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Do drifting and anchored Fish Aggregating Devices (FADs) similarly influence tuna feeding habits? A case study from the western Indian Ocean

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ABSTRACT

Anchored and drifting Fish Aggregating Devices (FADs) are intensively used in tropical tuna fisheries. In both small-scale and industrial fisheries, skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) are the main targets. The increasing development of this fishing practice by industrial purse seiners has raised the question of the impact of FADs on tuna communities, as they might act as an ecological trap. This study investigated the feeding habits of skipjack and yellowfin tuna associated with anchored and drifting FADs in the western Indian Ocean. The diet of 352 tunas was analysed taking into account the type of FAD, ontogenetic variations, and the resources richness of the area. Poor-food and rich-food areas were defined according to the abundance of stomatopod *Natosquilla investigatoris*, the main prey of tunas, on the fishing sites. Diet composition was expressed through functional groups of prey. Significant dietary differences were found between both FAD types, as well as an effect of individual size. Around anchored FADs tuna preyed on diverse assemblages of coastal fish and crustacean larvae and juveniles, whereas a low diversity of epipelagic prey dominated the tuna diet associated with drifting FAD. Compared to anchored FADs, the frequency of empty stomachs was significantly higher and the stomach content mass significantly lower among skipjack and small yellowfin tunas caught around drifting FADs. This was magnified in poor-food areas, where drifting FADs often evolved, suggesting that these FADs could negatively impact the growth of skipjack and small yellowfin tuna. Larger yellowfin tuna exhibited differences in their dietary habits between anchored and drifting FADs, and between poor-food and rich-food areas. However, drifting FADs did not impact them as strongly as juveniles of yellowfin or skipjack tunas. Our study gives new highlights on possible detrimental effects of FAD on tunas, and this has to be considered in future sustainable management strategies of tuna fisheries.

1. Introduction

Fish naturally associate with floating objects in almost all oceans in the world (Fréon and Dagorn, 2000; Castro et al., 2002). This aggregating behaviour is used in small-scale and industrial tuna fisheries so as to concentrate fish around man-made Fish Aggregating Devices (FADs), and then so increase the catches. Among fish, tropical tunas such as skipjack (*Katsuwonus pelamis*) and yellowfin tunas (*Thunnus albacares*) frequently associate with floating objects at the surface of the oceans (Gooding and Magnuson, 1967; Fontenau et al., 2000). As a consequence, since the early 1990's, drifting FADs are used in the open ocean and anchored FADs in inshore local tropical fisheries; these devices play an important role in all tropical and sub-tropical tuna fisheries nowadays (Fonteneau, 2000; IATTC, 2002). In the western Indian Ocean, anchored FADs are used in small-scale fisheries, and sets around drifting FADs are a common practice for the industrial purse seine fishery (Tessier et al., 2000).

The reason why fish aggregate so frequently with FADs at the surface of the ocean is still poorly understood. Six main hypotheses have been stated: sheltering, seamark in the ocean, meeting point, resting, feeding, and indication of area of high production (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Dagorn et al., 2000; Fréon and Dagorn, 2000; Castro et al., 2002). In addition, several authors suggested that tunas might be trapped around man-made FADs (Marsac et al., 2000), which could lead to an inappropriate habitat selection, and have detrimental effects on their short-term health (Hallier and Gaertner, 2008). According to the ecological trap hypothesis, man-made FADs could drift to non-productive areas and then reduce the feeding activities of associated tunas, which would negatively impact the dynamics of the populations. In the actual context of overfishing and rapid deple-

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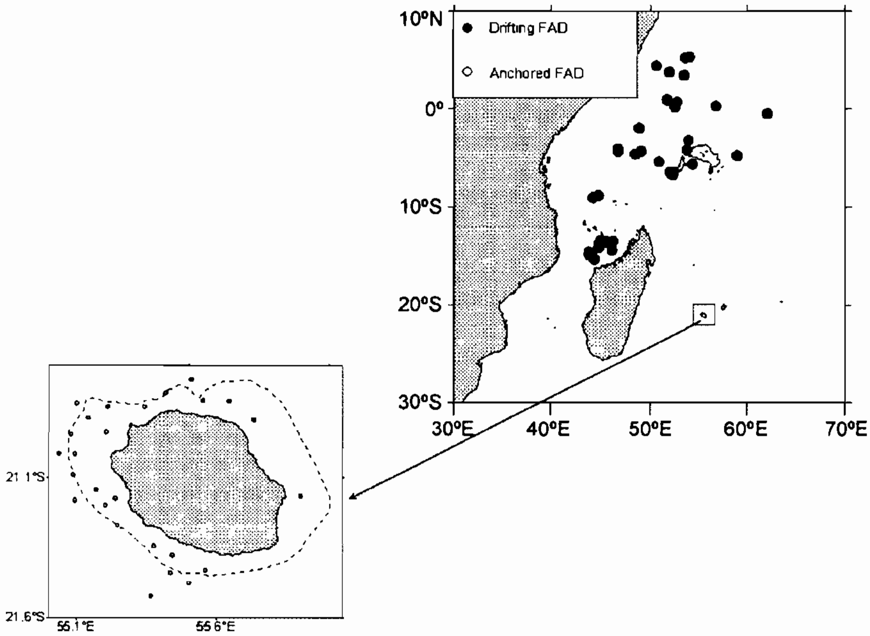

Fig. 1. Locations of drifting and anchored FADs sampled during the study.

tion of predatory fish communities worldwide (Myers and Worm, 2003), it is crucial to improve our understanding of the impacts of fishing activities, including the deployment of thousands of FADs in the oceans, on fish communities.

Studies on the diet of fish aggregated around FADs remain scarce. Food habits of FAD-associated tunas have been mainly investigated for yellowfin tunas (*T. albacares*) in the Pacific Ocean (Brock, 1985; Barut, 1988; Lehodey, 1990; Buckley and Miller, 1994; Grubbs et al., 2002; Graham et al., 2006), and in the Atlantic Ocean (Ménard et al., 2000a, 2000b). Results differ between studies of the different regions and this is mostly due to the opportunistic feeding behaviour of tunas (Ménard et al., 2006). Then additional studies have to be conducted to take into account regional specificities in stock management. Brock (1985) showed that FAD-associated tunas in Hawaii were less well-fed than their non-FAD relatives that can feed on deep-water shrimps to compensate for the decrease of usual prey. Recently Graham et al. (2006) showed that FAD-associated juvenile yellowfin tuna fed on

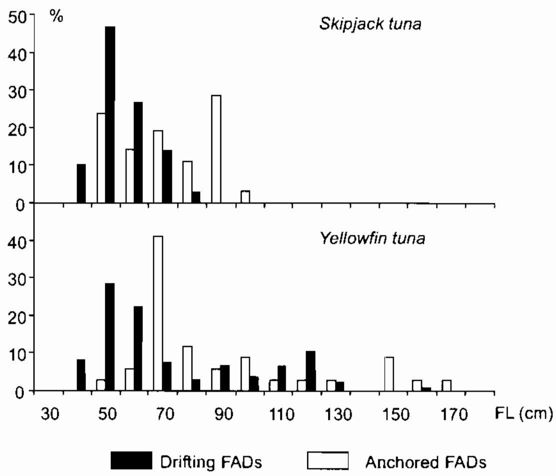

Fig. 2. Size frequencies of the tunas caught around drifting and anchored FADs. FL: fork length.

planktonic organisms inhabiting the shallow mixed layer, primarily stomatopod larvae and decapod crustaceans, whereas larger individuals targeted teleosts and vertically migrating mesopelagic species of shrimps. In French Polynesia FAD-associated yellowfin tuna preyed mostly on reef fish and stomatopod larvae (Lehodey, 1990). In the western Indian Ocean, previous studies have shown that free-swimming schools of surface tunas preyed mainly on epipelagic fish and pelagic crustaceans (Bashmakov et al., 1992; Roger, 1994a; Potier et al., 2004). To our knowledge, no study has been conducted on the feeding habits of tunas found in the vicinity of FADs.

In this study, we analysed the food habits and diet of yellowfin and skipjack tunas caught associated with anchored and drifting FADs in the western Indian Ocean. We aim at providing new insights on the impact of FAD on the feeding behaviour of tunas. For this purpose specific and ontogenetic-related differences in the diet composition by taxonomic and functional groups of prey were compared in tunas caught around drifting and anchored FADs. To highlight the impact of FADs, diet of tunas in free-swimming schools was used as reference of natural and undisturbed conditions.

2. Materials and methods

2.1. Study area and sample collection

The study was carried out in the tropical western Indian Ocean, off the Seychelles archipelago, in the northern Mozambique Channel, and off Reunion Island (Fig. 1). Between 2001 and 2006, 243 stomachs of yellowfin tuna (*T. albacares*) and skipjack tuna (*K. pelamis*) caught in drifting FADs were collected onboard purse seiners operating in the western Indian Ocean. In October 2002, to the north of the Seychelles, stomachs were collected in free-swimming schools (Potier et al., 2004) and around drifting FADs (this study), which were located in a region where large swarms of *Natosquilla investigatoris* were observed. This area was defined as rich-food area for tunas, as *N. investigatoris* made up the bulk of the tuna diet due to its huge availability in the surface layers (Potier et al., 2004). On the opposite, in May 2000 and 2001, tunas associated with drifting FADs were sampled in an area where no potential

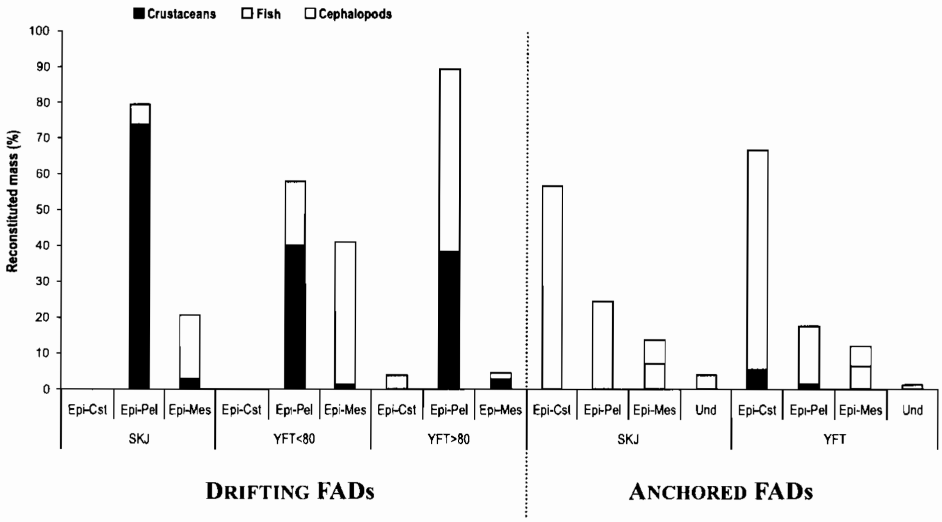

Fig. 3. Composition of the diet by mass of functional group of prey for skipjack and yellowfin tuna by type of FADs. See Section 2 for details.

food (poor-food area) was detected. Between August 2000 and 2006, 109 stomachs of yellowfin and skipjack tunas caught in the anchored FADs' web off Reunion Island were collected onboard game-fish boats. Around both FADs, individuals were caught early in the morning. Anchored FADs were distributed offshore in waters between 250 m and 1500 m in depth. For each fish, the fork length (FL) was measured onboard to the nearest cm. The stomach was stored in individual labelled plastic bags and frozen on board the seiners or conserved in a cool box on board game-fish boats. At the laboratory, all stomachs were kept frozen at −20 °C until further analyses.

2.2. Diet analysis

In laboratory stomach contents were thawed and weighed separately. Prey items were subsequently sorted and weighed individually, and the total number of individuals of each prey was counted. All prey were identified to the lowest possible taxonomic level, using published keys (Smith and Heemstra, 1986; Clarke, 1986; Smale et al., 1995), and comparison with reference specimens and diagnostic hard parts (e.g., otoliths, squid beaks, caudal of fish) of our own collection. On fresh prey, measurements on these diagnostic hard parts allowed us to reconstitute the size and the weight of the digested individuals. The fork (FL) and standard length (SL) of fish, the dorsal mantle length (DML) of cephalopods, and the total (TL) and telson length of crustaceans were measured to the nearest 0.1 mm. The fresh mass of all prey was estimated to the nearest 0.1 g. The sagittal otoliths of fish and the beak of cephalopods were collected. The Otolith Length (OL) and the Lower Rostral Length (LRL) of cephalopod beaks were measured to the nearest 0.01 mm with an optical micrometer and vernier caliper. All prey were then pooled in four functional groups in relation with their depth distribution: Epipelagic – coastal organisms, Epipelagic – pelagic (<200 m), Epipelagic – mesopelagic (200–400 m), Undetermined (http://www.marinespecies.org/).

The importance of each prey in the diet was assessed using the percentage of individuals in number and the frequency of occurrence. The reconstituted weight of the prey was calculated using published (Clarke, 1986; Smale et al., 1995) and our own allometric relationships. A stomach fullness index (SFI) was computed as: SFI = (content weight/(weight of fish − content weight)).

2.3. Data analysis

Yellowfin tunas associated with drifting FADs were separated in two size classes: individuals with Fork Length (FL) less or greater than 80 cm ($YFT_{D<80}$ and $YFT_{D>80}$, respectively). This partition allowed us to take into account age-related behavioural differences among individuals around drifting FADs. Individuals of 80 cm are approximately two years old, and only few individuals are mature at this age (Shung, 1973). In the Indian Ocean, the growth rate of the yellowfin tuna is maximal for this size (Marsac and Lablache, 1985). In general, small individuals are associated with skipjack tuna (SKJ_D) in mixed-schools near the surface. Large individuals often form monospecific schools or loose aggregations that are usually found deeper in the water column (Marsac et al., 2000; Sakagawa, 2000). Such distinction was not useful for yellowfin collected in anchored FADs (YFT_A), since individuals were always observed solitary or in small groups at the surface and caught with troll lines. The same pattern was observed for the skipjack (SKJ_A).

For a given class of tunas, we used three feeding indices: the frequency of prey occurrence in the stomachs (O), the mean proportion by number (MN) and the mean proportion by reconstituted weight (MRW). MN and MRW were calculated by taking the proportions of each prey species (or category) found in individual stomachs and then by calculating the average of proportions found

Table 1
Main characteristics of the study fish by species and type of FAD. Letters indicate significant differences ($p < 0.05$) by lines for the tested parameters between categories of fish. ISF: index of stomach fullness (see Section 2 for details).

	Skipjack tuna			Yellowfin tuna			
	Anchored	Drifting	Total	Anchored	Drifting FL < 80 cm	Drifting FL >80 cm	Total
Number of individuals	66	109	175	43	93	41	177
Mean length of fish (cm)	66.8 ± 15.3^{a}	50.4 ± 9.5^{b}	56.4 ± 14.3	87.5 ± 31.1^{c}	51.5 ± 9.7^{b}	105.7 ± 15.4^{d}	72.8 ± 29.6
Number of empty stomachs (%)	15.2	74.3	52.0	7.0	47.3	18.6	19.8
Mean mass of contents (g)	52.7 ± 94.5^{a}	$36.8 \pm 47.0^{a,b}$	47.4 ± 81.8	61.0 ± 97.7^{a}	53.6 ± 145.9^{b}	62.7 ± 93.1^{a}	57.8 ± 121.0
ISF	$0.57 \pm 0.76^{a,b}$	0.82 ± 0.80^{a}	0.65 ± 0.78	0.33 ± 0.30^{b}	0.54 ± 0.80^{b}	0.33 ± 0.48^{b}	0.44 ± 0.64

in all the stomachs. We thus treated individual fish as the sampling unit, allowing us to compute standard deviation.

The diet overlap between two fish categories was assessed using the Morisita-Horn index (see Potier et al., 2007b). Bootstrapping techniques based on 500 replications allowed us to estimate 95% confidence intervals for the overlap indices. A principal component analysis based on the occurrence of prey was performed in order to find which groups of prey structured the diet of the different predators. Computations were performed using R and the ade4 package.

3. Results

We analysed the stomach contents of 175 skipjack and 177 yellowfin tuna caught around FADs. Skipjack and yellowfin tuna caught associated with anchored FADs ranged from 41 to 96 cm (median 69 cm) and from 49 to 170 cm (median 70 cm) in fork length, respectively (Table 1, Fig. 2). Around drifting FADs, skipjack ranged from 31 to 74 cm (median 48 cm) and yellowfin tuna from 35 to 160 cm (median 58 cm). The size of the individuals collected associated with anchored FAD was significantly larger than with drifting FAD (Mann–Whitney: $U = 44.3$, $p < 0.01$ for skipjack; $U = 8.07$, $p < 0.01$ for yellowfin tuna). For the same type of FAD, skipjack were always smaller than yellowfin tunas (Mann–Whitney: $U = 6.93$, $p = 0.01$ for anchored FAD; $U = 23.06$, $p < 0.01$ for drifting FAD).

Around drifting FADs, the proportion of individuals with empty stomach was 3–5 times higher than around anchored FADs (Table 1). Indeed, around drifting FADs, almost 75% of skipjack and 48% of small yellowfin tunas (<80 cm) had empty stomachs. For large yellowfin tunas (>80 cm) associated with drifting FADs and individuals of the two species collected around anchored FADs, the percentage of empty stomachs was much lower (<20%). The fresh weight of non-empty stomachs displayed the same trend than for the size of the individuals with a mean weight of contents significantly lighter for skipjack compared to yellowfin tunas, and for individuals caught around drifting FADs (Table 1).

3.1. Diet composition

The food of skipjack and yellowfin tuna included a wide variety of organisms representing more than 40 families. Fish, cephalopods, and crustaceans were the three most important prey categories by mass, number, and frequency of occurrence. Other items were scarce (<1%) and include pteropods, plants, and one seabird fragment (feathers). A detailed list of the food items is presented by type of FAD and by tuna species (Appendix A). Overall, the difference in the diet composition was higher between the same tuna species caught around different FADs than between the two species caught around the same type of FAD (Mann–Whitney test $p < 0.05$, Fig. 3, Appendix A). Main differences were in the percentage of occurrence of the dominant prey items. The diversity of prey was higher around anchored FADs, and dominant functional groups of prey differ between types of FADs. The mass of coastal organisms in the diet was higher for tunas caught around anchored FADs, with a dominance of coastal fish, while epipelagic species were the main prey associated with drifting FADs (Fig. 3). Around drifting FADs the contribution of epipelagic fish changed with the tuna species and the size of the individuals, and is inversely correlated with epipelagic crustacean biomass. For skipjack tunas, the mantis shrimp *N. investigatoris* dominated the diet while fish were secondary prey items. This dominance of *N. investigatoris* declined between skipjack and yellowfin tunas and with the size in yellowfin tuna, while the contribution of epipelagic fish increased (Fig. 3). Epipelagic–mesopelagic organisms did not contributed strongly to the diet by mass, excepted cephalopods in the diet of skipjack and small yellowfin tunas around drifting FADs (Fig. 3).

3.2. Feeding overlap

For each pair of fish, Morisita-Horn indexes calculated on the number of prey and on the reconstituted weight showed similar patterns (Table 2). The standard deviation estimated by bootstrap confirmed that tunas collected associated with drifting FADs or with anchored FADs formed two distinct groups. By number, feeding overlap was significant between skipjack and small yellowfin (FL < 80 cm) caught around drifting FADs (0.64 ± 0.10). Feeding overlap was nearly significant for the following pairs: $YFT_{D>80}$–$YFT_{D<80}$; $YFT_{D>80}$–SKJ_D. By mass, feeding overlap is significant for skipjack and yellowfin tuna around anchored FADs, for skipjack and both small and large yellowfin tuna around drifting FADs and nearly significant for the pair $YFT_{D>80}$–$YFT_{D<80}$.

3.3. Structure of the diet

Results of the principal component analysis (Fig. 4) confirmed the differences observed between the diet of tunas caught associated with drifting and anchored FADs. The first axis (45% of the explained variance) is strongly structured around the type of FADs. Axis 2 (21% of the explained variance) is structured around the size of the predator. Nevertheless, the group of tunas caught under drifting FADs is not homogeneous. $YFT_{D>80}$ differed from the pair SKJ_D–$YFT_{D<80}$ (Fig. 3). The diet of the pair SKJ_D–$YFT_{D<80}$ is dominated by the stomatopod *N. investigatoris*, the portunid crab *Charybdis smithii*, squids of the ommastrephid family (*S. oualaniensis*, *Ornithoteuthis volatilis*), myctophid fish and fish larvae. Nomeidae (*Cubiceps pauciradiatus*), Onychoteuthidae, Bolitaenidae and to a latter extend molluscs of the pteropod order (*Cavolinia sp.*) structured the diet of large yellowfin tuna ($YFT_{D>80}$).

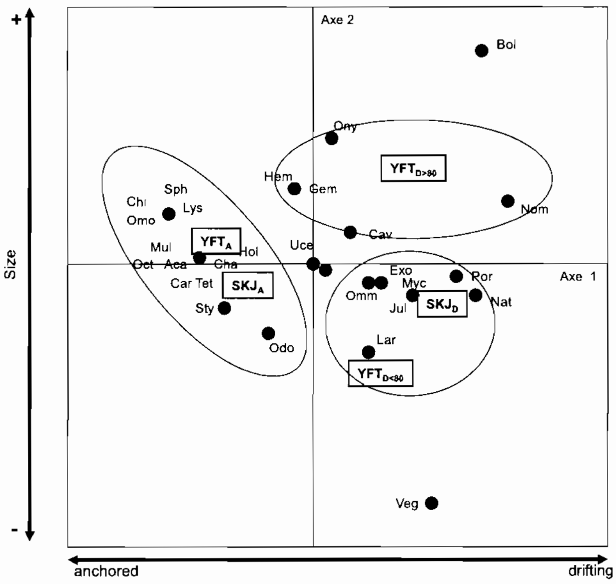

Fig. 4. Results of the principal component analysis carried out on the prey (in number) according to the type of FADs and the tuna species. Bol: *Bolitaenidae*, Car: *Carangidae*, Cav: *Cavoliniidae*, Cha: *Chaetodontidae*, Chi: *Chiasmondotidae*, Exo: *Exocoetidae*, Gem: *Gempylidae*, Hem: *Hemiramphidae*, Hol: *Holocentridae*, Jul: Juveniles of oceanic fish, Lar: Crab larvae, Lys: Lysiosquillidae, Mul: *Mullidae*, Myc: *Myctophidae*, Nat: *Natosquilla investigatoris*, Nom: *Nomeidae*, Oct: *Octopodidae*, Odo: *Odontodactyllidae*, Omm: *Ommastrephidae*, Omo: *Omosudidae*, Ony: *Onychoteuthidae*, Por: *Portunidae*, Sph: *Spyraenidae*, Sty: *Sternopthychidae*, Tet: *Tetraodontidae*, Uce: Unidentified cephalopods.

Table 2
Morisita–Horn's (±SD) overlap index of dietary composition based upon the mean proportion in number (RN) and reconstituted mass (RW) of prey between tuna categories. In bold are indicated significant feeding overlap (i.e. index > 0.6). SKJ: skipjack tuna, YFT: yellowfin tuna, A: anchored Fish Aggregating Devices, D: drifting Fish Aggregating Devices.

		RN				
		SKJ_A	SKJ_D	YFT_A	$YFT_{D<80\,cm}$	$YFT_{D>80\,cm}$
RW	SKJ_A		0.03 ± 0.02	0.47 ± 0.08	0.25 ± 0.08	0.18 ± 0.08
	SKJ_D	0.01 ± 0.01		0.02 ± 0.02	**0.64 ± 0.10**	0.50 ± 0.10
	YFT_A	**0.67 ± 0.16**	0.01 ± 0.01		0.23 ± 0.09	0.15 ± 0.06
	$YFT_{D<80}$	0.03 ± 0.03	**0.69 ± 0.18**	0.24 ± 0.13		0.54 ± 0.07
	$YFT_{D<80}$	0.06 ± 0.06	**0.61 ± 0.23**	0.02 ± 0.01	0.48 ± 0.22	

Skipjack and yellowfin tunas caught around anchored FADs have a diet dominated by stomatopods larvae, juveniles of reef fish (acanthurids, mullids, holocentrids) and mesopelagic fish of the sternopthychid and omosudid families.

3.4. Size of the prey

The size distributions showed that most of the preys were small (Table 3). Around anchored FADs (67.8 ± 21.7 mm), tunas ate larger squids than around drifting FADs (59.1 ± 6.1 mm). However, this difference was not related to the tuna species (Kruskal–Wallis test $H = 6.2$, $p = 0.19$). Whatever the type of FADs, fish of small size (45.5 ± 31.3 mm) dominated the diet of tunas. Large fish (maximum standard length of 400 mm) were eaten sometimes by large yellowfin tunas caught around drifting FADs ($YFT_{D>80}$) and yellowfin tunas associated with anchored FADs. Skipjack and small yellowfin tunas ($YFT_{D<80}$) preyed on fish of the same size range.

The mean size of crustaceans recovered from stomachs collected around drifting FADs increased with the size of the tunas. Tunas caught around anchored FADs fed on smaller crustaceans most of them being stomatopod larvae, and no significant difference was observed in the size of the crustaceans between skipjack and yellowfin tunas.

3.5. Feeding habits under drifting FADs: poor-food versus rich-food areas

The frequency of empty stomachs for tunas associated with drifting FADs was significantly higher in the poor-food area compared to the rich-food area ($\chi^2 = 38.49$, $p < 0.01$). In October 2002, when *N. investigatoris* was abundant, no difference occurred in the frequency of empty stomach between fish caught around drifting FADs or in free-swimming schools ($\chi^2 = 0.27$, $p = 0.61$) (Table 4). The mean stomach fullness index (SFI) exhibited almost the same pattern. In the rich-food area, this index did not differ between yellowfin and skipjack tunas associated with drifting FADs or in free-swimming schools. SFI for tuna caught around FADs in poor-food area were always significantly lower than for tunas caught in rich-food area (Table 4). In October 2002, the number of prey taxa found in the stomach contents was low (1 for skipjack and large yellowfin tuna and 4 for small yellowfin tuna around drifting FADs). The yellowfin and skipjack tunas caught in free-swimming schools had, in average, 3 prey taxa in their stomachs. In May 2000 and 2001, the stomach contents of the individuals had a higher number of prey taxa (12 for skipjack, 23 for small yellowfin tuna and 26 for large yellowfin tuna).

4. Discussion

In the western Indian Ocean, the feeding habits of tunas differ between individuals associated with anchored and drifting FADs. This difference is primarily related to the assemblages of prey available in their foraging habitats. On the one hand, in the vicinity of anchored FADs, a high diversity of coastal fauna is present and dominated by larval and juveniles stages of crustaceans and reef-fish. These results are similar to what Graham et al. (2006) found in Hawaii around near-shore FADs of Oahu, and Lehodey (1990) in French Polynesia. Moreover the frequency of empty stomach is low, indicating that food is few limiting in coastal environment. In the vicinity of anchored FADs, it has already been demonstrated that the associated fauna, dominated by larval and juveniles forms of fish, is more abundant and diversified compared to drifting FADs (IATTC, 1999). On the other hand, around drifting FADs, patterns in the dietary habits are more complex and are related to the prey availability in the vicinity of the devices, and overall, to the productivity of the pelagic waters where FADs and tunas move around. Tunas are supposedly attracted around FADs for several days (Holland et al., 1990). After this period the availability of prey in the vicinity of FADs can be reduced (Brock, 1985), consequently increasing intra- and inter-competition among individuals (Bromhead et al., 2000). In this situation, individual skills to detect prey, including the diving capacities related to the physiology of tunas (Block and Stevens, 2001), play an important role in the feeding success. Food in tropical waters is patchily distributed naturally (Bertrand et al., 2002), and tunas are adapted to such a situation. As a consequence, sets on free-schools of tunas mostly occur in rich-food area (Fonteneau, 1997). The fact that tuna schools are caught around drifting FADs in poor-food area suggests that these devices can trap the tunas in inappropriate feeding zones.

4.1. Regional comparison of feeding habits of tunas under anchored FADs

Coastal epipelagic teleosts dominate the diet of tunas caught under anchored FADs off Reunion Island (84% by reconstituted mass and 74% by number). This high proportion of fish is similar to the one found in the Philippines (Barut, 1988) and in the American Samoa (Buckley and Miller, 1994). In French Polynesia, crustaceans were the main prey and fish were secondary items (Lehodey, 1990). For Hawaii, the patterns were more complex for yellowfin tunas and they seem to be related to the size of the individuals (Graham et al., 2006). Brock (1985) found a dominance of crustaceans as Graham et al. (2006) found for small yellowfin tunas, while larger individuals were piscivores.

Although proportions differ between locations, the nature of the dominant prey species observe in Hawaii, French Polynesia, American Samoa, and in our study is overall similar, with coastal fauna as main prey items. Among fish prey, larval and juveniles' stages of reef-fish of the holocentrid, acanthurid, and balistid families dominate. In addition, in Reunion Island, small pelagic fish (*Decapterus* spp.) and individuals from the carapid family are important prey for large yellowfin tunas, like in American Samoa (Buckley and Miller, 1994). The main crustacean prey are similar in French Polynesia, American Samoa, Hawaii, and Reunion Island, and consist of planktonic larval stomatopods and crab megalopae. These results confirm the opportunistic feeding behaviour of tunas (Ménard et al.,

Table 3
Sizes of the different zoological groups of prey recovered from stomach contents of predators collected around drifting and anchored FADs. Letters indicate significant differences ($p < 0.05$) by lines for the tested size between categories of fish. SL: Standard length, TL: Total length, DML: Dorsal mantle length, SKJ: Skipjack tuna, YFT: Yellowfin tuna.

		Drifting FADs			Anchored FADs	
		SKJ	$YFT_{<80\,cm}$	$YFT_{>80\,cm}$	SKJ	YFT
SL (mm)	Fish					
Min-Max		27.0–32.0	18.0–164.0	30.0–400.0	18.0–181.0	19.0–197.0
Mean ± SD		30.9 ± 1.5^a	42.8 ± 34.6^a	105.8 ± 91.7^b	42.4 ± 20.7^c	49.1 ± 20.7^b
N		32	102	16	216	107
TL (mm)	Crustacean					
Min-Max		33.6–86.6	32.1–85.6	39.0–78.7	18.0–31.6	25.0–35.0
Mean ± SD		45.1 ± 10.6^a	59.6 ± 13.3^b	60.7 ± 9.5^b	25.4 ± 4.2^c	28.9 ± 4.5^c
N		78	225	117	7	44
DML (mm)	Squid					
Min-Max		50.2–65.9	56.0–65.9	46.1–63.5	38.4–77.6	30.5–116.9
Mean ± SD		59.7 ± 5.1	61.7 ± 4.6	56.4 ± 8.0	58.8 ± 11.2	74.8 ± 25.5
N		9	4	6	10	13

2006) that seem to target any abundant group of prey in their foraging habitats.

4.2. Anchored versus drifting FADs in the southwest Indian Ocean

Major differences are observed between functional group and prey species eaten by tunas associated with drifting and anchored FADs. Around drifting FADs, epipelagic crustaceans and fish, and to a lesser extend mesopelagic prey form the bulk of the diet of tunas. For skipjack and small yellowfin tunas, the pelagic stomatopod *N. investigatoris* is the foremost prey species. In 2001 and 2003, very dense and extensive swarms of this stomatopod occurred seasonally in the western Indian Ocean, and this prey has almost become the exclusive prey of free-swimming schools of tunas caught in the region (Potier et al., 2004, 2007a,b). On the contrary, in the 1980's and 1990's, this prey was absent from stomach contents of tunas and micronektonic assemblages (Bashmakov et al., 1992; Roger, 1994a,b). Losse and Merrett (1971) reported recurrent demographic explosions of this stomatopod that can explain its periodic dominance in the tuna diet.

As for individuals caught around anchored FADs, fish form the bulk of the diet of large yellowfin caught around drifting FADs (54.2% and 50.8% by mass and by number, respectively). However, fish prey around drifting FADs are dominated by epipelagic (flying fish) and mesopelagic teleosts, whereas larval stages are scarce. In the western Indian Ocean, the importance of the flying fish has already been observed in the diet of free-swimming schools of tunas (Bashmakov et al., 1992) and in the dolphinfish (*Coryphaena hippurus*) caught around drifting FADs (Taquet, 2004). They are also important prey of oceanic tropical seabirds of the western Indian that exclusively feed in the surface waters (Cherel et al., 2008; Catry et al., 2009). Finally, cannibalism or predation by large individuals on other scombrids is stronger than for small individuals, as observed in the Philippines (Barut, 1988).

The frequency of empty stomachs is high among skipjack and small yellowfin tunas caught around drifting FADs like in the Atlantic Ocean (Ménard et al., 2000a,b). For anchored FADs this percentage is lower and similar to the number of empty stomachs found around the anchored FADs in the French Polynesia (Lehodey, 1990). These differences suggest that tunas are attracted by FADs and that they can remain aggregated for long periods even if there is no food available. Such a result reinforces the idea that FADs might act as a trap for small surface tunas (Marsac et al., 2000; Hallier and Gaertner, 2008).

4.3. Impact of drifting FADs on the feeding habits of tunas in relation to the ocean productivity

Around drifting FADs, according to the species and the size of the individuals, tunas exhibit different feeding behaviours. In productive areas, food is not limiting and tuna diet around drifting FADs does not show major differences with that of free-swimming schools. Main differences are in the fullness of the stomach, which is, overall, higher for yellowfin tunas and positively correlated to the size of the individuals. In poor-food areas, the frequency of empty stomachs and the diet composition reveal that large yellowfin tuna are able to feed suitably, whereas small individuals and skipjack tuna are not so efficient to seek out food. Moreover, the diet of large tunas is similar to the diet of individuals caught in the same area by longline sets in relatively shallow depth (no greater than 185 m) (Potier et al., 2004, 2007a). Then, large yellowfin tunas seem able to shift from a schooling feeding behaviour in rich-food areas (i.e., when they detect, in surface waters, concentrations of favoured prey such as swarms of *N. investigatoris*) to a solitary feeding behaviour in poor-food areas (i.e., when tunas rather hunt individual prey at different depths up to deep waters). Such a result thus supports the hypothesis that large yellowfin tunas are relatively independent from FADs to acquire their food compared to small-sized tunas. This foraging behaviour has already

Table 4
Comparison of the number of empty stomachs, of the fullness of stomach (SFI) and the number of prey taxa between the skipjack, the small and the large sized yellowfin tunas caught around drifting FADs and free-schools in poor-food and rich-food areas (see text for definition). Letters indicate significant differences ($p < 0.05$) by lines for the tested parameters between categories of fish. SKJ: skipjack tuna, YFT: yellowfin tuna.

	Drifting FADs poor-food area			Drifting FADs rich-food area			Free-schools rich-food area		
	SKJ	$YFT_{<80\,cm}$	$YFT_{>80\,cm}$	SKJ	$YFT_{<80\,cm}$	$YFT_{>80\,cm}$	SKJ	$YFT_{<80\,cm}$	$YFT_{>80\,cm}$
Nb stomachs	93	74	35	16	19	6	8	*	3
Nb empty stomachs	80	24	8	1	0	0	0	*	0
Nb non empty stomachs	13	50	27	15	19	6	8	*	3
Frequency of empty stomachs	0.86^a	0.32^a	0.23^a	0.06^b	0^b	0^b	0^b	*	0^b
Stomach fullness index (SFI)	0.7 ± 0.8^a	0.4 ± 0.8^a	0.2 ± 0.2^a	0.9 ± 0.8^b	0.9 ± 0.7^b	1.2 ± 0.5^b	1.4 ± 0.7^b	*	1.2 ± 0.3^b
Mean nb of prey taxa per stomach	12	23	26	1	4	1	3	*	3

been described in Hawaii (Brock, 1985), and is related to the higher diving capacities of large tunas, which can exploit a large part of the ecosystem up to the mesopelagic realm (Block and Stevens, 2001). Small-sized yellowfin tunas and skipjack are physiologically constrained to forage in surface waters (Fonteneau, 2000; Block and Stevens, 2001), and they exhibit a similar feeding pattern when associated with drifting FADs. However the number of empty stomachs for skipjack is higher and the number of prey lower (Table 4). Skipjack and small yellowfin tunas associated with drifting FADs likely compete for food resources. Our results tend to support the hypothesis that small yellowfin tunas were more efficient than skipjack tunas in detecting prey in the vicinity of the FADs launched in poor-food areas. They also reinforce the idea that drifting FADs can impact negatively tunas by trapping them in poor-food area, as suggested by Marsac et al. (2000) and Hallier and Gaertner (2008). In that situation, large yellowfin tunas would have a competitive advantage compared to small individuals and to skipjack tunas, arising from their physiological abilities that allow them to explore deep layers (Block and Stevens, 2001). In poor-food areas, the induced aggregating behaviour of tunas would have different deleterious effects on the short-term health of the individuals according to the species and their size. Drifting FADs would fully act as an ecological trap for skipjack and small-sized yellowfin tunas until they reach maturation, and would have a minor impact on large yellowfin tunas. This result confirms previous observations in the Eastern pacific, which reveal a stronger association of skipjack tunas with FADs compared to yellowfin tunas (Arenas et al., 1999; IATTC, 2000).

5. Conclusion

Anchored and drifting FADs do not act similarly on tunas. Off Reunion, where coastal fauna is abundant, anchored FADs attract tunas, but do not impact individuals negatively. Although this result is in accordance with studies conducted in the Pacific, further investigations in the western Indian Ocean should be conducted like in the Comoros and the Seychelles to confirm our observations. For drifting FADs, the situation is more complex and the impact of FADs seems to be location-dependent, species-dependent and age-dependent. In rich-food areas, FADs have a reduce impact on the feeding pattern of tunas. In poor-food areas, drifting FADs may impact negatively tuna population dynamics by acting on the feeding activities of skipjack and small yellowfin tunas. Especially, for small tunas associated with FADs, the growth rate would be reduced and the natural mortality could increase. In this period of increasing climatic and anthropogenic perturbations on the marine environment, these additional deleterious effects of FADs have to be seriously considered in sustainable management plans and regulation of the fishing activities to reduce the depletion rate of tropical tuna resources.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.fishres.2010.11.011.

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