Aquat. Living Resour. 13 (2000) 233–240

S0990744000010664/FLA

Food consumption of tuna in the Equatorial Atlantic ocean: FAD-associated versus unassociated schools

Frédéric Ménard[a,d,*], Bernard Stéquert[a], Alex Rubin[a], Miguel Herrera[c], Émile Marchal[b]

[a] *IRD, Centre de recherches océanologiques, BP V 18 Abidjan, Ivory Coast*

[b] *IRD, Institut océanographique, 195 rue Saint-Jacques, 75005 Paris, France*

[c] *IOTC, PO Box 1011 Victoria, Mahe, Seychelles*

[d] *present address: IRD, Dep. HEA, BP 5045, 34032 Montpellier cedex 1, France*

Accepted 3 July 2000

Abstract – Since 1991, fishing operations on tuna schools associated with drifting Fish Aggregating Devices (FADs) have become widespread in the purse seine fishery in the Gulf of Guinea. In the offshore South Sherbro area (0–5° N, 10–20° W), FAD-associated catches represent about 75 % of the total catch. This FAD fishery exploits concentrations of skipjack mixed with a smaller amount of bigeye and yellowfin tuna of similar size (46 cm), and some large yellowfin. Catches on unassociated tuna schools are mainly composed of large yellowfin in breeding phase and skipjack. Here we studied tuna diet in relation with the aggregation mode (FAD-associated or unassociated tuna schools), species, and size. The stomach contents of around 800 fish were analysed. Numerous empty stomachs were found, especially in fish caught under FADs. Diets were similar for all small-size tuna sharing the same aggregation type. Small tuna mainly feed on *Vinciguerria nimbaria* (Photichthyidae), a mesopelagic fish of the micronekton, whereas large tuna mainly feed on Scombridae, mixed with *Cubiceps pauciradiatus* (Nomeidae) when they were caught in unassociated schools. The feeding habits of tuna are discussed with emphasis on the behavior of *V. nimbaria*. Estimations of the daily ration of similarly sized tuna with the same aggregation mode were very close. The low estimated rations for small, FAD-associated tuna show that logs do not have a trophic function, but rather are a refuge. In contrast, FADs seem to influence the diet of large tuna because of the Scombridae prey that probably is associated to the FAD.
© 2000 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

tuna feeding / daily ration / Fish Aggregating Devices / *Vinciguerria nimbaria* / purse seine / Atlantic Ocean

Résumé – Alimentation des thons dans l'Atlantique équatorial : comparaison sous DCP et en bancs libres. Depuis 1991, la pêche sous des Dispositifs de Concentration de Poissons (DCP) dérivants mis à l'eau par les senneurs s'est très fortement développée dans le golfe de Guinée. Dans la zone hauturière Sud Sherbro (0–5° N, 10–20° W), elle représente 75 % des captures totales. Cette pêche sous DCP exploite des concentrations plurispécifiques constituées surtout de listaos, et d'albacores et de patudos de taille similaire (46 cm), associés à quelques grands albacores. Les captures sur bancs libres sont constituées de gros albacores en reproduction et aussi de listaos. On compare ici l'alimentation des thons dans cette zone selon le type d'agrégation (bancs libres et DCP), l'espèce et la taille. Près de 800 contenus stomacaux ont été analysés. Les estomacs vides sont très nombreux, surtout sous les DCP. Le régime alimentaire varie suivant le type d'agrégation. Les petits thons se nourrissent essentiellement de *Vinciguerria nimbaria* (Photichthyidae), un poisson mésopélagique du micronekton dont le comportement particulier dans la zone est discuté. Les Scombridae sont les proies principales des grands thons sous DCP dérivants, alors qu'en bancs libres, ils se nourrissent aussi de *Cubiceps pauciradiatus* (Nomeidae). Les rations journalières des thons de même taille et capturés de la même façon ne montrent pas de différences importantes entre espèces. Les faibles rations estimées pour les petits thons sous DCP montrent que les épaves ne jouent pas un rôle alimentaire mais représentent plutôt un refuge. En revanche, les DCP semblent avoir un rôle dans l'alimentation des grands thons qui se nourrissent de petits Scombridae associés eux-mêmes aux DCP.
© 2000 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

alimentation des thons / ration journalière / Dispositifs de Concentration de Poissons / *Vinciguerria nimbaria* / pêche à la senne / océan Atlantique

*Corresponding author.
E-mail address: menard@ird.fr (Frédéric Ménard).

1. INTRODUCTION

In the Eastern Tropical Atlantic, tropical tuna, mainly yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye (*Thunnus obesus*), are exploited by surface purse seine fishery covering the whole area. Two main fishing modes are used: the search and the catch of free swimming tuna schools (mostly big-size tuna in mono-specific unassociated schools), and sets under artificial floating objects (drifting Fish Aggregating Devices, FADs), set afloat by the purse seiners. FADs concentrate tuna (mostly mixed concentrations of small-size tuna dominated by skipjack), but also other pelagic species associated with FADs: *Acanthocybium solandri*, billfish, Balistidae, *Sphyranea barracuda*, Coryphaena sp., *Elagatis bipinnulata*, Kyphosidae and sharks (Ménard et al., 2000). In the early 1990s, fishing operations on tuna schools associated with drifting FADs became widespread in the Eastern Tropical Atlantic (Ariz et al., 1993). At the moment catches using this fishing mode reach more than 50 % of the total surface catch (ICCAT data base).

Very few studies have undertaken the analysis of the impact of FADs on the feeding of tuna. Hunter and Mitchell (1967) studied the stomach contents of skipjack and yellowfin tuna associated with drifting logs (natural FADs) in the offshore waters of Costa Rica, and they showed that tuna do not feed on fish associated with the log. Other studies focus on the diet of yellowfin tuna associated with anchored FADs in the Hawaiian waters (Brock, 1985) and in the American Samoa (Buckley and Miller, 1994), or associated with anchored payaos in the Philippines (Yesaki, 1983; Barut, 1988). No link has been demonstrated between feeding behavior of yellowfin tuna and anchored FADs, except in the work of Yesaki (1983), who found cannibalism of large yellowfin tuna on small-size conspecifics associated with the anchored FADs.

The purpose of this paper is to study the tuna diet in relation with the aggregation type (unassociated tuna schools versus tuna concentrations around drifting FADs) in the South Sherbro area (0–5° N and 10–20° W) in the Equatorial Atlantic. The South Sherbro area developed into a major seasonal FAD fishing zone in the Eastern Tropical Atlantic (Ménard et al., 1999, Ménard et al., 2000) with high catches from November to January. During these three months, sets under FADs represented about 75 % of the total catch, and exploited mixed concentrations of small-size tuna (46 cm fork length), and some large yellowfin and bigeye tuna (less than 10 % of the catches in weight). Sets of unassociated tuna schools mainly occurred from February to April and targeted large-size yellowfin tuna, at this period in breeding condition, in the Gulf of Guinea (Albaret, 1977; Bard and Capisano, 1991). The influence of drifting FADs on the diet of tuna is investigated by comparing the stomach contents of tuna caught in the South Sherbro area, taken into account the type of association, the species, and the size. Daily rations are estimated following the methodology of Olson and Boggs (1986). Feeding habits of tuna are discussed with emphasis on the behavior of their main prey, *Vinciguerria nimbaria*, a mesopelagic fish of the micronekton.

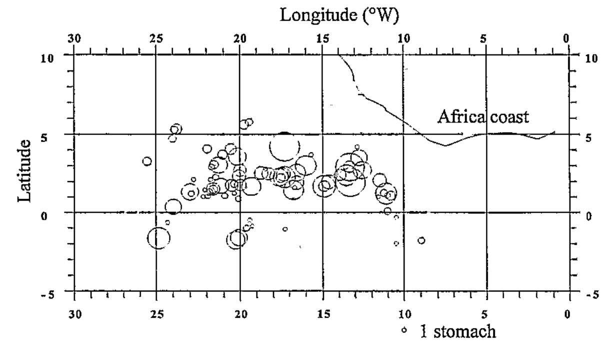

Figure 1. Sampling positions from which stomachs were collected in 1995, 1996, 1997 and 1998 in or near the South Sherbro area. Area of each circle is proportional to the number of stomachs.

2. MATERIALS AND METHODS

Stomachs were collected in 1995, 1996, 1997, and 1998 from tuna caught during daylight hours in or near the South Sherbro area (*figure 1*). The samples were collected by scientific observers on board vessels, by scientific technicians at the port of Abidjan during landings, or at tuna canneries in Abidjan. In order to study the influence of the size of the fish, the data was grouped in two size classes (smaller than 90 cm and bigger than 90 cm) that represent two distinct groups in the size catch distribution. Most of the fish were smaller than 90 cm, so only a few yellowfin tuna with a size greater than 90 cm have had their stomach collected and analysed. The length of each fish was measured and the stomach was either preserved in formalin or deep frozen. Stomachs were weighed, food was removed, and then contents were weighed and sorted according to the digested prey and its degree of digestion. The prey was identified to the lowest possible taxon. Four degrees of digestion were used according to the state of the prey. The degree of digestion four, the most advanced state of digestion, occurred in 60 % of our analyses.

Recognizable prey items were divided into six major categories for the fish that constituted the dominant phylum: *Vinciguerria nimbaria* (Photichthyidae), Scombridae (represented by *Auxis thazard* and *Katsuwonus pelamis*), *Cubiceps pauciradiatus* (Nomeidae), epipelagic fish (Balistidae, Clupeidae, Diretmidae and Exocetidae), mesopelagic fish (Astronesthidae, Gonostomatidae, Myctophidae, Nemichthyidae, Paralepididae and Gempylidae), and undetermined fish when the digestion state was too advanced. Planktonic crustaceans (mainly Euphausiaceae and natantia Decapods) constituted a separate category, as was the case for the Cephalopods (exclusively squids of the Teuthoidae family). The latter category was grouped with the remainder preys (undetermined pulp, tunicates such as Salpidae). The stomachs that contained only mucus or parasites were considered as empty.

To take into account the multivariate nature of the stomach contents data, we performed a correspondence analysis on the data matrix of the individual stomach contents of the six small tuna predators (skipjack, bigeye and yellowfin smaller than 90 cm, unassociated and FAD-associated), and on eight of the prey items. Scombridae was eliminated as an item because it was observed only once in the diet of a FAD-associated bigeye. Empty stomachs were also eliminated. Then a simple binary designation of presence or absence of each prey item was used in order to extract patterns from this data set.

In order to estimate daily rations, the process of gastric retention needed to be taken into account, i.e. the relationship between the amount of food remaining in the stomach and the time elapsed since the feeding. Such a process depends on the type of prey and on the prey sizes, and several models have been proposed; the most widely used assumes that gastric evacuation is exponential (Elliott and Persson, 1978). Olson and Mullen (1986) and Olson and Boggs (1986), in their very comprehensive study on the feeding of the yellowfin tuna of the Eastern Tropical Pacific, have proposed a food consumption model that does not require an a priori assumption of exponential gastric evacuation. Data from gastric evacuation experiments were fitted best by linear regression models for the different prey used to feed experimental tuna (mackerel *Scomber japonicus*, squid *Loligo opalescens*, smelt *Hypomesus pretiosus*, and nehu *Stolephorus purpureus*). The authors proposed to calculate the daily ration from the estimation of a feeding rate r (g·h^{-1}), computed as:

$$\hat{r} = \sum_i \frac{\bar{W}_i}{A_i}$$

with

A_i (h), the integral of the function that fits the gastric evacuation rate (i.e. the average amount of time required to evacuate the average proportion of ingested prey of type i present in the stomach at any time);

$\overline{W}_i$ (g), the average wet weight of prey of type i found in the stomach of the predator.

In the $\overline{W}_i$ calculus, empty stomachs are taken into account because, as a rule, they reflect the natural feeding conditions of the population. According to Maldeniya (1996) and due to the lack of experimental data for the gastric evacuation rates for the identified prey of the tuna in the South Sherbro area, we used the A_i values as they were estimated by Olson and Boggs (1986) with respect to the ecology of the species (*table I*). Assuming that tuna mainly feed during the daylight hours, the daily food intake is calculated by multiplying W$\hat{r}$ by 12 h. Daily rations correspond to the daily food intake expressed as a percentage of the average weight of the corresponding tuna predator. The weight of the stomach contents can be adjusted in order to take into account the stress due to the fishing. During the fishing operation, digestion continues until the death of the fish or until the preservation of the stomach (stress may also lead to a partial or total regurgitation of the stomach). Following Olson and Boggs (1986), we used an average duration of gear retention (2 h) in conjunction with gastric evacuation rates to calculate such an adjustment of the weight of the stomach contents at the time of gut removal (*table I*). Furthermore, to take into account the wet mass loss of the food in the stomachs observed within a few minutes after eating (Magnuson, 1969), $\hat{r}$ values were adjusted. Olson and Boggs (1986) interpreted the differences between the 100 %-value and the estimated intercept values of the gastric evacuation in linear models (*table I*) as a quick water loss. Thus, for each food item $\hat{r}$ values were increased by these differences.

3. RESULTS

The number of empty stomachs (85 %) was very high among tuna caught under FADs (*table II*). This was not the case for unassociated tuna, where the proportion of empty stomachs reached 25 %. *Figure 2* displays the status of the stomachs versus the time of the day. Under FADs, most of the tuna were caught before 8h00 in the morning, i.e. at dawn (7h00 at 15° W in the South Sherbro area), but the number of empty stomachs remained high, independent of the time. Non-empty stomachs were sampled before 08h00, 33 for a total of 305 sampled from 26 fishing sets. The composition of the prey and its degree of digestion varied greatly. The prey in the fullest stomach (around 1 kg) was a Scombridae recently eaten (degree of digestion: one) by a large-size yellowfin tuna. For unassociated tuna schools, non-empty stomachs of three bigeye and nine yellowfin tuna coming from the same fishing set occurring at 7h30, were analysed. The fish had fed almost only on *Vinciguerria nimbaria* and the degree of digestion ranged from one to four.

The average weights of the stomach contents were expressed as a percentage of the body mass of the predator (*table III*). The mass adjustments for gear retention led to an increase in the mean mass of the observed stomach contents between 14.8 and 23.5 %. Under the FADs, our estimations were very close for skipjack, small-size yellowfin (smaller than 90 cm) and bigeye tuna. Values of the stomach content mass were higher, but showed a great variability, for small-size unassociated tuna. Furthermore, the stomach content (% of body mass) decreased for increasing fish

Table I. Parameter values used in the estimations of the daily rations and for the adjustments of the stomach contents*.

Prey category	A_i	Intercept	Slope	Experimental food species
Vinciguerria nimbaria *Cubiceps pauciradiatus* Mesopelagic fish Epipelagic fish Undetermined fish	2.24	0.727	–0.0693	mackerel
Scombridae	5.29	0.856	–0.1182	nehu
Cephalopods	4.48	0.847	–0.0800	squid
Crustacea Other prey	3.77	0.805	–0.0859	mean of mackerel, squid, smelt, nehu

* Intercepts and slopes are the linear regression parameters of the proportion of food remaining as a function of time (*h*) passed since feeding; from Olson and Boggs (1986).

sizes (from 2.42 % to 0.47 %). Such a tendency was not found for yellowfin tuna caught under FADs.

Figure 3 displays the results of the correspondence analysis performed on the individual stomachs of the small-size tuna and their prey items. The first two axes explain 40 % of the inertia (first axis 22 %, second axis 18 %). The observed pattern shows that the second axis distinguishes tuna caught under FADs from unassociated tuna. Thus, the diet in the study area appears to be similar for all small-size tuna from the same aggregation type. *Vinciguerria nimbaria* and crustaceans are characteristic prey of unassociated tuna, whereas the intake of epipelagic fish and undetermined fish characterizes FAD-associated tuna. Afterwards all individual stomachs were grouped by tuna predator. *Figure 4* displays the mass proportions of each prey item. Fish, including undetermined fish species, were the main prey. Small-size tuna (smaller than 90 cm) mainly fed on *Vinciguerria nimbaria*, supplemented with cephalopods for tuna caught under FADs. Their diet showed a greater variability than for small tuna caught in unassociated schools. *Cubiceps pauciradiatus* and Scombridae formed the most important prey for large-size yellowfin tuna of unassociated schools (though with 65 % undetermined fish species), whereas large yellowfin under FADs almost exclusively fed on Scombridae (frigate tuna and skipjack). When samples coming from the same set of unassociated tuna schools were analysed together, we observed a high homogeneity in the prey and in the indices of digestion (degree of digestion). Under FADs, stomach contents rarely contained the same category of prey with the same degree of digestion, and for a given school, empty stomachs and more or less full stomachs were observed simultaneously.

Daily rations were estimated to be approximately 1.17 % of the body mass for the small-size tuna caught under FADs, and the ration was about 6.12 % for the small tuna caught in unassociated schools (*table IV*).

Table II. Number of tuna stomachs (N) sampled in the South Sherbro area and percentages of empty stomachs.

		FADs	Unassociated schools
Yellowfin	N	69	36
	% empty	65.2	16.7
Skipjack	N	333	115
	% empty	91	27
Bigeye	N	191	32
	% empty	82.7	25
Total	N	593	183
	% empty	85.3	24.6

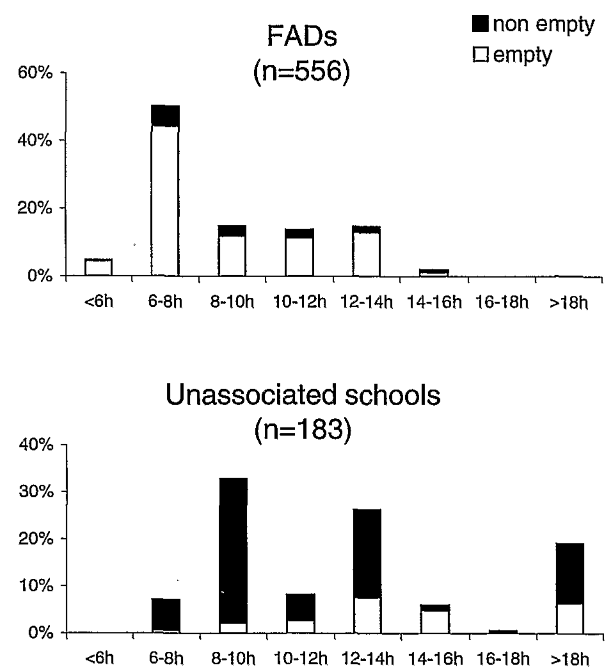

Figure 2. Tuna stomach samples versus time of the day with the proportion of empty stomachs.

Table III. Observed and adjusted stomach contents (% of body mass) and body mass (g) of tuna from which stomach samples were taken in the South Sherbro area.

		Body mass (g)			Observed Stomach contents			Adjusted stomach contents		
		Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
FADs	skj	790	8 224	2 046	0	7.82	0.19	0	9.68	0.23
	bet	796	11 530	3 142	0	6.86	0.22	0	8.30	0.27
	yft < 90 cm	812	12 735	3 137	0	2.97	0.13	0	3.68	0.16
	yft > 90 cm	15 040	81 003	46 167	0	4.66	0.85	0	5.32	0.98
Unassociated schools	skj	850	15 220	2 852	0	6.04	1.12	0	7.51	1.36
	bet	1 101	8 119	2 772	0	3.20	0.57	0	3.98	0.70
	yft < 90 cm	1 564	2 753	2 266	0	4.04	1.96	0	5.00	2.42
	yft > 90 cm	30 365	90 262	59 186	0	1.67	0.39	0	2.05	0.47

skj: skipjack; *bet*: Bigeye; *yft*: yellowfin tuna.

The latter estimation included the high value of 16.03 % computed for yellowfin tuna with a size smaller than 90 cm, that was probably overestimated because of the lack of samples for this tuna category (*table II*). Nevertheless, the daily ration was about five times higher than the one computed for small tuna under FADs. *Figure 5* displays the mass proportions of adjusted stomach contents and of daily food intake, for the small-size tuna grouped by aggregation type. For large yellowfin tuna, the ration was slightly greater under FADs (3.04 %) than in unassociated schools (2.59 %).

4. DISCUSSION

Vinciguerria nimbaria is a major chain in the local food web of the South Sherbro area, as was previously suggested by Roger and Marchal (1994). This mesopelagic fish of the micronekton has already been reported to be the most important forage item of skipjack and yellowfin tuna (Alverson, 1963; Legand et al., 1972; Dragovich and Potthof, 1972; Kornilova, 1981; Borodulina, 1982), but also of Bryde's whales (Kawamura and Hamaoka, 1981), and of spinner porpoise *Stenella longirostris* (Perrin et al., 1973). In the South Sherbro area, *V. nimbaria* represented 63 % of the daily food intake of the small tuna caught in unassociated schools, and 49 % for the small tuna under FADs (*figure 5*). Because tuna are generally considered to be opportunistic feeders, *V. nimbaria* must be abundant and accessible to tuna. This fish is often seen as a typical mesopelagic species, diving to depths of 500 m or more during the day, and migrating to the 0–90 m layer at night. Marchal and Lebourges

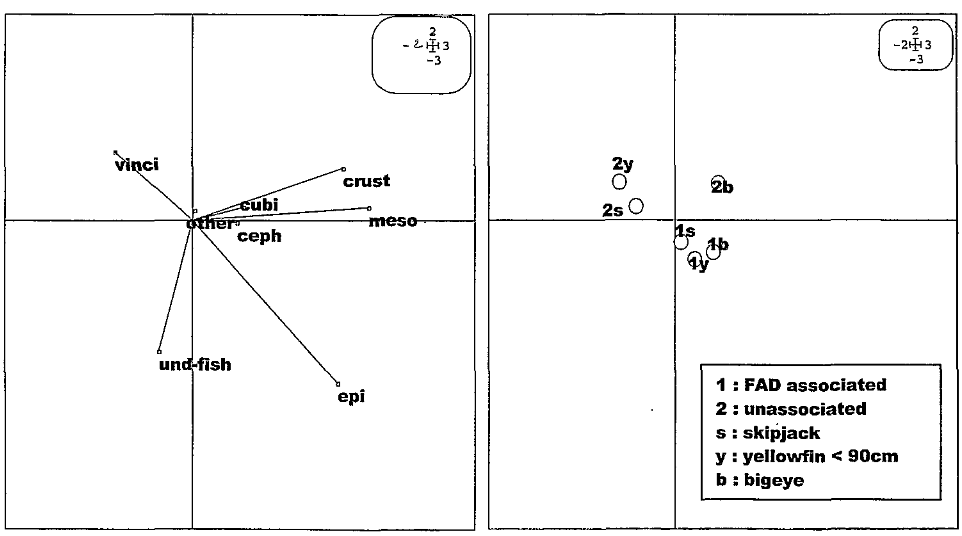

Figure 3. Correspondence analysis: projections on the factorial plane (two first axis with 22 and 18 % of the inertia, respectively) of the eight prey items and of the gravity centers of the six categories of small-size tuna predators; *vinci*: *Vinciguerria nimbaria*; *cubi*: *Cubiceps pauciradiatus*; *meso*: Mesopelagic fish; *epi*: Epipelagic fish; *und-fish*: Undetermined fish; *crust*: Crustacean; *ceph*: Cephalopod; *other*: other prey.

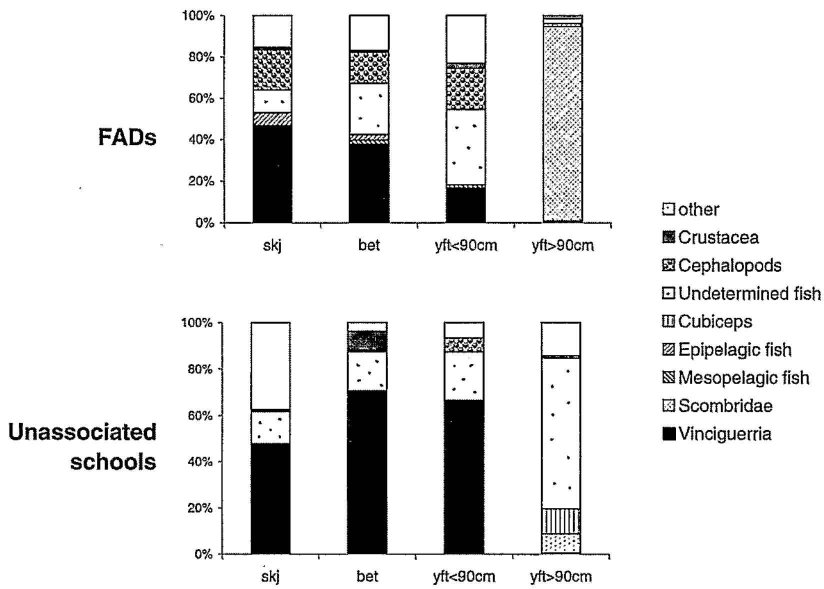

Figure 4. Mass proportions of prey found in skipjack (SKJ), bigeye (BET), yellowfin (YFT) stomachs, sampled in the South Sherbro area.

(1996) reported that the adult population of *V. nimbaria* have a peculiar diel behavior in the South Sherbro area, concentrating in mono-specific dense schools in the upper layers during the day where they become available to tuna predation. At night, they concentrate at or below the thermocline (80 m) mixed with other fish, squids and crustaceans. Lebourges-Dhaussy et al. (2000) showed that schools of *V. nimbaria* remained at the surface by day when a stable hydrological situation occurred with a well-mixed surface layer and a strong Deep Chlorophyll Maximum. *V. nimbaria* has a short life span (six to seven months) and a maximum standard length of 55 mm; instantaneous biomass was estimated by acoustic data to be around the megaton (unpublished data). This biomass, consisting of nearly-adult fish, renewed during the fishing period, must sustain the high concentrations of small tuna. The explanation for the peculiar behavior of the adults may be found in their feeding activity (Lebourges-Dhaussy et al., 2000).

The tuna purse seine fishery operates only during daylight hours. We therefore did not dispose of all the samples needed for covering a full diel cycle. However the feeding of surface tuna that are visual predators, takes place mainly during the daylight hours (Schaefer et al., 1963; Legand et al., 1972; Ortega-Garcia et al., 1992; Roger, 1994; Maldeniya, 1996), and very little (or not at all) at night for small-size surface tuna. Large bigeye and yellowfin tuna have been observed to feed during the night (Josse et al., 1998). Still, they are probably more active feeders during the daytime than at night (Kobayashi and Yamaguchi, 1971). In the Indian Ocean, Roger (1994) found that all the stomachs sampled from sets under FADs before sunrise were empty. Our results suggest that almost all the tuna caught by the purse seine fishers early in the morning have not fed yet, or have fed recently around dawn. In a great number of stomachs *V. nimbaria* very often seemed the only prey found, clearly showing that small tuna fed on this fish while schooling. Such

Table IV. Daily food intake (g) and daily rations (%) of tuna with respect to aggregation mode, species and size; *skj*: skipjack; *bet*: Bigeye, *yft*: yellowfin tuna.

		Daily food intake (g)	Daily ration (%)
FADs	skj	23.6	1.16
	bet	39.8	1.27
	yft < 90 cm	27.8	0.89
	yft > 90 cm	1 404.3	3.04
Unassociated schools	skj	157.1	5.51
	bet	133.6	4.82
	yft < 90 cm	363.2	16.03
	yft > 90 cm	1 530.9	2.59
FADs < 90 cm		29.3	1.17
Unassociated schools < 90 cm		170.5	6.12

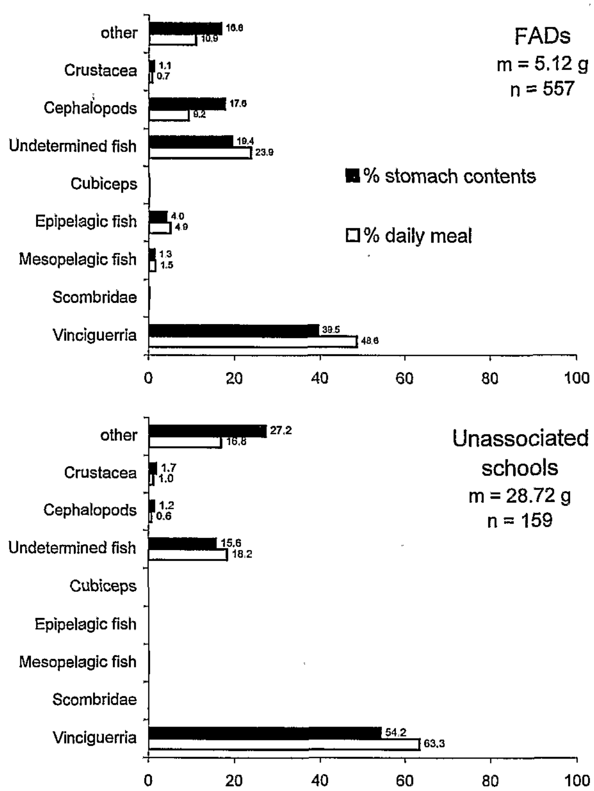

Figure 5. Mass proportions of adjusted stomach contents and of daily food intake, for the small-size tuna (skipjack, yellowfin, bigeye) of both aggregation types sampled in the South Sherbro area; *m*: mean weight (*g*) of the adjusted stomach contents; *n*: number of samples.

schools of *V. nimbaria* were only observed at the surface during daylight, whereas *V. nimbaria* was mixed in the upper layers at night together with other fish, squids and crustaceans coming from deeper layers. However, acoustic observations showed that they also concentrated in wide loose aggregations at night, most of the time inside or just below the layer. It is thus difficult to know whether they are mixed or not with other species. Another point is the role of the photophores, that fish such as *V. nimbaria* have, in the predation process: do they attract predators at night, or do they fight them off, especially when these fish concentrate? Until now, no direct observations have been able to answer this question. The degree of digestion may give some insights but this requires a precise measuring of the time elapsed between the beginning of the fishing operation and the preservation of the stomach. In our analysis, we thus chose a feeding period of 12 h, but we do not want to conclude that none of the tuna feed at night, because this may have been an artefact of the sampling.

Tuna are considered to have high food requirements due to their very high metabolic rates (Olson and Boggs, 1986; Dickson, 1995). However, few studies have undertaken analyses to estimate the food consumption of tuna from data about stomach contents sampled in the field. The order of magnitude of the tuna's food intake in our results is similar to the one estimated by Olson and Boggs (1986) for yellowfin tuna of the Eastern Tropical Pacific Ocean (from 3 to 5 % of the fish's body mass, depending of the size of the fish, but assuming a daily feeding period of 24 hours), and to those computed by Maldeniya (1996) for yellowfin in Sri Lanka waters (from 2.1 to 5.5 %). Such estimates strongly depend on the model chosen for food consumption and gastric evacuation that are similar in these latter approaches. Young et al. (1997), using an exponential rate of gastric evacuation (after Elliott and Persson, 1978 and Boisclair and Marchand, 1993), found an overall estimate of 1 % per day for the southern bluefin tuna (*Thunnus maccoyii*), although these authors indicated that daily ration estimates of farmed fish could reach 7 %. Seven percent of the weight of the fish was also the maximum capacity of the stomach of captive skipjack tuna, (Magnuson, 1969), but during an entire day they ate around 15 % of their body weight.

Assuming that the feeding activity is associated with the amount of food found in the stomach, the proportion of empty stomachs (85 % versus 25 % for unassociated schools) and the low daily ration estimates for the small-size tuna under FADs indicate that these fish do not feed under drifting FADs. Indeed, the biomass of the potential prey under the FADs, available for small-size tuna, is low. The tuna have to leave their FAD during the day and may form free swimming loose schools in order to feed actively on *Vinciguerria nimbaria* (not associated with the FAD). They may come back under floating objects they use as a refuge or meeting point (for review see Fréon and Misund, 1999). The large-size yellowfin tuna caught under FADs mainly feed on Scombridae themselves associated with the FAD and constituting a high biomass available for predation (Yesaki, 1983). It seems that FADs have a refuge function for small tuna, and a trophic function for large tuna, and probably for other associated pelagic species such as billfish and sharks.

References

Albaret, J.J., 1977. La reproduction de l'albacore (*Thunnus albacares*) dans le golfe de Guinée. Cah. Orstom sér. Océanogr. 15, 389–419.

Alverson, F.G., 1963. The food of yellowfin and skipjack tuna in the Eastem Tropical Pacific Ocean. Bull. Inter-Amer. Trop. Tuna Comm. 7, 293–396.

Ariz, J., Delgado, A., Fonteneau, A., Gonzales Costas, F., Pallares, P., 1993. Logs and tuna in the Eastern Tropical Atlantic. A review of present knowledge and uncertainties. ICCAT Coll. Sci.Vol. Pap. 40, 421–446.

Bard, F.X., Capisano, C., 1991. Actualisation des connaissances sur la reproduction de l'albacore (*Thunnus albacares*) en océan Atlantique. ICCAT Coll. Vol. Sci. Pap. 36, 158–181.

Barut, N.C., 1988. Food and feeding habits of yellowfin tuna *Thunnus albacares* (Bonnaterre, 1788), caught by handline around payao in the Moro Gulf. FAO, Indo-Pacific Tuna Development and Management Programme, IPTP/88/WP/18.

Boisclair, D., Marchand, F., 1993. The guts to estimate daily ration. Can. J. Fish. Aquat. Sci. 50 1969-1975.

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

Brock, R.E., 1985. Preliminary study of the feeding habits of pelagic fish around Hawaiian fish aggregating devices, or can fish aggregation devices enhance local fish productivity? Bull. Mar. Sci. 37, 40–49.

Buckley, T.W., Miller, B.S., 1994. Feeding habits of yellowfin tuna associated with fish aggregation devices in American Samoa. Bull. Mar. Sci. 55, 445–459.

Dickson, K.A., 1995. Unique adaptations of the metabolic biochemistry of tuna and billfishes for life in the pelagic environment. Env. Biol. Fish. 42, 65–97.

Dragovich, A., Potthoff, T., 1972. Comparative study of food of skipjack and yellowfin tuna off the coast of west Africa. Fish. Bull. 70, 1087–1110.

Elliott, J.M., Persson, L., 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47, 977–991.

Fréon, P., Misund, O., 1999. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment. Fishing News Books, Blackwell.

Hunter, J.R., Mitchell, C.T., 1967. Association of fishes with flotsam in the offshore waters of Central America. Fish. Bull. 66, 13–29.

Josse, E., Bach, P., Dagorn, L., 1998. Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. Hydrobiologia 371/372, 61–69.

Kawamura, A., Hamaoka, S., 1981. Feeding habits of the Gonostomatid fish, *Vinciguerria nimbaria* collected from the stomach of Bryde's whales in the Southern North Pacific. Bull. Plankton Soc. Jap. 28, 141–151.

Kobayashi, H., Yamaguchi, Y., 1971. Feeding ecology and hooking tendency of tuna and marlins in the Eastern Equatorial Pacific. Bull. Jpn. 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.

Lebourges-Dhaussy, A., Marchal, E., Menkès, C., Champalbert, G., Biessy, B., 2000. *Vinciguerria nimbaria* (micronekton), environment and tuna: their relationships in the Eastern Tropical Atlantic (ETA area). Oceanol. Acta 23, 515–528.

Legand, M., Bourret, P., Fourmanoir, P., Grandperrin, R., Guérédrat, J.A., Michel, A., Rancurel, P., Repelin, R., Roger, C., 1972. Relations trophiques et distributions verticales en milieu pélagique dans l'océan Pacifique intertropical. Cah. Orstom sér. Océanogr. 10, 303–393.

Magnuson, J.J., 1969. Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Trans. Am. Fish. Soc. 98, 379–392.

Maldeniya, R., 1996. Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. Env. Biol. Fish. 47, 101–107.

Marchal, E., Lebourges, A., 1996. Acoustic evidence for unusual diel behaviour of mesopelagic fish (*Vinciguerria nimbaria*) exploited by tuna. ICES J. Mar. Sci. 53, 443–447.

Ménard, F., Hervé, A., Fonteneau, A., 1999. An area of high seasonal concentrations of tuna: 2-4° N 10-20° W. The site of the PICOLO programme. In: Beckett J. (Ed.) Proc. ICCAT Tuna Symp. Part 1, 405-420.

Ménard, F., Fonteneau, A., Gaertner, D., Nordstrom, V., Stéquert, B., Marchal, E., 2000. Exploitation of small tuna by a purse seine fishery with fish aggregating devices and their feeding ecology in an Eastern Tropical Atlantic ecosystem. ICES J. Mar. Sci. 57, 525–530.

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.

Olson, R.J., Mullen, A.J., 1986. Recent developments for making gastric evacuation and daily ration determinations. Env. Biol. Fish. 16, 183–191.

Ortega-Garcia, S., Galvan-Mangana, F., Arvizu-Martinez, J., 1992. Activity of the Mexican purse seine fleet and the feeding habits of yellowfin tuna. Cienc. Mar. 18, 139–149.

Perrin, W.F., Warner, R.R., Fiscus, C.H., Holts, D.B., 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull. 71, 1077–1092.

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

Roger, C., Marchal, E., 1994. Mise en évidence de conditions favorisant l'abondance des albacores, *Thunnus albacares*, et des listaos, *Katsuwonus pelamis*, dans l'Atlantique Equatorial Est. ICCAT Coll. Vol. Sci. Pap. 32, 237–248.

Schaefer, M.B., Broadhead, G.C., Orange, C.J., 1963. Synopsis on the biology of yellowfin tuna *Thunnus* (*Neothunnus*) *albacares* (Bonnaterre) 1788 (Pacific Ocean). FAO Fish. Rep. 6, 538–561.

Yesaki, M., 1983. Observations on the biology of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tuna in the Philippine waters. FAO, Indo-Pacific Tuna Development and Management Programme, IPTP/83/WP/7.

Young, J.W., Lamb, T.D., Le, D., Bradford, R.W., Whitelaw, A.W., 1997. Feeding ecology and interannual variations in the diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. Env. Biol. Fish. 50, 275–291.