciradiatus* prey divided by the total number of non-empty stomachs), the fresh body mass (W_i = the total fresh body mass of *C. pauciradiatus* prey divided by the total weight of prey items), the numerical importance (N_i = the total number of *C. pauciradiatus* prey divided by the total number of prey items). To explore the role of *C. pauciradiatus* in the diet, O_i, W_i and N_i were computed with the data pooled across all stomachs for each predator. Data did not match the normality assumptions of analysis of variance. We thus performed Kruskal-Wallis and Kolmogorov-Smirnov tests (Zar 1999).

The number and the size distribution of the *C. pauciradiatus* otoliths recovered in the stomachs were tested using a forward stepwise regression taking into account different covariates: depth (surface, subsurface), zone (Seychelles, Somalia, Mozambique Channel), predator species (9 species) and predator size (EOFL or FL). For these analyses, the stomach was used as the sampling unit. Residuals were checked for normality by means of Shapiro tests, and for homocedaticity by plotting fitted values vs. residuals.

3 Results

3.1 Spatial distribution

The bigeye cigarfish was rarely caught in pelagic trawls carried out south of 20°S. A few specimens were captured in 40 trawls carried out in the South of the Madagascar Island. On the other hand, the bigeye cigarfish occurred from 20°N to 20°S the whole year long. In the eastern tropical Indian Ocean, the abundance of bigeye cigarfish remained low (<24 000 ind.nmi^{-2}) whatever the season. In the western Indian Ocean and during the South-West Monsoon, large concentrations of bigeye cigarfish were recorded in the Somalia area, in the east of the Seychelles archipelago and in the northern part of the Arabian Sea (Fig. 1a). During the North-East Monsoon, large patches (>50 000 ind. nmi^{-2}) occurred in the eastern part of the Seychelles archipelago, along the eastern coast of Africa and in the Arabian Sea (Fig. 1b). For both seasons, the differences in mean density between the western and the eastern basins were significant (Mann-Whitney test; $p < 0.01$ during the NE Monsoon and $p = 0.03$ during the SW Monsoon). On the other hand, the densities per basin did not differ significantly between the seasons (Mann-Whitney test; $p = 0.11$ in the eastern basin and $p = 0.22$ in the western basin). Most of the trawls, with bigeye cigarfish, were performed at night (greater than 95% for both seasons), and more than 50% of the total night hauls have captured bigeye cigarfish (56% during the NE Monsoon and 50% during the SW Monsoon). On the other hand, bigeye cigarfish was rarely recovered during the daytime (8.6% of the trawls during the NE Monsoon and 8.5% during the SW Monsoon). In the day hauls, the average density was always very low (1000 ind.nmi^{-2} during the NE Monsoon and 270 ind.nmi^{-2} during the SW Monsoon) The night average density decreased slightly but not significantly from 3536 ± 8215 ind.nmi^{-2} during the NE Monsoon to 2851 ± 10 639 ind.nmi^{-2} during the SW Monsoon (Kruskal-Wallis test, $H = 1.07$, $p = 0.30$).

3.2 Contribution to large pelagic fish diet

A total of 31 species of large pelagic predatory fishes have been sampled for diet studies during the longline and purse seine cruises (several were by-catches of each gear). Bigeye cigarfish occurred in the diet of ten fishes. It dominated by number (>50% of the fish prey) the diet of three surface tunas (albacore, yellowfin and bigeye tunas) and of sailfish. Bigeye cigarfish were also a significant part by number (from 15 to 50% of the fish prey) of the diet of swordfish and of barracuda. It was a minor part (<10% of the fish prey) of the diet of striped marlin, of longnose lancetfish, of two subsurface large tunas (yellowfin and bigeye tunas) together with two small surface scombrids (frigate mackerel and skipjack tuna).

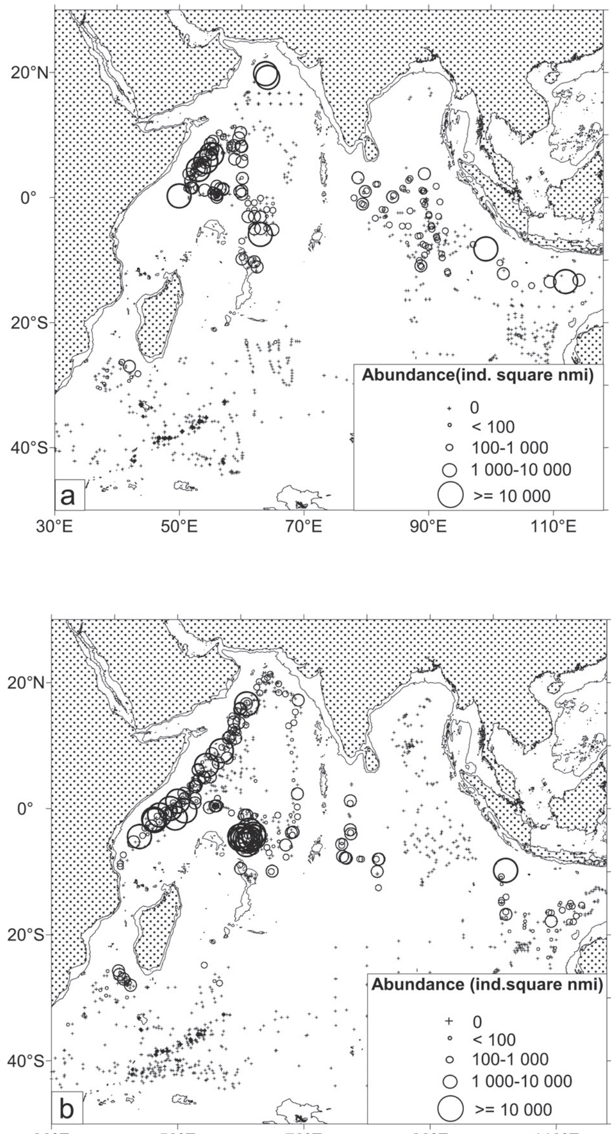

Fig. 1. Seasonal distribution of the bigeye cigarfish, *Cubiceps pauciradiatus* (number of specimens caught per square nautical mile) in trawling operations carried out during the YugNIRO cruises (see Table 1): (a) South-West Monsoon, (b) North-East Monsoon.

3.3 Surface predators

Most of the surface fish predators (86%) contained fresh remains in their stomachs. Fish dominated always their diet by mass (>50%) except for albacore tunas in which crustaceans were the main prey component (96%) (Table 2). However, long-term dietary changes were observed for skipjack and yellowfin tunas, with a shift from fishes to crustaceans during the recent years. Overall fish prey were found in 58% of the 848 sampled stomachs, and 54 314 fishes were identified. bigeye cigarfish was the most important fish prey (by number) in large tunas (yellowfin, bigeye and albacore) and in barracuda. It ranked second among fish prey in small tuna species (frigate mackerel and skipjack), whose diet was dominated by anchovies *Engraulis japonicus* (Table 3). Other important fish prey (>10% by number) included *Vinciguerria* *nimbaria*, Phosichtyidae, in the diet of barracudas. All other fish prey identified from stomach contents were recovered in small numbers (<5%).

3.4 Subsurface predators

Fresh remains were recovered in 88% of subsurface predators. Fish (>50%) dominated the diet of billfishes (sailfish, marlin and swordfish) and of large tunas (yellowfin and bigeye tunas) by mass (Table 2). It was a significant prey class (>10%) in two other species (lancetfish and albacore). Fishes occurred in 74% of the 594 stomachs, and 3682 fish items were identified. Bigeye cigarfish was the most important fish prey for swordfish and sailfish by number. It was also present in small numbers (<10%) in yellowfin and bigeye tunas, striped marlin and longnose lancetfish (Table 3). Other important fish prey (>10% by number) included: (i) myctophids of the genus *Diaphus* in the diet of albacore, yellowfin and bigeye tunas; (ii) the diretmid *Diretmichthys parini* in the diet of swordfish; (iii) mesopelagic fishes of the genus *Paralepis* in the diet of longnose lancetfish, yellowfin and bigeye tunas; (iv) two mesopelagic fishes *Omosudis lowei* and *Alepisaurus ferox* in the diet of longnose lancetfish (Table 3). All other fish prey identified from stomach contents were recovered in small numbers (<5%) only.

3.5 Abundance in the stomachs

Bigeye cigarfish occurred in the stomach contents of large pelagic fishes caught by purse seiners in the Seychelles waters, and by longliners in both Seychelles waters and Mozambique Channel. The species was not recovered in the diet of surface predators caught in the Mozambique Channel. For subsurface predators, the number of bigeye cigarfish per stomach was higher in the Seychelles waters than in the Mozambique Channel. For yellowfin tuna, bigeye tuna and swordfish, the number of prey per stomach increased from 3.0 ± 2.0 to 6.7 ± 9.2, 1.5 ± 0.7 to 8.0 ± 12.1 and from 2.6 ± 2.1 to 4.3 ± 4.5, respectively. However, the difference between both areas was significant for swordfish only ($p = 0.017$), and not for bigeye and yellowfin tunas ($p = 0.37$ and $p = 0.232$, respectively). Mean numbers of bigeye cigarfish per stomach content of surface predators sampled in the Seychelles waters during the 1980–1990's surveys were 171.1 ± 107.3 for yellowfin tuna, 118.5 ± 50.4 for bigeye tuna, 15.5 ± 7.0 for skipjack and 8.3 ± 2.3 for frigate tuna, while during the recent period (2000–2006), mean numbers were 26.0 ± 12.4 and 29.4 ± 32.5 for bigeye and yellowfin tunas, respectively. The differences between both seasons were significant ($H = 27.8$, $p < 0.01$, and $H = 36.7$, $p < 0.01$ for bigeye and yellowfin tunas, respectively). Furthermore, the number of bigeye cigarfish is always higher in the stomach contents of surface fish predators caught in the Seychelles area than in those of subsurface predators. The differences were significant for both bigeye and yellowfin tunas ($p < 0.01$ each). Stepwise regression results showed that depth factor ($p < 0.01$) and predator size ($p < 0.05$) were the most significant covariates explaining the number of *C. pauciradiatus* found in the stomach contents (Table 4).

3.6 Size of the prey

Predator fishes fed upon both adults and juveniles of bigeye cigarfish (Table 5, Fig. 2). A Kolmogorov-Smirnov test performed on the size (SL) distribution of bigeye cigarfish ingested by yellowfin tuna showed that subsurface individuals prey upon larger fish than surface tunas ($p < 0.01$) (Fig. 3). The same test performed on the body length distribution of bigeye cigarfish recovered in the stomachs of subsurface yellowfin tuna showed a significant difference between the Mozambique Channel and the Seychelles waters ($p < 0.03$): prey were larger in stomachs sampled in the Mozambique Channel than the ones collected in the Seychelles waters. Conversely, no difference was found in the size distribution of bigeye cigarfish eaten by swordfish caught in the two areas ($p = 0.13$) (Fig. 3). The stepwise regression performed on the distribution of *C. pauciradiatus* sizes recovered in the stomachs show that the zone effect had a lower impact ($p < 0.05$) than depth, predator species and predator size ($p < 0.01$ each; Table 4).

4 Discussion

This study highlights the trophic importance of the bigeye cigarfish *Cubiceps pauciradiatus* in the tropical pelagic ecosystem of the western Indian Ocean. The same results have already been observed in the eastern Atlantic (Ménard et al. 2000; Bard et al. 2002) and in the Pacific Oceans (Alverson 1963). In our study, *C. pauciradiatus* was found as a prey in nine species which are among the main fish predators of the pelagic ecosystem. The proportions by mass of the fish prey class (Table 2) and the proportions by number of bigeye cigarfish (Table 3) in the predator diets led us to consider that species as: (1) a major prey of the surface large tunas (yellowfin, bigeye and albacore), of sailfish and of swordfish; (2) a common prey of barracuda and skipjack tuna; (3) and a minor prey for frigate mackerel, striped marlin, longnose lancetfish and subsurface albacore, yellowfin and bigeye tunas. However, several fish predators have been poorly sampled in our study (e.g. barracuda, billfishes and albacore tuna), and therefore further investigations are needed for these species. The annual consumption of bigeye cigarfish by three predators (yellowfin, bigeye and skipjack tunas) was estimated to more than 20^6 metric tons in the Indian Ocean (Romanov and Zamorov 1999).

Additional information from predator diets was gained on the vertical distribution of bigeye cigarfish. According to prey size, predators grouped in three assemblages. Skipjack tuna, lancetfish, barracuda and sailfish, together with surface albacore, yellowfin and bigeye tunas foraged near the surface on small bigeye cigarfish (41.2 mm and 1.2 g on average). On the other hand, subsurface yellowfin and bigeye tunas preyed rather upon bigeye cigarfish of intermediate size (88 mm and 12 g), while swordfish consumed much larger individuals (107 mm and 19.8 g). Accordingly, swordfish and subsurface bigeye and yellowfin tunas fed significantly on adult bigeye cigarfish (96%, 46% and 41% of the total number, respectively), whereas the surface predators preyed on juveniles only (Table 5). Similar pattern of size selectivity of bigeye cigarfish

Table 2. Characteristics of predatory fishes caught in the western Indian Ocean during 2000-2006 IRD cruises (1) and during Russian cruises from 1961 to 1992 (2) and broad prey class composition of their diet. Length values (mean ± SD, in cm) and range. Frequency of occurrence (*FO*); Fresh body mass (*W*) expressed in percent.

	Predator Species	Specimens *n*	Length of predator Mean ± sd (cm)	Length of predator Range (cm)	Stomach with fresh remains	Cephalopods *FO*	Cephalopods *W* (%)	Crustacea *FO*	Crustacea *W* (%)	Fish *FO*	Fish *W* (%)	Others *FO*	Others *W* (%)
Surface	Sphyraenidae												
	Sphyraena barracuda	13	98 ± 15	77–110	9	2	0.1	3	12.4	7	87.5		
	Scombridae												
	Auxis thazard[1]	8	42 ± 3	34–45	3					3	100		
	Auxis thazard[2]	60	42 ± 4	33–49	60			5	1.8	55	98.2		
	Katsuwonus pelamis[1]	159	55 ± 10	31–74	79	5	1.1	59	90.1	21	8.7	1	0.1
	Katsuwonus pelamis[2]	182	53 ± 51	38–74	182	17	1.6	18	2.8	181	95.5	4	0.1
	Thunnus alalunga	4	102 ± 7	96–110	4	1	2	3	96.1	2	2		
	Thunnus obesus[1]	84	81 ± 31	41–160	62	17	10.5	25	31.7	37	57.8		
	Thunnus obesus[2]	25	118 ± 25	54–170	25				25	100			
	Thunnus albacares[1]	195	91 ± 36	35–160	170	32	0.9	108	78.3	88	20.7	3	0
	Thunnus albacares[2]	242	122 ± 26	55–158	242	6	0.7	4	0.8	74	98.5		
Subsurface	Scombridae												
	Katsuwonus pelamis	15	63 ± 5	53–71	12	4	6.8	11	91.4	2	1.8		
	Thunnus alalunga	11	104 ± 5	100-112	4	4	33.4	3	33.7	3	32.9		
	Thunnus obesus[1]	81	113 ± 22	60–167	53	44	31.9	19	13.6	34	54.5	1	0
	Thunnus obesus[2]	78	****		78	****	10.3	****	20.3	****	69.4		
	Thunnus albacares[1]	181	111 ± 21	48–174	149	112	12	98	31.6	122	56.4	10	0.1
	Thunnus albacares[2]	173	****		173	****	17.1	****	51.9	****	31	****	0
	Xiphiidae												
	Xiphias gladius	239	106 ± 29	56–192	206	149	45.9	89	2.2	179	51.8	1	0.1
	Istiophoridae												
	Istiophorus platypterus	19	166 ± 297	91–211	19	9	5.1	9	14.3	18	80.5	1	0.1
	Tetrapturus audax	4	186 ± 375	163–240	4	2	6.3	2	1.5	3	92.2		
	Alepisauridae												
	Alepisaurus ferox	172	119 ± 29	58–170	159	52	9.6	132	67.5	83	21.4	39	1.6

**** No data.

Table 3. Number of the main prey fish species (% in parentheses) in the diet of predatory fishes feeding on the cigarfish *Cubiceps pauciradiatus* in the western Indian Ocean. Data from surface (S)and subsurface (Su, in italics) individuals derived from recent (2000-2006) and historical periods (1961-1992) are pooled for each predator.

Family	Species	*Auxis thazard*	*Thunnus alalunga*		*Thunnus albacares*		*Thunnus obesus*		*Katsuwonus pelamis*	*Istiophorus platypterus*	*Tetrapturus audax*	*Xiphias gladius*	*Alepisaurus ferox*	*Sphyraen barracuda*
			S	Su	S	Su	S	Su	S	*Su*	Su	Su	Su	S
		n = 58	*n* = 2	*n* = 3[a]	*n* = 162	*n* = 295[a]	*n* = 62	*n* = 112[a]	*n* = 202	*n* = 18[a]	*n* = 3[a]	*n* = 179[a]	*n* = 83[a]	*n* = 7
Omosudidae	*Omosudis lowei*					39(3.1)	2 (0.1)	47(3.2)				1(0.2)	*38 (23.5)*	
Gempylidae	*Gempylus serpens*				22(0.1)	35(2.8)	1 (<0.1)	11(0.7)		4(3.4)		12(2.0)		
	Rexea prometheoides					2(0.2)								
	Nealotus tripes					3(0.2)		1(0.1)						
	Thyrsitoides marleyi				1 (<0.01)	1(0.1)						1(0.2)		
Nomeidae	*Cubiceps pauciradiatus*	124(4,3)	22 (100.0)		21 770 (55.0)	89(7.0)	2849 (75.4)	*32 (2.16)*	657 (8.2)	*73 (61.3)*	1(5)	*274 (45.7)*	4(2.5)	4 (17.4)
	Psenes arafurensis				1 (<0.01)	1(0.1)						6(1.0)		
Argentinidae	*Nansenia macrolepis*					2(0.2)								
	Microstoma microstoma							1(0.1)						
	Und. argentinids					2(0.2)								
Chauliodontidae	*Chauliodus* sp.							1(0.1)						
Paralepididae	*Paralepis spp.*					*191(15.1)*	1 (<0.1)	*107 (7.2)*		2(1.7)		5(0.8)	*30 (18.5)*	
	Lestrolepis intermedia				1 (<0.01)	15(1.2)		1(0.1)				1(0.2)		
	Lestidiops similis					1(0.1)		8(0.5)				2(0.3)		
	Und. paralepidids					20(1.6)								
Notacanthidae						1(0.1)								
Bregmacerotidae	*Bregmaceros* sp.					1(0.1)								
Scopelarchidae	*Scopelarchus analis*				2 (0.01)	5(0.4)								
Sternopthychidae	*Argyropelecus* sp.					2(0.2)								
	Argyropelecus affinis							1(0.1)						
	Polyipnus sp.							5(0.3)						
	Und. sternopthychids				1 (<0.01)	5(0.4)								
Alepisauridae	*Alepisaurus ferox*					73(5.8)		13(0.9)		2(1.7)		4(0.7)	*21 (13.0)*	
Bramidae	*Brama brama*				2 (0.01)	9(0.7)						17(2.8)	2(1.2)	
	Brama orcini											3(0.5)		
Myctophidae	*Diaphus spp.*			*25 (89.3)*	286 (0.7)	*106 (8.4)*		*509 (34.4)*	32 (0.4)			11(1.8)	2(1.2)	
	Diaphus perspicillatus				156 (0.4)			*646 (43.6)*						
	Diaphus lucidus				54 (0.1)									
	Electrona risso						1 (<0.1)							
Notosudidae	*Scopelosaurus hoedti*					1(0.1)		1(0.1)				2(0.3)		
Diretmidae	*Diretmus argenteus*				1 (<0.01)		2 (0.1)	16(1.1)				11(1.8)		
	Diretmichthys parini						1 (<0.1)	9(0.6)				*62 (10.3)*		1 (4.3)
Scopelarchidae	*Scopelarchus analis*							33(2.2)				33(5.5)		
Scomberesocidae	*Scomberesox saurus*					2(0.2)								
Phosichthyidae	*Vinciguerria nimbaria*					34(2.7)	1 (<0.1)	1(0.1)		1(0.8)			3(1.8)	4 (17.4)
Chiasmodontidae	*Chiasmodon niger*					46(3.6)		5(0.3)		5(4.2)			1(0.6)	1 (4.3)
Exocoetidae	*Exocoetus volitans*				34 (0.1)	4(0.3)	8 (0.2)	7(0.5)				4(0.7)	1(0.6)	
	Cheilopogon sp.				2 (0.01)	1(0.1)								
	Und. Exocoetids					*128 (10.1)*			1 (<0.01)					
Hémiramphidae	*Hyporhamphus* sp.					2(0.2)								
Oxyporhamphidae	*Oxyporhamphus micropterus*				2 (0.01)	1(0.1)			1 (<0.01)			1(0.2)		

Table 3. Continued.

Family	Species	*Auxis thazard*	*Thunnus alalunga*		*Thunnus albacares*		*Thunnus obesus*		*Katsuwonus pelamis*	*Istiophorus platypterus*	*Tetrapturus audax*	*Xiphias gladius*	*Alepisaurus ferox*	*Sphyraen barracuda*
			S	Su	S	Su	S	Su	S	*Su*	Su	Su	Su	S
		n = 58	*n* = 2	*n* = 3[a]	*n* = 162	*n* = 295[a]	*n* = 62	*n* = 112[a]	*n* = 202	*n* = 18[a]	*n* = 3[a]	*n* = 179[a]	*n* = 83[a]	*n* = 7
Clupeiformes					2(0.2)									
Engraulidae	*Engraulis japonicus*	2728(94.7)			13000 (32.9)		887 (23.5)		7230 (89.8)					
	Stolephorus sp.				1695 (4.3)									
Carangidae	*Decapterus macrosoma*				66(0.2)	23(1.8)	2 (0.1)							
	Decapterus macarellus	17 (0.6)			1018 (2.57)		7 (0.2)		23 (0.3)					
	Decapterus sp.				511 (1.29)	6(0.5)				6(5.0)		7(1.2)	1(0.6)	2 (8.7)
	Caranx sp.				4 (0.01)									
Scombridae	*Sarda orientalis*					1(0.1)								
	Katsuwonus pelamis	10 (0.3)			244 (0.6)	5(0.4)		1(0.1)	66 (0.8)					
	Auxis thazard	2 (0.1)			480 (1.2)	87(6.9)	7 (0.2)	1(0.1)	34 (0.4)		8(40)	2(0.3)	1(0.6)	1 (4.3)
	Und. scombrids					39(3.1)								
Monacanthidae	*Cantherhines* sp.				4 (0.01)	4(0.3)								
Balistidae	*Canthidermis maculata*			1(3.6)	86 (0.2)	15(1.2)	2 (0.1)					7(1.2)	16(9.9)	1 (4.3)
Diodontidae	*Diodon* sp.				3 (0.01)					1(0.8)			1(0.6)	2 (8.7)
Coryphaenidae	*Coryphaena equiselis*					4(0.3)				1(0.8)		1(0.2)		
Carapidae	*Echiodon* sp.					4(0.3)				2(1.7)				
Dactylopteridae	*Dactyloptena orientalis*				1 (<0.1)	3(0.2)				3(2.5)				
Acanthuridae	*Naso* sp.					7(0.6)							1(0.6)	
Ephippididae					3(0.2)									
Serranidae						1(0.1)		1(0.1)						
Menidae					2(0.2)									
Leiognathidae	*Leiognathus equula*					3(0.2)								
Scatophagidae					1(0.1)									
Holocentridae	*Myripristis* sp.				1 (<0.01)	6(0.5)								
	Sargocentron sp.					1(0.1)								
Stromateidae								1(0.1)						
Sparidae	*Chrysoblephus* sp.							2(0.1)						
Caproidae					9(0.7)									
Fistulariidae					2(0.2)									
Syngnathidae					3(0.2)									
Pentacerotidae						1(0.1)		1(0.1)						
Ostraciidae	*Ostracion cubicus*				1 (<0.1)	3(0.2)					2(10)		1(0.6)	
	Lactoria diaphana					8(0.6)								
Triacanthodidae	*Macrorhamphosodes* sp.							3(0.2)						
	Und. Triacanthodidae					3(0.2)		4(0.3)						
Tetraodontidae	*Cantigaster* sp.					11(0.9)								
	Lagocephalus lagocephalus					3(0.2)				1(0.8)		1(0.2)	3(1.9)	
	Arothron sp.							2(0.1)						
Echeneidae	*Remora brachyptera*				1 (<0.1)	2(0.2)		1(0.1)						
	Heniochus sp.					4(0.3)								
Coastal juveniles					7 (0.02)	8(0.6)								
High sea juveniles					11 (0.03)	9(0.7)								
Fish larvae					8 (0.02)	45(3.6)								
Und. Fish				2(7.1)	82 (0.2)	*114 (9.0)*	9 (0.2)	10(0.7)	6 (0.07)	*18 (15.2)*	9(45)	*132 (22.1)*	*40 (22.2)*	7 (30.4)
Total		2881	22	28	39558	1267	3780	1482	8050	119	20	600	166	23

Table 4. Results of the two stepwise regressions performed on the number (R^2 = 0.249) and on the size (otolith length) (R^2 = 0.730) of *Cubiceps pauciradiatus* recovered from the stomach contents of 10 predators. Depth, zone, predator species and predator size were assessed as covariates (see text).

	Regression coefficient	*SE*	*t*	$P(>\|t\|)$
Number of *C. pauciradiatus*				
Depth	19.163	3.617	5.298	< 0.01
Predator size	0.018	0.009	2.047	0.04
Predator species	−0.977	0.963	−1.015	0.31
Zone	−2.435	3.824	−0.637	0.53
Otolith length of *C. pauciradiatus*				
Depth	−2.905	0.091	−31.759	< 0.01
Predator size	−0.019	0.002	−11.509	< 0.01
Predator species	0.244	0.030	8.023	< 0.01
Zone	0.283	0.140	2.014	0.04

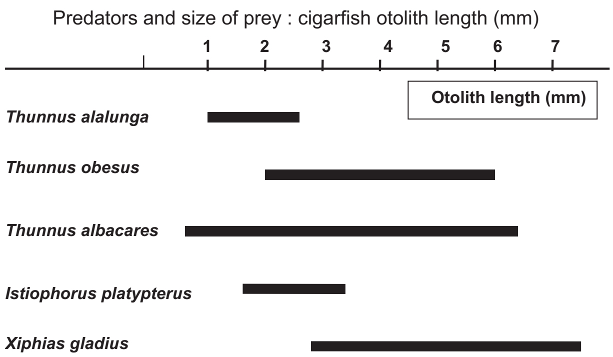

Fig. 2. Size distribution of otolith length (mm) of bigeye cigarfish recovered from stomach contents of five top predators in the western Indian Ocean. Size range of otoliths 1–8 mm corresponds to cigarfish size range 28–150 mm.

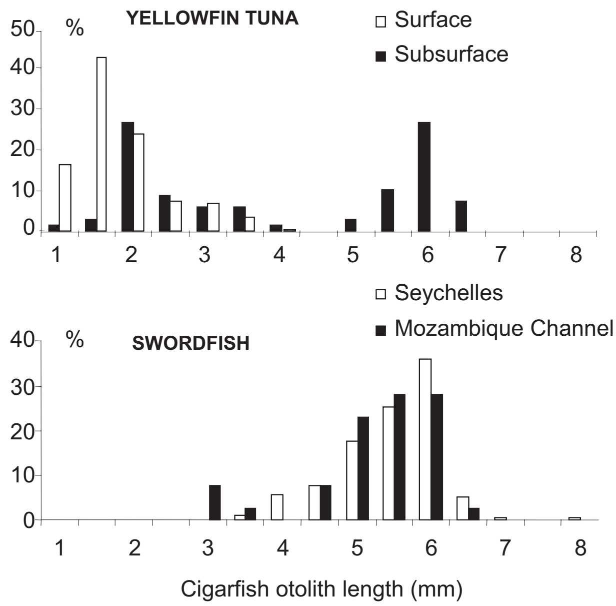

Fig. 3. Size distribution of otolith length (mm) of bigeye cigarfish found in the stomach contents in surface and subsurface caught predatory fishes: (a) from yellowfin tuna; size range of otoliths 1–6.5 mm corresponds to cigarfish size range 28–129 mm; (b) from swordfish caught in the Mozambique Channel and in Equatorial waters of the Seychelles archipelago; size range of otoliths 3–8 mm corresponds to cigarfish size range 65–150 mm.

were evidenced in the diet of predators from the Atlantic and Pacific Oceans (Fig. 4). These results are related to ontogenetic changes in the depth distribution of bigeye cigarfish. In the Atlantic Ocean, Salekhov (1990) observed that juveniles were epipelagic, while adults performed diel vertical migration from mesopelagic waters to the surface.

In open ocean ecosystems, large fish predators usually adopt an opportunistic feeding behaviour within their foraging range (Ménard et al. 2006). The differences in prey size distribution and in prey number observed in the stomachs of surface and subsurface fish predators can thus reflect the prey type availability in the environment. In the eastern Atlantic, Bard et al. (2002) showed that large schooling yellowfin tunas caught by purse seiners at sea surface were feeding on monospecific concentrations of bigeye cigarfish juveniles belonging to the same length class. In the same way, Ménard and Marchal (2003) investigated the foraging behaviour of surface tunas feeding on small schooling *Vinciguerria nimbaria* in the surface layers of the equatorial Atlantic, and Potier et al. (2007c) highlighted the role of the stomatopod *Natosquilla investigatoris* in the diet of tunas caught during the South-West monsoon in the Seychelles waters. In both cases, these concentrations of schooling prey were dominant in the surface layers prospected by tunas. Our results and these studies show that surface fish predators tend to feed on large concentrations of monospecific prey when they are available (Bard et al. 2002; Ménard and Marchal 2003; Potier et al. 2007c).

The subsurface predators did not exhibit the same feeding behaviour. They tended to feed on individual targets of larger size. If the bigeye cigarfish remained important in the diet of both swordfish and sailfish, it was less essential for subsurface tunas. Kornilova (1981) studied the detailed food composition of yellowfin and bigeye tunas caught by longline in the equatorial Indian Ocean from 1969 to 1973, and she did not mention bigeye cigarfish as a main prey. Our results are similar: in terms of mean proportions by number, the bigeye cigarfish represented 8% and 2% of the diet of yellowfin and bigeye tunas, respectively.

Our study, that combined historical (1962–1991) and recent (2000–2006) data, revealed the permanent trophic role of *C. pauciradiatus* in the diet of surface top predators in the western Indian Ocean. This role is dominant during the North-East Monsoon (December-April) when large concentrations of free schools of tunas are observed in the eastern part of the Seychelles archipelago. During that season, small bigeye cigarfish are always recorded in large number in the stomachs of schooling tunas (Bashmakov et al. 1992; Potier et al. 2007a) and schools of tunas are often observed in association with balaenopterid whales feeding on the same prey (Romanov 2002). The differences observed in the number of bigeye cigarfish preyed by schooling tunas between past and recent periods did not affect the catch per unit of effort (CPUE) of the French purse seiners operating on free schools in the same area during

Table 5. Characteristics of *C. pauciradiatus* prey eaten by top predators from the western part of the Indian Ocean. Values are means ±SD with ranges in parentheses.

	Predator Species	Number	Otolith size (mm)	Estimated Standard Length (mm)	Estimated Body Mass (g)	Adults (*SL* > 80 mm) (%)
Surface	Sphyraenidae					
	Sphyraena barracuda	3	2.1 ± 0.1 (2.0–2.2)	47 ± 2 (46–49)	1.3 ± 0.2 (1.1–1.5)	0
	Scombridae					
	Katsuwonus pelamis	3	1.9 ± 1.0 (1.2–3.1)	44 ± 20 (35–67)	1.6 ± 2.2 (0.3–4.2)	0
	Thunnus alalunga	28	1.9 ± 0.3 (1.0–2.6)	44 ± 7 (28–57)	1.1 ± 0.6 (2.8–5.7)	0
	Thunnus obesus	260	3.3 ± 0.4 (2.0–4.1)	70 ± 8 (46–86)	5.2 ± 1.9 (1.3–9.5)	0
	Thunnus albacares	420	1.6 ± 0.6 (0.6–3.6)	39 ± 11 (20–76)	1.1 ± 1.1 (0.1–6.5)	0
Subsurface	Scombridae					
	Thunnus obesus	27	4.0 ± 0.7 (3.4–6.0)	84 ± 13 (72–121)	9.6 ± 5.7 (5.4–28.2)	41%
	Thunnus albacares	76	3.8 ± 1.9 (1.0–6.4)	81 ± 35 (28–129)	12.7 ± 12.1 (0.2–34.0)	46%
	Xiphiidae					
	Xiphias gladius	210	5.2 ± 0.7 (2.8–7.5)	107 ± 13 (61–150)	19.8 ± 6.9 (3.2–54.4)	96%
	Istiophoridae					
	Istiophorus platypterus	57	2.5 ± 0.5 (1.6–3.4)	56 ± 88 (39–73)	2.5 ± 1.3 (0.6–5.5)	0
	Tetrapturus audax	1	2.9	63	3.5	0
	Alepisauridae					
	Alepisaurus ferox	4	2.3 ± 0.9 (1.4–3.6)	52 ± 17 (35–76)	2.4 ± 2.8 (0.4–6.5)	0

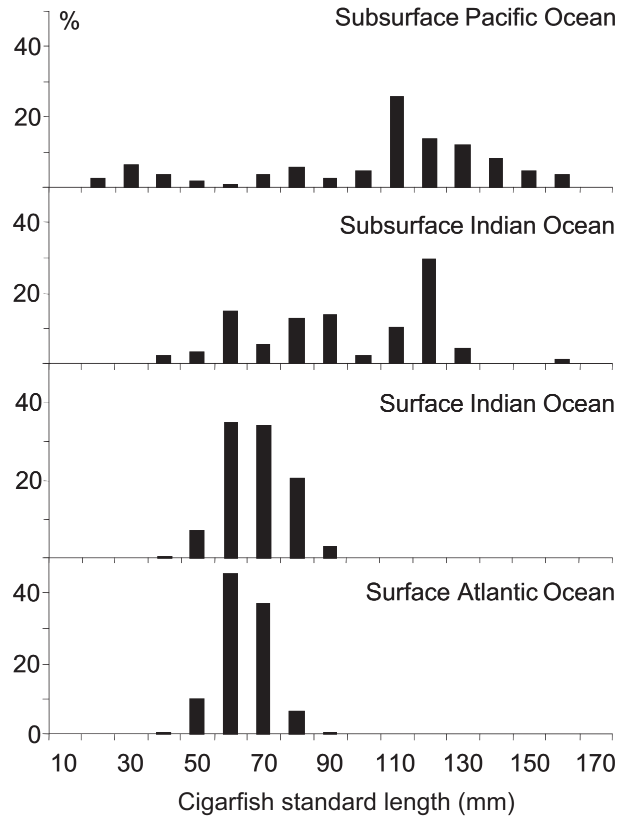

Fig. 4. Size distribution of bigeye cigarfish found in the stomach contents of surface and subsurface caught predactory fishes in different oceans.

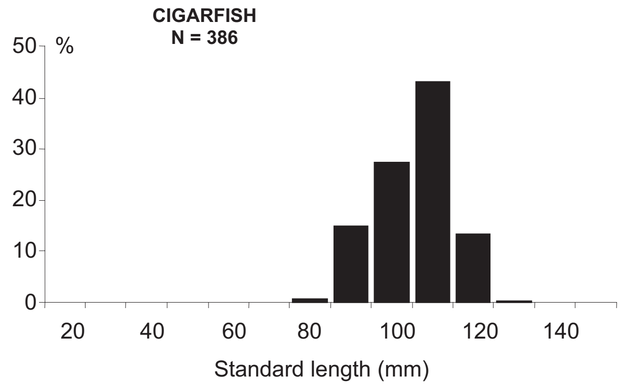

Fig. 5. Size distribution of bigeye cigarfish caught by midwater trawls in the east of Seychelles Islands.

the North-East Monsoon: 3.9 metric tons per standard fishing hour for the 1984–1990 period versus 4.3 tons per standard fishing hour for the 2000-2005 period, although the efficiency of the vessels increased substantially through the introduction of new fishing technology (sonars, birds' radars, etc.). This observed stability in the CPUEs could be due to a decrease in the availability of tuna prey such as concentrations of bigeye cigarfish.

In the Indian Ocean and Atlantic Ocean (Salekhov 1990), the important contribution of bigeye cigarfish to large pelagic fish diets fits well with the high catches of that species recorded in pelagic trawling data. Large aggregations of small bigeye cigarfish have been already observed visually at the sea surface (Bashmakov 1990, pers. comm.). Such aggregations likely indicated close spawning grounds and periods (from December-January to March-April in the East of Seychelles). Eastward of Seychelles, concentrations of small (Fig. 1) and mature (Fig. 5) bigeye cigarfish were located along southern streams of the South Equatorial Countercurrent (SECC) (Longhurst 1998; Schott and McCreary 2001; Schott et al. 2002) and within the South Equatorial Divergence. Both physical structures generate open ocean upwellings leading to increase of primary production (Longhurst 1998). In the same way, the highest densities of bigeye cigarfish in the Atlantic Ocean were recorded in zones of high productivity, such as the Equatorial Counter Current or the periphery of cyclonic gyres (Salekhov 1990; Lamkin 1997).

Our work highlitghs the usefulness of marine predators to gain valuable information on the biology and on the distribution of their prey (Cherel et al. 2004, 2007; Potier et al. 2007b, 2007c). Other nomeid fishes are important food items of various fishes, seabirds and marine mammals (Perrin et al. 1973; Pinaud et al. 2005). Our study shows that these poorly known fishes constitute, seasonally, a crucial link in the transfer of energy from lower trophic levels (zooplankton) to higher trophic levels (including surface tunas and swordfish). Juveniles of bigeye cigarfish consume a broad range of zooplanktonic organisms inhabiting the upper 100 m of the epipelagic zone (such as copepods or hyperiids), while adults are known to consume large amount of salps and occasionally small fishes (Gorelova et al. 1994). Therefore, *Cubiceps pauciradiatus* constitutes an important species of the intermediate trophic level in the tropical open ocean, connecting, through relatively short food chains, zooplankton to top predatory fishes.

Acknowledgements. The authors gratefully thank the Seychelles Fishing Authority (SFA), the crew of the longliner "*Amitié*", the crew of the longliner "*Cap Morgane*", and all the observers on board French and Soviet purse seiners for helping us to collect the samples. This work, a part of the THETIS programme of the IRD (Institut de Recherche pour le Développement), is also supported by the BIOPS project funded by Institut Français de la Biodiversité (N° CD-AOOI-07-013). We would like to acknowledge contribution of YugNIRO scientists in the long-term sampling of data in the Indian Ocean and the development of the database partially used in this paper. One of the authors (Romanov) was a member of that research team in 1985-2005. We thank three anonymous referees for their valuable comments and suggestions that helped us to improve the manuscript.

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