

Diet of three large pelagic fishes associated with drifting fish aggregating devices (DFADs) in the western equatorial Indian Ocean

M. A. Malone, K. M. Buck, G. Moreno & G. Sancho

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Abstract

Diet of three large pelagic fishes associated with drifting fish aggregating devices (DFADs) in the western equatorial Indian Ocean.— Several species of fish, aggregate around DFADs in marine tropical waters. We captured three predatory species: yellow fin tuna (*Thunnus albacares*), wahoo (*Acanthocybium solandri*) and dolphinfish (*Coryphaena hippurus*) from aggregations under DFADs in the Western Indian Ocean to characterize their diet and determine whether they fed on other DFAD associated organisms. Yellowfin tuna did not feed on DFAD-associated prey, while wahoo and dolphinfish did exploit resources aggregated by the DFADs, though they predominantly fed on other non-associated organisms. Opportunistic feeding on surface swarming stomatopod crustaceans was observed in yellowfin tuna and dolphinfish associated with FADs, but was not observed in wahoo.

Key words: FAD, Yellowfin tuna, Dolphinfish, Wahoo, Stomach contents, Diet.

Resumen

Dieta de tres peces pelágicos de gran tamaño asociados a agregaciones de peces bajo objetos flotantes (DFADs) en el Océano Índico ecuatorial occidental.— Los objetos flotantes congregan distintas especies de peces en aguas tropicales marinas. Se capturaron tres especies depredadoras: atún de aleta amarilla (*Thunnus albacares*), petos (*Acanthocybium solandri*) y llampugas (*Coryphaena hippurus*) en agregaciones bajo objetos flotantes en el Océano Índico occidental, para caracterizar su dieta y determinar si se alimentan de organismos asociados a las DFADs. Los atunes de aleta amarilla no se alimentaron de presas asociadas a objetos flotantes, mientras los petos y llampugas sí explotaron los recursos agregados a estos objetos flotantes, aunque predominantemente se alimentaron de otros organismos no asociados a ellos. En atunes de aleta amarilla y en llampugas asociados a FADs se observó una predación oportunista en la superficie de agrupaciones de crustáceos estomatópodos pero no así en los petos.

Palabras clave: Dispositivos agregadores de peces, Atún de aleta amarilla, Llampuga, Peto, Contenidos estomacales, Dieta.

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Margaret A. Malone, Kelly M. Buck & Gorka Sancho, College of Charleston, Grice Marine Lab., 205 Fort Johnson Road, Charleston, SC 29412, USA.— Gala Moreno, AZTI-Tecnalia, Herrera Kaia, Portualdea z/g, 20110 Pasaia, España (Spain).

Corresponding Author: Gorka Sancho. E-mail: sancho@cofc.edu

Introduction

Floating objects are known to aggregate fishes in tropical oceans. They can be natural or man-made objects, the latter often deployed specifically to act as Fish Aggregating Devices (FADs). Commercial tuna purse seine fisheries in tropical oceans deploy drifting FADs (DFADs) to target schools of tuna that aggregate underneath them. Other species of fish also aggregate under these floating objects, including epipelagic predatory fishes (Taquet et al., 2007). Although there has been an increase in the use of DFADs in tropical tuna fisheries in the past two decades, especially in the Western Indian Ocean (Fonteneau et al., 2004), the mechanisms underlying these floating objects are unknown (Fréon & Dagorn, 2000). Many hypotheses have been suggested to explain why these aggregations form, one of which is the 'concentration of food supply' hypothesis (Fréon and Dagorn, 2000). This hypothesis states that certain pelagic predators aggregate around FADs to feed upon the fauna of smaller fishes that also aggregate under these floating objects (Klima & Wickman, 1971; Fréon & Dagorn, 2000).

The diet of yellowfin tuna has been studied in many regions, including the Western Indian Ocean (Roger, 1994; Ménard et al., 2000; Somvanshi, 2002; Potier et al., 2004; 2007). Yellowfin tuna can be characterized as generalist predators that feed on a wide variety of small prey, including fish larvae, epipelagic and mesopelagic fishes, squid and pelagic crustaceans. Dietary studies of yellowfin tuna associated with anchored FADs generally show no feeding on FAD associated fish communities (Brock, 1985; Buckley & Miller, 1994; Graham et al., 2007). The few studies that analyze the feeding patterns of yellowfin tuna aggregated under DFADs show high percentages of fishes with empty stomachs (Ménard et al., 2000).

The feeding behavior of dolphinfish has also been extensively studied in tropical waters (*i.e.* Oxenford, 1999; Olson & Galvan-Magana, 2002). This epipelagic fish is characterized as a generalist predator that feeds on small epipelagic fishes, fish larvae and pelagic invertebrates. Dolphinfish have been shown to feed on prey associated with *Sargassum* mats (Oxenford, 1999). However, diets of dolphinfish caught under DFADs in Atlantic and Pacific waters were dominated by organisms that do not aggregate under floating objects (Oxenford, 1999; Olson & Galvan-Magana, 2002). Taquet (2004) found that a portion of the diet of dolphinfish under DFADs in the south western Indian Ocean came from prey associated with DFADs (14% when considering number of prey, 27% considering prey weight). Interestingly, juvenile flying gurnards (Dactylopteridae) and flyingfish (Exocoetidae) are a common teleost prey for dolphinfish all around the world (Oxenford, 1999; Olson & Galvan-Magana, 2002; Taquet, 2004).

Dietary studies of wahoo are not as common, but this species is characterized as predominantly piscivorous, consuming larger sized prey than yellowfin tuna and dolphinfish (Manooch & Hogarth, 1983).

This study describes the diet of three pelagic,

predatory species associated with DFADs in the Western Indian Ocean: yellowfin tuna (*Thunnus albacares*), dolphinfish (*Coryphaena hippurus*) and wahoo (*Acanthocybium solandri*), and addresses the 'concentration of food supply' hypothesis for DFADs in this environment.

Material and methods

Data were collected during four offshore cruises around the Seychelles archipelago (0° 01' N to 9° 06' S) that visited multiple DFADs deployed by the French and Spanish tuna purse seine fleets. The four cruises took place in October and February of 2004 and 2005. Fish were sampled for stomach contents from a total of 17 DFADs. Upon arrival at a DFAD, abundance and species composition of fish aggregations associated with the DFADs were visually estimated by divers (Taquet et al., 2007). A total of 32 fish species were identified aggregating with these DFADs, with an average abundance of 2680 fishes per aggregation (Taquet et al., 2007). During early morning and evening hours, fishes were caught by trolling artificial lures in close proximity to the DFADs. Most of the captured fishes were tagged with acoustic tags and released so that residence times around the DFADs could be monitored (Dagorn et al., 2007). Throughout the four cruises wounded yellowfin tuna, dolphinfish and wahoo that were not suitable for tagging because of their unlikely survival after release were sacrificed for stomach content analyses. Fork length measurements were made on deck and whole stomachs were quickly removed and frozen for future analysis.

In the laboratory, preserved stomachs were rinsed and opened, and their contents were removed. Mucous and gastric parasites were set aside and not taken into consideration. Extracted prey were gently blotted with paper towels, counted, weighed (wet weight) and identified down to the lowest possible taxonomic level using a dissecting scope. Dissected stomachs and their contents were fixed in 10% buffered formalin and preserved in 90% ethyl alcohol.

Prey items were grouped into seven categories: FAD-associated fishes (based on diver surveys done on each FAD; Taquet et al., 2007), non-FAD associated fishes (epipelagic and mesopelagic species combined), cephalopoda (squids), stomatopoda (almost exclusively *Natosquilla investigatoris*), crustaceans (non-stomatopod crustaceans, mainly decapod crabs and megalopa larvae), fish larvae (pelagic larvae of benthic and pelagic species), unidentified fishes (unrecognizable, digested fish remains) and other (items not belonging to the previous categories).

Mean stomach fullness was calculated as the weight of the stomach contents expressed as the percentage of the total fish weight, which was estimated using specific weight-length relationships for each species. Empty stomachs were defined as those with a stomach fullness value smaller than 0.01%.

The percent abundance (%N), percent weight (%Wt), and percent frequency (%F) of each prey category were calculated as described by Hyslop (1980). This information was used to calculate an

Table 1. Number of stomachs analyzed, % empty stomachs and stomach fullness (stomach content weight as % of fish body weight). *Natosquilla investigatoris* were regularly observed by divers in October 2004.

Tabla 1. Numero de estómagos analizados, % de estómagos vacíos, y contenido estomacal (peso de los contenidos estomacales expresados como % del peso total del pez). *Natosquilla investigatoris* fueron observados con regularidad por los buceadores en octubre del 2004.

		N	% Empty stomachs	Stomach contents (% body weight)	
				Mean	Max.
Yellowfin	All data	31	16.1	1.05	3.30
	X 04	20	15.0	1.45	3.30
	X 05, II 04, II 05	11	18.2	0.06	0.81
Dolphinfish	All data	83	25.3	0.91	6.60
	X 04	20	10.0	2.36	6.60
	X 05, II 04, II 05	63	30.2	0.45	3.82
Wahoo	All data	32	34.4	0.48	4.38
	X 04	16	31.2	0.49	4.38
	X 05, II 04, II 05	16	37.5	0.48	3.43

index of relative importance (*IRI*) that combines all three diet estimates (Pinkas et al., 1971):

$$IRI = (\%N + \%Wt) * \%F$$

A relative *IRI* (%*IRI*) was also calculated for each food category (*i*) to facilitate comparisons among the existent number (*n*) of food categories (Cortés, 1997):

$$\%IRI_i = 100IRI_i / \sum_{i=1}^n IRI_i$$

Though these previous indices have extensively been used to interpret stomach content data (Hyslop, 1980), mean percent abundance (%MN) and weight (%MWt) of prey items were also calculated, allowing for the calculation of standard errors (Graham et al., 2007). To calculate the mean percent abundances (%MN), the percent abundance (%N) was calculated for each individual stomach by dividing the abundance of each prey taxon by the total number of prey in that stomach. The mean of these values for all samples within each species was calculated by dividing the percent abundance (%N) of all the prey taxa in an individual stomach by the total number of prey items in that stomach. Percent abundance values from individual stomachs were averaged to yield single estimates of mean percent abundance (%MN) and standard error values for each of the three predatory species studied (Graham et al., 2007). This method was also used with prey weights to obtain mean percent weights (%MWt).

When analyzing stomach contents from individual cruises, data from February 2004 and February 2005 were combined due to overall lower captures in this month (*n* = 40 fishes in 2004 and 2005 combined).

Results

We analyzed the stomach contents of 31 yellowfin tuna, 80 dolphinfish, and 32 wahoo-associated DFADs (*n* = 17). Captured yellowfin tuna ranged from 29 to 124 cm in fork length (average = 52.6 cm), dolphinfish from 53 to 110 cm (average = 86.1 cm) and wahoo from 80.0 and 110.0 cm (average = 95.4 cm). Yellowfin tuna had the lowest percentage of empty stomachs (16%), followed by dolphinfish (25%) and wahoo (34%) (table 1). Overall mean stomach fullness values (weight of stomach contents as percentage of total body weight) were 1.45% (yellowfin), 0.91% (dolphinfish) and 0.48% (wahoo) (table 1).

The basic dietary descriptive indices (%N, %Wt and %F) for all three predatory species collected during the four cruises are presented in table 2. Yellowfin tuna exploited pelagic communities not aggregated by the FADs sampled, and no remains of FAD-associated organisms were found in yellowfin stomachs (table 2). Dolphinfish and wahoo did feed on FAD-associated fishes, though this prey category did not dominate either species' diet. Wahoo ingested large fishes associated with FADs (%Wt = 41.15), including tuna (Scombridae) and jacks (Carangidae), but their overall importance, based on %MN and %MWt, in the diet of wahoo does not seem to be as high as cephalopods and non-FAD associated fishes (fig. 1). Dolphinfish stomachs also contained FAD associated fishes, but the FAD associated fishes were not as important a part of their diet as the non-FAD associated fishes, cephalopods and stomatopods (table 2; fig. 1). FAD-associated fishes found in dolphinfish stomachs included triggerfish (Balistidae), mackerel (Scombridae), jacks (Carangidae), seahorses (Syngnathidae) and

Table 2. Percent abundance (%N), percent weight (%Wt), and percent frequency (%F) of prey items found in the three predatory species: yellowfin tuna (*Thunnus albacares*), dolphinfish (*Coryphaena hippurus*) and wahoo (*Acanthocybium solandri*).

Tabla 2. Porcentaje de abundancia (%N), porcentaje de peso (%Wt) y porcentaje de frecuencia (%F) de presas encontradas en las tres especies depredadoras: atunes de aleta amarilla (*Thunnus albacares*), llampugas (*Coryphaena hippurus*) y petos (*Acanthocybium solandri*).

Functional Prey Groups	Yellowfin tuna			Dolphinfish			Wahoo		
	%N	%Wt	%F	%N	%Wt	%F	%N	%Wt	%F
FAD-associated fishes	0.00	0.00	0.00	0.73	1.69	8.75	2.41	41.15	4.88
Non-FAD-associated fishes	0.00	0.00	0.00	2.30	26.65	25.00	10.84	40.46	19.51
Cephalopoda	0.64	0.38	9.68	14.09	10.49	33.75	54.22	7.12	41.46
Stomatopoda	93.51	92.78	58.07	73.17	42.06	15.00	0.00	0.00	0.00
Crustaceans	4.45	6.44	29.03	1.25	3.41	7.50	3.61	0.04	4.88
Larval fishes	0.13	0.02	3.23	4.07	3.50	18.75	1.20	0.03	2.44
Unidentified fishes	1.02	0.39	12.9	4.38	12.2	6.25	24.1	9.52	19.51
Other	0.00	0.00	0.00	0.00	0.00	0.00	3.61	1.68	7.32

barracuda (Sphyraenidae). It should be mentioned that the 'unidentified fishes' category consisted of very digested or partial remains that could not be identified to family level. If all unidentified fishes were to have been FAD-associated fishes, then wahoo (FAD-associated fishes %MN = 17.6; %MWt = 24.1) and dolphinfish (FAD-associated fishes %MN = 19.5; %MWt = 23.2) could be considered to prey on FAD-associated fishes as often as on fishes not associated with FADs. But if all unidentified remains were to be from non-FAD-aggregated species, then wahoo (non FAD-aggregated %MN = 28.9; %MWt = 37.5) and dolphinfish (non FAD-aggregated %MN = 32.6; %MWt = 33.6) would seem to mainly prey on fishes not associated with FADs and cephalopods, leaving FAD-associated fishes as the third most common food item.

When analyzing the stomach content data by cruises, clear seasonal and interannual differences in diets were observed. During the October 2004 cruise, the yellowfin tuna and dolphinfish sampled fed almost exclusively on *Natosquilla investigatoris*, a pelagic swarming Stomatopod crustacean, showing %IRI values of 99.2 and 95.9 respectively (fig. 2). Wahoo did not feed on the stomatopod *Natosquilla investigatoris* at any time, and in October 2004 fed primarily upon cephalopods and non-FAD-associated fishes (fig. 2), with flying fish (Exocetidae) being the most abundant fish prey (62% of all identified fishes). During the three other cruises (October 2005 and February 2004/2005) yellowfin tuna associated with drifting FADs had a more diverse diet, with stomach contents dominated by pelagic crustaceans (amphipods, megalopa larvae and the pelagic portunid crab *Charybdis edwardsi*), with some *Natosquilla investigatoris* found in October

2005 (fig. 2). Dolphinfish diet also showed increased diet diversity in February and October 2005, mainly consuming cephalopods in October 2005, and fishes not associated with FADs during the February cruises. Squid remained a strong component of their diet in the winter and some FAD-associated fishes were found in February samples (%IRI = 4.5; fig. 2). During both October cruises, wahoo predominantly fed on squid, and during February cruises they mainly fed on fishes, though mostly on non FAD-associated species (fig. 2).

The proportion of empty stomachs and fullness estimates did not vary seasonally for wahoo (table 1). Yellowfin tuna and dolphinfish during October 2004, when *N. investigatoris* dominated their diets, showed much lower proportions of empty stomachs and higher stomach fullness values than in other sampling periods (table 1).

Discussion

Yellowfin tuna did not feed on fishes aggregated under DFADs in the Western Indian Ocean. Wahoo did feed on DFAD aggregations, especially during the winter months when their diet was more piscivorous. Dolphinfish also fed on FAD associated fishes, but they were not a sizeable part of their diet.

The diet of yellowfin tuna captured under DFADs in this study was dominated by crustaceans, but also included cephalopods and larval fishes. These results coincide with most previous studies which characterized tuna associated with DFADs as generalist predators of small organisms, not exploiting other species associated with DFADs (Brock, 1985; Buckley & Miller, 1994). Ménard et al. (2000) described how small sized

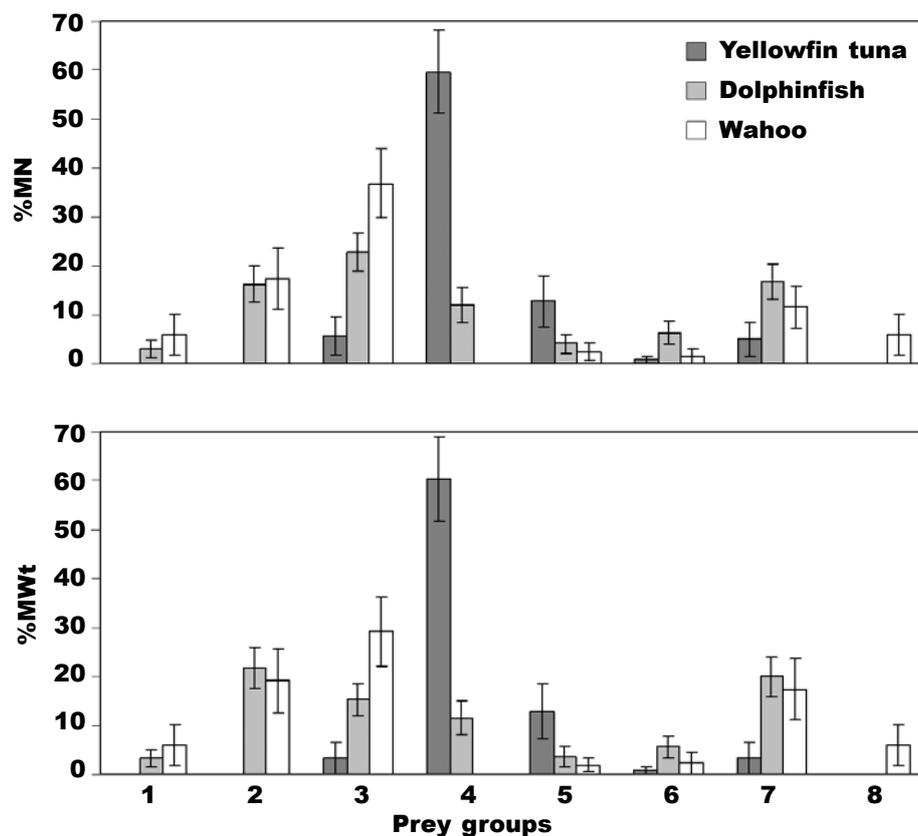


Fig. 1. Relative importance of seven prey groups in the diets of yellowfin tuna (*Thunnus albacares*), dolphinfish (*Coryphaena hippurus*), and wahoo (*Acanthocybium solandri*): A. Mean percent abundance (%MN); B. Mean percent weight (%MWT) \pm SE; 1. FAD-associated fishes; 2. Non-FAD-associated fishes; 3. Cephalopoda; 4. Stomatopoda; 5. Crustaceans; 6. Larval fishes; 7. Unidentified fishes; 8. Other.

Fig. 1. Importancia relativa de siete grupos de presas en las dietas de atunes de aleta amarilla (*Thunnus albacares*), llampugas (*Coryphaena hippurus*) y petos (*Acanthocybium solandri*): A. Porcentaje de abundancia media (%MN); B. Porcentaje de peso medio (%MWT) \pm EE; 1. Peces asociados a las FAD; 2. Peces no asociados a las FAD; 3. Cephalopoda; 4. Stomatopoda; 5. Crustacea; 6. Larvas de peces; 7. Peces no identificados; 8. Otros.

(< 90cm) yellowfin tuna associated with DFADs in the equatorial Atlantic fed on diverse prey not associated with DFADs. However, they observed that large (> 90 cm) yellowfin tuna associated with DFADs fed mainly on small epipelagic fishes, including small scombrids that commonly aggregate under FADs. Similar ontogenetic dietary shifts have also been observed in yellowfin tuna associated with anchored FADs in Hawaii (Graham et al., 2007), with small juvenile fishes (< 50 cm) mainly feeding on crustacean larvae and larger individuals (> 50 cm) feeding on mesopelagic shrimp, reef fish pelagic juveniles and epipelagic fishes. It is unknown whether the ingested epipelagic fishes were associated with the anchored FADs where the tuna were captured (Graham et al., 2007). All the yellowfin tuna analyzed in our study were smaller than 80 cm in fork length (average FL = 52.6 cm), except

for a single large tuna of 124 cm. Therefore we cannot address the possibility of large tuna feeding on small epipelagic fishes aggregated under DFADs in the Indian Ocean, but it is a question that should be addressed in future studies.

Dolphinfish have been described as opportunistic epipelagic predators, feeding both diurnally and nocturnally (Oxenford, 1999; Olson & Galvan-Magana, 2002). Our results agree with this general assessment, showing that dolphinfish mainly fed on squids, non-FAD associated fishes and crustaceans. Dolphinfish diet showed seasonal and interannual shifts, likely due to changes in prey availability in the epipelagic zone. Only during the February cruises, when dolphinfish displayed a mostly piscivorous diet, were FAD-associated fishes found in their stomachs. However, even during these winter cruises, the majority of fishes preyed

on by dolphinfish were epipelagic species not found in association with the FADs where the dolphinfish were captured. Taquet (2004) found dolphinfish in the southern Indian Ocean feeding on FAD-associated fishes at higher rates than we observed in this study. This might be explained by the significant proportion of unidentifiable, digested fishes found in stomach contents in our study. These prey fish could neither be classified as species associated with FADs nor as unassociated species. Another explanation could be related to the different fish communities aggregated under DFADS in both studies (Taquet et al., 2007), Equatorial commercial DFADS harbored much larger and more diverse fish communities, including schools of tuna, than tropical experimental DFADS in the southern Indian Ocean (Taquet, 2004; Taquet et al., 2007).

The diet of Indian Ocean wahoo caught around DFADS was similar to that of wahoo from the Eastern Atlantic and Gulf of Mexico, composed mainly of squid and fishes (Manooch & Hogarth, 1983). In February, wahoo had a piscivorous diet, mostly consuming fish species not aggregated by FADs (mainly flying fish), but also preying on some FAD aggregated fishes. In October, the diet of wahoo was dominated by squids, though fish remains were also recorded (from species both associated and not associated with FADs).

Ménard et al. (2000) found that the proportion of empty stomachs in Atlantic Ocean yellowfin tuna captured by purse seiners under drifting FADs (65%) was higher than in yellowfin tuna captured from free swimming schools (17%). Similarly, combining data from Atlantic and Indian Oceans, Hallier & Gaertner (2008) also found a higher proportion of yellowfin empty stomachs in purse seine caught tuna under FADs (49%) than in free schools (7%). Free swimming tuna captured in the Indian Ocean captured with longlines (Potier et al., 2007) and by trolling (Roger, 1994) also show low proportions of empty stomachs (13% and 8% respectively), indicating a high feeding activity. These results suggest that yellowfin tuna do not feed intensively under drifting FADs. The present study measured a low proportion of empty stomachs (16%), which indicates a higher feeding activity of yellowfin tuna captured by trolling under drifting FADs in the Indian Ocean. Our results were similar to the proportion of empty stomachs in yellowfin tuna captured by trolling around anchored FADs in Hawaii (17%; Graham et al., 2007). We suggest that these differences in empty stomach frequency are not due to ecological differences between different tuna populations, aggregation size or FAD characteristics, but more likely to be the result of the different sampling methods used. It is imaginable that capturing tuna associated with FADs with hook and line selects those individuals that are actively feeding at the time of capture, while purse seining captures all or most of the fishes aggregated under a FAD, independently of their feeding activity. This idea is further supported by the low proportions of empty stomachs found in dolphinfish captured by trolling in this study (25%) and in the Atlantic Ocean (11%; Oxenford, 1999), and the higher proportion of empty stomachs in dolphinfish caught by purse-seining in the Pacific Ocean (58%;

Olson & Galvan-Magana, 2002). Another factor could be the very likely different rates in regurgitation of stomach contents by fishes caught with hook and line and those caught in purse seines (Bowman, 1986). We hypothesize that fish in purse seines experience higher regurgitation rates because of the long time it takes to bring the fish on board. Future studies measuring feeding rates of FAD-associated predators should account for the differential selectivity of different sampling methods used.

In October 2004, yellowfin tuna and dolphinfish caught around DFADS fed intensively and almost exclusively on the pelagic, swarming stomatopod *Natosquilla investigatoris*. High concentrations of swarming *N. investigatoris* were noted by divers in the surface waters of the study area at this time. Little is known about the ecology and behavior of this crustacean in pelagic environments of the western Indian Ocean (Losse & Merret, 1971). Surface blooms of pelagic *N. investigatoris* have been recorded as periodic occurrences and were observed in 1933, 1944, 1965–1967, 1999 and 2000 (Losse & Merret, 1971; Potier et al., 2002; Kamukuru & Mgaya, 2004). In other regions, both yellowfin tuna and dolphinfish also engage in opportunistic feeding of very abundant, small prey (Oxenford, 1999; Ménard et al., 2000). The appearance of *N. investigatoris* swarms commonly results in opportunistic feeding by many shallow water predators (most tuna species, dolphinfish, marlin, swordfish, snapper, lancetfish), and likely has ecological effects on the whole western Indian Ocean (Losse & Merret, 1971; Potier et al., 2004; 2007). The low proportion of empty stomachs and high stomach fullness values measured for yellowfin and dolphinfish associated with DFADS in this study further supports this concept. Opportunistic feeding events like these could play an important role in population fluctuations of predators that exploit them, and they have been linked to increased catches of yellowfin tuna (Fonteneau et al., 2004). Efforts should be made to study the swarming events of *N. investigatoris* in the Indian Ocean.

In October 2005, no *N. investigatoris* were found in dolphinfish stomachs, while some were present in the diet of yellowfin tuna. Due to the epipelagic habits of dolphinfish when compared to yellowfin tuna, which are capable of feeding in deeper layers (Graham et al., 2007), the pattern observed in October 2005 could be explained if *N. investigatoris* were only to be found in deep waters and not swarming at the surface. Interestingly, wahoo did not take advantage of this opportunistic food resource, mainly feeding on squid in October 2004 and October 2005, and showing no seasonal changes in mean stomach fullness and empty stomach frequency. This is most likely due to the preference of wahoo for larger prey (Manooch & Hogarth, 1983). During *N. investigatoris* surface swarming events, interspecific competition between wahoo and other co-occurring epipelagic predatory fishes is greatly reduced.

In conclusion, our data suggest that yellowfin tuna associated to DFADS in the Indian Ocean do not feed on other species aggregated by FADs, as suggested by the 'concentration of food supply' hypothesis. This observation complements other studies of yellowfin

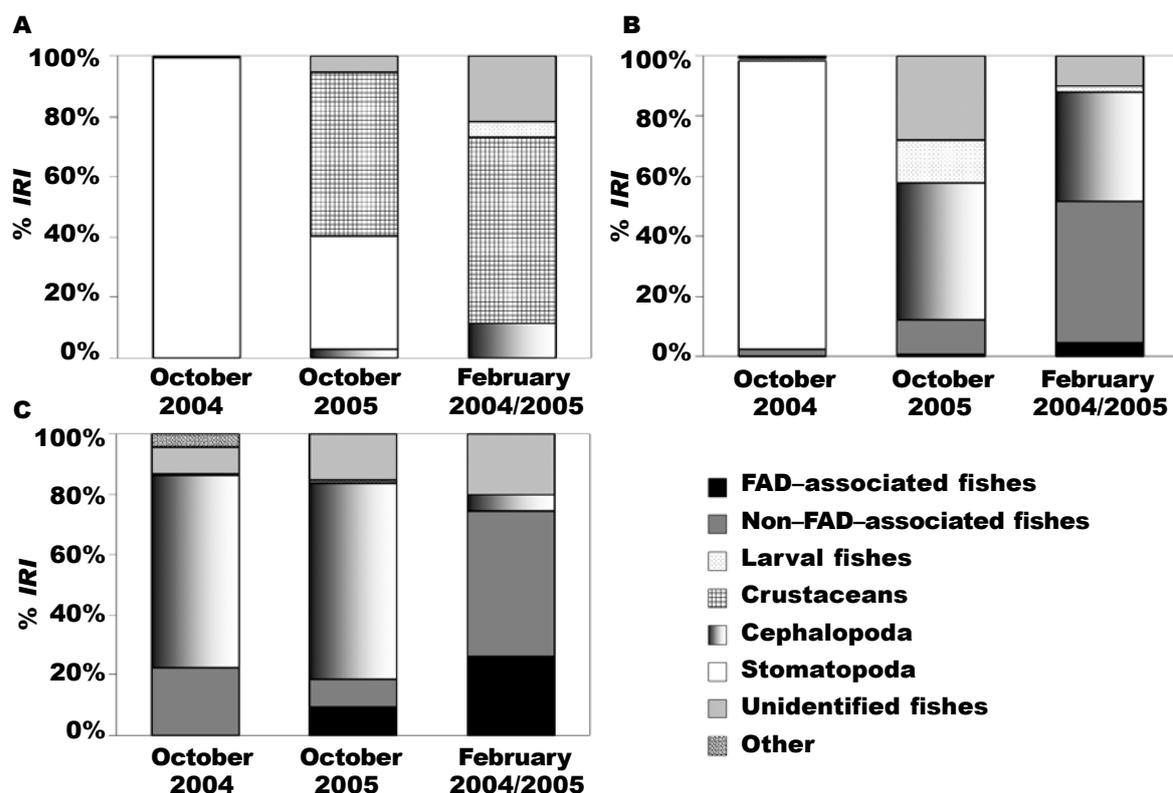


Fig. 2 Index of relative importance (% IRI) for the diets of: A. Yellowfin tuna (*Thunnus albacores*); B. Dolphinfish (*Coryphaena hippurus*); and C. Wahoo (*Acanthocybium solandri*) in October 2004, October 2005, and combined February 2004/2005.

Fig. 2. Índice de importancia relativa (% IRI) para las dietas de: A. Atunes de aleta amarilla (*Thunnus albacores*); B. *Llampugas* (*Coryphaena hippurus*) y C. *Petos* (*Acanthocybium solandri*) en octubre 2004, octubre 2005 y febrero 2004/2005 combinados.

tuna associated with FADs (Brock, 1985; Buckley & Miller, 1994; Graham et al., 2007). Yellowfin showed a relatively low proportion of empty stomachs, similar to studies that captured tuna by hook and line (Graham et al., 2006; Potier et al., 2007), but much lower than the proportion of tuna captured at FADs by purse seining (Ménard et al., 2000; Hallier & Gaertner, 2008). Yellowfin tuna displayed opportunistic intense feeding on *N. investigatoris* when surface swarms were observed in October 2004. Dolphinfishes have been described as opportunistic epipelagic predators, occasionally feeding on prey associated with *sargassum* algae and FADs (i.e. Oxenford, 1999; Olson and Galvan-Magana, 2002; Taquet, 2004). Our results support this idea, since dolphinfish did occasionally feed on FAD associated fishes, but switched diets and fed more intensively when an opportunistic resource (*Natsoquilla investigatoris*) became available. Wahoo seemed to seasonally exploit trophic resources available at FADs in the Indian Ocean, though their diet was always dominated by organisms not aggregated by FADs. This suggests that multiple factors are influencing the

aggregative behavior of dolphinfish and wahoo around FADs, though the concentration of potential prey items might be an important factor in the case of wahoo.

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References

- Bowman, R. E., 1986. Effect of regurgitation on stomach content data of marine fishes. *Environmental Biology of Fishes*, 16: 161–171.
- 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? *Bulletin of Marine Science*, 37: 40–49.
- Buckley, T. W. & Miller B. S., 1994. Feeding habits of yellow-fin tuna associated with fish aggregation devices in American Samoa. *Bulletin of Marine Science*, 55: 445–459.
- Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 726–738.
- Dagorn, L., Pincock, D., Girard, C., Holland, K., Taquet, M., Sancho, G., Itano, D. & Aumeeruddy, R., 2007. Satellite-linked acoustic receivers to observe behavior of fish in remote areas. *Aquatic Living Resources*, 20: 307–312.
- Fonteneau, A., Ariz, J., Hallier, P., Lucas, V., Pallares, P. & Potier, M., 2004. The Indian Ocean yellowfin stock and fisheries in 2003: overview and discussion of the present situation. Document IOTC 2004/WTTP/02: 1–17.
- Fréon, P. & Dagorn, L., 2000. Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. *Reviews of Fish Biology and Fisheries*, 10: 183–207.
- Graham, B. S., Grubbs, D., Holland, K. & Popp, B. N., 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Marine Biology*, 150: 647–658.
- Hallier, J. P. & Gaertner, D., 2008. Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series*, 353: 255–264.
- Hyslop, E. J., 1980. Stomach contents analysis – a review of methods and their application. *Journal of Fish Biology*, 17: 411–429.
- Kamukuru, A. T. & Mgaya, Y. D., 2004. The food and feeding habits of blackspot snapper, *Lutjanus fulviflamma* (Pisces: Lutjanidae) in shallow waters of Mafia Island, Tanzania. *African Journal of Ecology*, 42: 49–58.
- Klima, E. F. & Wickman, D. D., 1971. Attraction of coastal pelagic fishes with artificial structures. *Transactions of the American Fisheries Society*, 1: 86–99.
- Losse, G. F. & Merrett, N. R., 1971. The occurrence of *Oratosquilla investigatoris* (Crustacea: Stomapoda) in the pelagic zone of the Gulf of Aden and the equatorial western Indian Ocean. *Marine Biology*, 10: 244–253.
- Manooch, C. S. & Hogarth, W. T., 1983. Stomach contents and giant trematodes from wahoo, *Acanthocybium solanderi*, collected along the South Atlantic and Gulf coasts of the United States. *Bulletin of Marine Science*, 33: 227–238.
- Ménard, F., Stéquer, B., Rubin, A., Herrera, M. & Marchal, E., 2000. Food consumption of tuna in the Equatorial Atlantic Ocean: FAD-associated versus unassociated schools. *Aquatic Living Resources*, 13: 233–240.
- Olson, R. J. & Galvan-Magana, F., 2002. Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. *Fishery Bulletin*, 100(2): 279–298.
- Oxenford, H. A., 1999. Biology of the dolphinfish (*Coryphaena hippurus*) in the western central Atlantic: a review. *Scientia Marina*, 63: 277–301.
- Pinkas, L., Oliphant, M. S., Iverson I. L. K., 1971. Food habits of albacore, bluefin tuna, and bonito in Californian Waters. *California Fish and Game*, 152: 1–105.
- Potier, M., Lucas, V., Marsac, F., Sabatié, R. & Ménard, F., 2002. On-going research activities on trophic ecology of tuna in equatorial ecosystems of Indian Ocean. *IOTC Proceedings*, 5: 368–374.
- Potier, M., Marsac, F., Cherel, Y., Lucas, V., Sabatié, R., Maury, O. & Ménard, F., 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fisheries Research*, 83: 60–72.
- Potier, M., Marsac, F., Lucas, V., Sabatié, R., Hallier, J. P. & Ménard, F., 2004. Feeding partitioning among tuna taken in surface and mid-water layers: the case of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) in the Western Tropical Indian Ocean. *Western Indian Ocean Journal of Marine Science*, 3: 51–62.
- Roger, C., 1994. Relationships among yellowfin and skipjack tuna, their prey-fish and plankton in the tropical western Indian Ocean. *Fisheries Oceanography*, 3: 133–141.
- Somvanshi, V. S., 2002. Review of biological aspects of yellowfin tuna (*Thunnus albacares*) from the Indian Ocean. *IOTC Proceedings*, 5: 420–426.
- Taquet, M., 2004. Le comportement agrégatif de la dorade coryphène (*Coryphaena hippurus*) autour des objets flottants. Thèse de doctorat de l'Université de Paris 6, Océanologie biologique.
- Taquet, M., Aumeeruddy, R., Sancho, G., Itano, D., Wendling, B., Peignon, C. & Dagorn, L., 2007. Pelagic fish communities around drifting FADs in the Indian Ocean. *Aquatic Living Resources*, 20: 331–341.