Environmental Biology of Fishes 39: 161–172, 1994.

The plankton of the tropical western Indian ocean as a biomass indirectly supporting surface tunas (yellowfin, *Thunnus albacares* and skipjack, *Katsuwonus pelamis*)

Claude Roger
ORSTOM-HOT, B.P. 5045, 34032 Montpellier cedex 1, France

Received 4.12.1992 Accepted 10.8.1993

Key words: Trophic relationships, Prey, Food chain, Fishing, Scombroids

Synopsis

The biomass of available forage is a key factor in controlling the abundance and distribution of surface tropical tunas, as they have high energy demands and live in a poor environment. The direct estimate of this forage biomass is not possible with existing techniques. Thus we have investigated the lower link, i.e. the plankton organisms which are the food of fishes preyed upon by tunas. In a previous study, this fraction of the zooplankton has been identified, both by taxa and by size, by analysing the stomach contents of the fishes which are the preys of tunas. In this paper, we use 331 plankton samples from tuna fishing grounds of the tropical Indian ocean, to define the characteristics of the planktonic fraction actually participating in the tuna food chain. Main results are as follows: (1) Only 15–27% of the total zooplanktonic biomass (> 1 mm) is actually accessible for the fishes preyed upon by surface tunas. This 'useful' part of the zooplankton is a well defined fraction of the planktonic population which remains in the 0–170 meters water layer during daylight hours. This part of the zooplankton accounts for a variable percentage of its total biomass the different geographic areas and represents the most relevant parameter to assess the potential richness of a given area for surface tunas. (2) From areas where fishing for surface tunas is poor to those where fishing is successful, it is observed that the total zooplankton biomass increases by a factor of 4 whereas the biomass of the 'useful' fraction increases by a factor of 7. This disproportionate increase is due to the facts that the potential preys of fishes preyed upon by tunas represent a growing fraction of the zooplankton and that a growing proportion of this fraction remains by day in the 0–170 meter water layer, therefore becoming available for the day-feeders which comprise most of the prey-fishes of surface tunas.

Introduction

Tropical surface tunas, yellowfin and skipjack, pose a riddle: they have high metabolic demands (Kitchell et al. 1978, Olson & Boggs 1986) yet they live in a poor environment, i.e. the 0–200 m layer of tropical oceans (Yuen 1970, Dizon et al. 1978, Hunter et al. 1986, Yang & Gong 1987, Holland et al. 1990, Cayré 1991) where their potential food is scattered and unevenly distributed (Herbland 1990, Lemasson 1990).

Moreover, these tunas are essentially day-feeders, so that they have restricted access to the vertically migrating micronekton: by day the micronekton lies deeper than 400 m and comes up to the 0–200 m layer only at night when these tunas have a weak feeding activity (Kobayashi & Yamaguchi 1971, Legand et al. 1972, Roger & Grandperrin 1976, Sund et al. 1981, Borodulina 1982, Zavala-Camin 1986).

Prey organisms available to these tunas are thus mainly restricted to those which remain in the 0–200 m layer during the day (Nakamura 1965, Parin 1968, Dragovitch & Potthoff 1972, Grandperrin 1975, Valle et al. 1979, Kornilova 1981, Longhurst & Pauly 1987, Pelczarski 1988). Surface tunas can feed only partially on migrating micronekton such as squids, or under peculiar circumstances which induce the migrating fauna to stay in the subsurface layers during the day (Alverson 1961, Pitman & Ballance 1990, Bard & Pezennec 1991).

Most of the micronekton which remains by day in the upper 200 m comprises fast-swimming organisms, such as micronektonic fishes and squids, which are not caught by micronekton nets (Sund et al. 1981, Clarke 1983).

From these facts, it appears that (1) search for food is a major problem for these surface tropical tunas, which largely controls their abundance and distribution (Dizon et al. 1978, Sund et al. 1981, Petit & Stretta 1992, Stretta & Petit 1992) and (2) the direct assessment of the biomass of their forage is at present not possible.

Consequently, it is suggested to assess the potential richness of the oceanic areas for these tunas through indirect means. This strategy is illustrated in Fig. 1; it has been presented at an IPTP meeting in Mauritius (Roger[1]).

As a first step, stomach contents of tunas and of fishes found in their stomachs have been analysed. Table 1 summarises the importance of fishes as food for tunas. The preys of these prey-fishes are small zooplankton organisms, mainly copepods but also other crustaceans, which have been counted, identified at the taxon level and individually measured. Results of this first step of the research are reported elsewhere (Roger[2] submitted paper). It describes the fraction of the zooplankton, by taxon and sizes, which is actually taking part in the food chain leading to surface tropical tunas.

This zooplankton is adequately sampled by plankton nets. As a second step, we therefore analysed plankton samples originating from tunas fishing grounds and we sorted the fraction of the zooplankton which had been identified from the stomach contents analysis as the one involved in the tunas' food chain. The quantification of this fraction of the zooplankton provides an assessment of the potential richness of the area with regard to surface tunas. The present paper reports on this second step of the research.

There is good evidence that most of the epipelagic micronektonic fishes preyed upon by surface tunas are also day-feeders (Parin 1968, Roger & Grandperrin 1976, Medina-Gaertner 1988). Therefore, day samples of zooplankton will be considered as most representative of the potential richness of an area for surface tunas.

Material and methods

Plankton samples were collected from August 1988 to September 1989 during six cruises (Fig. 2) of the tuna purse-seiner Mascaroi of the Regional Tuna Association in charge of the Indian Ocean Tuna Programme. The net was a one-meter conical plankton net fitted with 1 mm mesh coloured in blue. Tows were oblique, from the surface to a mean depth of 170 m which is close to the theoretical 0–200 m layer where surface tunas live almost permanently and where almost the whole biomass of migrating zooplankton and micronekton concentrates at night. A Depth-Distance-Recorder TSK indicated the depth reached by the net, and the volume of water filtered. On board, samples were preserved in 10% formalin. In total, 331 stations were sampled: 140 by night and 191 by day.

In the laboratory, sorting of samples was achieved in two steps: exhaustive sorting of large individuals, then sorting of small individuals in subsamples. As a result, the fraction of the zooplankton which had been identified from the stomach contents analysis as being 'potential preys' (PP) of the prey-fishes was separated. This PP fraction com-

[1] Roger, C. 1988. Tunas and their food: a view from a lower link of the food-chain. Indo-Pacific Tuna Development and Management Programme (IPTP). Collective volume of working documents 3: 385–388.

[2] Roger, C. 1993. Relationships among yellowfin and skipjack tunas, their prey-fish and plankton in the tropical western Indian ocean.

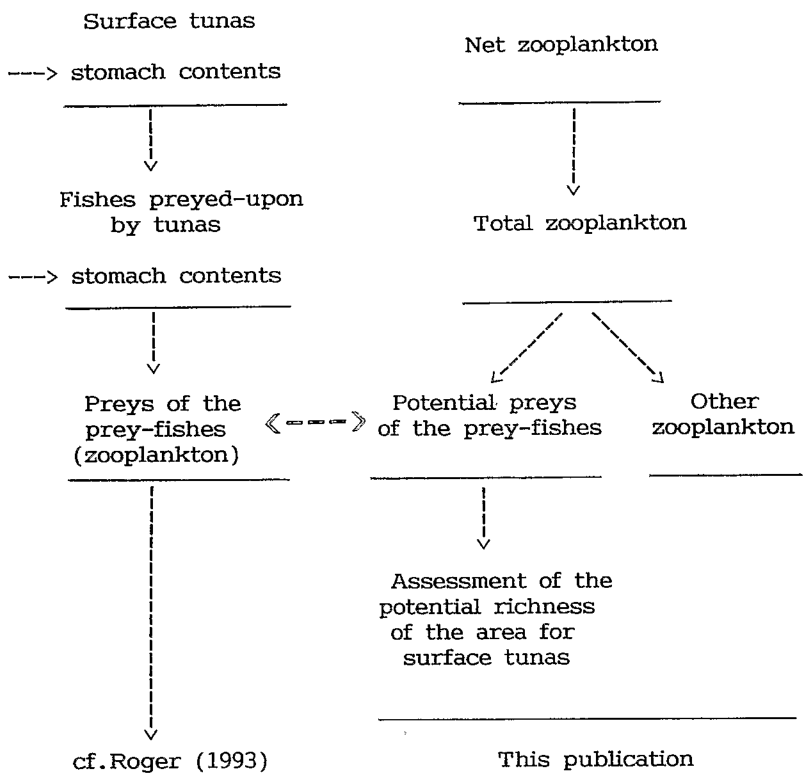


Fig. 1. Research strategy.

prised: a – all the copepods, *Lucifer* and ostracods, b – carids, sergestids, stomatopods, euphausiids, amphipods and megalopes whose length is less than 10 mm, c – chaetognaths and annelids less than 30 mm in length, and d – fishes and fish larvae less than 15 mm in length.

Other zooplankton organisms were considered for total biomass assessment, but not as potential preys of prey-fishes. Sorted organisms were dried at 65° C for 48 hours then weighed to ± 1 mg. In this paper, all biomasses are expressed in mg dry weight per 1 000 m^3 of water filtered.

It should be observed that no correction has been made to take into account the fact that plankton samples have been preserved for several months in 10% formalin prior to sorting. Such a correction has been estimated to be 1.24 for the plankton 1–10 mm in length (Giguère et al. 1989).

Table 1. Relative importance of fishes as food for surface tropical tunas of the western Indian ocean. Estimated % in volume. After Roger[2].

Fishing technique	Trolling and live-bait	Purse-seine
Yellowfin (*T. albacares*)	50%	85%
Skipjack (*K. pelamis*)	80%	95%

Results

A preliminary analysis showed that there was no difference between samples from morning stations (mean local time 1000 h) and afternoon stations (mean local time 1500 h) after Mann-Whitney, Kruskal-Wallis and Kolgomorov-Smirnov tests. Therefore, both have been considered as day stations. It should be also observed that biomasses in both day and night samples follow the log-normal distribution so that non-parametric tests should be used.

The list of taxa in each of the categories 'potential preys' (PP) and 'non-potential preys' of the prey-fishes is presented in Table 2. These two categories

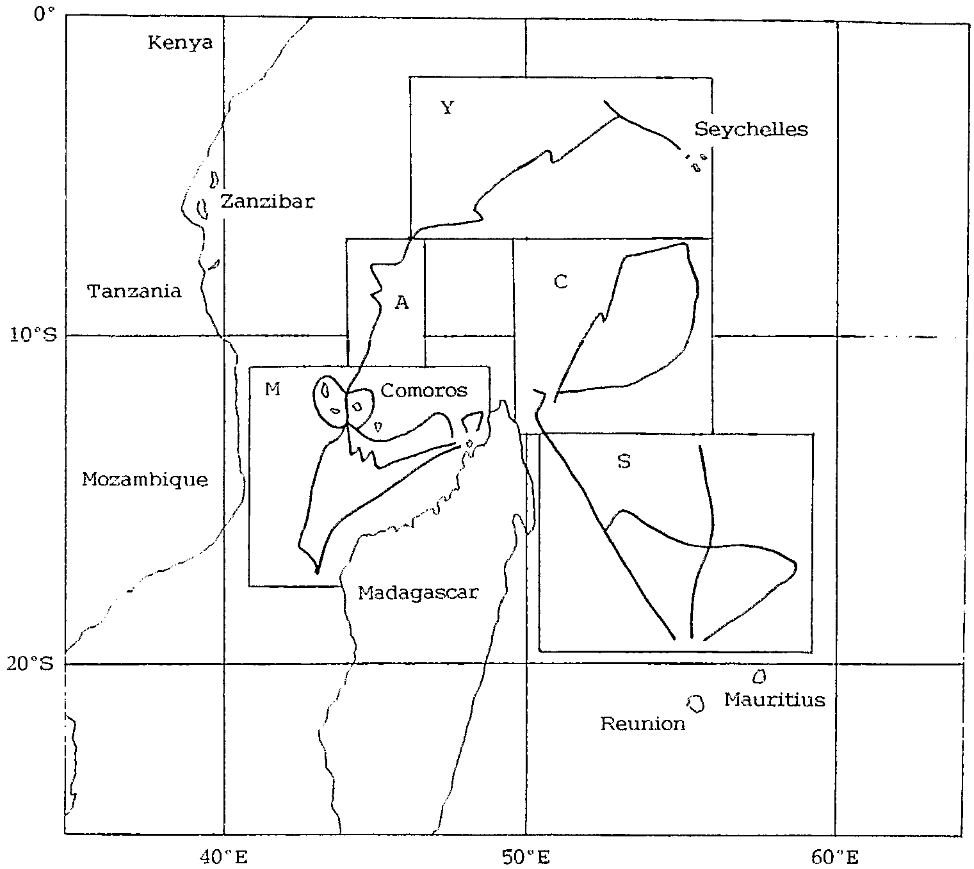


Fig. 2. Map of plankton cruises and limits of areas investigated: Y = Seychelles, A = Aldabra, C = Centre, M = Mozambique, S = South: number of plankton stations: Y = 39, A = 22, C = 54, M = 170, S = 43.

are identified from previously defined parameters, i.e. taxa and sizes of organisms found in the stomachs of fishes from tuna stomachs. Moreover, as most of the prey-fishes are mainly day-feeders, only potential prey which remain by day in the 0–170 m layer will be accessible to them (accessible potential preys = APP). From these facts, five parameters have been taken into account to characterise the plankton of tuna fishing grounds: a – Total biomass (TT) assessed from night samples, as most of the zooplankton concentrates at night in the upper 170 m. b – Biomass of the potential prey which remain by day in the upper 170 m. This is the part of the zooplankton which is actually accessible to the prey-fishes of tunas (APP). c – Day/night ratio of potential prey (APP/PP). This ratio measures the percentage of potential prey which remain by day in the upper 170 m. d – Percentage of accessible potential prey versus total biomass (APP/TT). e – Taxonomic composition of the APP fraction.

Mean values of these parameters are indicated in Table 2, together with some characteristics of the main taxa. It should be observed that, as a mean, 40% of the potential prey remain by day in the upper 170 m (APP = 515 mg per 1 000 m^3) and are therefore accessible to the day-feeders which comprise most of the prey-fishes of tunas. This biomass accounts for 56% of the zooplankton present by day in the upper 170 m, but only 19% of the total biomass of zooplankton (TT = 2 700 mg per 1 000 m^3).

In Fig. 2, five areas have been identified. In decreasing order of surface tunas yields (Stequert & Marsac 1986) these are Seychelles (Y), Aldabra (A), Mozambique (M), Centre (C) and South (S) areas. The analysis of the five selected parameters which describe the plankton characteristics in these five areas indicates a north-south trend following the M-A-Y and S-C-Y transects, for biomasses as well as for taxonomic composition.

Biomasses

The values of four of the selected parameters in the

Table 2. Sorted taxa and some of their characteristics.

Taxa	Mean individual dry weight mg	Ratio dry/wet weight mg (%)	Day stations n = 191 Zm = 164 m		Night stations n = 140 Zm = 178 m		Ratio day/night of biomasses
			Biomasses mg dry weight per 1 000 m³	% of PP	Biomasses mg dry weight per 1 000 m³	% of PP	
Potential prey of prey-fishes							
Copepods	0.15	12.8	150	29.1	343	26.9	0.44
Lucifer	0.10	12.3	22	4.3	32	2.5	0.69
Carids, stomatopods and sergestids < 10 mm	0.31	–	30	5.8	29	2.3	1.03
Euphausiids < 10 mm		14.4	80	15.5	468	36.8	0.17
Amphipods < 10 mm	0.25	12.8	38	7.4	110	8.6	0.35
Megalopes < 10 mm	–	–	10	1.9	19	1.5	0.53
Ostracods	–	–	4	0.8	7	0.6	0.57
Total crustaceans	–	**13.1**	**334**	**64.8**	**1008**	**79.2**	**0.33**
Fishes and larvae < 15 mm	0.27 to 1.63*	16.8	33	6.4	116	9.1	0.28
Chaetognaths < 30 mm	0.13	7.7	135	26.2	132	10.4	1.02
Annelids < 30 mm	–	–	4	0.8	6	0.5	0.67
Miscellaneous	–	–	9	1.8	11	0.9	0.82
Total potential prey	–	–	**515 = APP**	**100**	**1273 = PP**	**100**	**0.40 = APP/PP**
Other (non-potential prey)							
Carids and stomatopods > 10 mm	–	25.3	32		127		0.25
Sergestids > 10 mm	–	–	2		65		0.03
Peneids	–	–	–	–	23		–
Euphausiids > 10 mm	–	–	8		369		0.02
Amphipods > 10 mm	–	–	10		17		0.59
Megalopes > 10 mm	–	–	6		11		0.55
Total crustaceans	–		**58**		**612**		**0.09**
Fishes > 15 mm	–	19.5	23		267		0.09
Leptocephalids	–	4.7	6		18		0.33
Total fishes	–	–	**29**		**285**		**0.10**
Cephalopods	–	11.3	11		25		0.44
Heteropods	–	–	9		10		0.90
Chaetognaths > 30 mm	–	–	46		41		1.12
Gelatinous organisms	–	2.2	194		354		0.55
Miscellaneous	–	–	50		100		0.50
Total other	–	–	**397**		**1427**		**0.28**
Grand total	–	–	**912**		**2700 = TT**		**0.34**
			0.56**		**0.47 = PP/TT**		

n = number of stations
Zm = mean maximum depth reached by the net
APP = accessible potential prey (day 0 – 170 m)
PP = total potential prey (night 0 – 170 m)
TT = total biomass (night 0 – 170 m)
* = much variable according to station
** = APP/total day biomass

Table 3. Values of selected parameters in the five areas. Number of stations between brackets. d.w. = dry weight. TT = total biomass. APP = biomass of accessible potential prey. APP/PP = proportion of the potential prey which remain by day in the 0–170 m layer. APP/TT = proportion of the accessible potential prey in the total biomass.

Areas	Seychelles	Aldabra	Mozambique	Centre	South
TT mg d.w. per 1 000 m^3	4 379	3 393	2 659	2 709	1 017
	(19)	(11)	(65)	(23)	(22)
APP mg d.w. per 1 000 m^3	1 183	888	457	403	169
	(20)	(11)	(105)	(31)	(21)
APP/PP	0.60	0.54	0.33	0.44	0.35
APP/TT	0.27	0.26	0.17	0.15	0.17

five areas are shown in Table 3. The north-south trend of these parameters is presented in Fig. 3a (S-C-Y transect), 3b (M-A-Y transect) and 4 (all areas). The biomass of accessible potential prey (APP) at each station according to latitude along the S-C-Y transect is presented in Fig. 5. From areas where tuna fishing is poor to those where fishing is successful, several features are evident: a – the total zooplankton biomass (TT) rises from 1 017 to 4 379 mg per 1 000 m^3, that is by a factor of 4. b – the biomass of accessible potential prey (APP) rises from 169 to 1 183 mg per 1 000 m^3, that is by a factor of 7. It therefore accounts for a growing percentage of the total biomass (APP/TT increases from 0.15–0.17 to 0.27). c – a growing percentage of potential prey remains by day in the upper 170 m (APP/PP rises from 0.33–0.35 to 0.60).

It should also be observed that all these characteristics are closely related in Centre and Mozambique areas.

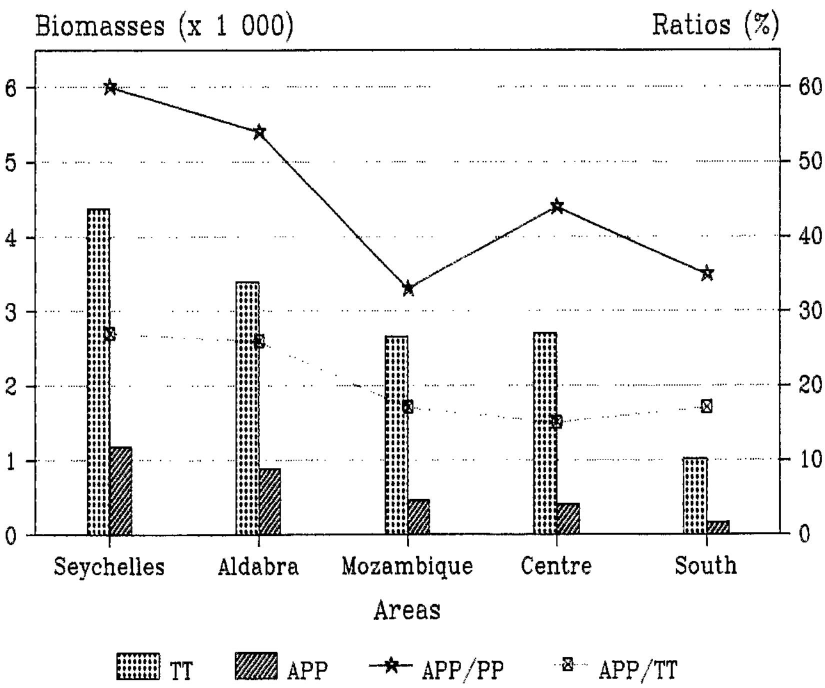
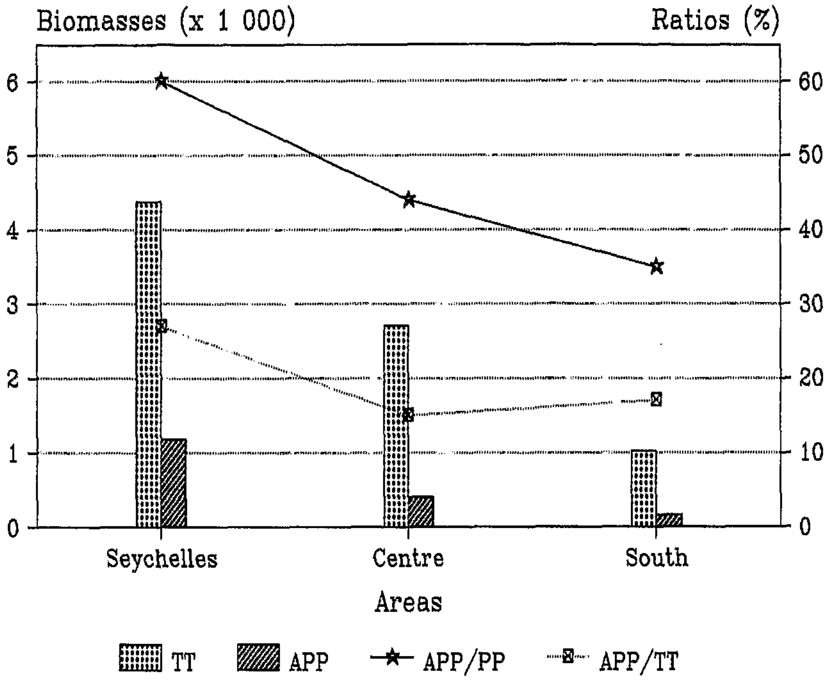
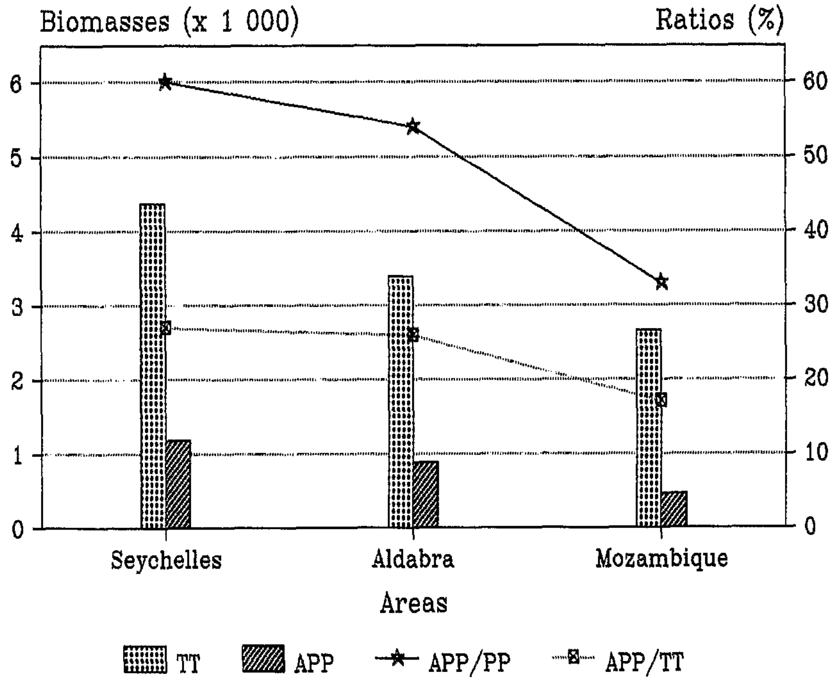


Fig. 4. Total biomasses (TT, night tows) and accessible potential prey biomasses (APP, day tows) in the five areas. Biomasses in mg dry weight per 1 000 m^3; PP – potential prey biomass (night tows).



a



b

Fig. 3. a-Total biomasses (TT, night tows) and accessible potential prey biomasses (APP, day tows) along the S-C-Y transect. b-same parameters along the M-A-Y transect. Biomasses in mg dry weight per 1 000 m^3; PP = potential prey biomass (night tows).

Seasonal variations

The question arises as to whether the above conclusions could be altered by taking into account seasonal variations. Seychelles and Aldabra areas were sampled only in August 1988, Centre area in Febru-

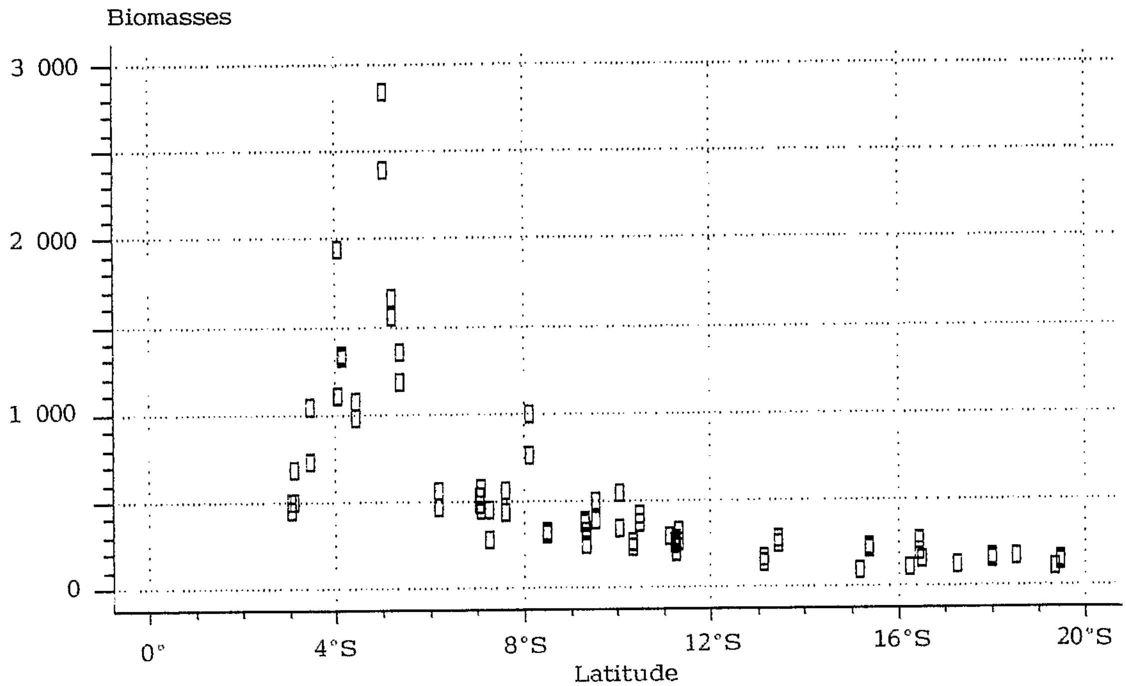


Fig. 5. Accessible potential prey biomasses (APP, day tows) according to latitude along the S-C-Y transect. Biomasses in mg dry weight per 1 000 m³.

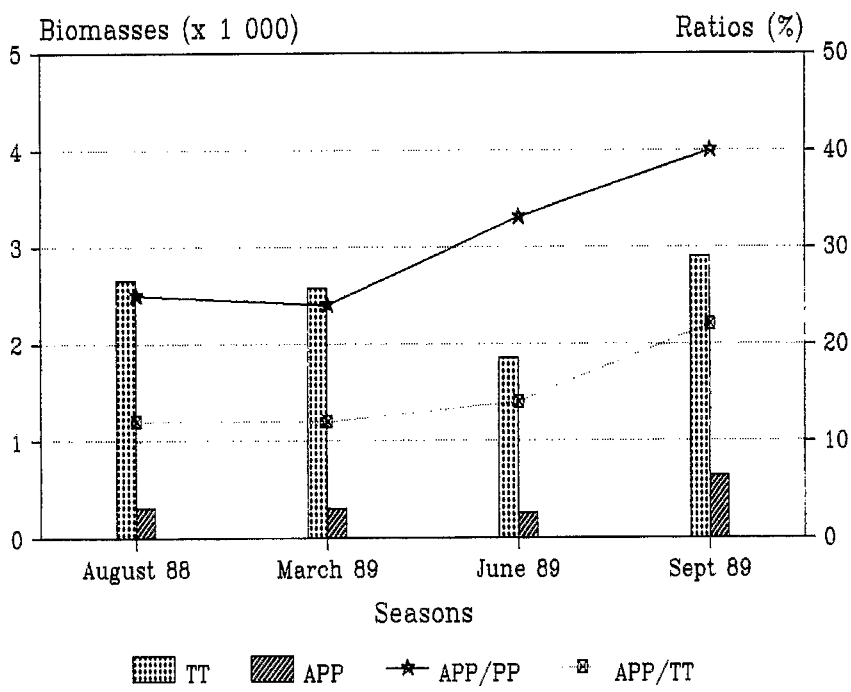


Fig. 6. Seasonal variations of total biomasses (TT, night tows) and accessible potential prey biomasses (APP, day tows) in the Mozambique area. Biomasses in mg dry weight per 1 000 m³.

ary-March 1989, and South area in November 1988. Only the Mozambique area was surveyed in several periods: August 1988, March, June and September 1989; the seasonal variations in this last area are presented in Fig. 6 where it is shown that variations in total biomass are weak. From March to September 1989 however, there is an increase in the paremeters considered as favourable for surface tunas: potential prey of the prey-fishes account for a growing fraction of the total zooplankton (APP/TT increases), and a growing proportion of these potential prey remains by day in the 0–170 m layer (APP/PP increases) thus becoming available for the day-feeders which comprise most of the prey-fishes of surface tunas.

In order to check the influence of seasonal variations, the four parameters have been represented in the areas Seychelles, Aldabra and Mozambique using only the data gained in August 1988 (Fig. 7). It can be seen that the north-south trend is the same as that found when using the whole set of data from all seasons (Fig. 3b). It is therefore considered that seasonal variations do not invalidate the conclusions previously obtained.

Taxonomic composition

A comparison between the taxonomic composition of the APP fraction which takes part in the tuna food chain and that of the total zooplankton (TT) caught by plankton nets at night, shows that: a – chaetognaths and *Lucifer* are four times more important (% dry weight) in APP than in TT; b – copepods, amphipods, ostracods and megalopes are twice as important; c – fishes and euphausiids are only one half as important.

From areas where tuna fishing is poor to those where fishing is successful, the APP fraction (Fig. 8) comprises an increasing percentage of copepods and chaetognaths (from 37 to 73%) and a decreasing percentage of fishes (larvae and juveniles) and euphausiids (from 37 to 12%). A similar situation is again observed in the Centre and Mozambique areas.

Discussion

Owing to the small size of individuals, zooplankton does not serve directly as food for tunas, but it is the forage of the micronektonic fishes which are the preys of tunas. As these prey-fishes are difficult to catch with existing techniques, the zooplankton which is their food represents the closest trophic level to tunas whose abundance is measurable. Its biomass therefore constitutes an assessment of the potential richness of an area for surface tunas.

It has been shown that only a small part of the zooplankton (15 to 27%, depending on areas) is actually used as food by the prey-fishes of surface tunas, if it is considered that these prey-fishes feed on small-sized organisms which remain by day in the 0–170 m layer. These characteristics of the zooplanktonic prey of the prey-fishes have been determined from stomach contents analysis.

On the other hand, it has been shown that the characteristics of this fraction of the zooplankton which serves as food for the prey-fishes are different from those of the total zooplankton, and that they are clearly linked with average tuna yields. In comparison with areas where surface tuna fishing is poor, the zooplankton of areas where fishing is successful exhibits distinct features: a – the total biomass is 4 times higher, but the biomass of the accessible potential prey of the prey-fishes is higher by a factor of 7. This relatively higher increase is due to the facts that potential prey account for a greater part of the total zooplankton and that a greater proportion of these potential prey remains by day in the 0–170 m layer and are therefore accessible to the prey-fishes of surface tunas. b – from the taxonomic point of view, in areas where tuna fishing is important, copepods, amphipods, *Lucifer*, ostracods, megalopes and chaetognaths are relatively more important in the plankton caught with nets, whereas fishes (and larvae) and euphausiids are less important.

Finally, it has been shown that these characteristics are not altered by seasonal variations.

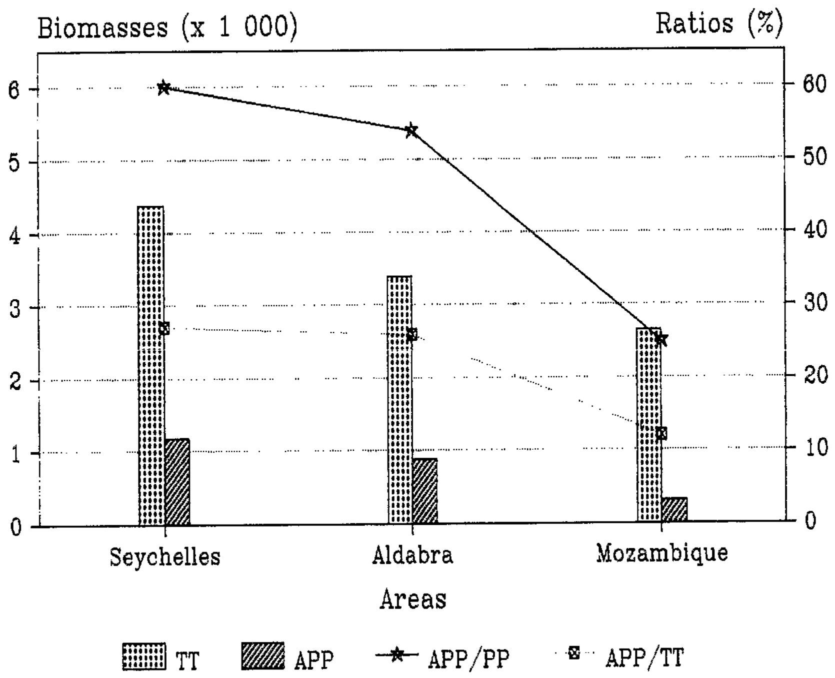


Fig. 7. Total biomasses (TT. night tows) and accessible potential prey biomasses (APP. day tows) along the M-A-Y transect in August 1988. Biomasses in mg dry weight per 1 000 m^3.

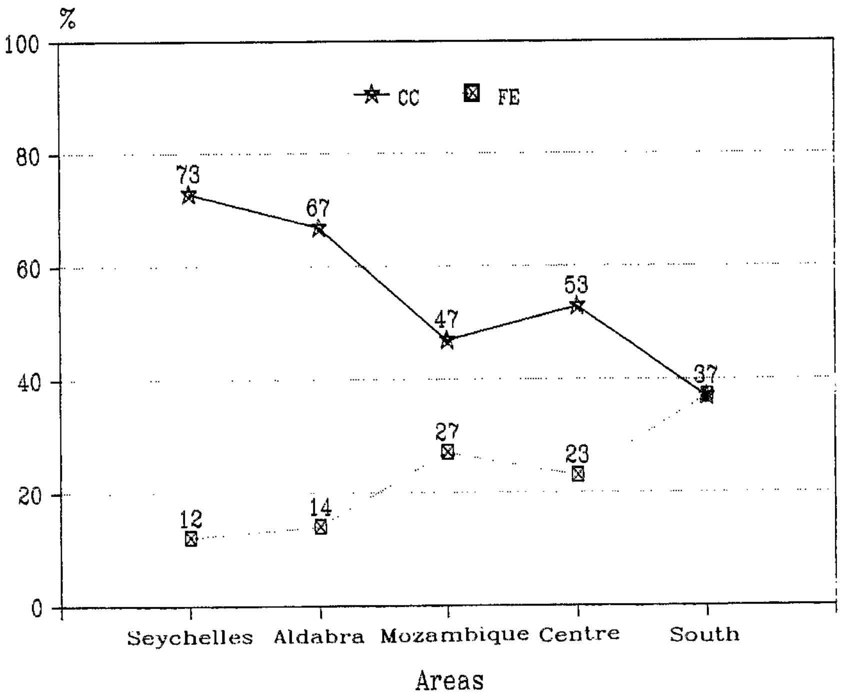


Fig. 8. Relative taxonomic composition of the accessible potential prey in the five areas: CC = copepods and chaetognaths, FE = fishes and euphausiids; percentages are calculated on dry weight biomasses.

Conclusions

The above considerations lead to three main findings: First, it is confirmed that the total zooplankton biomass is not representative of the available forage for the prey of surface tunas. This forage comprises only a well defined part of the total zooplankton and accounts for a variable percentage of its total biomass in different areas. Second, it is shown that there is a relationship between the biomass and the structure of plankton populations in the one hand, and abundance and distribution of surface tunas on the other. In this relationship, the structure of the plankton population (vertical distributions and migrations, and size spectra) appears to be as important as its total biomass. Finally, the most relevant parameter to assess the potential richness of an area for surface tunas is shown to be the biomass of the APP fraction of the zooplankton, whose characteristics have been previously defined.

Acknowledgements

Thanks are due to the crew of the purse-seiner Mascaroi for their excellent cooperation during the plankton sampling programme, and to M. Slepoukha for participating in plankton sampling.

References cited

Alverson, F.G. 1961. Daylight surface occurrence of myctophid fishes off the coast of South America. Pacif. Sci. 15: 483.

Bard, F.X. & O. Pezennec. 1991. Analyse des contenus stomacaux des albacores (*T. albacares*) pêchés à la senne dans le golfe de Guinée. ICCAT Collective volume of scientific papers 35, SCRS 90/67: 1–7.

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

Cayré, P. 1991. Behaviour of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish aggregating devices (FADs) in the Comoros Islands as determined by ultrasonic tracking. Aquat. Living Resour. 4: 1–12.

Clarke, T.A. 1983. Comparison of abundance estimates of small fishes by three towed nets and preliminary results of the use of small purse-seines as sampling devices. Biol. Oceanogr. 2: 311–340.

Dizon, A.E., R.W. Brill & H.S.H. Yuen. 1978. Correlations between environment, physiology and activity, and the effects of thermoregulation in skipjack tuna. pp. 233–260. *In:* G.D. Sharp & A.E. Dizon (ed.) The Physiological Ecology of Tunas, Academic Press, New York.

Dragovich, A. & T. Potthoff. 1972. Comparative study of food of skipjack and yellowfin tunas off the coast of West Africa. U.S. Fish. Bull. 70: 1087–1110.

Giguère, L.A., J.F.St Pierre, B. Bernier, A. Vezina & J.G. Rondeau. 1989. Can we estimate the true weight of zooplankton after chemical preservation? Can. J. Fish. Aquat. Sci. 46: 522–527.

Grandperrin, R. 1975. Structures trophiques aboutissant aux thons de Longue Ligne dans le Pacifique Sud-Ouest tropical. Thèse de Doctorat d'Etat, Université de Provence, Marseille. 296 pp.

Herbland, A. 1990. L'oligotrophie: un concept en évolution. ICCAT Collective volume of scientific papers 32, SCRS 89/61: 169–174.

Holland, K.N., R.W. Brill & R.K.C. Chang. 1990. Horizontal and vertical movements of yellowfin and bigeye tunas associated with fish aggregating devices. U.S. Fish. Bull. 88: 493–507.

Hunter, J.R., A.W. Argue, W.H. Bayliff, A.E. Dizon, A. Fonteneau, D. Goodman & G.R. Seckel. 1986. The dynamics of tuna movements: an evaluation of past and future research. FAO Fish. Tech. Paper 277: 1–78.

Kitchell, J.F., W.H. Neill, A.E. Dizon & J.J. Magnuson. 1978. Bioenergetic spectra of skipjack and yellowfin tunas. pp. 357–368. *In:* G.D. Sharp & A.E. Dizon (ed.) The Physiological Ecology of Tunas, Academic Press, New York.

Kobayashi, H. & Y. Yamaguchi. 1971. Feeding ecology and hoocking tendency of tunas and marlins in the eastern equatorial Pacific. Bull. Jap. Soc. Sci. Fish. 37: 83–89.

Kornilova, G.N. 1981. Feeding of yellowfin tuna, *Thunnus albacares* and bigeye tuna, *Thunnus obesus,* in the equatorial zone of the Indian Ocean. J. Ichthyol. 20: 111–119.

Legand, M., P. Bourret, P. Fourmanoir, R. Grandperrin, J.A. Gueredrat, A. Michel, P. Rancurel, R. Repelin & C. Roger. 1972. Relations trophiques et distributions verticales en milieu pélagique dans l'océan Pacifique intertropical. Cahiers ORSTOM, Sér. oceanogr. 10: 303–393.

Lemasson, L. 1990. Relations production halieutique-environnement. ICCAT Collective volume of scientific papers 32, SCRS 89/57: 133–136.

Longhurst, A.R. & D. Pauly. 1987. Ecology of tropical oceans. Academic Press, New York. 407 pp.

Medina-Gaertner, M. 1988. Relation entre l'alimentation des poissons et le zooplancton de la baie de Dakar. Inv. Pesq. 52: 155–192.

Nakamura, E.L. 1965. Food and feeding habits of skipjack tuna (*Katsuwonus pelamis*) from the Marquesas and Tuamotu Islands. Trans. Amer. Fish. Soc. 94: 236–242.

Olson, R.J. & C.H. Boggs. 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.

Parin, N.V. 1968. Ichthyofauna of the epipelagic zone. Translated by Israel programme for scientific translations 1970, IPST Cat. no. 5528. 206 pp.

Pelczarski, W. 1988. Examination of food of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) from the open waters of the Central Atlantic. ICCAT Collective volume of scientific papers 28, SCRS 87/55: 58–73.

Petit, M. & J.M. Stretta. 1992. Théorie cohérente du comportement des thonidés dans leur habitat. ICCAT Collective volume of scientific papers 39, SCRS 91/58: 332–336.

Pitman, R.L. & L.T. Ballance. 1990. Daytime feeding by Leach's storm-petrel on a midwater fish in the eastern tropical Pacific. The Condor 92: 524–527.

Roger, C. & R. Grandperrin. 1976. Pelagic food webs in the tropical Pacific. Limnol. oceanogr. 21: 731–735.

Stequert, B. & F. Marsac. 1986. La pêche de surface des thonidés tropicaux dans l'Océan Indien. FAO Doc. Tech. Pêches 282. 213 pp.

Stretta, J.M. & M. Petit. 1992. Determinisme du déplacement des thonidés et variabilité de l'environnement. ICCAT Collective volume of scientific papers 39, SCRS 91/57: 322–331.

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

Valle, S., N. Mezentseva & E. Rodriguez. 1979. Contenido estomacal del atun de aleta amarilla (*Thunnus albacares*) en el Atlantico Centro Oriental. Oceanogr. Trop. 18: 163–185.

Yang, W.S. & Y. Gong. 1987. The vertical distribution of tunas and billfishes, and fishing efficiency between Korean regular and deep longlines in the Atlantic Ocean. ICCAT Collective volume of scientific papers 26, SCRS 86/81: 184–187.

Yuen, H.S.H. 1970. Behavior of skipjack tuna *Katsuwonus pelamis* as determined by tracking with ultrasonic devices. J. Fish. Res. Board Can. 27: 2071–2079.

Zavala-Camin, L.A. 1986. Sobre el ciclo alimentario en los estudios de contenido estomacal de atunes y afines. ICCAT, Collective volume of scientific papers 26, SCRS 86/34: 582–583.