Feeding Partitioning among Tuna Taken in Surface and Mid-water Layers: The Case of Yellowfin *(Thunnus albacares)* and Bigeye *(T. obesus)* in the Western Tropical Indian Ocean

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Abstract—The trophic relations of two apex predators, yellowfin and bigeye tuna (*Thunnus albacares* and *T. obesus*), and their prey were investigated in the western tropical Indian Ocean. The contents of 173 non-empty stomachs were analysed from specimens caught with longlines and purse seine during scientific and fishing cruises. Diet data were processed by occurrence, by number, and by wet weight and a comparison of diets between surface and deep swimmers made. Crustaceans were the almost exclusive food source of surface-swimming bigeye tuna, with the stomatopod (*Natosquilla investigatoris*) being the sole prey item recorded in this category. The diet of deep-swimming yellowfin tuna was balanced between epipelagic fish, crustaceans and cephalopods. Bigeye tuna fed predominantly on cephalopods and mesopelagic fish (Scopelarchidae and Paralepididae), for which this predator appeared to be the most active chaser. The diet of the two predators reflects their ability to catch the prey, and their vertical distribution.

INTRODUCTION

In the tropical open oceans the epipelagic ecosystems are generally considered oligotrophic, but large predators such as tuna and tuna-like species are abundant and ubiquitous with high metabolic rates (Olson & Boggs, 1986). The survival of these pelagic predators depends on their efficiency to locate prey-rich areas (Sund et al., 1981; Bertrand et al., 2002). Forage resources in the ocean are patchy (Herbland, 1990) and large marine predators must forage over vast areas. The ecological role of apex predators in marine food webs is of interest because it is a critical in the assessment of the effects of fishing on ecosystems (Essington et al, 2002; Schindler et al., 2002; Cox et al., 2002; Watters et al., 2003). In the Central Pacific, Kitchell et al. (1999) found that no single fish species had a profound role at the highest trophic levels. However, new simulations conducted with ECOSIM model (Cox et al., 2002; Watters et al., 2003) suggest that tuna (yellowfin and skipjack) are likely to produce substantial structural changes in the ecosystem when removed by fishing. Such results are based on linkages between each food web component shown in a diet composition matrix. Therefore, the definition of the appropriate matrix for a given ecosystem is the starting point to any modelling approach. Ecosystem approaches to fisheries management are gaining increasing importance and it is a challenge to implement such an approach in the western Indian Ocean due to the rapid development of the large pelagic fisheries. Tuna catches have dramatically increased since the early eighties, when a purse seine fishery developed in the western

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part of the Indian Ocean. At the same time the Asian longline fisheries, which had been operating since 1952, also substantially increased their catches. In the period 1984–2001, tuna catches in the Indian Ocean rose from 0.2 to 1.1 million tonnes, purse seine contributing 34 % of the catch in 2001 (Anon, 2003).

A better knowledge of the feeding of apex predators is required in this region. The feeding habits of tuna have already been described around India (Sudarsan et al., 1991; Thomas and Kumaran, 1969; Thomas, 1969), South Africa (Shannon 1986) and in the western tropical part of the Indian Ocean (Kornilova, 1980; Zamorov et al., 1992; Roger, 1994a, Bashmakov et al., 1992, Potier et al., 2002). These authors showed the opportunistic behaviour of these fishes, which adapt their feeding to the available prey. In this paper, we focus on two species of tuna taken using two different gears, the longline and the purse seine, exploiting two different depth strata, respectively mid- and surface layers. The prey species composition is compared

in order to detect if significant partitioning of the forage resources occurs among these apex predators.

MATERIALS AND METHODS

The sampling area was located in the Western Indian Ocean, between 4°N–7°S and 46°E–60°E (Fig. 1). From 2001 to 2003, nine longline cruises were performed on board the longliner l'Amitié of the SFA (Seychelles Fishing Authority). Stomach contents were collected during fishing trips aboard a longliner and a purse seiner. During each cruise, 6 to 12 longline operations were performed. Samples from purse seines came from one trip made in October 2002 on board the French purse seiner Gueriden. During that cruise, 10 sets, made on drifting Fish Aggregating Devices (FADs), were sampled. Altogether 202 stomachs of yellowfin and bigeye tuna were analysed. Table 1 summarises the distribution of the stomachs by species and fishing gear.
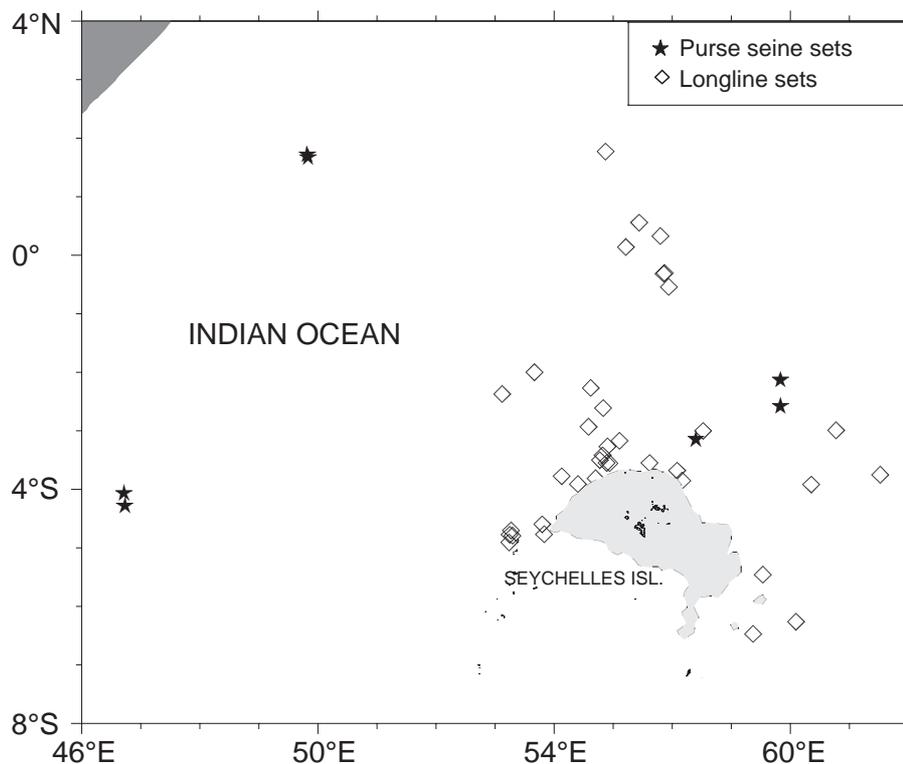
Fig. 1. Location of the longline and purse seine sets

Table 1. Distribution of the collected stomachs by species and fishing gear

Fishing gear	Yellowfin	Bigeye	Total
Longline	127	29	156
Purse seine	34	12	46
Total	161	41	202

Stomach analysis

The entire stomach was removed from the freshly caught fish when hauled on board. Size of the predator [LF1 (fork length) or LD1 (snout–first dorsal fin length)] and sex were recorded for each fish. Stomachs were frozen at -20°C. In the laboratory, each sample was thawed and drained. Then a three-step analysis was conducted (Fig. 2): (a) The total weight of the stomach contents was measured; (b) the content was sorted by large categories (fish, molluscs, crustaceans); and (c) the weight of each category was noted.

The different items constituting one category were sorted and counted. For each item, identifiable organs were used to determine the number of prey present in the stomach. For fish, the number of mandibles, parasphenoids or the maximum number of either left or right otoliths was assumed to reflect the total number of prey. For cephalopods, we used the greatest number of either upper or lower beaks. For crustacea, telsons or cephalo-thorax were counted.

The different items were determined to the lowest possible taxon using keys and descriptions of Clarke (1986), Nesis (1987), Smith & Heemstra (1986), Smale et al. (1995), Tregouboff & Rose (1978) and by comparison with the material held in our own reference collection.

Trophic and similarity indices

The dominance of the different items in the diet of the tuna was determined using the modified Costello diagram (Costello, 1990; Amundsen et al., 1996). The Costello diagram is based on a two-dimensional representation, where each point relates the occurrence of a prey taxon to its abundance (all in percent). Amundsen et al. (1996) modify the Costello diagram in order to overcome the problems inherent to the method. Abundance of a prey taxon is replaced by a new parameter, the prey-specific abundance (P_i) which equals:

Sampling: On board fishing vessels (purse seine and longline)

Storage: In the freezer

Analysis: (A) **Weighing of the stomach**

(B) **Sorting into large categories**
Fish   Molluscs   Crustacea
Weighing of the less abundant categories (ex: molluscs and crustacea) and weight of the main category (ex: fish) by subtraction

(C) **For every category**

Accumulated food ← sorting → Fresh food

Counting the recognisable organs (otoliths, beaks, mandibles, parasphenoids)

For every item
Systematics, counting and measurement of recognisable organs or entire individuals

Reconstituted weight of the diet

Fig. 2. Methodology used during the analysis of the stomach contents

$P_i = (\Sigma S_A / \Sigma S_t A) \times 100$

with ΣS_A = Total of prey A (expressed in number or weight), and $\Sigma S_t A$ = Total of prey (expressed in number or weight) in the stomachs with prey A. Information about prey importance and feeding strategy of the predator is given by the distribution of the points along the diagonals and the axes of the diagram (Fig. 3).

The degree of overlap between the different feeding regimes is given by the Morisita and Horn quantitative index of similarity (in Magurran, 1988):

$$C_{mh} = \frac{2\sum_{i=1}^{S} an_i \times bn_i}{(da + db)(aN \times bN)}$$

with S = total number of species of prey in the feeding regime of both predators;

aN = total number of prey in the feeding regime of predator A; and

bN = total number of prey in the feeding regime of predator B;

an_i = number of individuals of prey i in the feeding regime of predator A;

bn_i = number of individuals of prey i in the feeding regime of predator B;

$$da = \frac{\sum_{i=1}^{S} an_i^2}{aN^2} \quad \text{and} \quad db = \frac{\sum_{i=1}^{S} bn_i^2}{bN^2}$$

The feeding regimes are then compared by pair of predators. C_{mh} varies from 0 when the feeding regimes are completely distinct, to 1 when they are identical. Above 0.6 the overlap between feeding regimes is considered significant.

RESULTS

Feeding patterns

The size distribution of the fish whose stomachs were examined is given in Fig. 4. Of the 202 tuna stomachs, 29 were completely empty, and 173 contained prey remains (Table 2). None of the stomachs collected from purse seine sets were empty. For longline samples, the frequency of empty stomachs was low for yellowfin (13%) and high for bigeye (41%).

The repletion index expressed as gram of stomach content per kilogram of body weight was higher for surface tuna than for deep-dwelling tuna. The difference between surface and deep swimmers was lower for yellowfin tuna (rate purse seine/longline = 2.35) than for bigeye (rate of 9.88) (Fig 5). A Mann-Whitney test showed that differences are significant between fishing gear for a given species (Z = -3.67 p < 0.001, and Z = -5.84 p < 0.001 for bigeye and yellowfin, respectively), and between species for longline (Z = -3.58 p < 0.001). However, for the purse seine the test is not significant between species (Z = 0.47 p = 0.63). In wet mass and by large category, crustaceans formed the bulk of the diet for the yellowfin regardless of the fishing gear. It was also the main diet item for surface bigeye. On the other hand, the diet of longline bigeye was dominated by fish and squid.

$$Occurrence(\%) = \frac{\sum stomachs\ with\ prey\ A}{\sum stomachs\ with\ prey}$$

$$Prey\text{-}specific\ abundance\ (\%) = \frac{\sum prey\ A\ (number,\ weight)}{\sum all\ prey\ in\ stomachs\ with\ prey\ A}$$

Fig. 3. The theoretical Costello diagram (modified from Fig. 3 in Amundsen et al. 1996) and its interpretation to indicating feeding strategy. (BPC = between-phenotype component ; WPC = within-phenotype component)
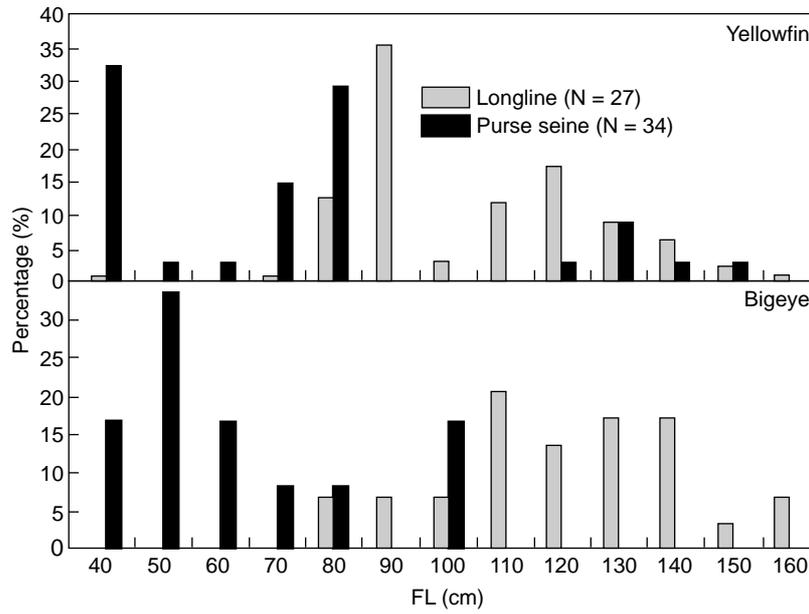
Fig. 4. Size distribution of fish sampled by species and fishing gear
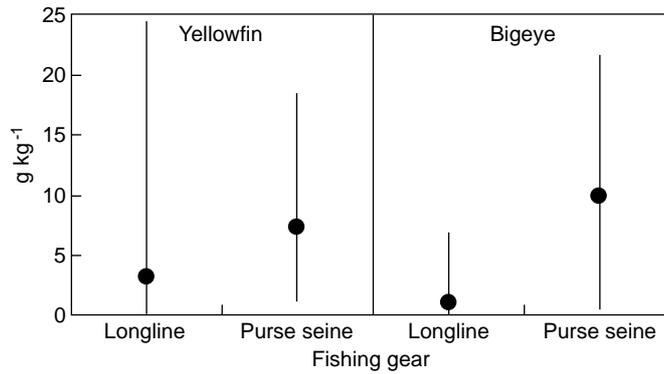
Fig. 5. Repletion index (mean and standard deviation) expressed in gram of stomach content per kilogram of body weight, by species and fishing gear

Table 2. Characteristics of the stomach contents by species and fishing gear

	Yellowfin			Bigeye		
	Empty	Non-empty	Mean content (g)	Empty	Non-empty	Mean content (g)
Longline	17	110	81.2 ± 145.7	12	17	42.1 ± 76.4
Purse seine	0	34	97.7 ± 135.1	0	12	83.2 ± 96.9
Total	17	144		12	29	

Prey species composition

1) Yellowfin tuna (*Thunnus albacares*)

The results of the analysis of the 144 yellowfin tuna stomachs are summarised in Table 3.

(A) LONGLINE STOMACHS:

A total of 44 families of prey were identified. Most of these prey items were crustaceans (4003 individuals), cephalopods (461 individuals) and fish (444 individuals). Organisms belonging to other groups like pteropods and heteropods were very

Table 3. Yellowfin tuna, *Thunnus albacares*. Frequency of occurrence and number of prey items recovered from stomach contents (total for all 110 deep and 34 surface-samples pooled)

		Occurrence		Number	
		n	**%**	**n**	**%**
LONGLINE					
Crustaceans		**78**	**70.9**	**4003**	**81.4**
Portunidae	*Charybdis edwardsi*	11	10.0	176	3.6
Oplophoridae	*Acanthephyra* sp.	4	3.6	4	0.1
	Oplophorus typus	4	3.6	73	1.5
Enoplometopidae	*Enoplometopus* sp.	3	2.7	16	0.3
crab larvae		45	40.9	3282	66.8
Squillidae	*Natosquilla investigatoris*	3	2.7	6	0.1
	Neoanchisquilla tuberculata	2	1.8	20	0.4
Odontodactylidae	*Odontodactylus scyllarus*	30	27.3	164	3.3
Lysiosquillidae	*Lysiosquilla tredecimendata*	20	18.2	39	0.8
Hyperiidae		30	27.3	188	3.8
Lycaeidae		7	6.4	7	0.1
Tyvidae		14	12.7	28	0.6
Fish		**90**	**81.8**	**444**	**9.0**
Scombridae	*Auxis sp.*	6	5.5	8	0.2
	Unidentified scombrids	19	17.3	42	0.9
Carangidae		5	4.5	18	0.4
Coryphaenidae	*Coryphaena equiselis*	2	1.8	2	0.0
Exocoetidae	*Exocoetus volitans*	3	2.7	4	0.1
Hemiramphidae	*Hyporamphus* sp.	1	0.9	2	0.0
Holocentridae	*Myripristis* sp.	4	3.6	4	0.1
Balistidae		4	3.6	9	0.2
Monacanthidae		3	2.7	3	0.1
Carapidae		1	0.9	2	0.0
Dactylopteridae	*Dactyloptena orientalis*	2	1.8	2	0.0
Ostraciidae	*Ostracion cubicus*	7	6.4	7	0.1
Omosudidae	*Omosudis lowei*	10	9.1	12	0.2
Paralepididae	*Paralepis atlanticus*	26	23.6	41	0.8
Alepisauridae	*Alepisaurus ferox*	10	9.1	10	0.2
Chiasmodontidae	*Chiasmodon niger*	1	0.9	1	0.0
Myctophidae	Unidentified myctophids	17	15.5	87	1.8
Nomeidae	*Cubiceps pauciradiatus*	12	10.9	84	1.7
Bramidae		1	0.9	1	0.0
Gempylidae	*Gempylus serpens*	2	1.8	2	0.0
Scopelarchidae	*Scopelarchus analis*	2	1.8	5	0.1
Argentinidae	*Nansenia macrolepis*	4	3.6	4	0.1
Phosichthyidae	*Vinciguerria nimbaria*	4	3.6	13	0.3
Unidentified fish		21	19.1	36	0.7
fish larvae		12	10.9	45	0.9

Table 3. continued

		Occurrence		Number	
		n	**%**	**n**	**%**
LONGLINE					
Cephalopods		**83**	**75.5**	**461**	**9.4**
Enoploteuthidae		7	6.4	15	0.3
Ommastrephidae		75	68.2	406	8.3
Mastigoteuthidae	*Mastigoteuthis* sp.	1	0.9	1	0.0
Onychoteuthidae		4	3.6	4	0.1
Cranchidae	*Taonius* sp.	4	3.6	4	0.1
Unidentified squids		10	9.1	21	0.4
Octopodidae		9	8.2	9	0.2
Argonautidae		1	0.9	1	0.0
Others		**5**	**4.5**	**8**	**0.2**
Heteropods	*Carinaria* sp.	2	1.8	2	0.0
Pteropods		1	0.9	4	0.1
Plants		2	1.8	2	0.0
Total		**110**		**4916**	**100.0**
PURSE SEINE					
Crustaceans		**31**	**91.1**	**1096**	**95.3**
Squillidae	*Natosquilla investigatoris*	31	91.1	1096	95.3
Fish		**5**	**14.7**	**5**	**.4**
Scombridae	Unidentified scombrids	5	14.7	5	.4
Cephalopods		**8**	**23.5**	**49**	**4.3**
Ommastrephidae		8	23.5	49	4.3
Total		**34**		**1150**	**100.0**

scarce. On average, 44.7 prey were found per stomach. Fish dominated the diet by occurrence (81.8%), and crustaceans by number (81%). Crab larvae, amphipods of the hyperiid family and *Charybdis edwardsi* were the most important prey item among the 12 families of crustaceans found in the stomach contents. By number (66.8% of the total) and by occurrence (> 40% of the stomachs) crab larvae dominated (Table 3). The stomatopod *Odontodactylus scyllarus* occurred in a quarter of the stomachs but it represented only 3.3% of the total number of prey items. Among the 22 families of fish prey, Paralepididae (23.6% of the stomachs), unidentified scombrids (17.3%) and myctophids (15.5%) were the most frequent items. The mesopelagic families of myctophids (87 individuals) and nomeids represented by the species *Cubiceps*

pauciradiatus (84 individuals) were the most numerous fish prey. However no family of fish exceeded 1.8% of the total prey. The main part of the cephalopod prey was made up of two ommastrephid species, *Stenoteuthis oualaniensis* and *Ornithoteuthis volatilis*. They occurred in two-thirds (68.2%) of the samples, and they formed 8.3% of the total number of prey. Other families represented a negligible proportion, by number (< 0.4%).

(B) PURSE SEINE STOMACHS:

Three families of prey were recorded and 1150 prey counted. Among them, crustaceans were represented by a single species (*Natosquilla investigatoris*), followed by cephalopods (n = 49 prey) and fish (n = 5 prey). In number, crustaceans dominated the diet (1096 prey, i.e. 95%).

cephalopods (family ommastrephids) formed 4.3% of the total number, and fish (scombrids) ranked third (0.4%). On average 33.8 prey per stomach were found.

2) Bigeye tuna *(Thunnus obesus)*
Table 4 summarises the results of the analysis of the 29 bigeye tuna stomachs.

a) LONGLINE STOMACHS:
A total of 154 prey items were recovered in the stomachs with 9.06 prey per stomach on average.

Among the prey items, fish were the most numerous (n = 73) followed by crustaceans (n = 41) and cephalopods (n = 40). No organisms belonging to other groups were observed. Cephalopods were present in 77% of the stomachs but they formed only a quarter (26.6%) of the total number of prey. Crustaceans were rarely found in the stomachs. Among the seven families recorded, the caridean shrimp *Oplophorus typus* and the stomatopod *N. investigatoris* were the most common crustacean prey item. They were recorded in 11.8% of the stomachs. *Oplophorus typus*

Table 4. Bigeye tuna, *Thunnus obesus*. Frequency of occurrence and number of prey items recovered from stomach contents (total for all 17 deep and 12 surface samples pooled)

		Occurrence		Number	
		n	%	n	%
LONGLINE					
Crustaceans		**7**	**41.2**	**40**	**26.0**
Portunidae	*Charybdis edwardsi*	1	5.9	1	0.6
Oplophoridae	*Acanthephyra* sp.	1	5.9	3	1.9
	Oplophorus typus	2	11.8	26	16.9
crab larvae		1	5.9	2	1.3
Squillidae	*Natosquilla investigatoris*	2	11.8	5	3.2
Hyperiidae		1	5.9	1	0.6
Tyvidae		1	5.9	2	1.3
Fish		**10**	**58.8**	**73**	**47.4**
Paralepididae	*Paralepis atlanticus*	5	29.4	13	8.4
Alepisauridae	*Alepisaurus ferox*	1	5.9	1	0.6
Myctophidae	Unidentified myctophids	4	23.5	8	5.2
Nomeidae	*Cubiceps pauciradiatus*	1	5.9	22	14.3
Diretmidae	*Diretmus argenteus*	1	5.9	1	0.6
	Diretmoides parini	3	17.6	4	2.6
Scopelarchidae	*Scopelarchus analis*	6	35.3	22	14.3
Unidentified fish		1	5.9	2	1.3
Cephalopods		**13**	**76.5**	**41**	**26.6**
Ommastrephidae		6	35.3	7	4.5
Histioteuthidae	*Histioteuthis* sp.	1	5.9	1	0.6
Onychoteuthidae		3	17.6	3	1.9
Unidentified squids		6	35.3	16	10.4
Octopodidae		4	23.5	13	8.4
Argonautidae		1	5.9	1	0.6
Total		**17**		**154**	**100.0**
PURSE SEINE					
Crustaceans		**11**	**91.7**	**533**	**93.0**
Squillidae	*Natosquilla investigatoris*	11	91.7	533	93.0
Fish		**1**	**8.3**	**1**	**0.2**
Unidentified fish		1	8.3	1	0.2
Cephalopods		**1**	**8.3**	**39**	**6.8**
Ommastrephidae		1	8.3	39	6.8
Total		**12**		**573**	**100.0**

accounted for 17% of the total number of prey. Other crustacean item remained rare. Six families of fish have been recorded. The scopelarchid *Scopelarchus analis* dominated strongly. This species occurred in 35% of the samples, and accounted for 14% of the total number. Other fish families are all mesopelagic ones: paralepids, alepisaurids, myctophids, nomeids and diretmids were respectively recorded in 29.4%, 5.9%, 23.5%, 5.9% and 23.5% of the stomachs. Together they contributed to 31.7% of the total number of prey. Ommastrephids were the most common family (36% of the stomachs) among cephalopod prey. However their contribution in number was low (4.5%). Four other families (histioteuthids, onychoteuthids, argonautids and octopoda) were recorded in the stomachs, but their contribution remained low.

B) PURSE SEINE STOMACHS:

A total of 573 prey were recorded, crustaceans, represented by one species *N. investigatoris*, dominated strongly the diet in number (93%). Cephalopods of the Ommastrephids family represented 7% of prey items. Only one fish was recorded in the stomach content (0.1% in number). On average, 47.8 prey per stomach were found.

Prey dominance and feeding strategy

For surface-caught fish of both species, the stomatopod *N. investigatoris* was by far the dominant prey, as shown by the upper-right location of this prey in the Costello diagrams (Fig. 6). In addition surface yellowfins exhibited a feeding specialisation for fish (scombrids) and bigeyes for squid (ommastrephids).

Mixed patterns were observed for deep swimmers. For bigeye, all prey were located below the prey importance axis (cf Fig. 3), indicating that this fish was exploiting a broad niche with a generalised feeding behaviour. For yellowfin swimming in deep waters, the feeding strategy was more balanced, with varying degrees from a generalised to a specialised type (notably on crustaceans such as crab larvae and the swimming crab *Charybdis edwardsi*).

Overlap of feeding regime

The Morisita and Horn indices, computed by pair of predators, were always very low, except for yellowfin and bigeye taken with the purse seine, where the value was almost = 1. It denotes a perfect overlap of the feeding regimes between these two species when swimming at the surface (Table 5).

PREY IDENTIFICATION:
CLA: Crab larvae
NAT: *Natosquilla investigatoris*
CHA: *Charybdis edwardsi*
SCO: *Scopelarchus analis*
SCB: Unidentified scombrids
PAR: *Paralepsis atlanticus*
UFI: Unidentified fish
OMM: Ommastrephids
USQ: Unidentified squids
OCT: Octopods

Fishing gear:
○ Purse seine
● Longline
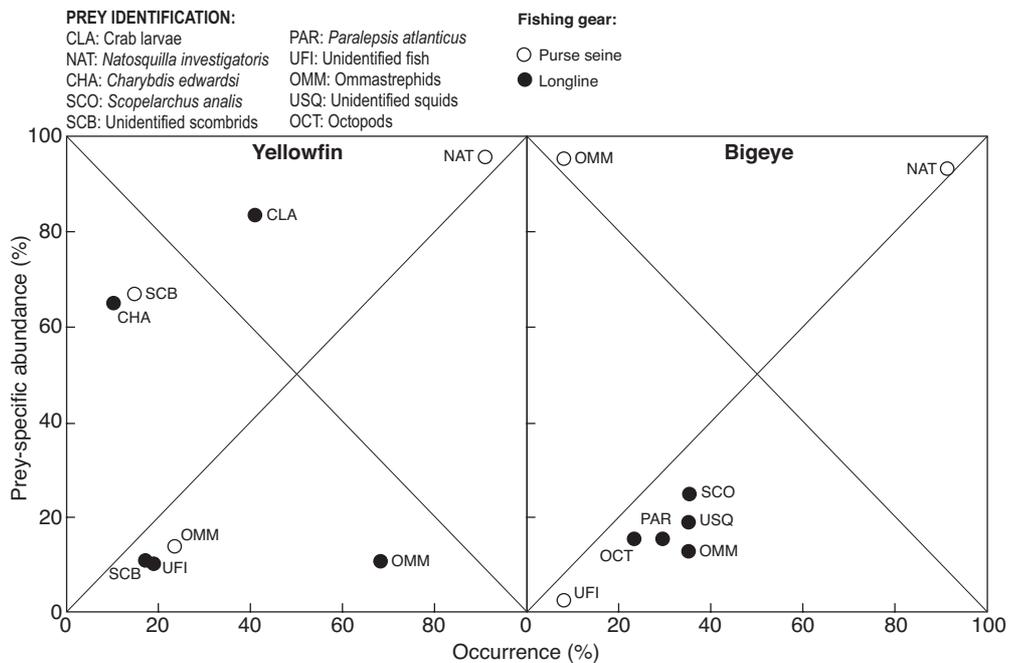
Fig. 6. Costello diagrams (Amundsen et al., 1996) by species and fishing gear.

Table 5. Results of the Morisita and Horn index calculated on the pairs of diet for fishing gear (pal = longline, sen = purse seine) and species (threshold of significance = 0.6). YF, yellowfin; BE, bigeye tuna

	YF_{pal}	BE_{pal}	YF_{sen}	BE_{sen}
YF_{pal}	1			
BE_{pal}	0.07	1		
YF_{sen}	0.01	0.07	1	
BE_{en}	0.02	0.08	**0.99**	1

DISCUSSION

Effect of the habitat stratification

Whether surface or deep swimmers, the diet of predators is dominated by three to five prey items. Three main systems of the vertical habitat were sampled: the upper layer for surface swimmers (caught by purse-seine), the mixed layer for yellowfin caught by longline, and the deeper part of the thermocline for deep-caught bigeye. Thus, the differences in prey composition we observed could be related to the differences in the vertical distribution of tuna (Bertrand et al., 2002).

The diet of yellowfin surface swimmers is very homogeneous, with the stomatopod *N. investigatoris* being the exclusive prey. Potier et al. (2002) observed the same phenomenon in the Somali region: yellowfin caught in surface schools by the purse seiners fed almost exclusively on *N. investigatoris*, which occured in dense swarms. These swarms were very frequently observed at a very large scale since 1999 by fishing vessels and by scientific on board observers (Potier et al., 2001 and unpublished data). Beaching of huge numbers of these animals was even observed in the Seychelles Islands, showing the importance of the population explosion for this species. Bashmakov et al. (1992) and Roger (1994b) found similar results in the western part of the Indian Ocean, but with a different species: *Engraulis japonicus* was indeed the almost exclusive prey of surface swimming yellowfin. We can notice the shift of the main prey from the pelagic fish *Engraulis japonicus* to *N. investigatoris*. Trophic levels found

in the literature, 3.1 to 3.4 for Engraulis sp. and 2.3 for squillidae (Christensen, 1995) seem to indicate a shortening of the food chain that has occurred the recent past.

The food of deep-dwelling yellowfin tuna is divided in almost equal parts between fish, crustaceans and cephalopods. Crustaceans dominated the diet by number. However this result could be biased by crab larvae which accounts alone for 66.8 % of the prey items. Along with crab larvae, the group of stomatopods and the swimming crab *Charybdis edwardsi* form the bulk of the crustacean prey. Such a result has already been observed in the western Indian Ocean by Zamorov et al. (1992). Alverson (1963) emphasised the role of the red crab *Pleurocondes planipes* in yellowfin tuna diet in the eastern Pacific. Epipelagic fish form the main part of the fish prey (69%) as the mesopelagic ones have a negligible impact on the diet of the yellowfin (18%). Thus, most of the yellowfin prey inhabit the shallower layers (Bertrand et al., 2002)

Bigeye surface swimmers exhibited a feeding behaviour similar to that of yellowfin surface swimmers, *N. investigatoris* being the almost exclusive prey. However cephalopods of the Ommastrephid family formed a non-negligible part of the diet. Deep-dwelling bigeye tuna fed predominantly on cephalopods and fish (Scopelarchidae). Mesopelagic fish were the exclusive fish prey observed during this study. These results show that great differences exist in the diet of deep dwelling bigeye and yellowfin tuna. Then bigeye tuna can prey upon fish species which are able to perform large vertical diel migrations or which remain deep in the water column during the night (Bertrand et al., 2002). In the Indian Ocean, Kornilova (1980) described a similar diet and Koga (1958) observed that bigeye stomachs contained significant quantities of mesopelagic fish (sternoptychids, alepisaurids) and decapods.

Predator behaviour and prey diversity

For surface swimmers, the diet was very homogeneous between species and among individuals of the same species, and the diversity of prey in terms of family remained low (n=3). As

noticed by Roger (1994b) and Ménard and Marchal (2003), once a prey concentration of one target species is detected, tuna can feed on this concentration until satiation. It appears to have been the case in an earlier study, where a huge abundance of the stomatopod *N. investigatoris* was found in tuna stomachs (Potier et al., 2001).

For deep swimmers, the diversity of the diet is higher. The number of families found in the stomachs was 44 for yellowfin and 18 for bigeye tuna. Borodulina (1974) in the Gulf of Guinea (equatorial Atlantic) and Kornilova (1980) in the area of the present study observed similar diversity. In Sri Lankan waters, Sudarsan & John (1994) found higher diversity. These different results are related to the fact that the Sudarsan & John study covered coastal regions, whilst the present one and the Kornilova study covered open-sea ecosystems. However, with respect to bigeye tuna, the diversity of fish prey in our samples was very low compared to other areas, a result which is different from that of Kornilova (1980), based on information collected in the period 1969–1973. The relatively low number of stomachs analyzed in the present study may explain such differences.

CONCLUSION

Considering the importance of yellowfin and bigeye biomass, these species exert a significant predation pressure on the epi- and mesopelagic communities. Different ecological preferences induce a variation of the major prey item between predators and between surface and deep swimmers. However, whatever the predator or its swimming behaviour, a limited number of items always composes the bulk of the diet.

To explain such result two hypotheses can be formulated; the dominance of few items reflects their relative abundance in the ecosystem, or being in dense schools their representation in the predator's diet (mainly surface swimmers) is enhanced. For deep swimmers, there is a clear separation of the prey resources between yellowfin and the deep-dwelling bigeye. Studies in the other oceanic areas confirm this result. Conversely, we found a perfect overlap of the feeding regime among surface swimmers. In the western Indian Ocean, a short food chain leading to tuna may exist as crustacean and small-sized individuals are dominant in the diet. In recent years, the shift in the diet of tuna from fish to crustaceans may have lowered the trophic level of these top predators.

REFERENCES

Alverson, F.G. (1963) The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. Inter-Am. Trop. *Tuna Comm. Bull.* **7:** 293–396.

Amundsen, P.-A., Gabler, H.-M., & Staldvik, F.J. (1996) A new approach to graphical analysis of feeding strategy from stomach contents data - modification of the Costello (1990) method. *J. Fish Biol.* **48:** 607–614.

Anon.(2003) Indian Ocean Tuna Fisheries Data Summary, 1992– 2001, IOTC Data Summary No. 23, 112 p.

Bashmakov, V.F., Zamorov, V.V. & Romanov, E.V. (1992) Diet composition of tunas caught with long lines and purse seines in the western Indian Ocean. TWS/91/31 Workshop on stock assessment of yellowfin tuna in the Indian Ocean. 7–12 october 1991, Colombo, IPTP: 53–59.

Bertrand, A., Bard, F.-X. & Josse, E. (2002) Tuna food habits related to the micronekton distribution in French Polynesia. *Mar. Biol.* **140:** 1023–1037.

Borodulina, O.D. (1974) The feeding of the bigeye tuna (*Thunnus obesus*) in the Gulf of Guinea and its place in the trophic system of the pelagic zone. J. Ichthyol. **14:** 766–775.

Borodulina, O.D. (1982) Food composition of yellowfin tuna Thunnus albacares (Scombridae). *J. Ichtyol.* **21:** 38–46.

Christensen, V. (1995) A model of trophic interactions in the North Sea in 1981, the year of stomach. *Dana* **11:** 1–28.

Clarke, M.R. (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, 273 pp.

Costello, M.J. (1990) Predator feeding strategy and prey importance : a new graphical analysis. *J. Fish Biol.* **36:** 261–263.

Cox, S.P., Essington, T.E., Kitchell, J.F., Martell, S.J.D., Walters, C.J., Boggs, C. & Kaplan, I. 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. *Can. J. Fish. Aquat. Sci* **59:** 1736–1747.

Essington, T.E., Schindler, D.E., Olson, R.J., Kitchell, J.F., Boggs, C., & Hilborn, R. (2002) Alternative fisheries and the predation rate of yellowfin tuna in the eastern Pacific Ocean. *Ecological Applications* **12:** 724–734.

Herbland, A. (1990) L'oligotrophie: un concept en évolution. ICCAT Coll. Vol.Sci. Pap., 32, SCRS 89/**61:** 169–174.

Kitchell, J.F, Boggs, C.H., He, X. & Walters, C.J. (1999) Keystone predators in the Central Pacific. In: Ecosystem Approaches for Fisheries Management. Alaska Sea Grant College Program, AK-SG-99-01, Fairbanks, pp. 665–683.

Koga, S. (1958) On the difference of the stomach contents of tunas and black marlin in south equatorial Pacific Ocean. *Bull. Fac. Fish.*, Nagasaki Univ. **7:** 21–30.

Kornilova, G.N. (1980) Feeding of yellowfin tuna, *Thunnus albacares*, and bigeye tuna *Thunnus obesus,* in the equatorial zone of the Indian Ocean. *J. Ichthyol.* **20:** 111–119.

Magurran, A.E. (1988) Ecological diversity and its measurement. Princeton University Press, 192p.

Ménard, F. & Marchal, E. (2003) Foraging behaviour of tuna feeding on small schooling *Vinciguerria nimbaria* in the surface layer of the equatorial Atlantic Ocean. *Aquatic Living Resources* **16:** 231–238.

Nesis, K. N. (1987) Cephalopods of the world. T. F. H. Publications, 351 p.

Olson, R.J.& Boggs, C.H. (1986) Apex predation by yellowfin tuna (Thunnus albacares): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Can. J. Fish. Aquat. Sci.* **43:** 1760–1775.

Potier, M., Sabatié, R., Ménard, F., & Marsac, F. (2001) Preliminary results of tuna diet studies in the West equatorial Indian Ocean. 3rd session of the IOTC working party on tropical tunas, Seychelles, 19–27/06/2001. WPTT/01/03. IOTC Proceedings **4:** 273-278.

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. 4th session of the IOTC working party on tropical tunas, Shangai, China, 3-11/06/2002. WPTT/02/24. *IOTC Proceedings* **5:** 368–374.

Roger, C. (1994a) Relationships among yellowfin and skipjack tuna, their prey-fish and plankton in the tropical western Indian Ocean. *Fish. Oceanogr.* **3:** 133–141.

Roger, C. (1994b) On feeding conditions for surface tunas (yellowfin, *Thunnus albacares* and skipjack, Katsuwonus pelamis) in the western Indian Ocean. In: Ardill J D. (Ed.) Proceedings of the expert consultation on Indian Ocean Tunas, 5Th session, Mahé, Seychelles, 4-8 Oct. 1993, IPTP Coll. Vol. Work. Doc 8: 131–135.

Schindler, D.E., Essington, T.E., Kitchell, J.F., Boggs, C., & Hilborn, R. (2002) Sharks and tunas: fisheries impacts on predators with contrasting life histories. Ecological Applications **12:** 735–748.

Shannon, L.V. (1987) The tunas of the Benguela region off Southern Africa. A synthesis. ICCAT, Coll. Vol. of scientific papers XXVI (SCRS 1986): 566–581.

Smale, M.J., Watson, G. & Hecht, T. (1995) Otolith Atlas of southern African marine fishes. Ichthyological Monographs. J/L/B/ Smith Institute of Ichthyology, Grahmastoxn, South Africa, 253 pp.

Smith, M.M. & Heemstra, P.C. (1986) Smiths' sea fishes. Southern Book Pub., 1047 p.

Sudarsan, D. & John, M.E. (1994) Further studies on biological aspects of yellowfin tuna in the Indian EEZ. In: Ardill J D. (Ed.) Proceedings of the expert consultation on Indian Ocean Tunas, 5Th session, Mahé, Seychelles, 4–8 Oct. 1993, IPTP Coll. Vol. Work. Doc. 8: 135–141.

Sudarsan, D. John, M.E. & Nair, K.N.V. (1991) Some biological considerations of yellowfin tuna, Thunnus albacares (Bonnaterre) taken by longline gear in the Indian EEZ. IPTP, Workshop on stock assessment of yellowfin tuna in the Indian Ocean, Colombo, Sri Lanka, TWS/91/11: 18–28.

Sund, P.N., Blackburn, M. & Williams, F. (1981) Tunas and their environment in the Pacific ocean: a review. *Oceanogr. Mar. Biol. Annu. Rev.* **19:** 443–512.

Thomas, P.T. (1962) The food of *Katsuwonus pelamis* (Linnaeus) and *Neothunnus macropterus* (Temminck and Schlegel) from Minicoy waters during the season 1960–61. Proc. Symp. Scombroid fishes, MBAI, 2: 626–630.

Thomas, P.T. & Kumaran, M. (1962) Food of indian tunas. *FAO Fish. Rep.* **6:** 1559–1667.

Tregouboff, G. & Rose, M. (1978) Manuel de planctonologie méditerranéenne. CNRS, Paris, 2 vol.

Watters, G.M. , Olson, R.J., Francis, R.C., Fiedler, P.C., Polovina, J.J., Reilly, S.B., Aydin, K.Y., Boggs, C.H., Essington, T.E., Walters, C.J., & Kitchell, J.F. (2003) Physical forcing and the dynamics of the pelagic ecosystem in the eastern tropical Pacific: simulations with ENSO-scale and global-warming climate drivers. Can. J. Fish. Aquat. Sci **60:** 1161–1175.

Zamorov, V.V., Spiridinov, V.A. & Napadovsky, G.V. (1992) On the role of the swimming crab Charybdis smithi (Mc Leay 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 Coll. Vol. Work. Doc. 6: 70–75.