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ORIGINAL PAPER

Diel behaviour of tuna and non-tuna species at drifting fish aggregating devices (DFADs) in the Western Indian Ocean, determined by fishers' echo-sounder buoys

Jon Lopez[1] · Gala Moreno[1,2] · Leire Ibaibarriaga[3] · Laurent Dagorn[4]

Abstract As tropical pelagic species are attracted by floating objects in the surface of the ocean, industrial purse seiners deploy thousands of man-made drifting fish aggregating devices (DFADs) to facilitate their catch of tunas. However, the sharp increase in the use of DFADs leads to some ecological concerns, such as producing higher amount of by-catch or alteration of natural behaviour of fish. We used fishers' satellite-linked GPS buoys equipped with echo-sounders to continuously collect acoustic samples under remote DFADs and investigate the diel behaviour patterns of the associated fish (i.e., non-tuna species and small and large tunas) and their potential biological interactions. Results showed a strong correlation between the presence of non-tuna species and small tunas, and between small and large tunas. Diel biomass dynamics were highly variable and seem to be both species and region-specific, which may suggest adaptive behaviour patterns. Tuna associated with DFADs in the Somalia area showed a clear night-time associative behaviour. In contrast, tuna in the NW Seychelles associated with DFADs to a greater degree during daytime. In the Mozambique Channel, large tuna showed daytime associative behaviour, while small tuna showed a maximum biomass at sunrise, decreasing over the day. The associative behaviour of non-tuna species was slightly variable, being uniform near the equator or showing two peaks when increasing latitude. This study shows the importance and effect of biological factors on the associative behaviour of the fish and serves as a first step towards improving pre-set selectivity of purse seine fisheries using DFADs. The fish presence and density may improve DFAD attraction and detectability and the observed periodicity by species and area shows both similarities and differences with published literature.

Keywords Tuna · Behaviour · Echo-sounder buoys · By-catch · Purse seiners · FAD · Multi-species aggregations

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Introduction

Numerous pelagic fish species are known to associate with floating objects on the surface and in subsurface waters of tropical and subtropical oceans, from small reef fish to large pelagics, such as sharks, billfishes, and tunas (Castro et al. 2002). Although the motivations for, and advantages of, associating with floating objects (also called fish aggregating devices or FADs) remain largely unknown (Fréon and Dagorn 2000), fishers have been increasingly taking advantage of this aggregative behaviour to increase their chances of fishing. Starting in the late 1970s, modern man-made FADs were anchored all over the world (e.g., the South Pacific, Caribbean sea, and Maldives) to attract tuna and other species and support local artisanal fisheries and food security (Taquet 2004; Scott and Lopez 2014). However,

the majority of FADs used worldwide are drifting FADs (DFADs) exploited by industrial tropical tuna purse seine fleets (Fonteneau et al. 2013). Most DFADs consist of bamboo rafts with nets hanging below and are equipped with satellite-linked buoys to allow them to be located remotely (Lopez et al. 2014).

This fishing mode is essential for the current purse seine fleets in all oceans: more than 50% of the sets are made on floating objects, exceeding 70% some years in the Indian and Eastern Pacific Oceans (Dagorn et al. 2012b; Scott and Lopez 2014). The majority of the remaining tuna catch comes from sets on free-swimming schools (i.e., unassociated schools). Whereas skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) are targeted by the tropical tuna purse seine fishery, by-catch species in DFAD-associated sets are common. Romanov (2002) showed that in the western Indian Ocean, by-catch was found in 93% of the sets around DFADs. Because of the increased use of DFADs in the past three decades [i.e., about 100,000 DFADs are estimated to be deployed annually worldwide (Baske et al. 2012; Scott and Lopez 2014; Ushioda 2015)], the impacts that this global fishery has on the ecosystem have recently received much attention (Dagorn et al. 2012a). Main concerns over DFAD-related fishing are common for the different tuna regional fisheries management organizations (*t*-RFMOs): (1) reduction in yield per recruit of some target species; (2) increased by-catch and perturbation of pelagic ecosystem balance; and (3) deleterious alteration of the normal movements of the species associated with DFADs (Bromhead et al. 2003; Morgan 2011; Dagorn et al. 2012b).

Recently, several mitigation techniques are under investigation by the scientific community, including measures that can be taken before the set is conducted (e.g., non-entangling FADs, echo-sounder buoys, and behavioural patterns) (Itano and Restrepo 2011). However, effective conservation strategies require the collection of large-scale data on species' spatial and temporal dynamics and on their interaction with the fishing gear (Moreno et al. 2015). Experiments in which FAD-associated fish were tagged with ultrasonic transmitters have provided useful information on species-specific fine-scale horizontal and vertical movements, including residence times (Table 1). In addition, associated fauna around FADs has been studied through alternative techniques, such as underwater visual surveys (Taquet et al. 2007b) or scientific acoustic surveys (Doray et al. 2007; Moreno et al. 2007b), which provided new insights into understanding individual and collective behaviours of fish at FADs. Because DFADs are hardly accessible and ephemeral, these data cannot be systematically collected due to the associated human and economic costs. Consequently, the information available on the behavioural ecology of tropical tunas, and other species,

associated with DFADs is still scarce [but see Schaefer and Fuller (2013)], particularly in some regions of the Western Indian Ocean. For example, there are no references on the specific behavioural patterns of FAD-associated target and non-target species in the Somalia area, where DFAD fishing is particularly intense (Davies et al. 2014). This lack of basic data on fish aggregations dynamics at DFADs is one of the main constraints to better understand the potential impacts of DFADs on the ecosystem and to define wise conservation measures.

One of the most significant advances of tropical tuna purse seine fleets in the last years is the use of satellite-linked buoys equipped with echo-sounder (Lopez et al. 2014). Fishing crews use the biomass estimates from the buoys as very important complementary information to decide on the best DFAD to visit next. Recently, researchers investigating DFADs have recognized the potential of fishers' echo-sounder buoys to serve scientific purposes (i.e., continuous data collection of fish biomass at DFADs via autonomous acoustic sampling) (Moreno et al. 2015). Up to date, the lack of scientific validation of the acoustic data provided by fishers' echo-sounder buoys has precluded the use of this data with scientific purposes. However, a recent research conducted by Lopez et al. (2016) has allowed, for the first time, the use of continuous stream of data at DFADs using these devices.

Studying the simultaneous associative behaviour of target and non-target species within large multi-species aggregations associated with DFADs at large scale will improve our knowledge on species-specific vulnerability to purse seine fisheries as well as on the potential ecological and biological links between species (i.e., attraction power, orientation cues for DFAD location), and would likely provide clues on how mitigate the effect of fishing on exploited resources. Thus, the objective of our study is to investigate the fine-scale (24-h) dynamics of multi-species aggregations at DFADs in different areas of the Western Indian Ocean, using data from fishers' echo-sounder buoys.

Materials and methods

Data collection

The sampling was conducted in the Western Indian Ocean from July 2008 to May 2010. The study area was stratified into four regions based on ZET (zones d'echantillonnage thonière) areas defined by Pianet et al. (2000) (Fig. 1). Eight new DFADs equipped with Satlink echo-sounder buoys (Satlink, Madrid, Spain, http://www.satlink.es) were deployed at sea by a Spanish tuna purse seiner during regular fishing trips, and two more DFADs were found at sea and equipped with the same echo-sounder buoys

Table 1 Summary of the most significant tagging experiments at fish aggregating devices (FADs) investigating tunas and non-tunas species associative behaviour sorted by species, FAD type and date [*AFAD* Anchored FAD, *DFAD* drifting FAD, *YF* yellowfin (*Thunnus albacares*), *SKJ* skipjack (*Katsuwonus pelamis*), *BE* Bigeye (*Thunnus* *obesus*), *RR* rainbow runner (*Elegatis bipinnulata*), *TR* Triggerfish (*Canthidermis maculata*), *DLP* Dolphinfish (*Coryphaena hippurus*), *WIO* Western Indian Ocean, *MZC* Mozambique Channel, *CPO* Central Pacific Ocean, *EPO* Eastern Pacific Ocean]

Author	Species	Area	FAD type	Acoustic tagging	Diel associative behaviour	Excursions
Forget et al. (2015)	RR/TR	MZC	DFAD	Passive	RR = Night	RR = Daytime
					TR = No clear pattern	TR = Fairly uniform
Taquet et al. (2007a, b)	DLP	WIO	DFAD	Passive	No clear pattern	Short (<2 h), daytime (60%)
Holland et al. (1990)	YF/BE	Hawaii	AFAD	Active	Diurnal	Nightime
Cayré (1991)	YF/SKJ	Comoros Islands	AFAD	Active	YF = Diurnal	YF = nightime
					SKJ = not associative	SKJ = not associative
Klimley and Holloway (1999)	YF	Hawaii	AFAD	Passive	Mostly diurnal	Mostly nightime
Ohta and Kakuma (2005)	YF/BE	Japan	AFAD	Passive	Mostly diurnal	Nightime
Babaran et al. (2009)	YF < 30 cm/RR	Philippines	AFAD	Passive	No clear pattern	No clear pattern
Mitsunaga et al. (2012)	YF < 30 cm	Philippines	AFAD	Passive	Diurnal	Nightime
Mitsunaga et al. (2013)	YF < 30 cm	Philippines	AFAD	Passive	Diurnal	Nightime
Govinden et al. (2013)	SKJ/YF	Maldives	AFAD	Passive	No clear pattern	SKJ = seasonal
						YF = no clear pattern
Schaefer and Fuller (2005)	SKJ/BE	EPO	AFAD/DFAD	Passive	SKJ = night	SKJ = Daytime
Matsumoto et al. (2006)	SKJ/YF/BE	CPO	DFAD	Active	No clear pattern	Fairly uniform
Govinden et al. (2010)	SKJ/YF/BE	MZC	DFAD	Passive	Diurnal	Nightime
Schaefer and Fuller (2013)	SKJ/YF/BE	EPO	DFAD	Passive and active	SKJ = mostly diurnal	SKJ = nightime (60%)
					BE = fairly uniform	–
					YF = mostly nocturnal	–
Matsumoto et al. (2014)	SKJ	CPO	DFAD	Passive and active	Mostly diurnal	Nightime

during a scientific cruise in the Mozambique Channel. All the DFADs were left to drift freely with no constraints on distance, orientation or time. A total of 1856 acoustic samples were collected, covering 315 observation days (average = 5.9 samples/day and 63.8 days/DFAD) (Table 2). Acoustic samples were managed and monitored through the ELB3010 manager software (Satlink, Madrid, Spain, http://www.satlink.es). This software allows the acquisition, control, and monitoring of echo-sounder buoy data and enables continuous communication with buoys to request real-time location information or change the configuration of the sampling frequency of the buoy.

The Satlink buoy contains a Simrad ES12 sounder, which operates at a frequency of 190.5 kHz with a power of 140 W (beam angle at −3 dB: 20°). The observation depth range extends from 3 to 115 m (with a transducer blanking zone from 0 to 3 m) and is composed of ten homogeneous layers, each with a resolution of 11.2 m. At an angle of 40°, the cone of observation under the buoy has a diameter of 83.71 m at a depth of 115 m. The echosounder provides acoustic information (area backscattering coefficient, s_a, m^2 m^{-2}; MacLennan 2002) for each depth layer. The sounder was programmed to operate for 40 s every hour. During this period, 32 continuous pings were sent from the transducer and an average of the backscattered acoustic response was computed and stored in the buoy until they were transmitted via satellite (Inmarsat-C). Various satellite connection errors impeded reliable data transfer, resulting in loss of part of the original data. Echo-sounder buoys were calibrated before the survey by the manufacturer at origin. Volume backscattering strength [S_v, dB re 1 m^{-1}; Maclennan et al. (2002)] lower than −45 dB was automatically removed by the internal module of the buoy, because they likely correspond to organisms smaller than tuna [e.g., organisms of the sound

Fig. 1 Survey regions in the Western Indian Ocean (delimited by *grey lines* and defined from Pianet et al. 2000) and spatial distribution of the acoustic samples. Different *shapes of dots* correspond to actual drifting fish aggregating devices (DFADs) (MZC1, MZC2, NW Sey1, NW Sey2, etc). Each dot represents consecutive observations taken by the Satlink echo-sounder buoys (http://www.satlink.es, Madrid, Spain) attached to the same ten DFADs. A total of 1856 acoustic samples were collected in 315 observation days from the ten DFADs
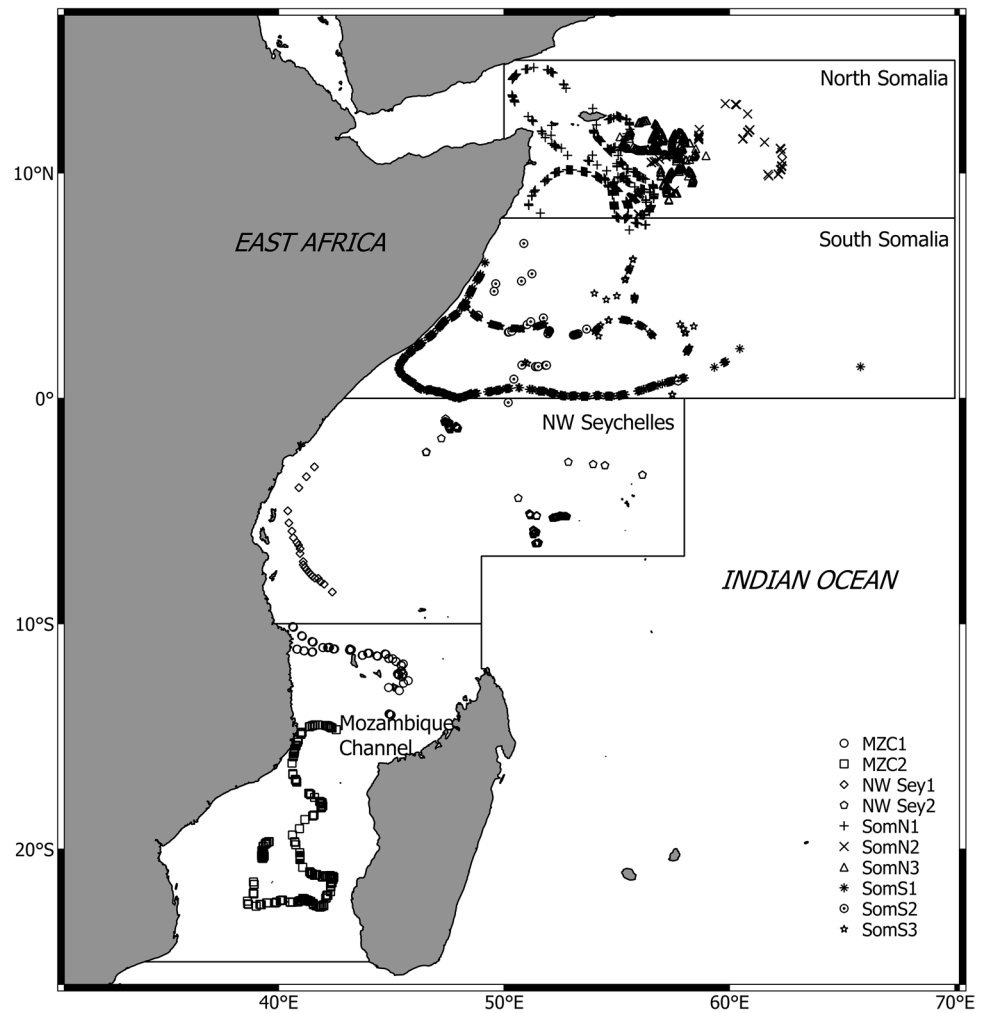
Table 2 Spatial–temporal distribution of the samples: number of acoustic samples and accumulated observation days by region, as well as the average number of samples by buoy or drifting fish aggregating device (DFAD) by each region of the present study and the number of samples collected by quarter (Q)

	Nb. Samples	Observation days	Average (sample/day)	Q1	Q2	Q3	Q4
North Somalia	738	130	5.68	–	–	475	263
South Somalia	665	94	7.07	174	290	128	73
NW Seychelles	171	25	6.84	–	–	118	53
Mozambique Channel	282	66	4.27	122	160	–	–
Total	1856	315	5.89	296	450	721	389

scattering layers (MacLennan and Simmonds 1992; Josse et al. 1998; Josse and Bertrand 2000; Oshima 2008)].

Published information on the vertical behaviour of DFAD-associated fish in the Indian Ocean (Moreno et al. 2007b; Taquet et al. 2007b; Forget et al. 2015) was used to merge the original ten layers of the buoy into three new layers. Whereas s_a from the first two depth layers (3–25.4 m) were assigned to non-tuna species, s_a from 25.4 to 80 m (layers 3 to 7) and from the deepest three layers (layers 8 to 10; from 80 to 115 m) were assumed to correspond to small and large tunas, respectively. In the present work, small tunas refer to skipjack of any size and juveniles of yellowfin and bigeye tuna (~50 cm fork length), while large tunas refer to adults of yellowfin and bigeye tunas (>100 cm fork length). Similar depth limits were adopted in the previous studies with the use of the same echo-sounder buoys to separate non-tuna species from tuna in the Indian Ocean (Lopez et al. 2010, 2016; Robert et al. 2013b). Additional

information obtained from 25 echo-sounder buoys deployed in the Indian Ocean between 2009 and 2012 (a total of about 2000 acoustic samples) supported this vertical segregation (Lopez et al. unpublished data). The plot of the average s_a recorded by each echo-sounder buoy depth layer (Fig. 2), combined with the behavioural information in the references cited above, suggested a potential segregation of tuna size increasing with depth, indicating a greater likelihood of larger tuna occupying waters deeper than 80 m (individuals with swim bladders). The large amount of acoustic backscatter recorded in the first 25 m could be due to the presence of non-tuna species, which are known to occur close to the sea surface and also have swim bladders. Skipjack tuna, the main target species of the fleet fishing around DFADs, is usually known to occupy medium depths and has no swim bladder. This vertical segregation seems to be in agreement with the previous findings
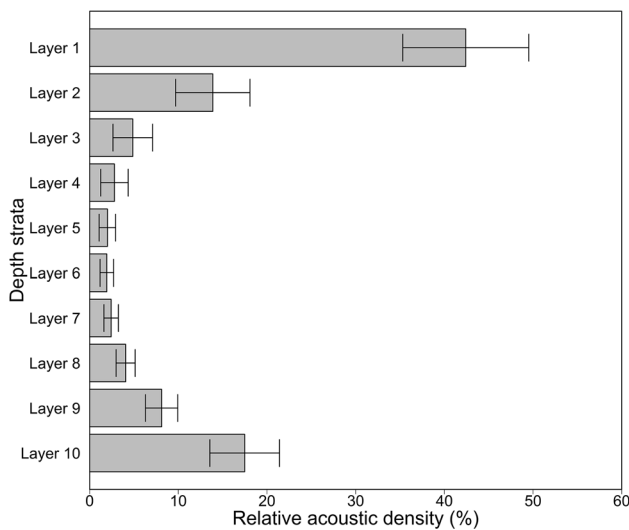

Fig. 2 Average percentages of acoustic backscatter (*black bars*) and their standard errors (*lines*) recorded at sunrise from about 2000 acoustic samples taken by 25 Satlink echo-sounder buoys attached to drifting fish aggregating devices (DFADs) in the Indian Ocean between 2009 and 2012 [Layers' depth ranges (m): *Layer 1* = 3–14.2; *Layer 2* = 14.2–25.4; *Layer 3* = 25.4–36.6; *Layer 4* = 36.6–47.8; *Layer 5* = 47.8–59; *Layer 6* = 59–70.2; *Layer 7* = 70.2–81.4; *Layer 8* = 81.4–92.6; *Layer 9* = 92.6-103.8; *Layer 10* = 103.8–115]

obtained through the conventional scientific echo-sounders around DFADs in the Indian Ocean (Moreno et al. 2007b).

In addition, GMT times recorded by the buoy were transformed to time of day (24 h) according to their geographical location.

Data analysis

Area backscattering coefficients for each new layer were transformed into biomass estimates (in metric tons) using a depth layer echo integration procedure (Simmonds and MacLennan 2005), based on (1) the target strengths suggested by Doray et al. (2007) and Moreno et al. (2007b), for non-tuna and tuna species aggregations (non-tunas −42 dB; small tunas −35.1 dB; and large tunas −29.9 dB), respectively, and (2) the weight of the most common sizes of fish found at FADs [i.e., 1 kg for non-tuna species (F. Forget, pers. comm.); 2 and 21 kg for small and large tuna, respectively (Floch et al. 2012)]. The estimated fish biomasses were assumed to represent the DFAD-associated biomass for the different fish categories.

Dynamics of fish biomass for area and for the three fish categories were investigated at a diel scale (i.e., 24 h) using time of day as a covariate in generalized additive models [GAMs; Hastie and Tibshirani (1990)]. The biomass of fish groups was log-transformed [Log_e(Biomass + 0.05)] to normalize the data (i.e., 0.05 is half the smallest non-zero value). GAMs with Gaussian error distributions with identity link functions were used in the modelling. Pearson correlations were performed to summarise the correlation between the log-transformed biomasses (Table 3). To investigate the potential ecological relationships existing between fish groups (i.e., attraction power, orientation cues, etc), log-transformed biomasses of non-tuna and small tuna were also introduced in the models when appropriate following the most logical trophic level hierarchy of the different fish categories [i.e., covariates were not introduced into the model when correlation was high between terms to avoid overfitting (Wood 2006)]. Thus, the effect of non-tuna species was considered in both small and large tuna models, but not the other way. Similarly, the effect of small tunas was considered in large tuna models but not vice versa. To avoid overfitting and to simplify the interpretation

Table 3 Pearson correlations between biomass of different fish categories at drifting fish aggregating devices (DFADs) by study region [*NT* non-tuna species, *ST* small tunas, *LT* Large tunas]

	North Somalia (n = 738)		South Somalia (n = 665)		NW Seychelles (n = 171)		Mozambique Channel (n = 282)	
	ST	LT	ST	LT	ST	LT	ST	LT
NT	0.248***	-0.054	0.173***	0.135***	0.432***	0.206*	0.294***	−0.024
ST	–	0.398***	–	0.752***	–	0.834***	–	0.447***

Signif. codes: *** 0, ** 0.001, *0.01

Sample size (*n*) added for information

of the results, two additional precautionary measures were taken into the account when establishing GAMs. First, the penalty (gamma) was increased from default 1 to 1.4, which puts a heavier penalty on each degrees of freedom in the GCV score and forces models to be a little smoother than they might otherwise be (Wood 2006; Zuur et al. 2009). Second, the maximum degrees of freedom (measured as number of knots k) allowed to the smoothing functions were limited to the main effects at $k = 6$ (Cardinale et al. 2009; Giannoulaki et al. 2013; Jones et al. 2014). It has been suggested that using these prudent defences against overfitting can largely correct this without compromising model fit (Kim and Gu 2004; Wood 2006). Therefore, the following models were fitted for each area and fish group:

$$\text{Biomass}_{\text{non-tuna}} = c(\text{Time of day}, k = 6), \text{gamma} = 1.4.$$

$$\text{Biomass}_{\text{small tuna}} = c(\text{Time of day}, k = 6) + s(\text{Biomass}_{\text{non-tuna}}, k = 6), \text{gamma} = 1.4.$$

$$\text{Biomass}_{\text{large tuna}} = c(\text{Time of day}, k = 6) + s(\text{Biomass}_{\text{non-tuna}}, k = 6) + s(\text{Biomass}_{\text{small tuna}}, k = 6), \text{gamma} = 1.4.$$

Where Biomass is the relative abundance of the fish group in log scale, c specifies a cyclic penalized cubic regression spline smooth, s represents a penalized thin plate regression spline type smoother based on generalized cross validation [GCV; Craven and Wahba (1978)], k is the maximum degrees of freedom allowed to the smoothing function, and gamma $= 1.4$ is an ad hoc way of avoiding overfitting (Kim and Gu 2004). When the estimated degrees of freedom of the splines of the biomass explanatory variables were close to their lower limit (i.e., close to 1 for univariate smoothing), the covariate in question was considered to be linear (Wood 2008).

The GAMs used the "mgcv" package [version 1.7-29; Wood (2014)] of the R program (Team 2013). "Deviance explained" (analogous to variance in a linear regression), adjusted r^2, and GCV scores were calculated for each GAM (Table 4). The shapes of the functional forms for the selected covariates were plotted. When the slopes of the functional forms are positive, the covariates are related positively to the dependent variables, or vice versa. Selected models allowed prediction of biomass in unsurveyed hours.

Data interpretation

Two fisheries data sources were used to explore factors that may affect diel behaviour: (1) catch data and (2) fishing activity information (i.e., setting time). Non-tuna and tuna species composition by region, and for the surveying period were extracted and analysed from AZTI's observer data and the IRD's SARDARA catch database (a database including corrected catch effort and size frequencies for

tropical tunas and other major exploited species), respectively. Whereas non-tuna species and skipjack tuna were analysed as a single size group (i.e., percentage of the presence in the total catch and no matter the size), relative catch of yellowfin and bigeye tuna species was estimated for two size classes (i.e., small and large, limit at 10 kg.) following the criteria proposed by Fonteneau et al. (2000).

In addition, a total of 2908 FAD sets were analysed from Spanish skippers' logbooks (2009–2010, ANABAC ship owners association's data) to study their distribution along a 24-h time period and by considered region. As with buoy times, the original GMT times recorded in the logbooks were transformed to time of day according to their geographical location. The time when the set started was used to calculate the hourly distribution of setting times in the four study areas.

Results

Model interpretation

Setting times

The analysis showed that a large proportion of the DFAD sets were carried out in the early morning, before or just after sunrise, a pattern found to be very similar for all the studied areas: 45% of the DFAD sets were initiated prior to or at 7 AM and a second slight peak was identified between 9 and 10 AM, accounting for about 15–20% of the total number of sets. Overall, 77% of all the sets were initiated before noon (Fig. 3).

Catch species composition

Skipjack tuna dominated the catch everywhere (43–76%), followed by small yellowfin (11–15%) and small bigeye (5–12%). In general, small tuna accounted for about 90%, or more, of the total catch. However, in NW Seychelles, small tuna represented only 64% of the total catch, where large yellowfin (>10 kg.) reached 35% (usual values between 3 and 10%). The amount of large bigeye found in the total catch was low everywhere (<0.5%). An analysis of the small tuna catch composition in detail indicated that values were similar in every region. Skipjack tuna dominated the catch (i.e., about 70–80%), while yellowfin and bigeye tunas accounted for between 15 and 20% and between 5 and 15% of the total catch, respectively (Fig. 4).

Four-to-six species comprised more than the 80% of the total catch of non-tuna species in every region (Fig. 5). Triggerfish (*Canthidermis maculata*) dominated non-tuna species catches (40–65%), followed by rainbow runner (*Elegatis bipinnulata*) (5–35%). In addition, both species
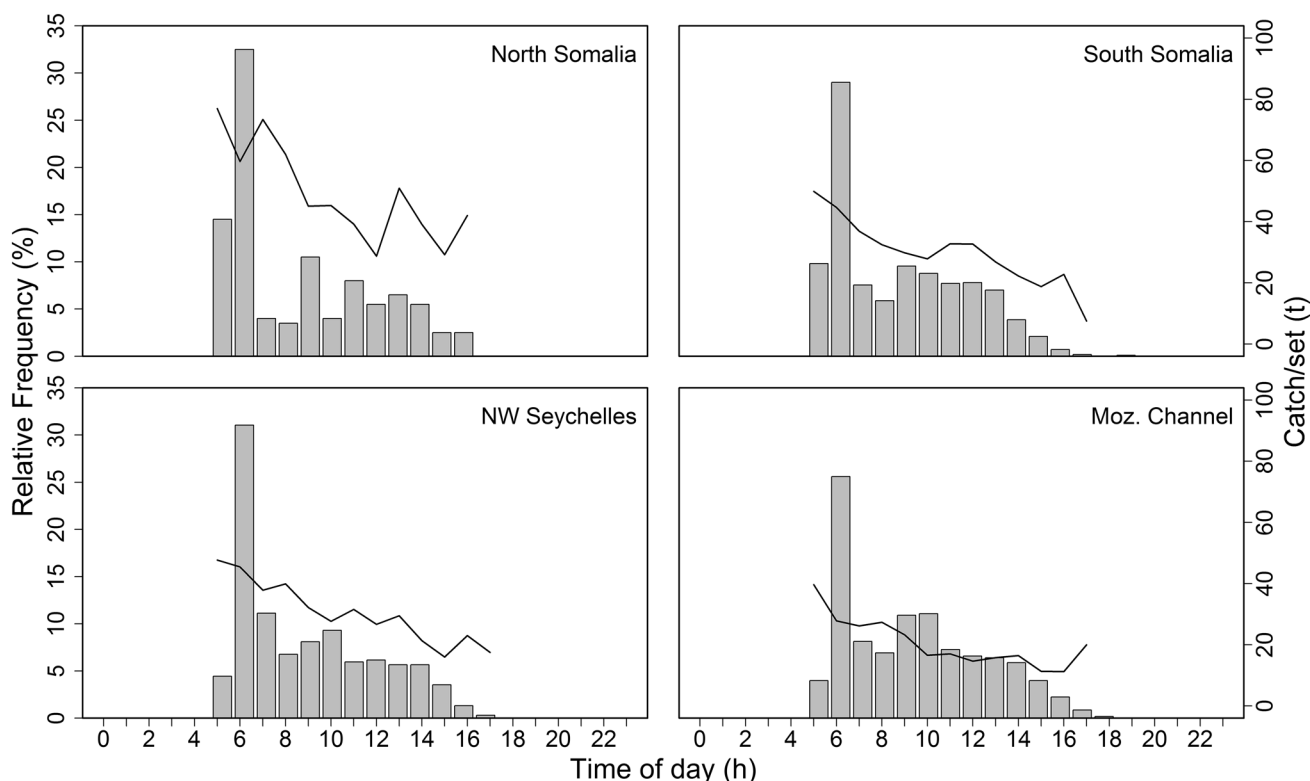
Fig. 3 Percentage of drifting fish aggregating device (DFAD) sets observed on the Spanish fleet in each region as a function of time of day when the set started. In addition, catch rates (*t*) of the Spanish fleet as a function of time of day when the set started are presented for each of the region considered in the study

Fig. 4 Average species composition (**a**) and size (**b**) of drifting fish aggregating device (DFAD)-associated purse seine catches in the Western Indian Ocean by region (*N Som*. North Somalia, *S Som*. South Somalia, *NW Sey*. North West Seychelles; *Moz. C*. Mozambique Channel) and for the period of the acoustic sampling as recorded in the SARDARA database
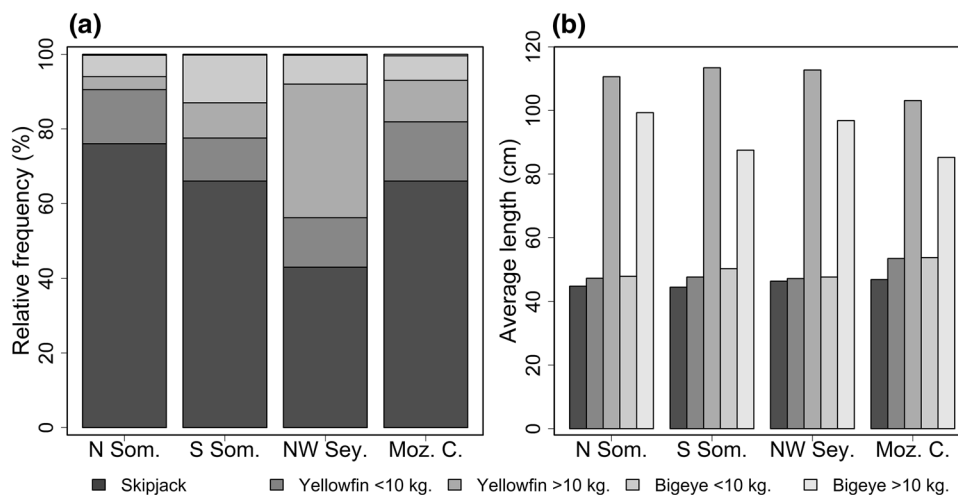
were the only ones found in all the regions. Dolphinfish (*Coryphaena hippurus*) and Starry Triggerfish (*Abalistes stellatus*), although absent in the NW Seychelles area, were also a commonly caught species in the study area, accounting for near 5–10% of the total non-tuna catch. Other species, in aggregate, accounted for about 10–15% of the total catch.

Effect of time of day and biological factors on tuna and non-tuna species

Selected GAMs for each fish category and region are summarized in Table 4. Effective covariates differed among the various models. All the smooth terms were always significant ($P < 0.05$) or highly significant ($P < 0.001$), except for

Fig. 5 Average species composition of drifting fish aggregating device (DFAD)-associated purse seine non-tuna species catches in the Western Indian Ocean by region (*N Som.* North Somalia; *S. Som.* South Somalia; *NW Sey.* North West Seychelles; *Moz. C.* Mozambique Channel) and for the period of the acoustic sampling as recorded in the AZTI's observer database

Non-tuna species
- ☐ Other spp.
- ☐ Platax teira
- ☐ Kyphosus cinerascens
- ☐ Decapterus macarellus
- ☐ Aluterus monoceros
- ☐ Coryphaena hippurus
- ☐ Abalistes stellatus
- ☐ Elagatis bipinnulata
- ■ Canthidermis maculata
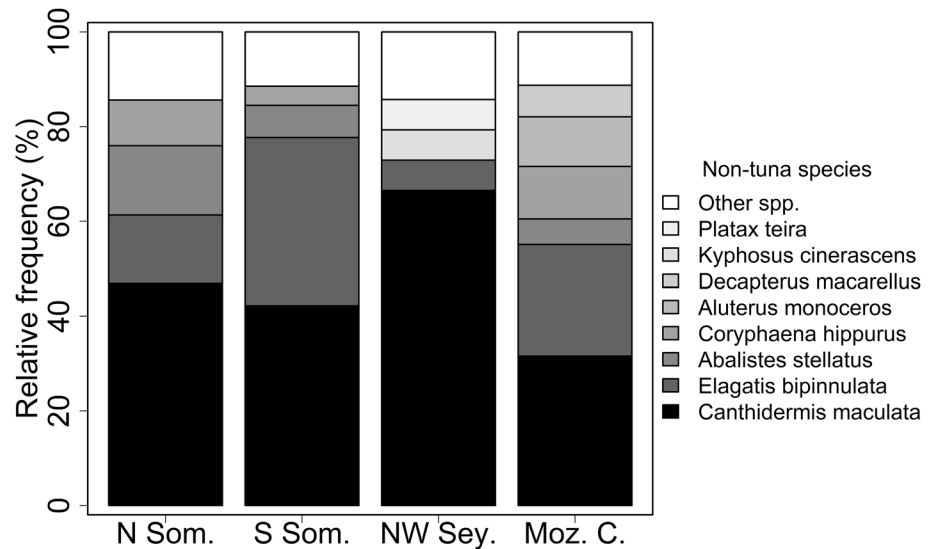
time of day for non-tuna species in South Somalia and NW Seychelles. In general, adjusted r^2 and deviance explained increased from non-tuna to small tuna models, and from small tuna to large tuna models. The exception was NW Seychelles, where the model for small tunas showed slightly better results than large tuna model. For example, adjusted r^2 improved from 0.018 to 0.355 for non-tuna to large tuna models in North Somalia, respectively, and so did the deviance explained from 2.2 to 36.4.

The shapes of the functional forms for selected covariates for the different fish categories by region are illustrated in Figs. 6 and 7, where the ordinates represent the relative importance of the predictor variable on the response variable (i.e., fish biomass). These figures indicate that biomasses for each category depended, in general, non-linearly on the covariates.

Day–night patterns

The impact of time of day appeared to be higher for tuna species than for non-tuna species (Table 4). Significant differences are shown between the associative behaviour of tunas and non-tuna species everywhere (Fig. 6). Whereas non-tuna species displayed similar behaviour patterns whatever the geographical location, with maximum biomasses observed around sunrise followed by a second peak at noon, tuna species showed large differences between regions. The two different size classes of tuna showed similar behaviour patterns in all locations except in the Mozambique Channel, where small and large tunas presented differences (Fig. 6).

In general, tuna displayed two marked behaviour patterns according to their geographical location. Whereas larger total tuna biomasses seemed to associate with DFADs during night-time in the northern regions of the

Western Indian Ocean (i.e., Somalia areas), DFADs in the southern regions (i.e. NW Seychelles and Mozambique Channel) showed higher tuna biomasses at daytime. In the Somalia area, maximum biomasses of both small and large tunas were recorded few hours before sunrise, usually followed by a slight second peak approximately at noon or few hours later. Functional shapes for both small and large tunas in the NW Seychelles followed a Gaussian-shaped pattern with maximum values recorded at noon. In the Mozambique Channel, the moment at which both small and large tuna presented their maximum values of biomass did not converge. The functional form elucidated by the GAMs for small tunas indicated maximum biomass in the moments prior to sunrise, while large tunas' abundance peaked at noon (Fig. 6).

Biological interactions

Table 3 shows differences on the correlations between biomass of different fish categories across regions. In general, the abundances of non-tuna and large tuna were positively correlated with small tuna biomass. In particular, the correlation between biomass of tunas of different sizes (min = 0.398; max = 0.834) was stronger than between non-tuna and small tuna (min = 0.173; max = 0.432). In contrast, non-tuna biomass was positively correlated with large tuna in South Somalia and Northwest Seychelles, but non-significantly correlated in North Somalia and Mozambique Channel (Table 3).

Functional forms of the effect of biological parameters (i.e., biomass of a given group) on a known fish category for each region are shown in Fig. 7. The presence of non-tuna species had normally positive effects on both small and large tuna biomass (either with linear or Gaussian-shaped patterns with maximum values at medium–high

Table 4 Results of the GAMs showing the effect of time of day and biological factors on non-tunas (NT), small tunas (ST), and large tunas (LT) [-covariate not included in the model]. Time of day was always included in the models as covariate, while biological covariates were included in the models following the most logical trophic level hierarchy of the different fish categories. Thus, the effect of non-tuna species was considered in both small and large tuna models, but not the other way. Similarly, the effect of small tunas was considered in large tuna models but not vice versa, except in South Somalia and NW Seychelles to avoid overfitting, where correlation was high between terms

Parameter	North Somalia			South Somalia		
	NT	ST	LT	NT	ST	LT
Adjusted r2	0.018	0.237	0.355	0	0.191	0.308
Deviance explained (%)	2.2	24.2	36.4	0	19.7	31.4
GCV score	0.97	0.867	0.578	0.148	0.338	0.72

Covariates	NT df	NT P	ST Df	ST P	LT Df	LT P	NT Df	NT P	ST Df	ST P	LT Df	LT P
	(North Somalia)						(South Somalia)					
NT	–	–	1	<0.0001	1.209	<0.0001	–	–	1	<0.0001	2.121	<0.0001
ST	–	–	–	–	4.811	<0.0001	–	–	–	–	–	–
Time of day	3.502	<0.01	3.891	<0.0001	3.835	<0.0001	0	0.743	3.787	<0.0001	3.918	<0.0001

Parameter	NW Seychelles			Mozambique Channel		
	NT	ST	LT	NT	ST	LT
Adjusted r^2	0	0.29	0.213	0.117	0.276	0.346
Deviance explained (%)	0	30.5	23.2	12.9	28.9	37.7
GCV score	0.043	1.516	1.869	0.572	1.323	0.163

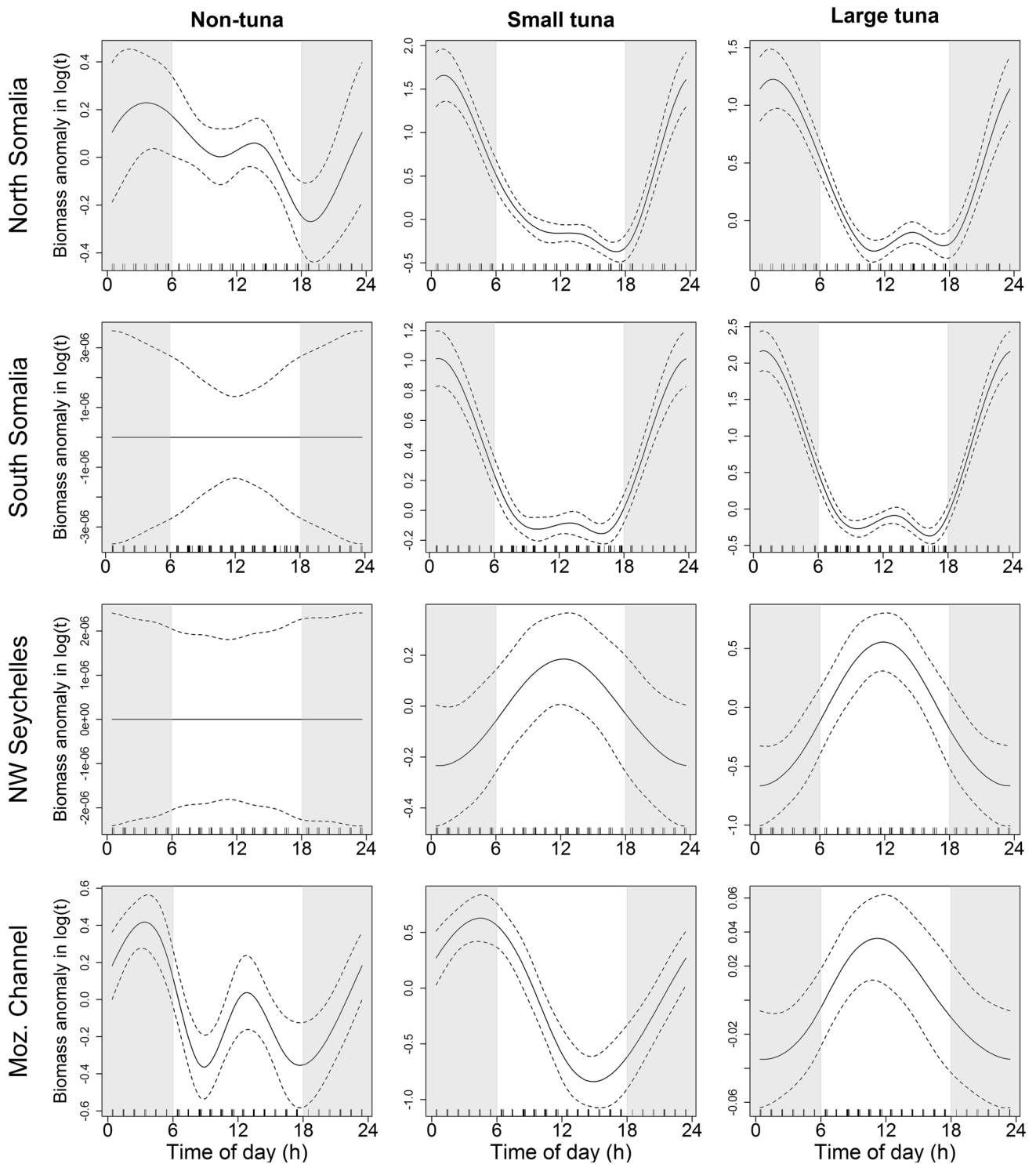| Covariates	NT Df	NT P	ST Df	ST P	LT Df	LT P	NT Df	NT P	ST Df	ST P	LT df	LT P
	(NW Seychelles)						(Mozambique Channel)					
NT	–	–	2.427	<0.0001	2.034	<0.0001	–	–	2.47	<0.0001	2.059	<0.01
ST	–	–	–	–	–	–	–	–	–	–	4.525	<0.0001
Time of day	0	0.666	1.234	<0.05	2.009	<0.0001	3.792	<0.0001	2.61	<0.0001	1.98	<0.1

Fig. 6 Smoothed fits of time of day modelling the biomass abundance of different fish categories considered in the present study. *Shadowed area* reflects night periods. *Tick marks* on the *x-axis* are observed data points. The *y-axis* represents the spline function. *Dashed lines* indicate 95% confidence bounds

non-tuna biomass levels), except in North Somalia and Mozambique Channel, where negative trends close to linear were shown for large tuna.

The effect of small tuna biomass on large tuna biomass was positive in both North Somalia and in Mozambique Channel, for which positive peaks were identified at low
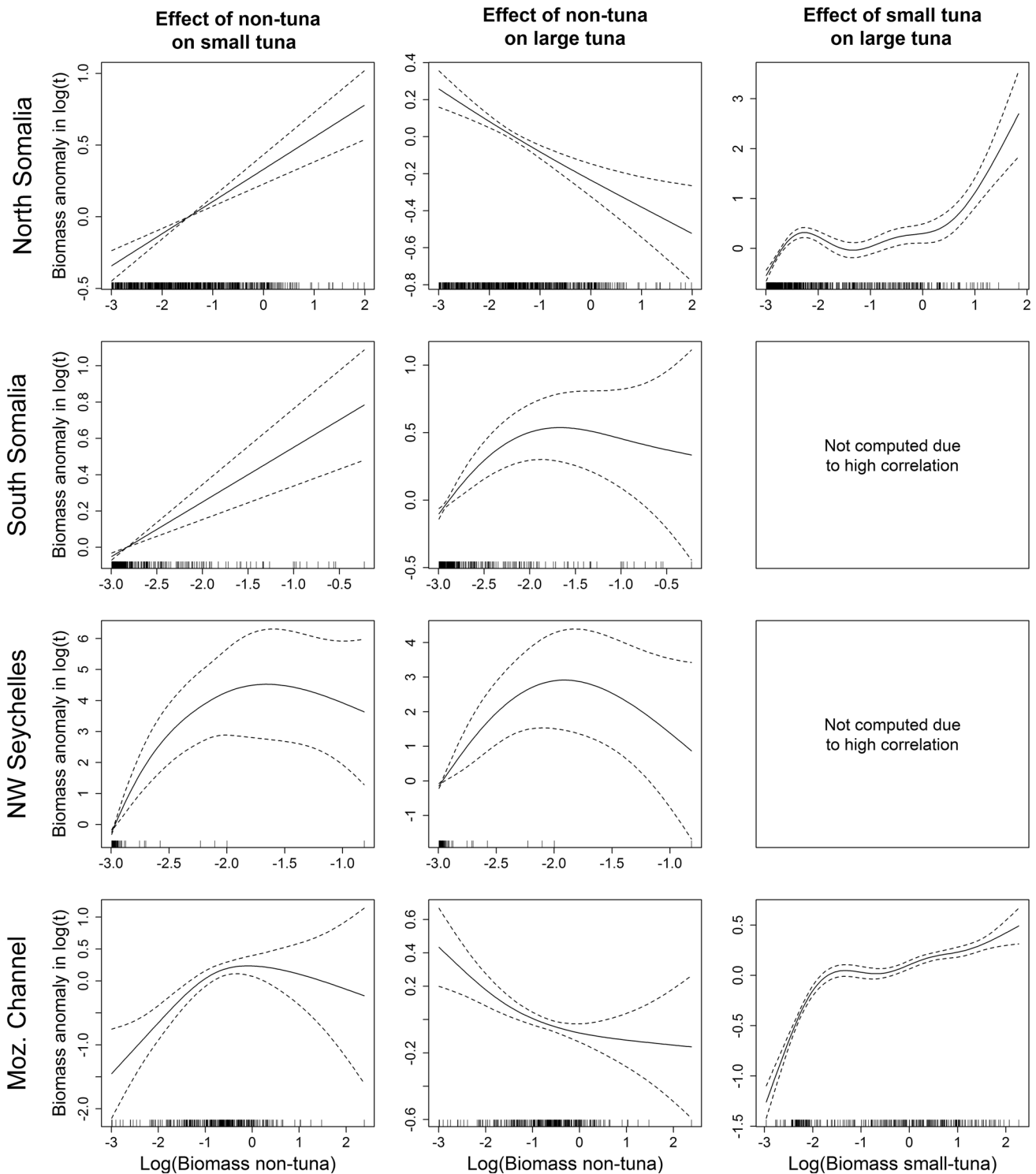
Fig. 7 Smoothed fits showing the relative effect of biological factors (biomass of non-tunas and small tunas) on the biomass abundance of different size classes of tuna (i.e., small and large tuna). *Tick marks* on the *x-axis* are observed data points. The *y-axis* represents the spline function. *Dashed lines* indicate 95% confidence bounds

small tuna biomass values. No relationship between small tunas and large tunas in South Somalia and NW Seychelles could be established in the GAMs due to the high positive collinearity between both variables. This prevented us from estimating the shape of their functions but reflected that the presence of large tunas was strongly and positively related to the amount of small tunas in these regions also.

Discussion

Using for the first time echo-sounder buoy data, this study provides information on the region-specific dynamics of fish aggregations at DFADs around the day-night cycle. The present work reveals that tuna associated with DFADs in the Somalia area showed a clear night-time associative behaviour, while tunas associated with DFADs in the Southern areas (i.e., NW Seychelles, Mozambique Channel) showed a more diurnal associative behaviour, with the exception of small tunas in Mozambique Channel, who showed a night-oriented associative behaviour. This study also shows that the presence and amount of other individuals at DFADs may be of great interest for tuna species. In general, an increasing biomass of fish at DFADs had positive effects on the associative behaviour of tunas in a 24 h scale, suggesting that potential ecological interactions exist between fish categories (e.g., FAD-attraction, orientation cues, and fish density-dependent behavioural patterns), which will be discussed in detail later.

The individual associative behaviour of several species around FADs has been investigated for many years (Table 1). Various authors (Ohta and Kakuma 2005; Dagorn et al. 2007; Taquet et al. 2007a; Robert et al. 2012, 2013a; Govinden et al. 2013; Schaefer and Fuller 2013; Forget et al. 2015) have recorded presences and absences of several hours for tagged tuna and non-tuna species associated with FADs, and suggested the existence of regular temporal patterns with a periodicity of 24 h. For example, Ohta and Kakuma (2005) revealed that tunas returned to moored FADs in Japan typically around 9 PM, while Doray et al. (2009) found repeated maximum abundances of tunas at 11 AM in AFADs in Martinique using traditional acoustics. To date, most of the tagging studies done around FADs have found higher detection rates of individuals during daytime; although it should be noted that other studies found the opposite or no clear patterns (Table 1). Regional and species-specific differences have also been detected when investigating excursion activity: whereas some studies found greater departure-arrival events at night, other investigations have reported higher excursion rates during daytime (Table 1). Thus, tagging evidence suggests that the behaviour of fish species associated with FADs is variable.

However, the majority of studies available are based on tagging individuals, and not on the collective dynamics of fish aggregations. Our study, focusing on the dynamics of the aggregations also found periodicity and region and species-specific associative behaviours (see the first lines of discussion or Sect. 3.2.1 for details). The reasons behind these different associative behaviours are difficult to infer, especially when in situ biological sampling is lacking for verifying the taxonomic composition at studied DFADs. An exploration of catch statistics showed potential regional differences in the species and size compositions of the fish associated with our DFADs. However, these differences may be not the only responsible of the observed behaviour variability as the associative behaviour of fish is a result of an unknown combination of factors (Leroy 2013). The abiotic (i.e., oceanographic variables, DFAD densities, seasonality, etc) and biotic components of the environment (i.e., occurrence of other conspecifics and allospecifics, presence of predators, etc) may also influence the associative behaviour of the fish. In that sense, prey availability has been reported to be significant in determining the daily and seasonal distribution of large pelagic species (Pitcher and Parrish 1993; Bakun et al. 1998; Lemos and Gomes 2004; Miller 2007; Marsac et al. 2014; Leroy et al. 2015). Unfortunately, no automatic recording tool currently exists for monitoring the abundance of tuna prey around DFADs. Scientific surveys coupling acoustics with experimental fishing or video recorders around DFADs to infer the potential prey density of a particular area would improve our understanding on the associative behaviour-environment relationship. Likewise, comparing residence times of species at DFADs with fine-scale remote sensing data would also contribute to better understand the effect of local community structure, prey availability, and environmental drivers on the associative behaviour of the fish.

Seasonality of the Indian Ocean is highly marked by monsoonal pattern (Schott et al. 2007) which includes two monsoon periods (northeast from December to March and southwest from June to September) and two inter-monsoon periods (northeast from October to November and southwest, from April to May). It is widely accepted that the Indian monsoon regulates the climate by instilling an annual cycle that affects the marine ecology (Jury et al. 2010). As climatic and oceanographic variability may drive the seasonal distribution and behaviour of tunas and non-tuna species, a non-seasonal sampling should be conducted in all the western Indian Ocean when possible and extend current data and analysis. However, this imply significant logistical difficulties for balanced scientific sampling as Indian Ocean tuna fishing is highly seasonal [e.g., fishery only enters to Mozambique Channel from March to May (Davies et al. 2014)]. Accessing to larger echo-sounder buoys data sets, including those fishers' buoys that are no more operational for fishing purposes but still are recording information or data transfer with reasonable time delays (i.e., months and years) would significantly improve our knowledge on the behavioural patterns of the species by region. Bearing in mind that fishing companies may buy and use 45,000–70,000 new buoys annually (Baske et al. 2012), international bodies should support and guarantee reliable science-industry data transfer to use the final findings in favour of sustainable management of exploited resources.

This study shows that, on a diel scale, the greater the presence and amount of other animals at DFADs the larger the biomass of associated tunas (except in North Somalia and Mozambique Channel, where negative relationships were found between non-tuna species and large tuna). The causes driving this positive correlation may be various. On one hand, tuna associative behaviour may be fish density-dependent (Doray et al. 2009), and thus, an increasing abundance of fish at DFADs could lead to stronger attraction and retention behaviours. Thus, small-scale, aggregative processes could modulate the diel biomass variability of tunas. The biological interactions between fish have also been suggested by other authors (Ohta and Kakuma 2005; Soria et al. 2009; Capello et al. 2011; Robert et al. 2012, 2014), who highlighted the importance of social stimuli on determining behaviour patterns of tunas and other species at AFADs.

On the other hand, the presence of other individuals, especially non-tuna species due to their demonstrated near continuous occurrence at DFADs throughout the day, may facilitate tuna to locate and associate with floating objects. In fact, sound produced by other animals or the anchoring structure (Ghazali et al. 2013), as well as other sensory signals (chemicals, etc.) (Dempster and Kingsford 2003) have been suggested as potential attraction and orientation cues for relocating AFADs after excursions. In that sense, the presence of fish at DFADs, which lack the anchoring structure, may play a significant role in the detection process of the DFAD. Studies investigating the aggregation–segregation phenomenon in detail would be necessary as understanding the key drivers of the associative behaviour of fish is of primary importance for an adequate management of exploited resources.

The 24 h dynamics of the aggregations showed by both small and large tunas seem to be similar across the different regions of the Western Indian Ocean, except for the Mozambique Channel, where behaviour appears to be size specific (Fig. 6). Reasons behind this phenomenon are unclear and may range from having different biological needs, such as prey class preferences or survival practices, to the special hydrographic characteristics supported by each region. It could also be possible that overlap exist between the different sizes of tunas in the fixed vertical limits. However, the size-specific behaviour observed in the Mozambique Channel suggests that the used limits are able to reflect the differences existing between groups when occurring. The Mozambique Channel is known for having a complex circulation influenced by mesoscale eddies and fronts (Tew Kai and Marsac 2010) and for being a region less affected by man-made DFAD deployments in the Western Indian Ocean (Dagorn et al. 2013). According to fishers, these features mean that fish have very specific behaviour in the area; moving from free-swimming

schools to DFADs, or vice versa, very rapidly. These particular conditions in the area may interweave with the associative behaviour of different size classes of tuna. Up to date, the behavioural interaction and communication between different sizes of tunas have not been investigated in depth. Very few studies have simultaneously considered different size classes of tunas in their tagging experiments [except Schaefer and Fuller (2005); Robert et al. (2012)], and hence, the basic principles of size-specific behaviour traits and their relationships remain uncertain. Further investigations should examine these interactions in detail by coupling telemetry techniques and acoustic technology (i.e., scientific echo-sounders or echo-sounder buoys), since understanding size-specific behaviour patterns appears to be critical for future experiments and behavioural assumptions.

Analysis of the distribution of the setting times of Spanish purse seines (Fig. 3) showed that tuna catch may not always be maximized following current practice. The time at which Spanish purse seiners more frequently set on DFADs (around 6 AM) did not always match the maximum abundance of tunas at DFADs. Conversely, it normally coincided with the non-tuna species maximum abundance, although biomass variability of this group is believed to be relatively temporally stable (Moreno et al. 2007a; Dagorn et al. 2012a) (reflected in this study by the low scores of GAM parameters of this group). As non-tuna species associate very strongly with DFADs and leaving them only for short periods of time (<2 h) (Forget et al. 2015), the continuous presence of non-target species at DFAD is virtually ensured day and night. Considering the high variability of the biomass of tunas at DFADs in a daily basis, managing the setting time of the purse seines may have significant positive effects on the conservation of non-target species. In fact, monitoring pre-set non-tuna to tuna catch ratio has been suggested as an advantageous tool to control and mitigate the effects of tropical tuna purse seine fishery on the pelagic ecosystem, and especially on non-target species (Dagorn et al. 2012a). We believe that, in a full retention policy and ecosystem-based fishery management scenario (Pikitch et al. 2004), which is currently under discussion in t-RFMOs, new tools that provide continuous information on this ratio should be a priority.

This study demonstrates that echo-sounder buoys, in conjunction with new quantitative methods and an appropriate sampling strategy, can be used to remotely infer the potential non-target to target species proportion of the catch at a given time of the day. The information and results provided by the current work should be considered a first step to address non-target species conservation issues based on monitoring pre-set non-tuna to tuna catch ratio. Further investigations combining both scientific acoustics and echo-sounder buoys and tagging should confirm the

observed collective behavioural patterns by fish category to suggest region-specific management measures. Similar experiments should also be extended to other oceans and regions as this information could be used to assist fishery managers and decision makers in the future (Moreno et al. 2015).

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