Feeding ecology of silky sharks *Carcharhinus falciformis* associated with floating objects in the western Indian Ocean

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The silky shark *Carcharhinus falciformis* is commonly associated with floating objects, including fish aggregating devices (FADs), in the Indian Ocean. While the motives for this associative behaviour are unclear, it does make them vulnerable to capture in the tuna purse seine fishery that makes extensive use of FADs. Here, the diet of 323 *C. falciformis*, caught at FADs in the Indian Ocean, was investigated to test the hypothesis that trophic benefits explain the associative behaviour. A high proportion of stomachs with fresh contents (57%) suggested that extensive feeding activity occurred while associated with FADs. Multiple dietary indices showed that typical non-associative prey types dominated, but were supplemented with fishes typically found at FADs. While the trophic benefits of FAD association may be substantial, our results suggest that associative behaviour is not driven solely by feeding.

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INTRODUCTION

Several species of fishes share the tendency to associate with objects drifting in the open ocean. The range of species that exhibit this trait spans several taxonomic groups and trophic levels (Gooding & Magnuson, 1967; Taquet *et al.*, 2007). A near equal diversity is shown in the range of hypotheses proposed to explain why some fishes behave in this way (Fréon & Dagorn, 2000; Castro *et al.*, 2002; Dempster & Taquet, 2004). Several proposed ideas are specific to certain types of fishes, often thought of as either predators or prey (Gooding & Magnuson, 1967; Fréon & Dagorn, 2000), but as Fréon & Dagorn (2000) suggest, they are not necessarily mutually exclusive and some, such as the meeting-point and indicator-log hypotheses, could apply to both groups. Early

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hypotheses centred around the idea that juvenile fishes seek protection from predators (Hunter & Mitchell, 1967; Feigenbaum *et al.*, 1989; Rountree, 1989) by seeking refuge close to drifting objects. Conversely, the motivations for predatory species to aggregate appear to be far more complex and to date remain largely unknown. A general lack of consensus for explaining the associative behaviour of both predators and prey means the driving forces behind this behaviour remain largely uncertain. Three species of tunas, skipjack tuna *Katsuwonus pelamis* (L. 1758), yellowfin tuna *Thunnus albacares* (Bonnaterre 1788) and bigeye tuna *Thunnus obesus* (Lowe 1839), display a strong tendency to aggregate around floating objects. As a result, tuna purse-seine fisheries now deploy thousands of drifting objects, known as fish aggregating devices (FAD) as a highly effective tool facilitating their capture. Approximately half of the global catch of these three species come from such aggregations (Dagorn *et al.*, 2013). In terms of biomass, these tunas often constitute >95% of an aggregation, which can, at times, reach several hundred t in size (Dagorn *et al.*, 2012). The majority of hypotheses set forth to explain the aggregative phenomenon in recent years have focused on tunas (Fréon & Dagorn, 2000). The role that feeding plays in the associative behaviour of tunas has been investigated by several authors (Hunter & Mitchell, 1967; Brock, 1985; Ménard *et al.*, 2000*a*, *b*) and largely the findings have suggested that aggregated tunas derive little to no trophic enrichment through their association with floating objects. Given the extensive size of tuna aggregations and the lack of sufficient prey biomass within the total aggregation to feed so many tunas, these findings appear plausible. A feeding hypothesis was proposed, however, for predatory species that occur at lower densities, such as *Coryphaena hippurus* L. 1758 (Kojima, 1956; Hunter & Mitchell, 1967), large tunas, sharks and billfishes (Ménard *et al.*, 2000*b*). To date, few studies on non-tuna species have investigated this relationship directly (Taquet, 2004; Duffy *et al.*, 2015). The silky shark *Carcharhinus falciformis* (Müller & Henle 1839) and the oceanic whitetip shark *Carcharhinus longimanus* (Poey 1861) are the two shark species most often found associated with floating objects, but *C. falciformis* is far more common. As a result of the tendency to associate with floating objects, *C. falciformis* is regularly taken as by-catch in the FAD-based tuna purse-seine fishery.

Behavioural studies have found that juvenile *C. falciformis* remain associated with the same floating objects for several weeks at a time (Filmalter *et al.*, 2011, 2015). Furthermore, *C. falciformis* in known to display strong diel patterns in vertical behaviour when associated with floating objects and regularly undertake short excursions during the night which last several hours (Filmalter *et al.*, 2015). Diel vertical behavioural patterns are characterized by limited vertical movement during daylight hours and increased vertical oscillations during portions of the night, suggestive of foraging activity (Filmalter *et al.*, 2015).

A recent study by Duffy *et al.* (2015) found that FAD-associated *C. falciformis* in the eastern tropical Pacific Ocean derive significant foraging benefits from the aggregated biomass, suggesting that feeding may be an important driver of associative behaviour in this region. Similar predator–prey relationships for FAD associated *C. falciformis* from other regions remain poorly understood. Observations, however, of *C. falciformis* consuming fishes encircled within purse seines during fishing operations have been observed throughout the extent of this fishery (Bane, 1966; Duffy *et al.*, 2015). Gaining insight into the factors that drive the associative behaviour of *C. falciformis* is an important component for investigating the effect that changing fisheries practices are having on this vulnerable species. As modern tuna purse-seine fisheries continue to

deploy increasing numbers of drifting objects (FADs) throughout the tropical oceans, the vulnerability of this species to fishery mortality continues to rise (Dagorn *et al.*, 2013; Poisson *et al.*, 2014).

The current study aimed to test the hypothesis that increased trophic benefits explain the associative behaviour for this species in the western Indian Ocean, through the analysis of stomach contents of *C. falciformis* caught at drifting objects in this region.

MATERIALS AND METHODS

STOMACH CONTENT ANALYSIS

Carcharhinus falciformis were captured by French and Spanish flagged tuna purse-seine vessels when they set their nets on FADs in the western Indian Ocean between 2001 and 2012. Between one and four sharks were randomly collected from selected fishing sets and either frozen dry in a blast freezer or in brine at −15° C with the tuna catch by the vessel's crew. The date and location of each capture were recorded. Samples were collected from an extensive geographic area that covered tropical and subtropical waters of the central western Indian Ocean as well as the northern portion of the Mozambique Channel (Fig. 1). On return to shore, the sharks were defrosted in the laboratory, weighed to the nearest 0·1 kg, fork length (L_F) measured to the nearest mm and the stomachs removed in a semi-frozen state. Once the stomachs were completely thawed, excess water was drained and six treatment steps were performed, following the methods of Potier *et al.* (2007*a*).

All items that were very fresh and were likely to have been consumed inside the net were removed and completely disregarded from the analyses. The total content of each stomach was weighed to the nearest g. Hard parts (*i.e.* cephalopod beaks and fish otoliths and bones) accumulated from fully digested prey items (no flesh attached) were removed and disregarded in the analysis to prevent over emphasis of certain prey types in the diet. Contents were then divided into four broad categories (fishes, cephalopods, crustaceans and other) and weighed to obtain the wet-mass proportion of each category in the diet. Single items within each category were then sorted, weighed and measured. Items were enumerated using identifiable fresh remains. For crustaceans, counts were made using the highest number of either pairs of eyes, pairs of chelae or cephalo-thoraxes. For fishes, the number of parasphenoids, mandibles or greatest number of either left or right otoliths was used. For cephalopods, the maximum number of either lower or upper beaks was used. The items were then identified to the lowest possible taxonomic level using published identification keys and descriptions (Clarke, 1986; Smith & Heemstra, 1986; Smale *et al.*, 1995) and a personal reference collection. Specific measurements were then taken according to the type of each prey item. For crabs, the length of the propodus was measured (mm), for cephalopods the lower rostral length (L_{LR}, mm) was recorded and for fishes standard length (L_S, mm) was used. Additionally, when fish prey was partially digested, the lengths of hard structures (otoliths, parasphenoids or dentary) were measured and whole prey size estimated using species-specific regression equations between the structure's length and L_S (Potier *et al.*, 2011).

Using the size of each prey item, whole masses were reconstituted using published allometric equations (Clarke, 1986; Smale *et al.*, 1995; Potier *et al.*, 2011). If no species-specific equation was available, masses were calculated from closely related or morphologically similar species. Furthermore, when no measurement was obtainable from an identified prey item, the average size of that item from all stomachs was used. When items could not be identified to at least the family level, the measured wet mass was used.

Prey items were divided into broad ecological categories reflecting their known behavioural patterns and position in the water column. These categories were: epipelagic, mesopelagic and coastal. Epipelagic species constituted those found within the upper 200 m of the water column throughout the day and night. Mesopelagic organisms are those that undertake diel migrations during ephemeral periods, moving from depths greater than 200 m during the day to the surface layers during the night. Coastal species consisted of those known to primarily occur in coastal
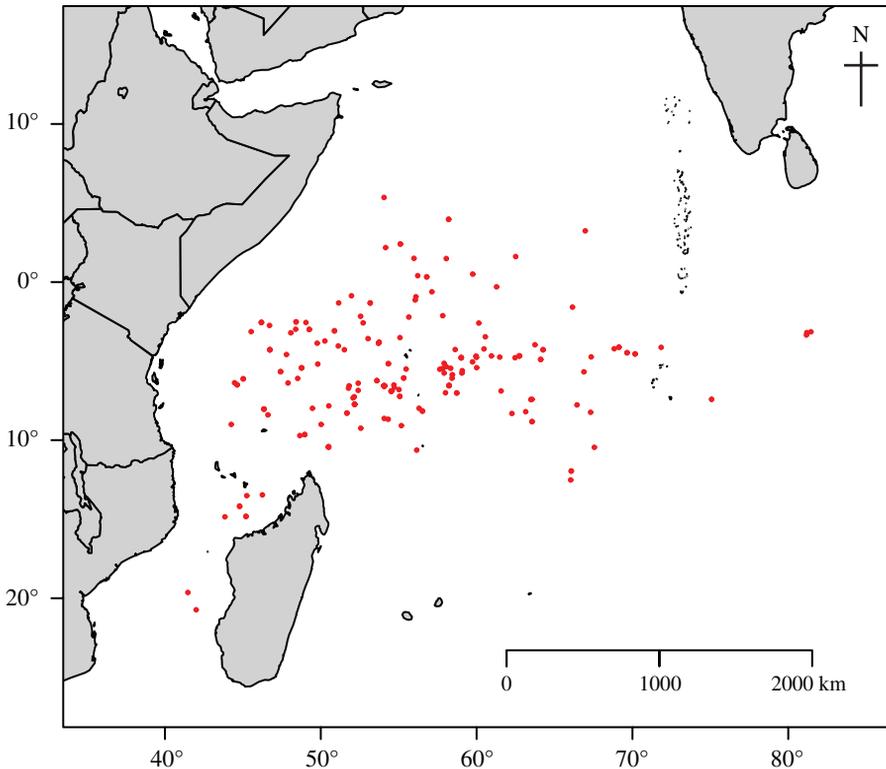
FIG. 1. Spatial distribution of sampling of *Carcharhinus falciformis* caught at floating objects in the western Indian Ocean. Red dot indicates capture locations of one or more *C. falciformis*.

waters, at depths <100 m. Furthermore, all prey items were also designated as either aggregative [*i.e.* known to occur at drifting objects in the Indian Ocean from Taquet *et al.* (2007)] or non-aggregative.

DATA ANALYSIS

In order to assess the representativeness of the sampled stomachs in describing the diet of *C. falciformis*, a cumulative prey curve was constructed following the methods of Ferry & Cailliet (1996). The order in which the stomachs were assessed was randomized 1000 times and the mean cumulative number and s.D. of unique prey items calculated for each stomach assessed, following the equation $S_n f(n)$, where S is the number of unique prey items observed in (n) stomachs analysed.

Three indices were used to describe the importance of each prey item and each broad category (cephalopods, crustaceans and teleosts) in the diet of *C. falciformis*: frequency of occurrence (O_n, the numerical occurrence and $O\%$, the percentage occurrence in non-empty stomachs); mean numerical proportion expressed as a percentage $\left(\overline{N}\%\right)$; mean proportion by reconstituted mass expressed as a percentage $\left(\overline{M}_R\%\right)$. $\overline{N}\%$ and $\overline{M}_R\%$ were calculated using the proportion that each species or category represented in each stomach and then calculating the mean proportion across all stomachs. In this way, each individual *C. falciformis* was treated as the sampling unit, which facilitated the calculation of an s.D. for each prey species or category.
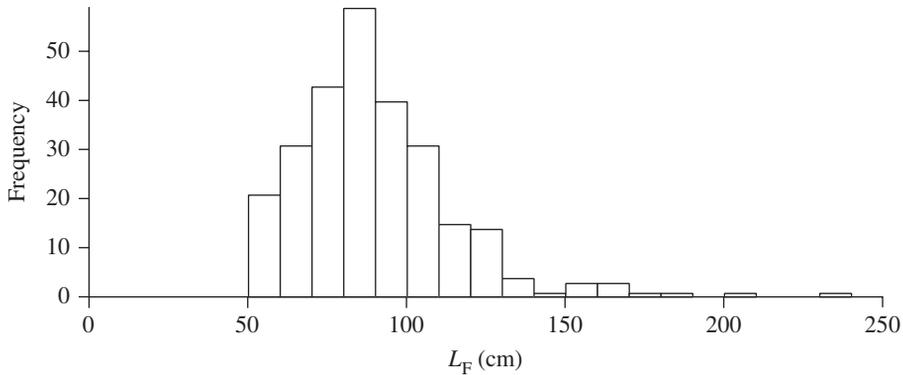
FIG. 2. Fork length (L_F) frequency distribution of *Carcharhinus falciformis* caught at floating objects in the western Indian Ocean and sampled for dietary analysis ($n = 269$).

RESULTS

Three hundred and twenty-three (141 females, 127 males, 55 unknown) *C. falciformis* were sampled for dietary analysis. Length measurements were collected for 269 individuals. Sizes ranged from 52 to 234 cm with a median L_F of 86·9 cm (Fig. 2). Of the sampled sharks, 82 (25·5%) had empty stomachs. Additionally, 35 (10·8%) sharks had only fishes ingested during the purse-seine operation in their stomachs and were therefore considered as being empty as well. Hence, the total number of empty stomachs was 117 (36·2%). A further 23 individuals (7·1%) had only accumulated hard parts of digested prey. The remaining 183 (57·3%) stomachs were found to contain a variety of prey species including both epipelagic and mesopelagic organisms. The prey curve suggests that sufficient stomachs were sampled to characterize the diet of *C. falciformis* in this environment despite the curve not having reached an asymptote (Fig. 3).

DIET COMPOSITION

The mean reconstituted mass of stomach contents from all individuals was 199 g (range: 0–2655 g). Considering all prey items identified to the class level, teleosts formed the most important prey category across all indices ($\overline{N}\%$, $\overline{M}_R\%$, $O\%$; Fig. 4). Crustaceans were marginally less important in terms of $\overline{N}\%$ and $\overline{M}_R\%$ than teleosts. Cephalopods were consistently third in rank. Prey items from 43 taxa including identification to class, family and species were observed (Table I). Diversity was lowest for crustaceans, with only two species identified; however, the swimming crab *Charybdis smithii* was the most common of all prey items and occurred in almost 40% of non-empty stomachs. While a large number of mantis shrimp *Natosquilla investigatoris* were also found, they were observed in few stomachs. Eleven cephalopod species from 10 families were found with fresh remains. Cephalopods were typically low in occurrence, with most species observed with fresh remains only once. The enoploteuthid, *Ancistrocheirus lesueurii* was the most common cephalopod species recorded. While not considered in the calculation of dietary indices, the diversity of cephalopod species was greater (17 species) when accumulated material (beaks) were also considered (Table II). Teleosts were the most diverse prey class. Fifteen species and 16 families
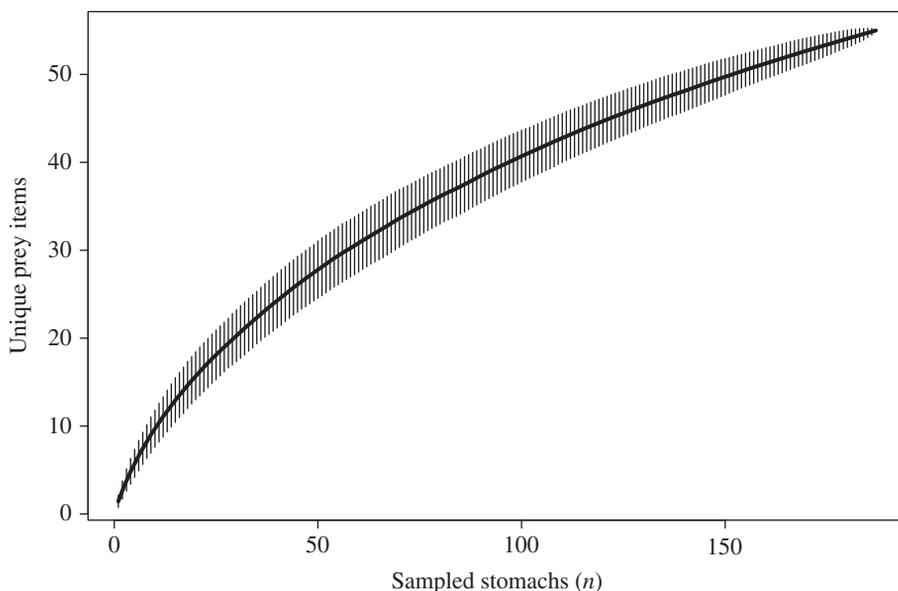
FIG. 3. Cumulative prey curve showing the relationship between new unique prey items and the number of stomachs of *Carcharhinus falciformis* examined. |, S.D. following 1000 randomizations of the order in which the stomachs were examined.

were identified. Identified teleosts were dominated by scombrids and carangids, across all indices. Within these families, *Decapterus macarellus* (Cuvier 1833) and *K. pelamis* were the most important identified species.

Eighty-eight per cent of all fresh prey items were identified to the family level. The level of importance of each of the top three families, which constituted by far the majority of the diet, was consistent across all three indices (Table III). The top 10 families,
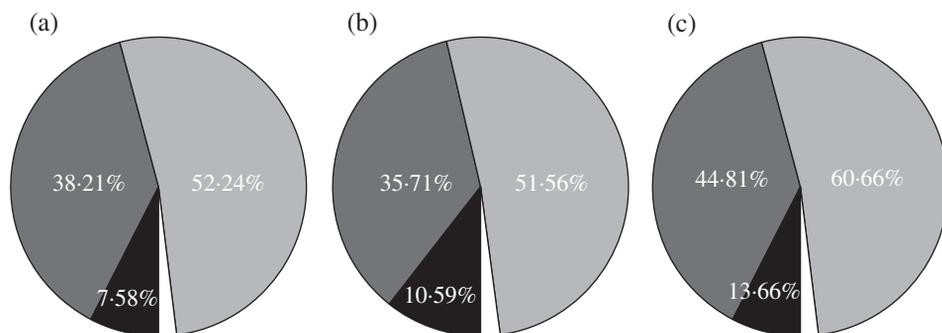

FIG. 4. The relative proportion of each prey functional group (□, teleosts; ▨, crustaceans; ■, cephalopods; □, other) for *Carcharhinus falciformis*, derived using three dietary indices: (a) mean numerical proportion expressed as a percentage $\left(\overline{N}\%\right)$, (b) mean proportion by reconstituted mass expressed as a percentage $\left(\overline{M}_{R}\%\right)$ and (c) the percentage occurrence in non-empty stomachs ($O\%$).

TABLE I. Summary information from fresh prey items identified from the stomach contents of 183 *Carcharhinus falciformis* associated with floating objects in the western Indian Ocean

Prey class	Prey family	Prey species	O_n	$O\%$	$\overline{N}\%$	$\overline{M}_R\%$	Association	Eco. Cat.
Cephalopoda		All Cephalopoda	25	13·66	7·58 ± 24·47	10·59 ± 28·64		
	Alloposidae	*Haliphron atlanticus*	1	0·55	0·55 ± 7·39	0·55 ± 7·39	No	Mesopelagic
	Argonautidae	*Argonauta argo*	1	0·55	0·18 ± 2·46	0·00 ± 0·06	No	Epipelagic
	Cranchidae	*Taonius* sp.	1	0·55	0·18 ± 2·46	0·24 ± 3·26	No	Mesopelagic
	Enoploteuthidae	*Ancistrocheirus lesueurii*	7	3·83	2·14 ± 13·20	3·48 ± 17·71	No	Mesopelagic
	Histioteuthidae	*Stigmatoteuthis hoylei*	1	0·55	0·08 ± 1·06	0·39 ± 5·30	No	Mesopelagic
	Mastigoteuthidae	*Mastigoteuthis* sp.	1	0·55	0·01 ± 0·07	0·41 ± 5·60	No	Mesopelagic
	Octopoteuthidae	*Octopoteuthis rugosa*	2	1·90	0·46 ± 4·43	0·63 ± 6·21	No	Epipelagic
	Ommastrephidae	*Ornithoteuthis volatilis*	1	0·55	0·55 ± 7·39	0·55 ± 7·39	No	Epipelagic
		Sthenoteuthis oualaniensis	2	1·90	0·55 ± 7·39	0·72 ± 7·75	No	Epipelagic
	Onychoteuthidae	*Walvisteuthis rancureli*	1	0·55	0·02 ± 0·28	0·28 ± 3·74	No	Mesopelagic
		Unknown Onychoteuthid	1	0·55	0·02 ± 0·28	0·00 ± 0·01	No	Mesopelagic
	Tremoctopodidae	*Tremoctopus violaceus*	1	0·55	0·55 ± 7·39	0·55 ± 7·39	No	Epipelagic
	Unknown		4	4·37	2·30 ± 13·50	2·80 ± 14·94	No	
Crustacea		All Crustacea	82	44·81	38·21 ± 46·26	35·71 ± 45·52		
	Portunidae	*Charybdis smithii*	71	39·89	34·13 ± 45·14	31·85 ± 44·28	No	Epipelagic
		Uknown portunid	2	1·90	0·13 ± 1·50	0·16 ± 2·07	No	Epipelagic
	Squillidae	*Natosquilla investigatoris*	6	3·28	3·22 ± 17·53	3·00 ± 16·7	No	Epipelagic
	Unknown		1	1·90	0·73 ± 7·78	0·70 ± 7·68	No	
Other Arthropoda	Halobates	*Halobates* sp.	3	0·55	0·55 ± 7·39	0·55 ± 7·39	No	
Teleostei		All Teleostei	112	60·66	52·24 ± 47·02	51·56 ± 47·41		
	Balistidae	Uknown balistid	3	1·64	1·00 ± 8·59	0·98 ± 8·70	Yes	Epipelagic
	Belonidae	Uknown belonid	3	1·64	0·84 ± 7·91	0·94 ± 8·60	Yes	Epipelagic
	Carangidae	*Decapterus maccarellus*	5	2·73	2·23 ± 13·86	2·22 ± 13·85	Yes	Epipelagic
		Decapterus macrosoma	1	0·55	0·54 ± 7·32	0·13 ± 1·80	No	Epipelagic

TABLE I. Continued

Prey class	Prey family	Prey species	O_n	$O\%$	$\overline{N}\%$	$\overline{M}_R\%$	Association	Eco. Cat.
		Decapterus sp.	6	3·28	2·38 ± 13·61	2·59 ± 15·21	Yes	Epipelagic
		Naucrates ductor	3	1·64	1·06 ± 10·08	1·12 ± 10·02	Yes	Epipelagic
		Unknown carangid	10	5·46	3·84 ± 18·23	3·62 ± 17·99	No	Epipelagic
	Chiasmodontidae	*Chiasmodon niger*	1	0·55	0·52 ± 6·99	0·14 ± 1·91	Yes	Mesopelagic
	Coryphaenidae	*Coryphaena equiselis*	1	0·55	0·27 ± 3·70	0·33 ± 4·43	Yes	Epipelagic
	Coryphaenidae	*Coryphaena hippurus*	2	1·90	1·09 ± 10·43	1·09 ± 10·43	Yes	Epipelagic
	Diodontidae	Unknown diodontid	1	0·55	0·55 ± 7·39	0·55 ± 7·39	Yes	Coastal
	Echeneidae	*Remora brachyptera*	2	1·90	0·25 ± 2·63	0·56 ± 6·26	No	Epipelagic
	Exocoetidae	*Exocoetus volitans*	1	0·55	0·55 ± 7·39	0·55 ± 7·39	No	Epipelagic
		Uknown Exocoetid	12	6·56	4·24 ± 18·75	4·71 ± 20·09	No	Epipelagic
	Gempylidae	*Gempylus serpens*	1	0·55	0·04 ± 0·49	0·05 ± 0·64	No	Mesopelagic
	Holocentridae	Unknown holocentrid	1	0·55	0·55 ± 7·39	0·55 ± 7·39	Yes	Coastal
	Kyphosidae	*Kyphosus* sp.	1	0·55	0·55 ± 7·39	0·55 ± 7·39	Yes	Coastal
	Lobotidae	*Lobotes surinamensis*	3	1·64	1·64 ± 12·73	1·64 ± 12·73	Yes	Coastal
	Monacanthidae	Unknown monacanthid	2	1·90	0·96 ± 9·22	0·64 ± 7·49	Yes	Coastal
	Scombridae	*Euthynnus affinis*	1	0·55	0·55 ± 7·39	0·55 ± 7·39	Yes	Epipelagic
		Katsuwonus pelamis	8	4·37	4·10 ± 19·53	4·13 ± 19·62	Yes	Epipelagic
		Thunnus albacares	1	0·55	0·55 ± 7·39	0·55 ± 7·39	Yes	Epipelagic
		Thunnus spp.	3	1·64	1·37 ± 11·03	1·63 ± 12·69	Yes	Epipelagic
		Unknown scombrid	22	12·20	8·57 ± 26·07	8·92 ± 26·95	Yes	Epipelagic
	Sphyraenidae	*Sphyraena barracuda*	1	0·55	0·55 ± 7·39	0·55 ± 7·39	Yes	Epipelagic
	Unknown		18	19·67	13·47 ± 31·47	12·30 ± 30·24		
Plant	Plant	Macroalgae	7	2·73	1·43 ± 10·78	1·58 ± 12·25		

Association, reflects whether prey is known to associate with floating objects or not; Eco. Cat., the broad ecological category of the prey item; $\overline{M}_R\%$, the percentage in mean reconstituted mass ± S.D.; $\overline{N}\%$, the percentage in mean number ± S.D.; $O\%$, the percentage of stomachs where each prey type was observed; O_n, the numerical frequency of occurrence of each item.

TABLE II. The number and diversity of cephalopods consumed by *Carcharhinus falciformis* associated with floating objects in the western Indian Ocean. Both fresh and accumulated prey items are included. Accumulated items were identified from remaining beaks

Species	Fresh	Accumulated	Total
Ancistrocheirus lesueurii	7	15	22
Argonauta argo	1		1
Walvisteuthis rancureli	1	1	2
Chiroteuthis sp.		1	1
Cranchia scabra		2	2
Cycloteuthis sirventi		3	3
Haliphron atlanticus	1		1
Stigmatoteuthis dofleini		2	2
Stigmatoteuthis hoylei	1	3	4
Mastigoteuthis sp.	1		1
Octopoteuthis rugosa	2	2	4
Onychoteuthis sp. 1		1	1
Onychoteuthis sp. 2		1	1
Ornithoteuthis volatilis	1		1
Sthenoteuthis oualaniensis	2	20	22
Taonius sp.	1	4	5
Tremoctopus violaceus	1		1

according to the $\overline{M}_R\%$ analysis, consisted of five associative (Scombridae, Carangidae, Lobotidae, Corypheanidae and Balistidae) and five non-associative (Potunidae, Exocoetidae, Enoploteuthidae, Squillidae and Ommastrephidae) families.

Based on the identified families, almost half of the diet comprised organisms known to be associated with floating objects (Fig. 5). Furthermore, when prey items were characterized according to their ecological niche (epi- or mesopelagic), epipelagic items were found to strongly dominate the diet of *C. falciformis* $\left(\overline{N}\% = 96{\cdot}2, \overline{M}_R\% = 94{\cdot}5 \right)$.

DISCUSSION

This study provides the first detailed assessment of the diet of *C. falciformis* associated with drifting objects in the Indian Ocean. The size range of sharks sampled [median $L_F = 87{\cdot}6$ cm, *c.* total length $(L_T) = 108$ cm] corresponds well with the reported mode (100 cm) of the size range of *C. falciformis* taken by the French tuna purse-seine fleet in the Indian Ocean (Amandè *et al.*, 2008b), but is slightly smaller than that reported for the Spanish fleet which peaks between 110 and 119 cm L_T (González *et al.*, 2007). The majority of individuals were early juveniles [50% maturity = 210–220 cm L_T; Joung *et al.* (2008)] with only a few adults being captured. Amandè *et al.* (2008a) noted that large individuals were infrequently taken in the western Indian Ocean purse-seine fishery. The broad geographic range from which samples were collected also extends over the majority of the area where fishing on floating objects typically occurs (Kaplan *et al.*, 2014).

TABLE III. Comparisons between prey families consumed by *Carcharhinus falciformis* associated with floating objects in the western Indian Ocean. Families are ranked according to the index of relative importance

Rank	Family	$O\%$	$\overline{M}_R\%$	$\overline{N}\%$	Association
1	Portunidae	41·79	39·72 ± 47·82	41·85 ± 47·82	No
2	Scombridae	19·31	19·23 ± 38·75	18·76 ± 37·66	Yes
3	Carangidae	13·66	11·72 ± 30·63	12·61 ± 31·29	Yes
4	Exocoetidae	7·11	6·12 ± 22·82	5·72 ± 21·78	No
5	Enoploteuthidae	3·83	4·01 ± 18·98	2·94 ± 16·08	No
6	Squillidae	3·28	3·45 ± 17·88	3·79 ± 19·04	No
7	Lobotidae	1·64	1·89 ± 13·65	1·92 ± 13·78	Yes
8	Coryphaenidae	2·45	1·87 ± 13·51	1·71 ± 12·44	Yes
9	Ommastrephidae	2·45	1·46 ± 11·44	0·65 ± 8·01	No
10	Balistidae	1·64	1·33 ± 10·03	1·28 ± 9·75	Yes
11	Belonidae	1·64	1·14 ± 9·44	1·12 ± 9·13	Yes
12	Octopoteuthidae	1·90	0·89 ± 8·55	0·85 ± 8·42	No
13	Echeneidae	1·90	0·83 ± 7·61	0·41 ± 4·16	No
14	Monacanthidae	1·90	0·74 ± 8·04	1·19 ± 10·51	Yes
15	Sphyraenidae	0·55	0·63 ± 7·93	0·64 ± 8·01	Yes
16	Alloposidae	0·55	0·63 ± 7·93	0·64 ± 8·01	No
17	Tremoctopodidae	0·55	0·63 ± 7·93	0·64 ± 8·01	No
18	Kyphosidae	0·55	0·63 ± 7·93	0·64 ± 8·01	Yes
19	Diodontidae	0·55	0·63 ± 7·93	0·64 ± 8·01	Yes
20	Holocentridae	0·55	0·63 ± 7·93	0·64 ± 8·01	Yes
21	Mastigoteuthidae	0·55	0·48 ± 6·00	0·01 ± 0·08	No
22	Histioteuthidae	0·55	0·45 ± 5·68	0·09 ± 1·14	No
23	Cranchidae	0·55	0·39 ± 4·92	0·32 ± 4·00	No
24	Onychoteuthidae	0·55	0·32 ± 4·04	0·05 ± 0·64	No
25	Chiasmodontidae	0·55	0·16 ± 2·05	0·61 ± 7·57	No
26	Gempylidae	0·55	0·05 ± 0·69	0·04 ± 0·53	No
27	Argonautidae	0·55	0·01 ± 0·07	0·21 ± 2·67	No

Association, reflects whether prey is known to associate with floating objects or not; $\overline{M}_R\%$, the per cent mean reconstituted mass ± S.D.; $\overline{N}\%$, the percentage in mean number ± S.D.; $O\%$, the percentage of stomachs where each family was observed.

DIET COMPOSITION

The diet of *C. falciformis* remains poorly studied throughout most of its cosmopolitan distribution and in many areas information on the species' food habits stem from published reports based on the examination of few stomachs containing prey: Strasburg (1958) seven; Bane (1966) two; Mearns *et al.* (1981) two; Stevens (1984*a*, *b*) two each; Branstetter (1987) four; Stevens & McLoughlin (1991) five; Bowman *et al.* (2000) 36. General conclusions from these studies suggest that *C. falciformis* are opportunistic feeders, ingesting a wide variety of prey types (Compagno, 1984; Bonfil, 2008). The functional group of prey that dominates the diet appears to be area specific and may reflect differential abundances of various prey types across the distribution of the species. For example, the comprehensive study conducted by Cabrera Chávez-Costa *et al.* (2010) found that the diet of *C. falciformis* from two areas in Baja California
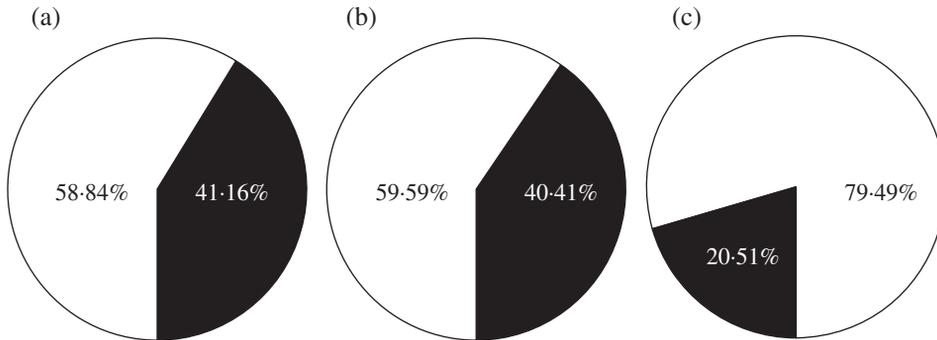
(a)   (b)   (c)

Fig. 5. Proportion of the diet of *Carcharhinus falciformis* associated with floating objects in the western Indian Ocean as a function of the recognized association of the prey (■, species known to associate with floating objects; □, prey that do not associate with floating objects). (a) Mean numerical proportion expressed as a percentage $\left(\overline{N}\%\right)$, (b) mean proportion by reconstituted mass expressed as a percentage $\left(\overline{M}_{R}\%\right)$ and (c) the percentage occurrence in non-empty stomachs (*O*%).

Sur were dominated by red crabs *Pleuroncodes planipes* (index of per cent relative importance, $I_{RI}\% = 83\%$) and jumbo squids *Dosidicus gigas* ($I_{RI}\% = 43\%$), respectively. Owing to the dominance of specific prey types in the diet, these authors considered that *C. falciformis* in this region are selective predators. Other authors have described the species as a generalist predator, feeding on various crustacean, cephalopod and fish species. Recently, Duffy *et al.* (2015) examined a large number of stomachs from across the eastern Pacific Ocean and concluded that *C. falciformis* is indeed an opportunistic feeder in this region. The findings of the current study align well with these results as a high diversity of prey items from three main faunal groups (teleosts, crustaceans and cephalopods) were observed.

Teleosts dominated the diet, in terms of $\overline{N}\%$, $\overline{M}_{R}\%$ and *O*% and consisted largely of species known to aggregate around floating objects, principally members of the families Scombridae and Carangidae. Non-associative Exocoetidae were, however, also prominent. These results mirrored those from *C. falciformis* from the eastern Pacific Ocean, most of which were collected at FADs, where the diet was well represented by these families (Duffy *et al.*, 2015).

Crustaceans formed a major part of the diet of *C. falciformis* and were dominated by two species, the stomatopod *Natosquilla investigatoris* and the decapod *Charybdis smithii*. The latter appears to be a highly important food resource for *C. falciformis* in this region. Previously, Romanov *et al.* (2009) found a lower occurrence (*O*% = 11·8) of *C. smithii* in a small sample of *C. falciformis* (21 individuals) caught during tuna purse-seine operations around floating objects in the western Indian Ocean. They noted, however, that the species was more common (*O*% = 28·2) in the stomachs of *C. falciformis* (*n* = 113) caught on longlines. These differences may be a result of contrasting sampling effort as the smaller number of stomachs assessed in the study may have led to underrepresentation of certain prey types. In the current study, where substantially more sharks were sampled, the frequency of occurrence of *C. smithii* was higher (39·9%) than previously reported for either gear type. Romanov *et al.* (2009) suggested that this species represents an important prey resource for a multitude of pelagic predators within this region and was consistently the main prey of *T. albacares* and lancet fish

Alepisaurus ferox Lowe 1833. The stomatopod *N. investigatoris* is known to undergo periodic cycles of increased abundance, with higher abundance generally coinciding with lower abundance of *C. smithii*. All observations of *N. investigatoris* recorded here, occurred during one such period of high abundance between 2000 and 2005 (Potier *et al.*, 2007b). Oceanic crustaceans clearly form an important component of the diet of juvenile *C. falciformis* in this region. The relative abundance of these two species in the diet probably reflects fluctuations in local abundance with time.

Cephalopods formed the third most important functional group in the diet of *C. falciformis* in this study. While this group only contributed *c.* 10% of the $\overline{M}_R$ and a frequency of occurrence of 14%, a wide variety of cephalopod species were identified. Ménard *et al.* (2013) reported a higher frequency of occurrence of cephalopods (20%) in the stomachs of *C. falciformis* sampled from longlines and purse-seine vessels in the same region. This difference may reflect a different feeding strategy when not associated with floating objects. Interestingly, these authors found that the epipelagic flying squid *Sthenoteuthis oualaniensis* was by far the most common species in their sample, while only two individuals were observed in the fresh remains during the current study. When both fresh and accumulated items were considered, however, this species was observed 22 times, making it equally as common as the mesopelagic *Ancistrocheirus lesueurii*. The observation of the marine insect *Halobates* sp. and of macroalgal material in some stomachs are believed to reflect accidental consumption during feeding activity at the surface. Strasburg (1958) suggested the opportunistic feeding habits of many pelagic sharks often lead to the consumption of items with little to no nutritive value. Similar items were observed in the stomachs of shortfin mako sharks *Isurus oxyrinchus* Rafinesque 1810 (Stillwell & Kohler, 1982; Maia *et al.*, 2006).

When compared with other dietary studies on fishes associated with FADs, these results suggest that *C. falciformis* feed more actively than tunas when associated with FADs. This is apparent from the high proportion of *C. falciformis* stomachs containing food (57 %) compared with the generally empty stomach of tunas (85%, Ménard *et al.*, 2000a). This difference may simply reflect higher metabolic and digestive rates of tunas (Magnuson, 1969; Olson & Boggs, 1986), which evacuate their stomachs completely in <24 h. Without comparable information for *C. falciformis*, however, the reasons for such a difference remain unclear. Compared with other predators that occur at low densities around drifting objects (Taquet *et al.*, 2007), results on the percentage of empty stomachs are more similar to present results for *C. falciformis*. Taquet (2004) found only 9% of stomachs of *C. hippurus* associated with floating objects in the Indian Ocean to be empty. *Coryphaena hippurus* fed on a combination of associative and non-associative organisms, but mesopelagic migrating species dominated the diet. Ménard *et al.* (2000b) observed a large proportion of scombrids in the diet of large *T. albacares* from aggregations at floating objects and concluded that, for this size category, which generally represent a small percentage of the aggregated tunas, the abundance of small scombrids commonly associated with floating objects provides a trophic resource. Considering the results obtained here, there appear to be commonalities in the feeding strategy between the larger and less numerous predators that are found in floating object aggregations.

FEEDING PATTERNS

The percentage of completely empty stomachs or those with only accumulated hard parts (33%) was low in comparison with many other studies on *C. falciformis* which

were not captured in association with floating objects (Branstetter, 1987; Cabrera Chávez-Costa *et al.*, 2010), but similar to that reported for this species from floating objects in the eastern Pacific Ocean (30%; Duffy *et al.*, 2015). As all fresh prey deemed to have been eaten within the seine were excluded, it is believed that the relatively low percentage of empty stomachs observed here, compared with many other shark dietary studies (Wetherbee & Cortés, 2004), is an unbiased reflection of the feeding behaviour of juvenile *C. falciformis* during associations with floating objects, caught at the surface during the day. Wetherbee & Cortés (2004) suggested that the general high frequency of empty stomachs and often few, well digested prey items, encountered in shark dietary studies, supports the view that the majority of sharks are intermittent feeders. Considering the high percentage of empty stomachs found in other diet studies of *C. falciformis* (Branstetter, 1987; Cabrera Chávez-Costa *et al.*, 2010), the results of this study suggest that juveniles may feed more frequently when associated with floating objects, than when encountered away from FADs.

Carcharhinus falciformis regularly undertake excursions away from the floating object at night and display rapid vertical oscillations, suggestive of foraging behaviour away from floating objects (Filmalter *et al.*, 2015). The occurrence of epipelagic and mesopelagic cephalopods and some mesopelagic fish species in the stomachs sampled here, probably reflect feeding activity during these nocturnal excursions when these species migrate to the surface layers (Galván-Magaña *et al.*, 2013; Ménard *et al.*, 2013). Furthermore, Romanov *et al.* (2009) found that the swimming crab, *C. smithii*, which was a principle component of the diet of the sharks in this study, also undertake diel vertical migrations and are significantly more abundant in the upper 100 m of the water column between dusk and dawn than during the day. In total, 43% of the diet $\left(\overline{M}_{\mathrm{R}}\right)$ consisted of prey items that migrate into the surface layers during the night, illustrating that, at a minimum, almost half of the consumed food was probably eaten at night. During the day, juvenile *C. falciformis* typically remain within the upper 60 m of the water column (Filmalter *et al.*, 2015), where they are less likely to encounter such prey taxa.

FEEDING AT FADS

The principal result of this study suggests that *C. falciformis* associated with drifting objects in the Indian Ocean do not feed exclusively on other species from the FAD-associated assemblage. Nonetheless associative species do form a significant portion of the diet. This result was consistent across all dietary indices. Interestingly, in the only other extensive study on the diet of *C. falciformis* associated with drifting objects, Duffy *et al.* (2015) found that *C. falciformis* in the Pacific Ocean relied heavily on the associated biomass as a food resource. Such findings may suggest regionally specific feeding habits, but also suggest the underlying factors driving associative behaviour may differ regionally within a species. Indeed, it is also possible that the abundance of food resources in the surrounding environment could strongly affect the diet of predatory species such as *C. falciformis*. In the Indian Ocean, the ubiquitous *C. smithii* probably represent a readily available and easily accessible food resource for *C. falciformis* associated with floating objects, thus negating the need to target more mobile prey species in the associated aggregation. The lack of a comparable resource in the eastern Pacific Ocean may result in *C. falciformis* from this region preying more on resources provided by the aggregation itself. The higher proportion of scombrids found in the diet of *C. falciformis* in the Pacific Ocean lend support to this hypothesis.

Nonetheless, the results of these two studies indicate that the underlying reasons for associating with a floating object are complex and probably involve multiple factors, of which the availability of food is only one. Additional factors driving associative behaviour may include predator avoidance (especially during early juvenile stages), location of conspecifics or other species, such as tunas, which may increase the likelihood of finding prey. In both cases, the aggregated biomass probably serves as a food reserve for *C. falciformis*, which it can access when non-associative prey abundance is low. Taquet (2004) proposed the same hypothesis for *C. hippurus*, after comparing the diet of associated and non-associated individuals in the Indian Ocean and finding that during association with a floating object, only 27% of the diet consisted of other associated prey. Following this hypothesis, it is impossible to reject the hypothesis that *C. falciformis* associate with floating objects to obtain trophic benefits. The results of this study, however, show that food resources available to the species in floating-object aggregations are of lesser importance, with the predation of non-associative free-swimming prey being the primary foraging strategy in the Indian Ocean.

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