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Relationships among yellowfin and skipjack tuna, their prey-fish and plankton in the tropical western Indian Ocean

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ABSTRACT

Stomach contents of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tuna caught by trolling and purse seining in the tropical western Indian Ocean, together with those of the prey-fish found in their stomachs, have been analysed. Epipelagic fish are the main prey of these tunas, whereas no vertically migrating fish, which inhabit subsurface layers at night, have been found in their stomachs. These tunas are thus considered day-feeders. Purse-seine-caught tunas, which belong to large schools, have a much higher number of prey-fish in their stomachs than tunas caught by trolling on small schools. Similarly, prey-fish from purse-seine tunas have a much higher number of planktonic prey in their stomachs than those from troll-caught tunas. Therefore, these tunas adopt a wandering strategy in small schools when food resources are scarce and form large schools when they are abundant. The planktonic organisms found in the stomachs of prey-fish are described by taxa and sizes; they represent the fraction of the planktonic biomass actually supporting the stock of tuna. Size ratios between the three links tuna–prey-fish–plankton are very high, suggesting that these tunas benefit from a short food chain which is probably efficient from the energetic point of view.

Key words: feeding, trophic relationships, Indian Ocean, yellowfin, skipjack tuna

INTRODUCTION

Yellowfin (YFT, *Thunnus albacares*) and skipjack (SKJ, *Katsuwonus pelamis*) tuna are very active pelagic fish which require a large amount of energy (Kitchell *et al.*, 1978; Crowder and Magnuson, 1981; Olson and Boggs, 1986). Nevertheless, they live in the upper layer (0–200 m or so) of tropical seas (Yuen, 1970; Dizon *et al.*, 1978; Yang and Gong, 1987; Cayré, 1991), which is "one of the most unproductive environments" (Sund *et al.*, 1981). These well-known facts lead to the conclusion that food availability is a key factor in determining their abundance and distribution (Blackburn, 1969; Sund *et al.*, 1981; Petit, 1991; Stretta, 1991).

The aim of this study is to describe the successive links of a food chain culminating with these tunas in this region, by analysing stomach contents of tunas together with those of the prey found in their stomachs. Among the prey of these tunas (fish, cephalopods, crustaceans), only fish are suitable for reliable stomach contents analysis. The first step of the study is thus to check whether prey-fish represent the main prey of these tunas so as to ensure that the chain plankton → prey-fish is prominent in tuna feeding. The second step is to describe the plankton used as food by these prey-fish, in order to identify the fraction of the planktonic biomass actually supporting this food chain.

METHODS AND MATERIAL

Tunas were obtained both from fishing carried out during the Indian Ocean Tuna Programme and from commercial purse seiners. All fishing operations were carried out during daylight. Working areas are indicated on Fig. 1.

In the Mozambique area, tunas originated both from purse-seine fishing which was carried out when large schools were encountered, and from trolling on schools too small to justify the use of the purse seine. In the Seychelles area, all samples were obtained from commercial purse seiners fishing on large schools. Troll-caught yellowfin amounted to 65 individuals, among which 5 had empty stomachs and 15 contained only unidentifiable remains; the figures are 75, 27 and 10 respectively for skipjack. No such information is available for purse-seine-caught tunas, as only non-empty stomachs were sent to the laboratory.

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Figure 1. Working areas in the western Indian Ocean.

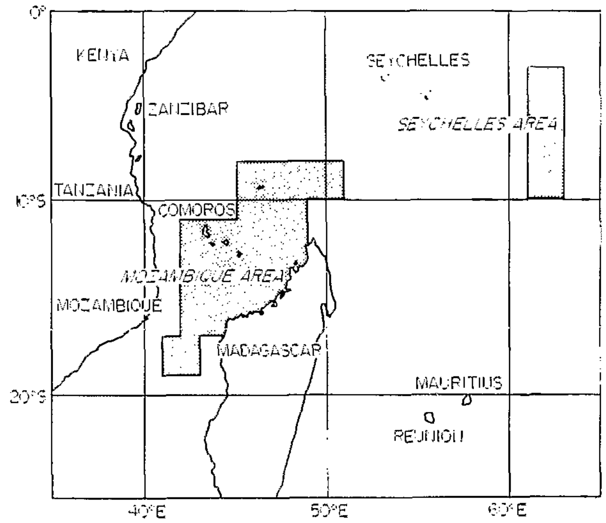
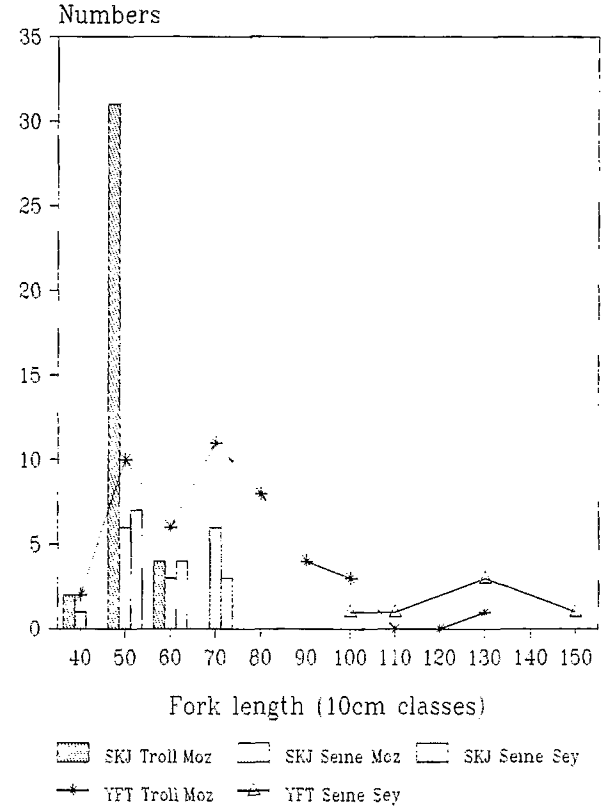


Figure 2. Lengths of the 119 tunas used for stomach contents analysis (SKJ, Skipjack; YFT Yellowfin; Moz, Mozambique area; Sey, Seychelles area).



Number, size, date, fishing technique and geographical origin of the 119 tunas with non-empty stomachs used for stomach content analysis are indicated in Table 1. The length distribution of these tunas is shown in Fig. 2.

In every case, stomach contents were removed immediately after fishing. In order to estimate the relative importance of the main categories of prey (fish, cephalopods, crustaceans), displacement volume measurements were made only when fish was not the sole prey. Prey-fish were preserved in 10% formalin for further analysis of their stomach contents.

In the laboratory, the 4025 prey-fish found in the 119 tuna stomachs were measured and their stomach contents analysed under binocular microscope; subsamples were used when prey-fish occurred in large numbers in any single stomach. Planktonic organisms were sorted by taxa, counted and measured using 0.5 mm size categories.

Table 1. Origin and characteristics of the 119 tunas used for stomach contents analysis. FL, fork length; f.o., fishing operation; σ, standard deviation.

Method and date	Skipjack		Yellowfin	
	Number	FL (cm)	Number	FL (cm)
Trolling, Mozambique area				
March–April 1989	15 (from 12 f.o.)	50.8 (σ = 5.3)	18 (from 14 f.o.)	76.7 (σ = 11.8)
May–July 1989	12 (from 6 f.o.)	50.9 (σ = 4.6)	9 (from 7 f.o.)	72.3 (σ = 23.5)
Aug–Sept 1989	11 (from 9 f.o.)	51.3 (σ = 2.6)	18 (from 13 f.o.)	61.6 (σ = 15.5)
Total	38 (from 27 f.o.)	51.0 (σ = 4.3)	45 (from 34 f.o.)	70.3 (σ = 16.9)
Purse seining, Mozambique area				
May–July 1989	16 (from 8 sets)	60.2 (σ = 9.3)	–	–
Purse seining, Seychelles area				
Jan 1990, Oct–Dec 1990	14 (from 5 sets)	58.1 (σ = 6.9)	6 (from 4 sets)	125.7 (σ = 17.9)

RESULTS

Stomach contents of tunas

A preliminary observation should be reported. When purse-seine fishing was operated around floating logs before sunrise, almost all tunas had empty stomachs. In the Mozambique area, 519 tunas from 10 different net deployments were examined; all of them, with the exception of two yellowfins, had empty stomachs. In the Seychelles area, more than 1300 tunas were examined; 99% of them had empty stomachs (Stequert, pers. comm.). This fact leads to the conclusion that these tunas do not feed by night and/or do not find any food under floating material such as logs.

The analysis of the 119 stomach contents originating from trolling and purse seining carried out during daylight leads to the following results.

All tunas caught by purse seine feed almost exclusively on fish, both in the Mozambique area as in the Seychelles area (Table 2, Fig. 3). Prey-fish occur in large numbers in each tuna stomach: means of 53, 82 and 135 according to species and area (Table 3, Fig. 4). Their mean length is in the range 32–42 mm and almost all of them belong to the family Engraulidae and are probably of the same species. In the Mozambique area, 5 skipjack out of 16 have fed in addition on large-sized prey-fish (mean length, 129 mm) such as flying fish, juvenile tunas, Paralepididae, *Diplospinus* sp., and *Hemiramphus* sp. Only 14 prey-fish out of 1317 belonged to this large-sized category, but their importance in volume is not negligible. It should be noted that all prey-fish are epipelagic.

The stomach contents of tunas caught by trolling in the Mozambique area showed some differences from those caught by purse seine. Fish is the dominant prey, but crustaceans account for 9% of the stomach volume in skipjack and 24% in yellowfin. Most of these crustaceans are stomatopod larvae and amphipods; small numbers of carids and megalopa larvae have also been found. Small cephalopods (mean mantle length 24 mm, standard deviation 19 mm) represent 4–6% of the stomach content volume. All prey-fish are epipelagic, with the exception of 6 (out of 319 prey-fish) mesopelagic fish in skipjack stomachs. Only 24 (out of 1122 prey-

Table 2. Stomach contents of 119 tunas.

		Prey type					
		Fish		Crustaceans		Cephalopods	
Fishing method and area	Predator	% Occurrence	% Volume	% Occurrence	% Volume	% Occurrence	% Volume
Trolling in Mozambique area	Skipjack	100	87	47	9	16	4
	Yellowfin	100	70	72	24	41	6
Purse seine in Mozambique area	Skipjack	100	99	13	Trace	6	Trace
Purse seine in Seychelles area	Skipjack	100	99	21	Trace	7	Trace
	Yellowfin	100	96	67	3	33	Trace

Table 3. Number of prey-fish per stomach of tuna.

	Predator					
	Skipjack			Yellowfin		
Fishing method and area	Mean number of prey	Standard deviation	Range	Mean number of prey	Standard deviation	Range
Trolling in Mozambique area	8.4	16.8	1–100	18.5	44.8	1–300
Purse seine in Mozambique area	82.3	76.0	3–240	–	–	–
Purse seine in Seychelles area	53.1	24.0	24–94	135.5	78.7	56–273

Figure 3. Prey of tuna (% by volume) in the two fishing areas and caught by different fishing methods.

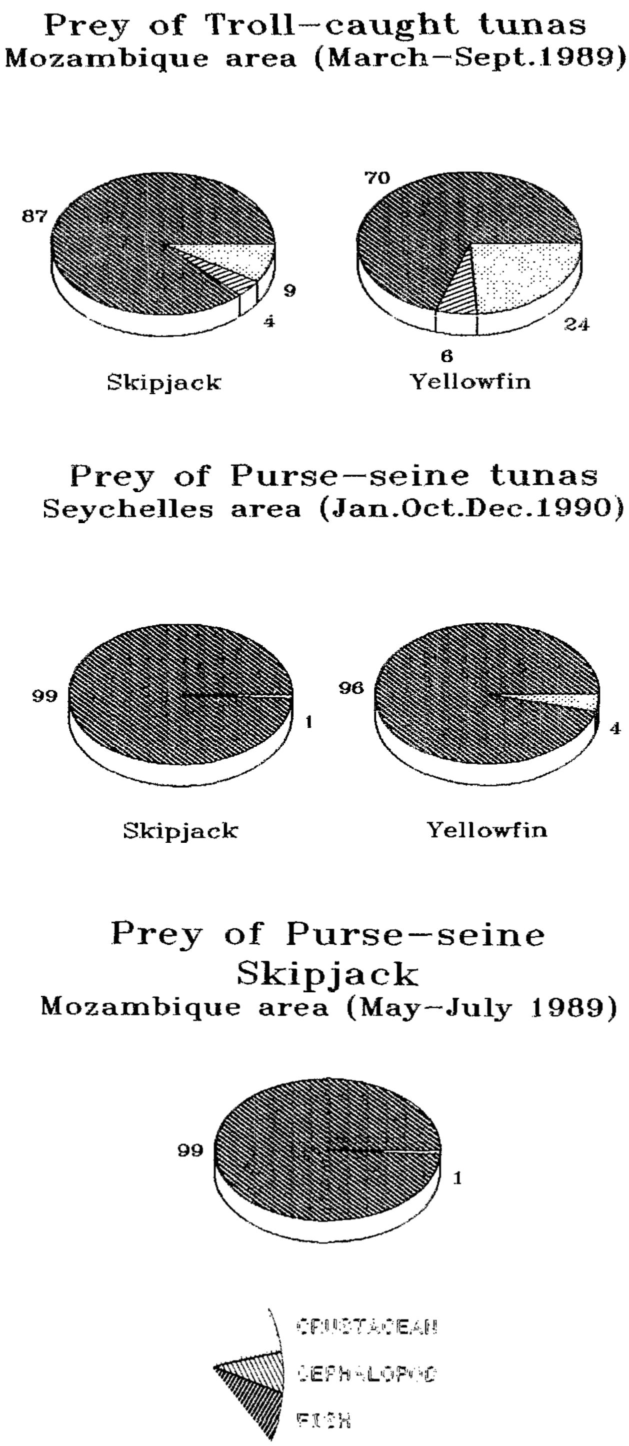
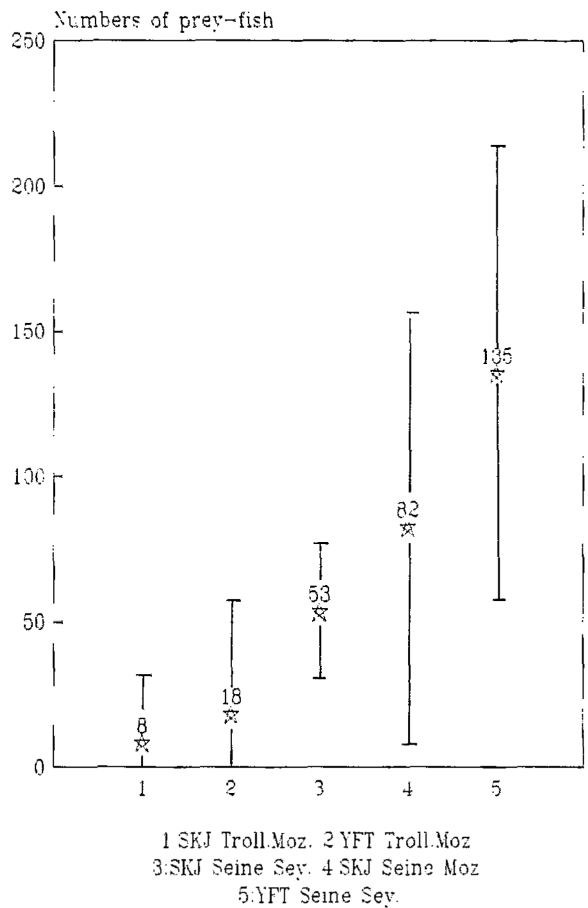


Figure 4. Numbers of prey-fish per stomach of tuna (mean and standard deviation). See legend of Fig. 2 for key.



fish) are large-sized. The mean size of the other prey-fish is in the range 25–27 mm, which is a little smaller than the Engraulidae consumed by purse-seine-caught tunas.

These prey-fish are of a somewhat different nature from those of purse-seined tunas: they belong to various families, among which Balistidae, Diodontidae, Ostracionidae, Nomeidae and Engraulidae are the more numerous. Also, the number of prey-fish per tuna stomach (8–18 as a mean) is much smaller than in purse-seined tunas (Fig. 5). The Mann–Whitney test shows a highly significant difference ($P < 0.001$) for the number of prey-fish per stomach in skipjack of the Mozambique area depending on their origin (trolling on small schools: 8.4 prey-fish per stomach; purse seining on large schools: 82.3 prey-fish per stomach).

Numbers, types and sizes of prey-fish according to geographical origin and fishing technique are presented in Table 4.

Stomach contents of prey-fish

The characteristics of the plankton found in the stomachs of the 352 prey-fish analysed are shown in Table 5. Copepods are by far the main prey in number, and

Table 4. Type and size of prey-fish.

	Mozambique area			Seychelles area (purse seine)	
	Trolling		Purse seine		
	Skipjack	Yellowfin	Skipjack	Skipjack	Yellowfin
Number of stomachs of tunas analysed (total 119)	38	45	16	14	6
Number of prey-fish (total 4025)	319	833	1317	743	813
Type and size of prey-fish					
Mesopelagic[a]					
Number	6	0	0	0	0
Occurrence (%)	8	–	–	–	–
Mean size (mm)	28	–	–	–	–
Large-sized[b]					
Number	3	21	14	0	0
Occurrence (%)	5	22	31	–	–
Mean size (mm)	95	139	129	–	–
Other					
Number	310[c]	812[c]	1303[d]	743[d]	813[d]
Occurrence (%)	100	93	81	100	100
Mean size (mm)	27 ($\sigma = 11$)	25 ($\sigma = 13$)	42 ($\sigma = 11$)	32	40

[a]5 Myctophidae and 1 *Sternoptyx*.
[b]Flying fish, juvenile tunas, Paralepididae, *Diplospinus* sp., *Hemiramphus* sp.
[c]Various epipelagic species: Balistidae, Diodontidae, Ostracionidae, Nomeidae, Engraulidae etc.
[d]99% Engraulidae.

also in volume as judged from visual examination under binocular microscope. Other crustaceans (amphipods, ostracods, *Lucifer*, euphausiids and decapods) occur frequently but their quantitative importance is low. Other prey as chaetognaths, annelids and fish larvae are also of secondary importance. Only in prey-fish stomachs originating from yellowfin caught by trolling in the Mozambique area, are prey other than copepods significant.

Lengths of copepods ranged from 0.5 to 4 mm (Fig. 6). Other crustaceans had a mean length of 4.6 mm and a maximum length usually under 10 mm. Most chaetognaths and annelids were less than 30 mm and fish larvae less than 15 mm in length. These taxa and sizes depict the plankton which supports this tuna food-chain.

Mean numbers of planktonic prey per stomach of prey-fish are illustrated in Fig. 7(A). Important differences are obvious between trolling material (23.6 and 16.4 planktonic prey per prey-fish stomach) and purse-seine material (51.2, 130.3 and 94.7 planktonic prey per prey-fish stomach).

DISCUSSION AND CONCLUSIONS

Fish are by far the dominant prey of surface yellowfin and skipjack tuna caught by trolling and purse seining in this region. Nearly all the prey-fish are epipelagic since almost no vertically migrating fish, such as Myctophidae, which rise by night in subsurface layers, were found. Many other studies have reported similar observations (Nakamura, 1965; Dragovitch, 1970; Dragovitch and Potthoff, 1972; Legand *et al.*, 1972; Grandperrin, 1975; Borodulina, 1982; Pelczarski, 1988; and others) which support the generally accepted opinion that these tunas are day-feeders.

Tunas fished by purse seine (therefore belonging to large schools) feed heavily on engraulid concentrations, and large schools of prey-fish are associated with large schools of tuna. Tunas fished by trolling on small schools feed to a larger extent on crustaceans and cephalopods and contain fewer prey-fish per stomach and these are from a wider range of taxonomic groups. Obviously these tunas are in search of richer areas and in

Table 5. Stomach contents of prey-fish.

	Origin of prey-fish					
	Mozambique			Seychelles		
	Trolling		Purse seine	Purse seine		Total or mean
	Skipjack	Yellowfin	Sipjack	Skipjack	Yellowfin	
Number of prey-fish stomachs analysed	65	193	49	29	16	352
Stomach contents of prey-fish						
Copepods						
Occurrence (%)	92.3	73.1	91.8	96.6	93.8	89.5
Total number	1459	2564	2446	3707	1457	11 633
Mean number per stomach	24.3	18.2	54.4	132.4	97.1	65.3
% Prey by number	95.3	80.8	97.5	98.1	96.2	93.6
Mean size (mm)	0.92	1.31	0.97	0.81	1.05	1.01
Amphipods						
Occurrence (%)	9.2	13.5	14.3	0	25.0	12.4
Total number	7	50	15	0	12	84
Ostracods						
Occurrence (%)	9.2	5.2	6.1	6.9	0	5.5
Total number	13	25	6	2	0	46
Lucifer						
Occurrence (%)	3.1	5.7	6.1	41.4	43.8	20.0
Total number	18	57	7	19	15	116
Euphausids and Decapods						
Occurrence (%)	20.0	24.4	38.8	62.1	68.8	42.8
Total number	19	165	31	32	23	270
Mean size (mm)	4.6	5.8	4.1	3.7	4.8	4.6
(Standard deviation)	(1.9)	(3.0)	(3.2)	(1.0)	(2.7)	–
Chaetognaths						
Occurrence (%)	4.6	13.5	6.1	20.7	18.8	12.7
Total number	6	251	4	18	4	283
Annelids						
Occurrence (%)	1.5	4.2	0	3.5	12.5	4.3
Total number	1	15	0	1	4	21
Fish larvae						
Occurrence (%)	12.3	16.1	2.0	0	0	6.1
Total number	8	47	1	0	0	56
Mean size (mm)	13.5	11.3	10.0	–	–	11.6
(Standard deviation)	(11.1)	(4.3)	–	–	–	–
Total number of planktonic prey	1531	3174	2510	3779	1515	12 509
Mean number per prey-fish stomach	23.6	16.4	51.2	130.3	94.7	35.5
(Standard deviation)	(27.4)	(22.0)	(76.8)	(94.5)	(67.2)	–

the meantime feed on variously scattered prey they meet.

By analysing the stomach contents of the fishes which comprise the main prey of these tunas, the nature of the plankton supporting the stock of yellowfin and skipjack in the western Indian Ocean has been described. Copepods are of primary importance, then other crustaceans less than 10 mm, annelids and chaetognaths less than 30 mm and fish larvae less than 15 mm in length. The few studies reporting on the feeding behaviour of the epipelagic fish forming the prey of tuna indicate that these could be diurnal feeders (Parin, 1968; Roger,

Figure 5. Lengths of the 2018 prey-fish found in the 99 tunas caught in the Mozambique area (not including 38 large-sized prey-fish, 95–139 mm, see Table 4). See legend of Fig. 2 for key.

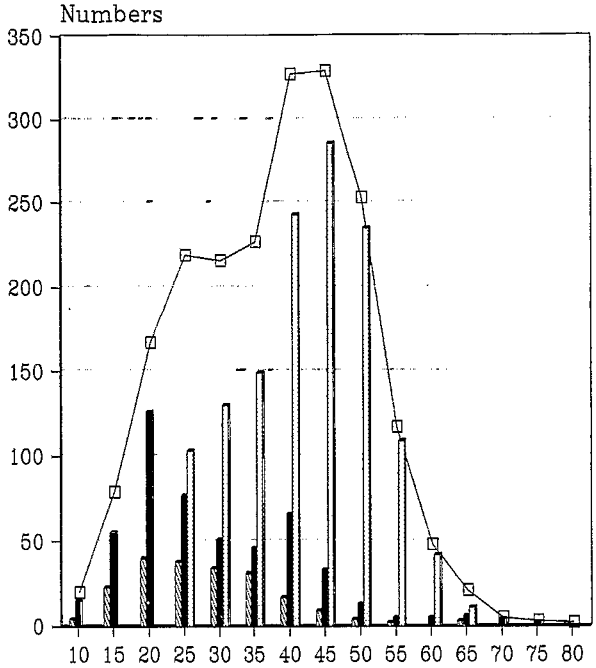
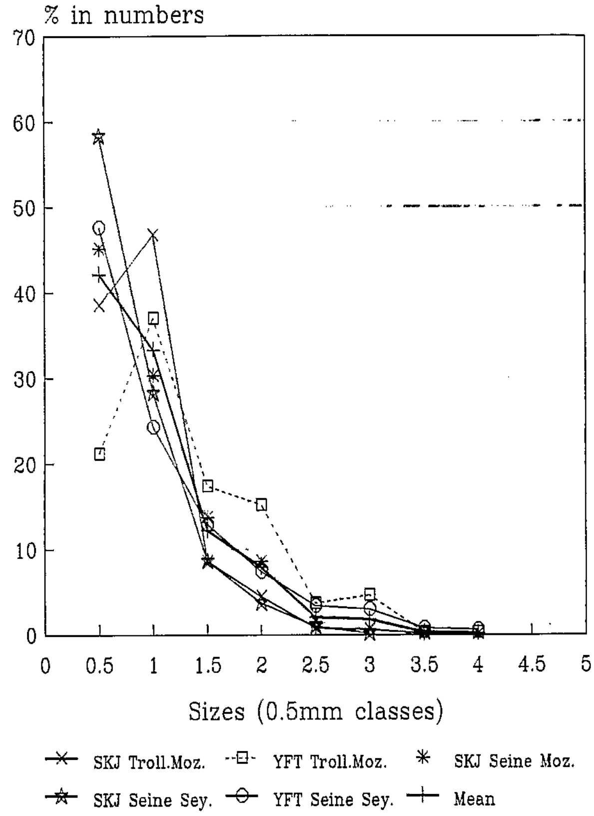


Figure 6. Lengths of copepods found in the stomachs of prey-fish. See legend of Fig. 2 for key.



1974; Roger and Grandperrin, 1976). According to this view, the biomass of plankton supporting this tuna food-chain would thus comprise the above cited organisms which remain by day in the 0–200 m layer. The biomass and taxonomic composition of this fraction of the zooplankton is markedly different from that of the zooplankton as a whole (Roger, 1982, 1986).

Table 6 reports on mean lengths of tunas, their prey-fish and the copepod prey of the latter. The length ratios between these three links attain very high values. It thus appears that yellowfin and skipjack tuna here take advantage of a short food-chain which is probably efficient from the energetic point of view.

By multiplying the mean number of prey-fish per tuna stomach by the mean number of planktonic prey per prey-fish stomach (Table 7), we obtain the mean num-

Table 6. Length ratios between tunas, prey-fish and copepods.

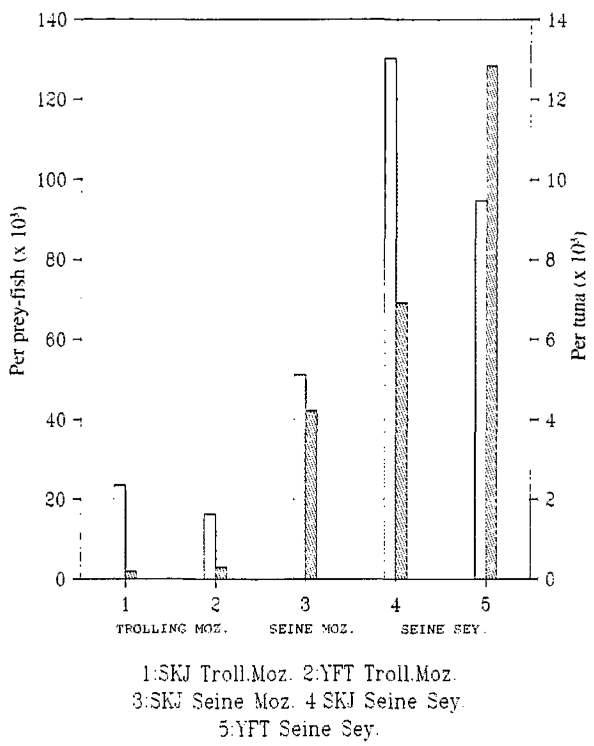
Tuna, method and area	1 Mean length of tuna (cm)	2 Mean length of prey-fish (mm)[a]	Ratio 1:2	3 Mean length of copepods (mm)	Ratio 2:3	Ratio 1:3
Skipjack, trolling, Mozambique	51.0	27	19	0.92	29	554
Yellowfin, trolling, Mozambique	70.3	25	28	1.31	19	537
Skipjack, purse seine, Mozambique	60.2	42	14	0.97	43	621
Skipjack, purse seine, Seychelles	58.1	32	18	0.81	40	717
Yellowfin, purse seine, Seychelles	125.7	40	31	1.05	38	1197

[a]The 38 (out of 4025) large-sized prey-fish are excluded.

Table 7. Numbers of prey per stomach.

Tuna, method and area	Number of prey-fish per tuna stomach	Number of plantonic prey per prey-fish stomach	Number of planktonic prey per tuna stomach
Skipjack, trolling, Mozambique	8.4	23.6	198
Yellowfin, trolling, Mozambique	18.5	16.4	303
Skipjack, purse seine, Mozambique	82.3	51.2	4214
Skipjack, purse seine, Seychelles	53.1	130.3	6919
Yellowfin, purse seine, Seychelles	135.5	94.7	12832

Figure 7. Mean number of planktonic prey per stomach of prey-fish (□), and of tuna (▨). See legend of Fig. 2 for key.



ber of planktonic prey per tuna stomach. Striking differences are obvious (Fig. 7) between the poor feeding conditions of tunas caught by trolling (small schools) in the Mozambique area (198–303 planktonic prey per tuna stomach) and the much better feeding conditions of the purse-seined tunas (large schools): 4214 planktonic prey per tuna stomach in the same area, 6919 and 12 832 in the Seychelles area which thus appears as even richer. Therefore, it can be inferred that these tunas adopt a wandering strategy in small schools when feeding conditions are poor (few prey-fish for tuna and few planktonic prey for prey-fish) and form large schools when feeding conditions are good. Using a completely different strategy in their research, based on theoretical optimum energetic yield, Petit (1991) and Stretta (1991) reached the same conclusion.

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