
Drifting along in the open-ocean: The associative behaviour of oceanic triggerfish and rainbow runner with floating objects

Forget Fabien ^{1,2,*}, Cowley Paul ², Capello Manuela ¹, Filmalter John D. ², Dagorn Laurent ¹

¹ MARBEC, University of Montpellier, CNRS, IFREMER, IRD, Sete, France

² South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

* Corresponding author : Fabien Forget, email address : fabienforget@gmail.com

Abstract :

Multispecies aggregations at floating objects are a common feature throughout the world's tropical and subtropical oceans. The evolutionary benefits driving this associative behaviour of pelagic fish remains unclear and information on the associative behaviour of non-tuna species remains scarce. This study investigated the associative behaviour of oceanic triggerfish (*Canthidermis maculata*) and rainbow runner (*Elagatis bipinnulata*), two major bycatch species in the tropical tuna purse seine fishery, at floating objects in the western Indian Ocean. A total of 24 rainbow runner and 46 oceanic triggerfish were tagged with acoustic transmitters at nine drifting FADs equipped with satellite linked receivers. Both species remained associated with the same floating object for extended periods; Kaplan-Meier survival estimates (considering the censored residence time due to equipment failure and fishing) suggested that mean residence time by rainbow runner and oceanic triggerfish was of 94 and 65 days, respectively. During daytime, the two species increased their home range as they typically performed short excursions (<2 h) away from the floating objects. Rainbow runner performed more excursions per unit time than oceanic triggerfish; the mean excursion index was 0.86 (± 0.8 SD) for oceanic triggerfish and 1.31 (± 1.1 SD) for rainbow runner. Ambient light intensity appears to be the stimulus triggering the onset and end of the associative modes. The observed prolonged residency of these two major bycatch species suggests that they are more vulnerable to the tropical tuna purse seine gear than the targeted tuna species.

Highlights

► The associative behaviour of oceanic triggerfish (*Canthidermis maculata*) and rainbow runner (*Elagatis bipinnulata*) were investigated using acoustic telemetry satellite linked receivers at floating objects in the western Indian Ocean. ► Both species remained associated with the same floating object for extended periods with mean residency estimated at 94 days for rainbow runner and 65 days for oceanic triggerfish. ► A strong diel pattern was observed for both species with short excursions (<2 h) away from the floating objects observed during the day. ► Ambient light intensity appears to be the stimulus triggering the onset and end of the associative modes. ► The observed prolonged residency of these two major bycatch species suggests that they are more vulnerable to the tropical tuna purse seine gear than the targeted tuna species.

37 Introduction

38 Large multispecies aggregations at floating objects are a common feature of the world's
 39 tropical and subtropical oceans. While a total of 333 species have been recorded at floating
 40 objects [Castro2001], it appears that far fewer, approximately 20 species, regularly associate
 41 with floating objects [Kingsford1993, Taquet2007]. Numerous hypotheses have been
 42 proposed to explain the causes of this associative behaviour [Castro2001, Freon2000]. An
 43 initial hypothesis was that fish use floating objects as shelter to reduce predation
 44 [Gooding1967, Hunter1967, Rountree1989]. While underwater observations provide some
 45 support to this hypothesis for small fish [Gooding1967], it does not appear to be valid for
 46 larger schooling species such as tunas. Other authors have suggested that association could be
 47 driven by trophic advantages, by predated on associated fish [Gooding1967, Kojima1956].
 48 While predation events have been observed at fish aggregating devices (FADs)
 49 ([Hunter1967], unpublished personal observation), diet studies of tropical tunas and dorado
 50 (*Coryphaena hippurus*) tend to indicate that the associated fauna does not represent a major
 51 component of the diet of predators at floating objects [Taquet2004, Menard2000]. The
 52 meeting point hypothesis suggests that fish use the floating object as a spatial reference point
 53 to facilitate schooling behaviour and form larger schools [Dagorn1999, Freon2000]. Another
 54 motive that has been suggested is that floating objects act as good indicators of productive
 55 environments by accumulating in rich frontal areas [Bakun2006, Hall1992].
 56 A striking characteristic of multispecies aggregations is that the community appears to be
 57 spatially structured relative to the floating objects. [Kojima1960] was the first to propose a
 58 categorisation of the community based on radial distribution relative to the floating objects.
 59 [Parin1992] then proposed three broad categories of spatial distribution: intranantant (< 50 cm
 60 from the object), extranantant (50 cm to 2 m from the object) and circumnattant (> 2m from the
 61 object) and subsequently, [Freon2000] proposed some distance modifications for these
 62 categories. However, none of these categories were determined empirically [Girard2007].
 63 Acoustic telemetry studies have allowed for empirical investigations on the distribution range
 64 of FAD-associated species, which varied from 300-400 m for dorado [Taquet2007a] to 5-10
 65 km for tunas [Dagorn2000c, Holland1990, Matsumoto2014]. With similar intent,
 66 [Moreno2007a] used acoustic surveys to observe the spatial distribution of biomass at
 67 floating objects and while distinct structures could be identified, species specific details could
 68 not be determined. Other than tunas, oceanic triggerfish (*Canthidermis maculata*) and
 69 rainbow runner (*Elagatis bipinnulata*) often form the bulk of the aggregations around floating
 70 objects [Romanov2002b, Lezama-Ochoa2015a, Amande2011], yet little is known about their
 71 associative behaviour, ecology or potential role in multispecies aggregation dynamics.
 72 Large schools of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye
 73 tuna (*T. obesus*) are found at floating objects and fisherman have used floating objects as a
 74 visual cue to locate pelagic fish in the open ocean. In the early 80's, tropical purse seiners
 75 started to deploy man-made floating objects (i.e. FADs), which were subsequently equipped
 76 with electronic buoys to facilitate their relocation [Fonteneau2000]. This strategy proved to
 77 be highly effective and rapidly lead to a massive increase in FAD deployments
 78 [Fonteneau2000]. Moreover, since the mid 2000s, FADs were equipped with echosounder
 79 buoys that provided fishermen with biomass estimates of target tuna species, allowing them
 80 to locate larger schools and considerably increased their fishing efficiency [Fonteneau2013,
 81 Lopez2014]. The annual landing of the tropical tuna purse seine fishery accounts for 5
 82 million tons of tuna of which about 60% originates from fishing on floating objects
 83 [Dagorn2013, ISSF 2019]. In the Indian Ocean, the total catch of tropical tuna is about 1
 84 million tons with the purse seine fishery . The recent implementation of a yellowfin tuna
 85 quota in the Indian Ocean considerably increased the effort on FAD fishing as the proportion

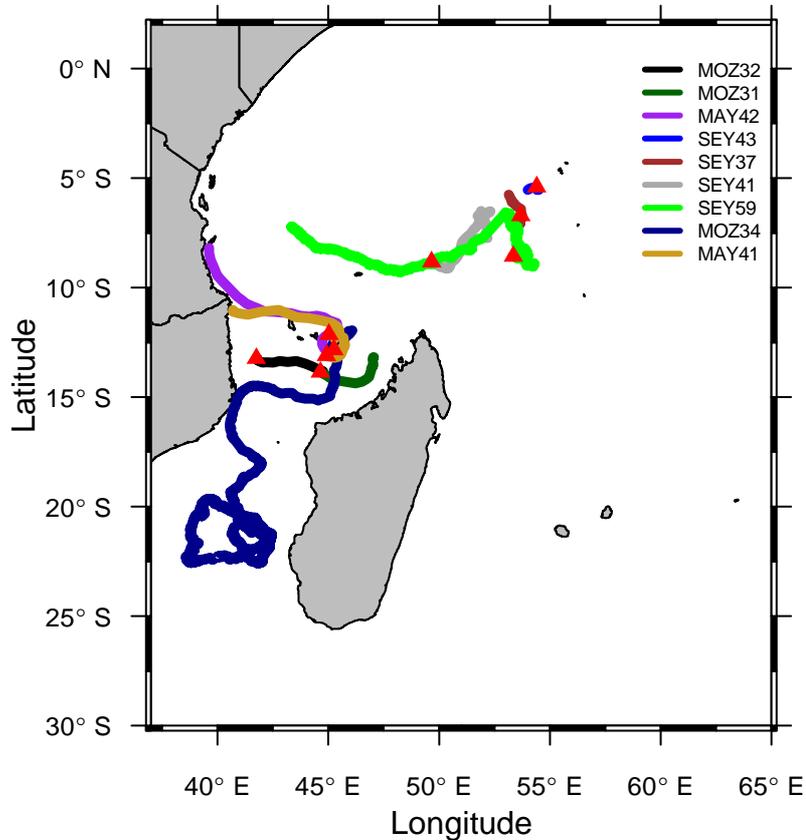
86 of FAD sets by purse seine fleets now represents between 90-96% (fleet dependent) of total
87 sets [Fiorellato et al. 2019]. The multispecies nature of aggregations around floating objects
88 means that this practice generates 2.8–6.7 times (ocean dependant) more bycatch than when
89 fishing on free-swimming tuna schools [Dagorn2013]. The most dominant incidentally
90 captured non-target species at FADs include dorado, rainbow runner, oceanic triggerfish,
91 wahoo (*Acanthocybium solandri*) and silky shark (*Carcharhinus falciformis*) [Amande2011a,
92 Amande2011, Romanov2002b]. Owing to higher bycatch rates and the preponderance of the
93 FAD-based fishery, concerns have been raised on its impacts on pelagic ecosystems and the
94 sustainability of this fishing practice has been questioned [Hall1996, Hall2000, Gilman2011].
95 Moreover, some authors suggested that drifting FADs could act as an ecological trap for
96 associated species. The ecological trap hypothesis suggests that massive seeding of drifting
97 FADs could have negative impact on the populations of associated species by altering the
98 natural movements of populations towards less favourable environments which could lead to
99 an increase in natural mortality and population declines [Marsac2000, Hallier2008a].
100 Currently, little to no data is available on the basic biology, ecology and behaviour of oceanic
101 triggerfish and rainbow runner associated with FADs. Information on their behaviour may
102 contribute towards a better understanding of the causes driving associative behaviour and
103 provide essential elements to a holistic understanding of multispecies aggregations at floating
104 objects. Additionally, with an increased emphasis placed on ecosystem based management,
105 key ecological parameters of captured species are required to evaluate the impacts of fishing
106 mortality on the ecosystem. This study aimed to characterise the associative behaviour of
107 oceanic triggerfish and rainbow runner at floating objects using acoustic telemetry. The
108 objectives were to 1) estimate the residency at floating objects 2) examine temporal patterns
109 in association, 3) determine if there is a species specific associative pattern and evaluate the
110 degree of similarity between individuals of the two species.

111 **Materials and methods**

112 **Acoustic tagging**

113 Four scientific cruises were conducted in the western Indian Ocean between March 2010 and
114 April 2012. These cruises took place in the Mozambique Channel and around the Seychelles
115 Archipelago. Drifting FADs were located through collaboration with European purse seine
116 skippers. Firstly, a VR4-Global (VEMCO, Amarix Ltd., Canada) acoustic receiver was
117 attached to the drifting FAD. These receivers utilise the Iridium satellite system to transmit
118 acoustic detection logs from tagged individuals on a daily basis. Oceanic triggerfish and
119 rainbow runner were caught using rod and reels or hand lines. Coded acoustic transmitters
120 (V9, V9P, V9TP and V9AP (120 s nominal delay, 69 kHz, 1H; Table 1) were surgically
121 implanted into the peritoneal cavity following the standard methods implantation technique
122 [Dagorn2007a, Schaefer2004]. Captured individuals were brought onboard using a scoop net
123 and placed on V-shaped tagging table. The fish were then rapidly examined to verify that no
124 injuries were sustained during capture. Only individuals that appeared to be in good condition
125 were tagged. The head of the fish was covered with a wet cloth, a hose pumping seawater
126 was placed by the mouth to irrigate the gills and a small incision (~2 cm) was made close to
127 the ventral midline into the peritoneal cavity. The tag was implanted into the peritoneal cavity
128 and two independent sutures were made to close the incision, the length of the fish was then
129 measured to the closest 0.5 cm (fork length for rainbow runner and total length for oceanic
130 triggerfish) and the fish was then released in close proximity (<100 m) to the monitored
131 FAD. Once tagging was complete, the FAD and attached VR4-Global receiver were left to
132 drift and the data was relayed remotely. Daily detection logs and position logs from the VR4-
133 Global receiver were then consolidated into a database for subsequent analysis. The FAD

134 drift patterns were constructed using positions obtained by the VR4-Global receiver (Figure
 135 1).



136
 137 Figure 1: Drift trajectories of the nine experimental FADs monitored in the western Indian
 138 Ocean. Red triangles indicate the starting point of the experiments.

139 Data Analysis

140 Residency

141 The total residence time (TRT) provides an indication of the residency of tagged fish at
 142 FADs. TRT is defined as the amount of time between the first detection and last detection
 143 before the fish permanently left the FAD. The time when an individual first associated with
 144 the floating object, prior to the experiment, is unknown. Hence, the real residency of
 145 individuals remains unknown. Additionally, some experiments were prematurely interrupted
 146 by either commercial fishing operations, resulting in the capture of the entire FAD
 147 aggregation, or by equipment failure. TRTs that were not interrupted artificially indicate that
 148 the individuals left the FAD of their own accord and were recorded as “natural departures”.
 149 In order to standardise the varying experimental durations to allow comparisons between the
 150 different FADs where tagging was conducted, a residency index was calculated for each
 151 individual. This index was calculated by dividing the TRT by the experimental duration for
 152 each FAD (Table 1). This standardised index ranges from 0 to 1 and is commonly used in
 153 acoustic telemetry to provide estimates of the relative residency of tagged individuals within
 154 an acoustic telemetry array [Afonso2012, Ledee2015]. In order to estimate the durations of
 155 residency of the two species at FADs, a survival analysis of the TRT was conducted. Survival
 156 analysis was used to analyse data where the outcome variable is the time until the occurrence
 157 of a particular event (here departure from FAD) with the added ability to handle censored

158 observations (i.e. truncations). Survival analysis has previously been used in acoustic
159 telemetry experiments with truncated data [Ohta2005, Robert2012a, Stehfest2013]. Kaplan-
160 Meier estimates of the survivor function of TRTs was calculated with 95% confidence
161 intervals. For comparative purposes, two Kaplan-Meier survival functions were generated
162 using i) TRTs considering censored data (i.e. stratified into natural departures and censored
163 data) and, ii) all TRTs with no censoring considered (i.e. all TRTs) to provide residence time
164 estimations and assess the effect of censored data on estimates. A log-rank test was used to
165 test the differences in survival functions between the two species. An exponential survival
166 regression model was then fitted to each of the censored and uncensored curves to provide an
167 estimation of residency for the two species at FADs. A constant hazard assumption was made
168 for the regression model, whereby the probability of leaving the FAD was independent of
169 time. Additionally, the mean of the uncensored TRT was calculated to allow comparisons
170 with other studies reporting residency at FADs.
171

172 **Temporal patterns in association**

173 Detection timelines were constructed for each FAD depicting all detections of tagged
174 individuals and were visually inspected to assess the patterns in the detection rates.
175 Additionally, detection time series were converted into hourly detection time series and
176 hourly chronograms were constructed to examine temporal patterns in associative behaviour.
177

178 Cyclical patterns in the associative behaviour of each individual were examined through a
179 fast fourier transformation (FFT) applied to the hourly detection rates and the resulting
180 spectral density was plotted. FFT indicates whether rhythmic patterns existed in the presence
181 of tagged individuals at FADs [Barnett2012]. Distinct peaks in the spectral density indicates
182 the presence of cyclic rhythms and the time scale at which they occur, denoting the
183 periodicity. The spectral analysis was performed on individuals that had ≥ 5 days of data to
184 ensure sufficient sample size for the analysis. Additionally, a continuous wavelet
185 transformation (CWT) was computed to examine the stability of the cyclic rhythms, such as a
186 diel pattern, over time. The CWT decomposes a time series into time-frequency space
187 [Percival2000] and has previously been used to examine cyclic rhythms in fish behaviour
188 [Alos2012a, March2010]. Morlet wavelets, using the “dplr” package in R, was used to
189 construct a 2-dimensional wavelet spectrum and calculate a point wise test with a 95%
190 significance level. Spectrograms were then inspected to determine how persistent the cyclic
191 rhythms were over time according to the significance of the signal.
192

193 Gaps in the detection time series are indicative of periods when individuals ventured outside
194 the range of the receiver. Excursions were defined as a detection gap of > 1 hour and were
195 used as temporal units to describe movements away from the FAD [Capello2015]. To assess
196 the level of variability in the excursion behaviour amongst individuals an excursion index
197 (EI) was calculated by dividing the total number of excursions by the TRT. This time
198 standardised index reflects the excursion activity of individuals and provided the number of
199 excursions per day. A high index value indicates more frequent excursions per unit time. The
200 distribution and durations of excursions were then examined over 24 hrs.
201

202 A cluster analysis was conducted to determine the degree of similarity, and synchronicity,
203 amongst individuals and whether there was a species-specific pattern in associations.
204 First, the detection time series were converted into hourly presence-absence time series to
205 remove the potential effect of detection variance and acoustic collisions. Secondly, for each
206 FAD, the hourly presence-absence time series were trimmed synchronously to obtain the

207 same time segments for each individual. Finally, a hierarchical clustering was computed
 208 using the Ward algorithm on euclidean distance matrices based on the presence-absence time
 209 series at each FAD using the R software [RCoreTeam2014].

210

211

212

213

214 Results

215 A total of 24 rainbow runner and 46 oceanic triggerfish were tagged at nine drifting FADs
 216 (Fig.1). Details of the tagging information are provided in Table 1. All 70 individuals were
 217 detected at the FAD where they were released. The cumulative number of observation days at
 218 FADs was 919.5 d for oceanic triggerfish and 538.1 d for rainbow runner, yielding a total of
 219 273 866 and 114 397 detections, respectively.

220

221 Table 1: Metadata of oceanic triggerfish (TRI) and rainbow runner (ELA) tagged at drifting
 222 FADs. TRT is the total residence time. * Denotes TRT with natural departures from FAD.

223 Rainbow runner lengths are given in FL and oceanic triggerfish lengths by TL.

224

Tagging		Species	Size (TL/FL cm)	FAD ID	Acoustic tag		Experiment		Excursion	
Date	Time				Type	ID	Duration (days)	TRT	Num.	Index
15/04/11	11:56	TRI	31.0	MAY41	V9TP	3601	21.4	20.7	1	0.0
15/04/11	11:42	TRI	30.0	MAY41	V9TP	3603	21.4	21.3	1	0.0
15/04/11	16:27	TRI	32.0	MAY41	V9P	64826	21.4	20.7	11	0.5
15/04/11	16:04	TRI	30.0	MAY41	V9P	64827	21.4	20.7	58	2.8
15/04/11	22:01	TRI	33.0	MAY41	V9P	64828	21.4	20.5	14	0.7
16/04/11	07:15	TRI	33.0	MAY41	V9P	64829	21.4	20.7	16	0.8
16/04/11	23:48	TRI	34.0	MAY41	V9P	64830	21.4	21.1	9	0.4
16/04/11	21:46	TRI	30.0	MAY41	V9P	64831	21.4	21.12	20	0.9
16/04/11	22:25	TRI	36.0	MAY41	V9P	64832	21.4	21.12	38	1.8
16/04/11	-	TRI	30.0	MAY41	V9P	64834	21.4	1.6*	0	0.0
20/04/11	11:59	ELA	24.0	MAY42	V9TP	3599	26.9	16.8*	1	0.1
20/04/11	12:16	ELA	23.0	MAY42	V9P	30112	26.9	24.3	70	2.9
20/04/11	18:45	ELA	23.0	MAY42	V9P	30114	26.9	24.6	81	3.3
20/04/11	08:02	ELA	23.5	MAY42	V9P	64819	26.9	24.7	56	2.3
21/04/11	-	ELA	23.5	MAY42	V9P	64835	26.9	24.7	66	2.7
20/04/11	11:46	TRI	32.5	MAY42	V9P	3605	26.9	24.3	16	0.7
20/04/11	11:05	TRI	32.5	MAY42	V9P	30113	26.9	10.5*	4	0.4
20/04/11	07:43	TRI	36.5	MAY42	V9P	64820	26.9	10.1*	2	0.2
20/04/11	07:10	TRI	34.0	MAY42	V9P	64821	26.9	8.0*	13	1.6
20/04/11	07:01	TRI	31.0	MAY42	V9P	64822	26.9	8.0*	6	0.7
21/04/11	16:50	TRI	32.0	MAY42	V9P	64823	26.9	9.1*	8	0.9
21/04/11	16:35	TRI	35.0	MAY42	V9P	64824	26.9	9.0*	9	1.0
15/03/10	18:21	TRI	33.0	MOZ31	V9P	64810	11.6	11.5	2	0.2
15/03/10	18:13	TRI	33.0	MOZ31	V9P	64811	11.6	7.3*	1	0.1
16/03/10	18:06	TRI	31.0	MOZ31	V9P	64813	11.6	10.8	28	2.6
16/03/10	17:58	TRI	32.0	MOZ31	V9P	64814	11.6	10.8	3	0.3
16/03/10	17:45	TRI	33.0	MOZ31	V9P	64815	11.6	9.3	2	0.2
16/03/10	07:37	TRI	33.0	MOZ31	V9P	64816	11.6	10.8	0	0.0
16/03/10	16:17	TRI	33.0	MOZ31	V9P	64817	11.6	10.8	1	0.1

21/04/11	07:04	TRI	32.0	MOZ32	V9P	64809	10.8	11.0	0	0.0
08/03/10	11:25	ELA	45.0	MOZ34	V9P	64804	67.0	67.0	172	2.6
08/03/10	11:39	ELA	43.0	MOZ34	V9P	64805	67.0	67.0	172	2.6
09/03/10	18:53	TRI	28.0	MOZ34	V9	54304	67.0	26.8*	18	0.7
09/03/10	11:13	TRI	31.0	MOZ34	V9	54305	67.0	66.2	171	2.6
09/03/10	11:59	TRI	39.0	MOZ34	V9P	64806	67.0	66.2	80	1.2
09/03/10	12:05	TRI	34.0	MOZ34	V9P	64807	67.0	12.5*	9	0.7
09/03/10	07:19	TRI	30.0	MOZ34	V9P	64808	67.0	26.4*	34	1.3
22/06/11	17:40	ELA	65.0	SEY37	V9TP	3593	16.6	13.5	5	0.4
23/06/11	17:00	ELA	62.0	SEY37	V9TP	3595	16.6	15.4	1	0.1
24/06/11	14:05	ELA	79.5	SEY37	V9TP	3597	16.6	7.8*	3	0.4
24/06/11	14:30	ELA	77.0	SEY37	V9P	3621	16.6	11.4	1	0.1
23/06/11	17:45	TRI	30.5	SEY37	V9P	3617	16.6	10.8	0	0.0
23/06/11	18:00	TRI	28.0	SEY37	V9P	3618	16.6	10.8	0	0.0
24/06/11	13:52	TRI	30.0	SEY37	V9P	3619	16.6	10.1	1	0.1
24/06/11	14:15	TRI	30.5	SEY37	V9P	3620	16.6	13.5	3	0.2
13/04/12	14:48	ELA	63.5	SEY41	V9AP	4668	21.4	27.7*	36	1.3
14/04/12	08:56	ELA	28.5	SEY41	V9P	7072	21.4	29.8	75	2.5
14/04/12	11:30	ELA	30.0	SEY41	V9P	7073	21.4	29.8	77	2.6
14/04/12	18:32	TRI	29.0	SEY41	V9AP	4672	21.4	29.5	17	0.6
13/04/12	16:55	TRI	33.5	SEY41	V9P	7069	21.4	27.6*	93	3.4
14/04/12	07:40	TRI	30.5	SEY41	V9P	7070	21.4	29.9	50	1.7
14/04/12	08:02	TRI	30.0	SEY41	V9P	7071	21.4	29.9	30	1.0
18/06/11	14:00	ELA	30.5	SEY43	V9P	3586	4.4	3.4	1	0.3
19/06/11	10:59	ELA	57.0	SEY43	V9P	3588	4.4	3.3	2	0.6
19/06/11	11:20	ELA	32.0	SEY43	V9TP	3590	4.4	3.3	1	0.3
19/06/11	11:45	ELA	34.0	SEY43	V9P	3606	4.4	1.9	1	0.5
19/06/11	13:15	ELA	61.5	SEY43	V9TP	3607	4.4	2.3	1	0.4
19/06/11	13:45	ELA	79.0	SEY43	V9TP	3610	4.4	4.3	1	0.2
18/06/11	14:35	TRI	32.0	SEY43	V9P	3611	4.4	4.2	3	0.7
18/06/11	14:45	TRI	30.5	SEY43	V9P	3612	4.4	4.2	2	0.5
18/06/11	14:55	TRI	34.0	SEY43	V9P	3613	4.4	4.2	2	0.5
18/06/11	15:15	TRI	26.5	SEY43	V9P	3614	4.4	2.8	0	0.0
18/06/11	15:30	TRI	30.5	SEY43	V9P	3615	4.4	4.2	3	0.7
26/04/12	11:34	ELA	64.0	SEY59	V9AP	4680	85.2	16.8*	7	0.4
26/04/12	11:57	ELA	61.0	SEY59	V9AP	4682	85.2	17.0*	22	1.3
26/04/12	13:37	ELA	44.5	SEY59	V9AP	4684	85.2	16.7*	17	1.0
26/04/12	17:50	ELA	35.0	SEY59	V9AP	4686	85.2	84.9	206	2.4
26/04/12	10:15	TRI	30.5	SEY59	V9AP	4674	85.2	57.9*	17	0.3
26/04/12	10:27	TRI	35.0	SEY59	V9AP	4676	85.2	66.4*	23	0.3
26/04/12	10:33	TRI	32.0	SEY59	V9AP	4678	85.2	64.4*	16	0.2

225

226

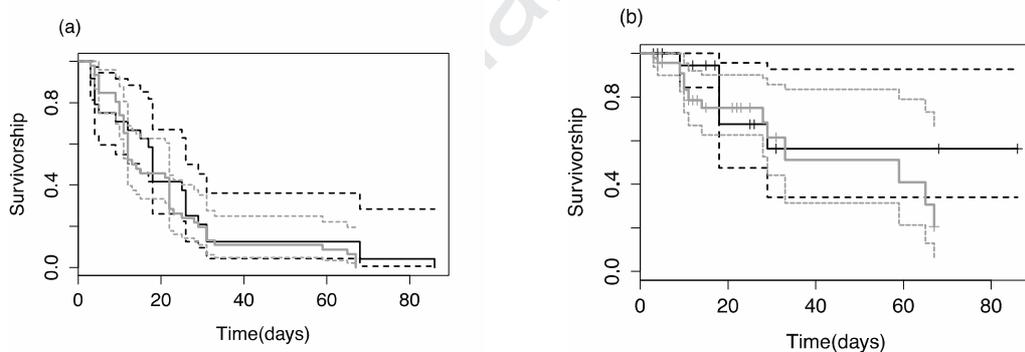
227

228

229

230 Residency

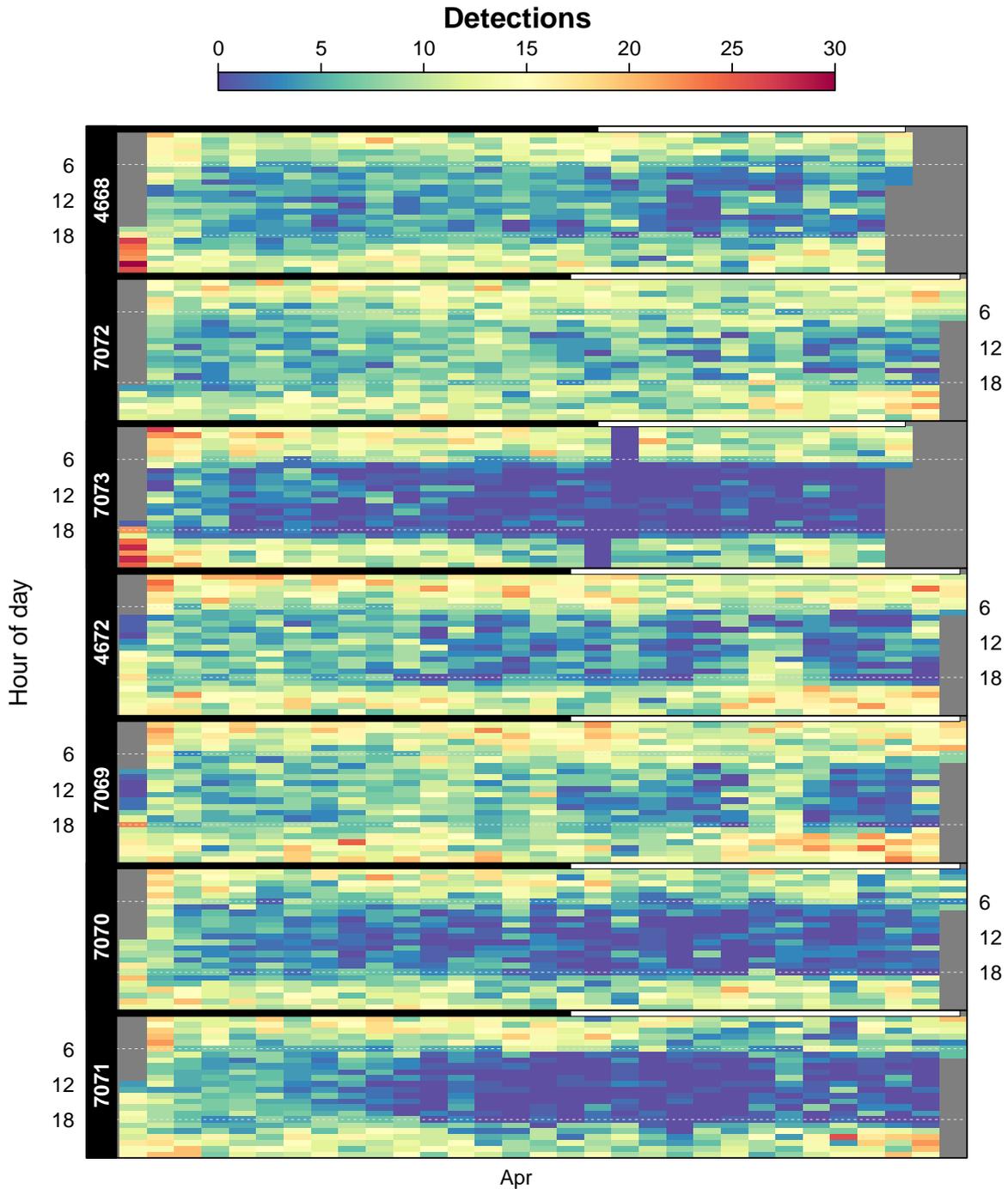
231 TRT at FADs for the rainbow runner ranged between 1.9 to 84.9 days and 2.8 and 66.4 days
 232 for the oceanic triggerfish. The large range in residency was not always indicative of natural
 233 behaviour as observations were often terminated prematurely due to either fishing operations,
 234 which resulted in the capture of the FAD-associated fish, or equipment failure (Table 1). A
 235 high residency index score was obtained for both oceanic triggerfish (0.75 ± 0.28 , mean \pm
 236 SD) and rainbow runner (0.75 ± 0.25 , mean \pm SD). Kaplan-Meier survival curves revealed
 237 considerable overlaps in confidence intervals for both species suggesting that they displayed
 238 similar residency patterns (Fig. 2). This was confirmed by the log-rank test of comparison as
 239 no significant difference was observed between the survival functions of the two species
 240 (censored curve: $\chi^2 = 0.8$, $df = 1$, $p = 0.36$, uncensored: $\chi^2 = 0.9$, $df = 1$, $p = 0.344$). Kaplan-
 241 Meier survival curves considering the censored TRT did not reach 0 as the longest TRTs
 242 were censored due to equipment failure and suggest that the maximum residence time of
 243 rainbow runner and oceanic triggerfish was underestimated. The Median values from the
 244 Kaplan-Meier survival curves with censoring was 59 days for oceanic triggerfish but could
 245 not be determined for rainbow runner as the curve did not decrease below 0.5 due to the
 246 censoring of the longest TRTs. Instead, the survivorship at 60% was used for comparisons.
 247 The Kaplan-Meier survival curves with censoring estimated that 60% of oceanic triggerfish
 248 and rainbow runner remained associated with FADs for approximately 30 days and 25 days
 249 respectively (Fig. 2(b)). Using uncensored data, the estimation was reduced to approximately
 250 15 days for oceanic triggerfish and 17 days for rainbow runner (Fig. 2(a)). Mean residence
 251 time estimation using the survival regression model on censored data was 65 days for oceanic
 252 triggerfish and 94 days for rainbow runner. The overall mean TRT (no regression model) was
 253 of 21.01 days (± 17.59 SD) for oceanic triggerfish and 23.5 days (± 21.80 SD) for rainbow
 254 runner



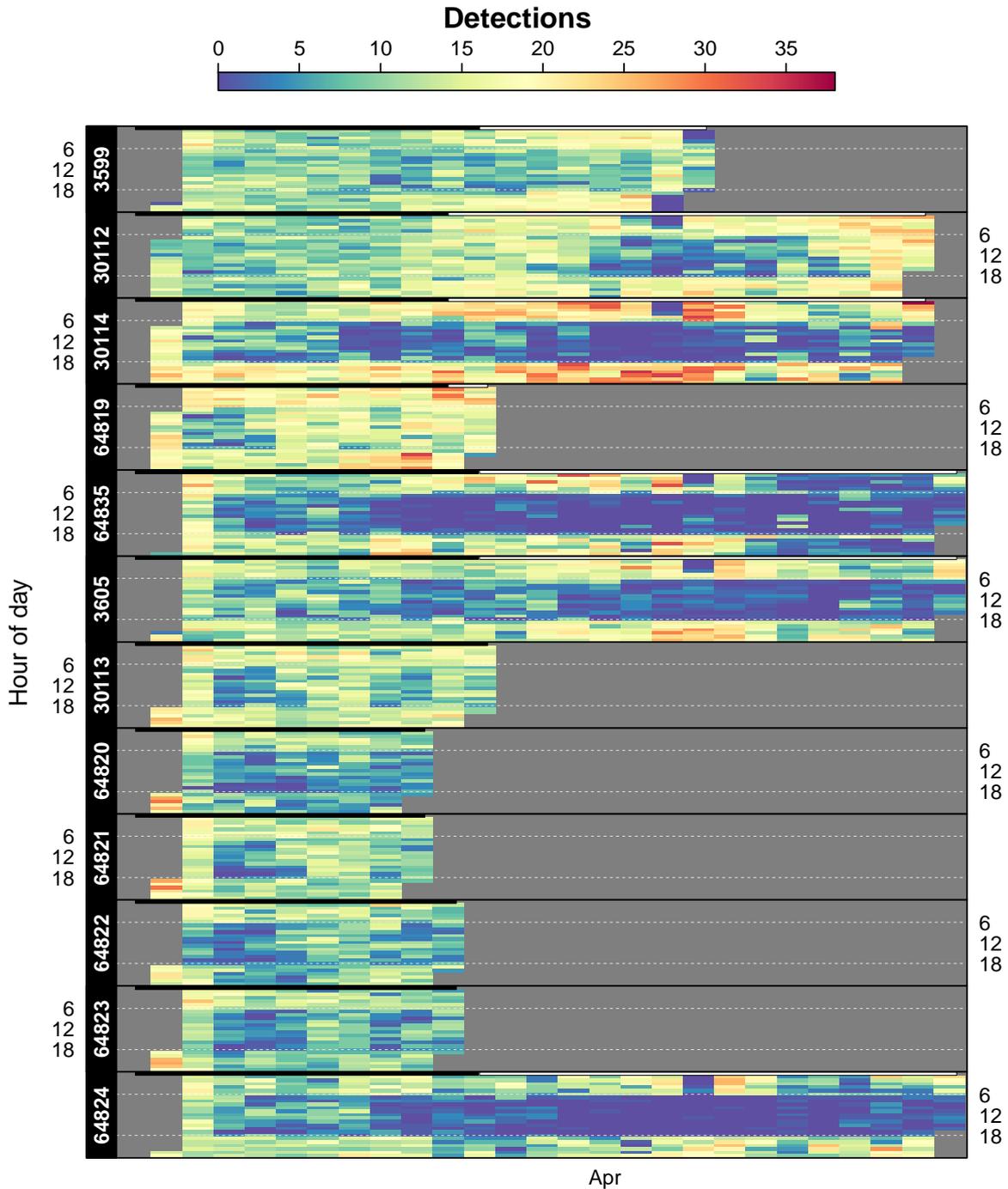
255
 256 Figure 2: Kaplan-Meier survival functions for oceanic triggerfish (grey line) and rainbow
 257 runner (black line) for (a) all TRTs and (b) natural departure TRTs and censored TRTs.
 258 Horizontal ticks indicate censored data points. Dotted lines represent 95% confidence
 259 interval.
 260

261 Temporal patterns in association

262
 263 In general, both species remained within the reception range of the receiver throughout most
 264 of the day (Figs. 3,4). Gaps in detections indicate when individuals were out of the reception
 265 range, away from the FADs (Fig. 3,4, S1).
 266



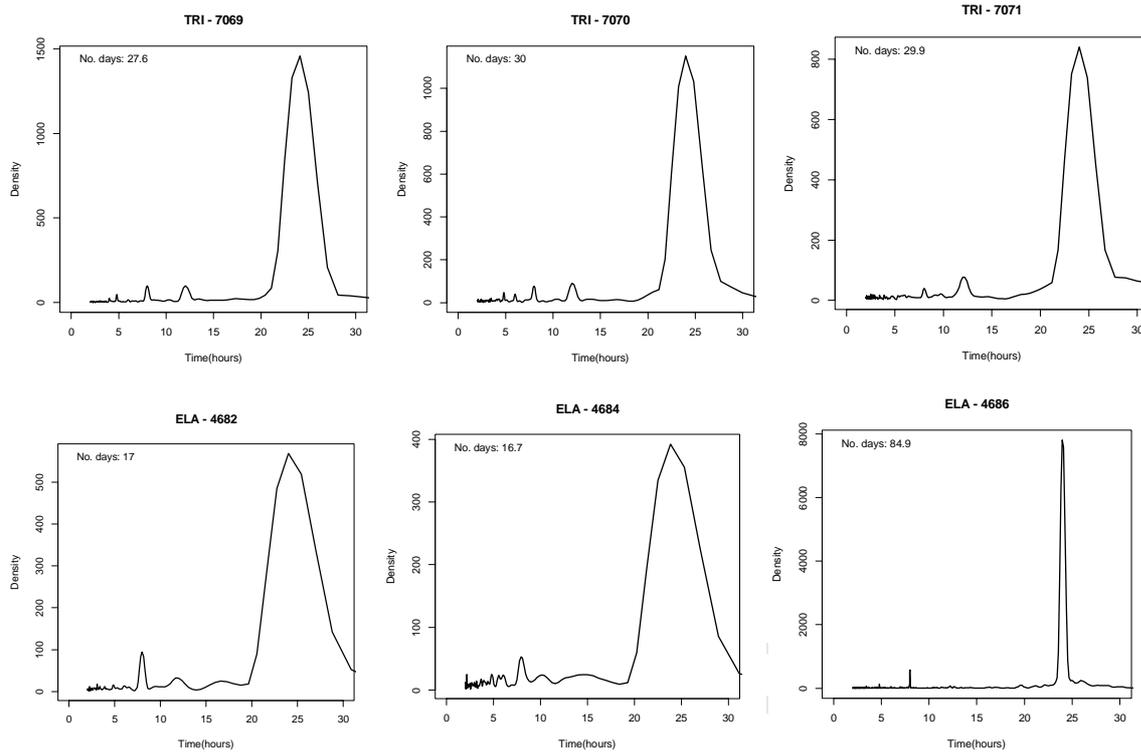
267
 268 Figure 3: Examples of hourly detection chronogram for rainbow runner (ID# 4668, 7072,
 269 7073) and oceanic triggerfish (ID# 4672, 7069, 7070, 7071) at FAD SEY41. Each strip
 270 illustrates the hourly detections of an individual (ID# on the left). Hour of the day is on the y-
 271 axis and time (days) on the x-axis. The scale denotes the corresponding number of detections.



272
 273
 274
 275
 276
 277
 278

Figure 4: Examples of hourly detection chronogram for oceanic triggerfish (ID# 3605, 30113, 64820, 64823, 64824, 64822, 64821) and rainbow runner (ID# 30112, 64835, 64819, 30114, 3599) at FAD MAY42. Each strip illustrates the hourly detections of an individual (ID# on the right). Hour of the day is on the y-axis and time (days) on the x-axis. The scale denotes the corresponding number of detections.

279
 280



281

282

283

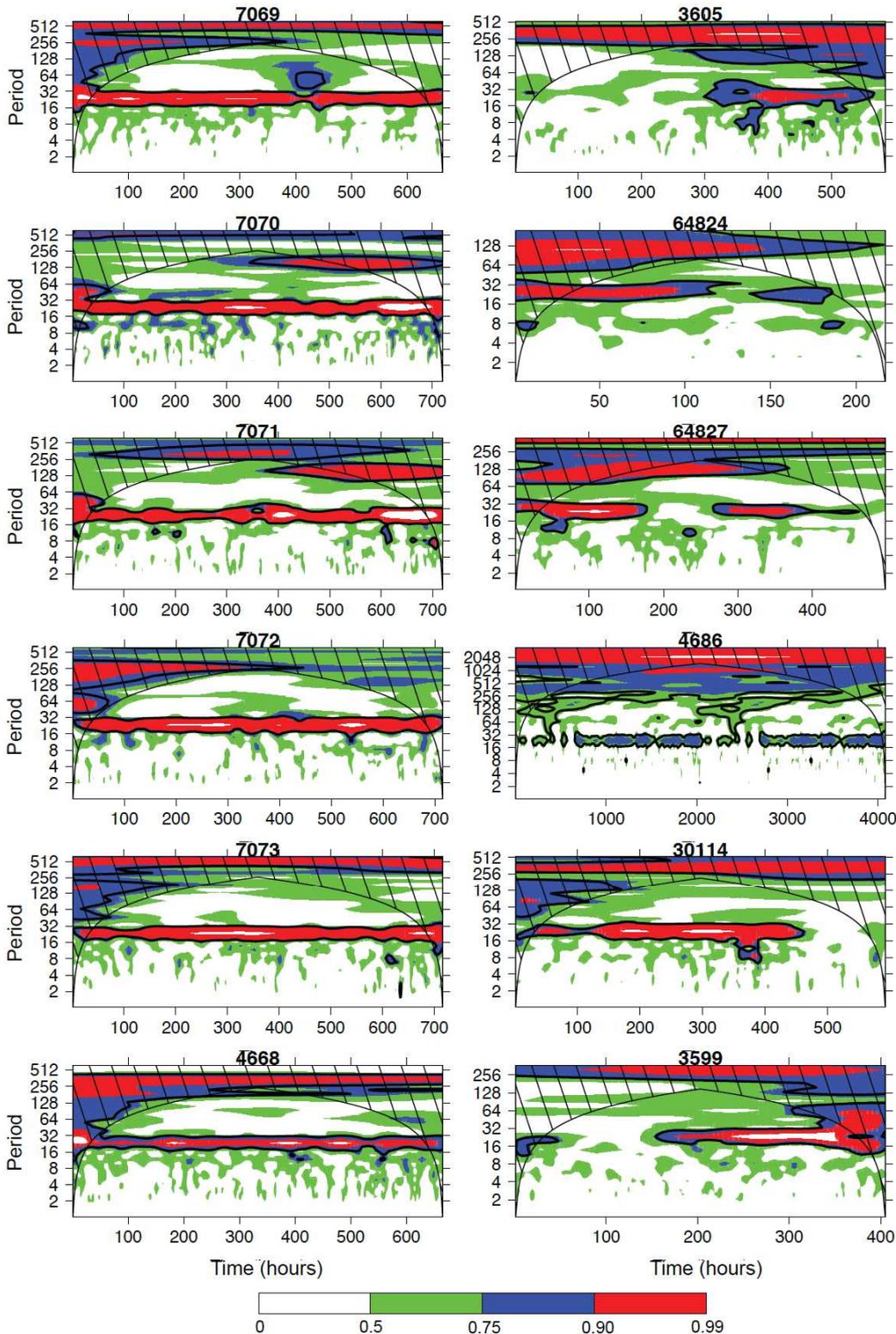
284

285

286

287

Figure 5: Examples of fast fourier transform (FFT) spectral densities for three oceanic triggerfish (top) and three rainbow runner (bottom) at drifting FADs.



288

289

290 Figure 6: Wavelet spectrum examples of oceanic triggerfish (Top; ID# 7069, 7070, 7071,

291 3605, 64824, 64827) and rainbow runner (bottom; ID# 7072, 7073, 4668, 4686, 30114, 3599)

292 using Morlet wavelet of hourly detections showing persistent diel behaviour (left) and

293 intermittent diel behaviour (right). Barred area represents the cone of influence (COI). Values

294 inside the COI cannot be interpreted due to edge effects. The thick black contour lines

295 represent 95% confidence level and the scale bar represents the intensity of the time-

frequency space over time.

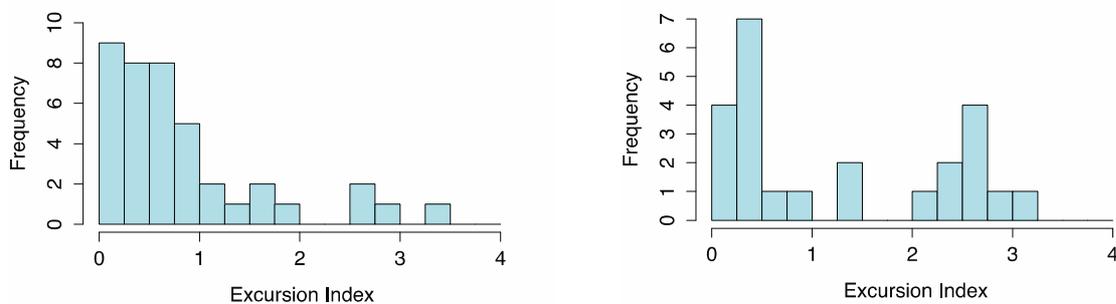
296 Temporal patterns in association using FFT spectral analysis revealed a strong periodicity in
 297 the association of both species at FADs with a distinct peak at 24 h (Fig. 5). This pattern was
 298 observed for all analysed individuals of both species (rainbow runner n = 18, oceanic
 299 triggerfish n = 40) with sufficient data (> 5 days), indicating the presence of a distinct diel
 300 pattern in their associative behaviour. This diel pattern is characterised by a stronger
 301 association during the night and excursions away from the FAD during the day.

302

303 Moreover, the 24 h periodicity was clear on the wavelet spectrograms with a significant
 304 signal (Fig. 6). However, intraspecific variability in the persistence of the 24 h periodicity
 305 was apparent (Fig. 6). Examples in Fig. 6 illustrates different patterns in the persistence of
 306 periodicity; some individuals exhibited continuous periodicity (oceanic triggerfish: ID# 7079,
 307 7070, 7071; rainbow runner: ID# 7072, 7073, 4668) throughout their residency at FADs
 308 while others displayed intermittent periods of periodicity (oceanic triggerfish: ID# 3605,
 309 64824, 64827; rainbow runner: ID# 4686, 30114, 3588). These observed differences in
 310 pattern were not FAD specific, but rather reflects individual behavioural variability.

311

312 Overall, 82% of tagged oceanic triggerfish performed excursions while all tagged rainbow
 313 runner performed at least one excursion (Table 1). The distributions of the excursion index
 314 was not unimodal (Fig. 7). A second mode was observed in the excursion index distributions
 315 of rainbow runner and to a lesser extent for oceanic triggerfish. This indicates a different
 316 modality in the associative behaviour; some individuals performed ~2-3 times more
 317 excursions per day than their conspecifics (Fig. 7). Rainbow runner performed more
 318 excursions per day than oceanic triggerfish; the mean excursion index was of 0.86 (\pm 0.8 SD)
 319 for oceanic triggerfish and 1.31 (\pm 1.1 SD) for rainbow runner. The mean duration of
 320 excursions was of 2.0 hours (\pm 1.6 SD) for oceanic triggerfish and 2.4 hours (\pm 2.2 SD) for
 321

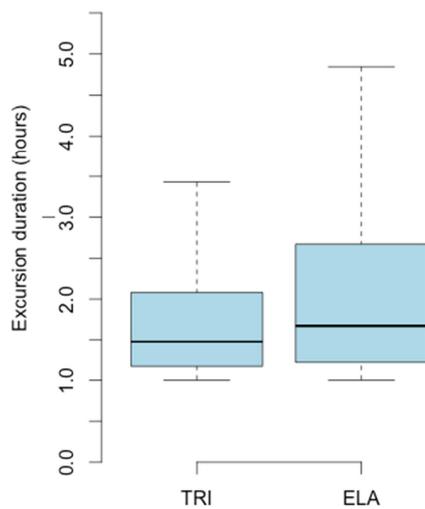


322

323 Figure 7: Frequency histogram distributions of excursion index for oceanic triggerfish (left)

324 and rainbow runner (right)

325



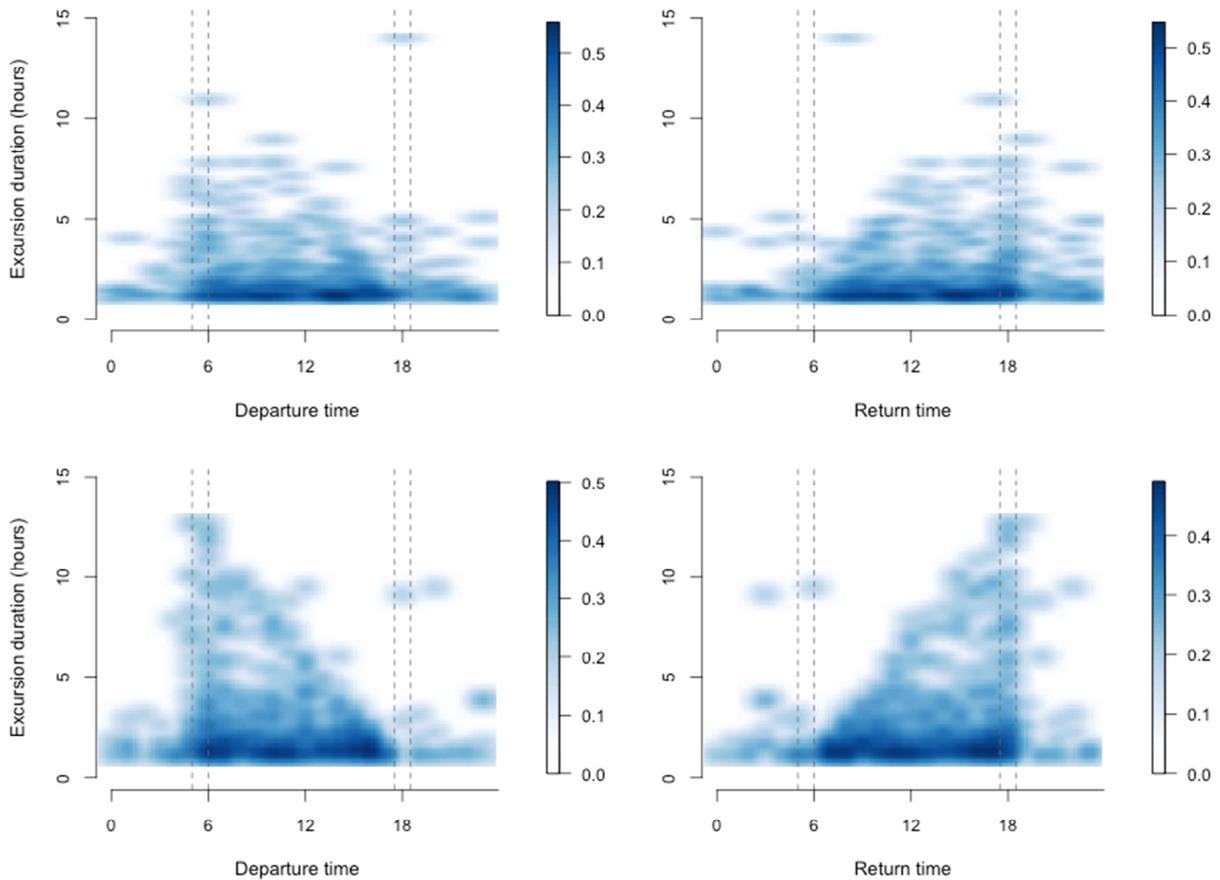
326
327 Figure 8: Box and whisker plots of excursion durations of oceanic triggerfish (TRI) and
328 rainbow runner (ELA).

329

330

331 The distribution and durations of excursions were then examined at a 24 h scale at all the
332 FADs. The heatmap (Fig. 9) indicates that the majority of the excursion activity (departures
333 and returns) occurred during the daytime for both species (rainbow runner: 72.5 %, oceanic
334 triggerfish: 81.2%). A sharp increase in excursion departure occurred at sunrise and a
335 decrease at sunset irrespective of the excursion duration. While excursion durations were
336 typically short (Fig. 8), the pattern observed for longer excursions was distinct; for both
337 species, there was a linear decrease in the longer excursion which ended before sunset (Fig.
338 9).

339



340

341 Figure 9: Heatmap of departure and return time (local time) of excursions with corresponding
 342 durations for oceanic triggerfish (top) and rainbow runner (bottom) at all the FADs. Densities
 343 are represented on the scale bars. Areas between dotted lines represent sunrise and sunset
 344 hours.

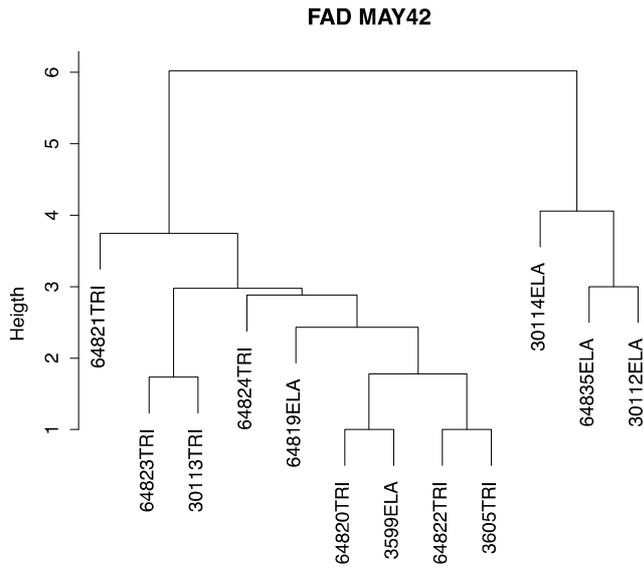
345

346

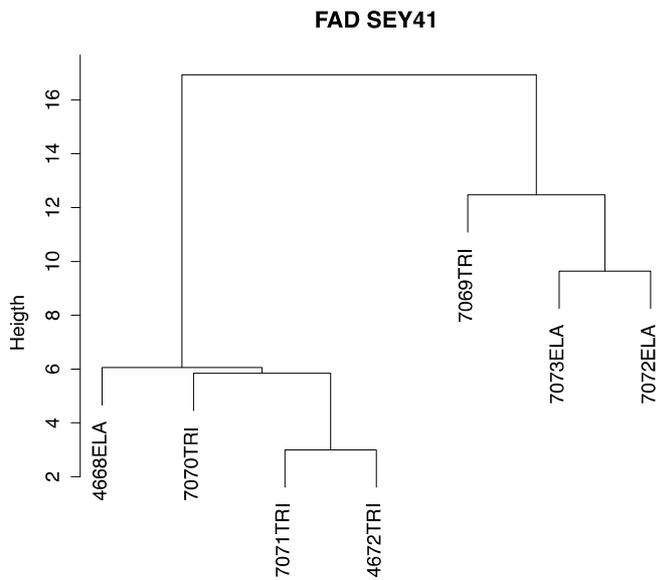
347 The variability in the associative behaviour amongst individuals of the two species as well as
 348 temporal variability of individuals during their association is depicted in Figs. 3,4 and 6.

349 While some detection gaps may appear to be synchronous, they do not appear to be
 350 systematic amongst individuals of the same species. The clustering analysis revealed that
 351 there was no clear species-specific grouping in the associative patterns; some triggerfish
 352 displayed more similar associative behaviours to rainbow runner than their conspecifics (Fig.
 353 10).

354



355



356

357 Figure 10: Examples of cluster dendrogram of hourly presence-absence segments for FAD
 358 SEY41 and MAY42. End nodes are denoted by ID number and species code (TRI = oceanic
 359 triggerfish, ELA = rainbow runner).

360

361

362

363

364

365

366

367

368 Discussion

369 Residency at FADs

370 Both rainbow runner and oceanic triggerfish remained associated with the same floating
 371 object for extended periods. The maximum residence time at the same drifting FAD recorded
 372 during this study (i.e. 84.6 days for rainbow runner and 66.4 days for oceanic triggerfish)
 373 represents the highest values ever reported for FAD-associated fishes. [Dagorn2007] was the
 374 first study to tag both tuna and non-target species (121 fish of 7 different species) at drifting
 375 FADs. Their study provided a general mean residence time for yellowfin tuna (mean: 1.04
 376 days, \pm 2.23 SD), skipjack tuna (mean: 0.91 days, \pm 2.17 SD), bigeye tuna (mean: 1.43 days,
 377 \pm 1.46 SD) silky sharks (mean: 5.33 days, \pm 3.16 SD), wahoo (mean: 1.57 days, \pm 2.73 SD),
 378 dolphinfish (mean: 3.96 days, \pm 3.86 SD), silky sharks (mean: 5.33 days, \pm 3.16 SD) and
 379 oceanic triggerfish (mean: 12.49 days, \pm 6.08 SD), while [Filmlalter2015] reported a mean
 380 residence time of 14.03 days at drifting FADs for silky sharks. [Taquet2007a] reported that
 381 the mean residence time of dorado at drifting FADs was of 6.25 days (median of 5.09 days).
 382 The overall mean residence time in this study was 21.03 days for oceanic triggerfish and 23.5
 383 days for rainbow runner which is considerably longer than what was reported above. No
 384 previous investigations have reported on the residency of rainbow runners at drifting FADs.
 385 While the 'raw' mean residence time provides some general indication of residency, it is
 386 biased by observation lengths and truncations. Indeed, the mean residence time estimation
 387 from the regression model of censored data was considerably higher with 65 days for oceanic
 388 triggerfish and 94 days for rainbow runner. Using mean values as a descriptor of the
 389 survivorship can be misleading due to the skewed nature of the survival functions. It is
 390 therefore recommended that median values from Kaplan-Meier survival curves (with
 391 censoring) are jointly reported in order to allow appropriate comparisons of residency time
 392 estimations between studies. The residency index also indicated high residency with scores
 393 above 0.75 being comparable to those obtained for resident reef species [Alos2012a,
 394 Mason2010, Toole2011].
 395 The ecological trap hypothesis suggests that massive seeding of drifting FADs could have a
 396 negative impact on the populations of associated species [Hallier2008c, Marsac2000]. To
 397 date, there no clear evidence in favour of this hypothesis and the few studies that have
 398 investigated this topic have focused on tunas [Hallier2008c, Menard2000, Robert2014]. In a
 399 hypothetical ecological trap scenario, the impacts on populations of oceanic triggerfish and
 400 rainbow runner, due to their long residency, should be more prominent. However, as
 401 highlighted by [Robert2014], demonstrating the presence of an ecological trap scenario is not
 402 trivial and requires baseline information on biological parameters (e.g. physiological
 403 condition, reproductive success, etc). While the two studied species could be good candidates
 404 to study the ecological trap hypothesis, the difficulty remains in finding a control to test this
 405 hypothesis.

406

407 Temporal patterns in association

408 Diel pattern in association with FADs have been reported for yellowfin, bigeye and skipjack
 409 tuna at anchored FADs [Holland1990, Marsac1998, Ohta2005, Yuen1970] and drifting FADs
 410 [Forget2015, Schaefer2013, Matsumoto2014] with a closer association during the day.
 411 Similarly, silky sharks displayed a stronger association during the day [Filmlalter2015,
 412 Forget2015] while no clear pattern was found for dorado at FADs [Taquet2007a]. A distinct
 413 diel pattern in the associative behaviour with FADs was observed here for oceanic triggerfish
 414 and rainbow runner. Contrastingly, the diel pattern observed for these two species was
 415 opposite to that of other pelagic species described above. During daytime, the two species

416 increased their home range as they performed excursions away from the FAD, out of the
417 receiver's reception range. This diel pattern is more commonly observed in reef associated
418 species [Koeck2014, Alos2011]. The studies mentioned above have suggested that nocturnal
419 feeding behaviour drives the switch in the associative mode of tunas and silky shark as they
420 move away from the FAD and feed on the deep scattering layer. An opposing diel pattern in
421 the pelagic realm observed for oceanic triggerfish and rainbow runner is intriguing and may
422 reflect differences in foraging strategy or predator avoidance mechanisms. Information on
423 their vertical movement behaviour to investigate the depth strata usage and feeding ecology
424 may help elucidate this different diel associative pattern.

425 Ambient light intensity appears to be the stimulus triggering the onset and end of the
426 associative modes. After sunrise, the two species typically increase their home range and
427 perform excursions away from the FAD. The average excursion duration of oceanic
428 triggerfish (2.05 h) and rainbow runner (2.45 h) suggests that individuals, generally, do not
429 venture far from the FAD. Considering a swimming speed of 1 body length per sec, the
430 maximum home range size of the two species (assuming constant speed and a linear
431 movement away from FAD) during a typical excursion could range between 1.1 and 2.2 km.
432 During an active tracking experiment conducted on FAD SEY41, the maximum measured
433 distance of oceanic triggerfish away from the FAD (during an excursion), while tracking a
434 silky shark, was 800 m [Filmlalter2015]. The homing abilities and mechanisms used by fish to
435 return and relocate FADs has intrigued scientists for many years. Tunas perform extended
436 nocturnal excursions away from FADs and active tracking studies have revealed that, during
437 this time, they can be found within a radius of 5-10 km from the FAD [Dagorn2000c,
438 Holland1990, Matsumoto2014]. The ability of tuna to relocate FADs from such large
439 distances demonstrates their navigational and homing capabilities [Holland1990].
440 [Girard2007] investigated the homing abilities of dorado through displacement experiments
441 and acoustic telemetry and reported successful homing up to 1.6 km from the FAD.
442 [Filmlalter2015] actively tracked a silky shark at a drifting FAD during one day and reported
443 a maximum straight line distance of 1.2 km between the shark and the FAD. [Ibrahim1990]
444 investigated the ability of various small (< 40 cm TL) FAD-associated species to relocate
445 FADs by displacing fish tagged with floats at various distances from the FAD and reported
446 that a maximum homing distance of 180 m. In their pioneer study, [Hunter1967] looked into
447 the homing ability of oceanic triggerfish by tagging and releasing 10 individuals at 7.5, 15
448 and 30.5 m from their original drifting log. None of the fish released at 30.5 m returned to the
449 original log. The authors concluded that the greatest distance was outside the visual range of
450 the fish and thus the fish could not orientate towards it. The results from this study, however,
451 indicate that both oceanic triggerfish and rainbow runner are capable of returning to the FAD
452 after several hours out of its visual range (several hundred meters) and as highlighted by
453 previous studies [Dempster2003, Ibrahim1990] vision cannot be of aid from such large
454 distances. It is conceivable that other sensory cues, such as sounds generated by the floating
455 object or the fishes in close proximity to it, may be used by FAD associated species for
456 homing, however, the hearing capabilities of pelagic fish and its use for navigation remains
457 unclear [Dempster2003].

458 The motive of excursions away from FADs displayed by tunas, dorado and silky shark has
459 largely been attributed to foraging activities [Filmlalter2015, Holland1990, Taquet2007a].
460 Foraging could also be the primary motive causing the increase in home range of the two
461 studied species. If so, the fact that excursions occur during the day suggests that the two
462 species have a different foraging strategy to that of tunas and silky sharks; which tend to be
463 more active nocturnally. [Klima1971] proposed that floating objects act as a spatial reference
464 point that fish use to orientate in an otherwise unstructured environment. The two species

465 may temporarily increase their home range for feeding while using the FAD as a reference
466 point.

467 The cluster analysis revealed that there was no species-specific grouping of the associative
468 behaviour at FADs. Variability was observed in the associative behaviour amongst
469 individuals of the two species and the fact there was no systematic synchronisation in
470 absences from FAD amongst individuals suggests that oceanic triggerfish and rainbow runner
471 do not form unique monospecific schools at FADs and are more likely to form several sub
472 schools. Some individuals of the two species performed 2 to 3 times more excursions per unit
473 time than their conspecifics. This intraspecific difference in behaviour was more apparent for
474 rainbow runner and suggests the presence of a different behavioural mode. The fact that
475 individuals at the same FAD experiencing the same abiotic and biotic environmental
476 conditions display different behaviours indicates behavioural polymorphism. Behavioural
477 variability in fishes has been observed at fine scales under controlled laboratory conditions
478 [Raimondi1990] and has also been used to explain differences in large scale movements,
479 such as migration [Kerr2009]. Explaining behavioural variability is challenging as the
480 interplay between genetic variability, historical shifts in selection pressures and adaptive
481 behaviour is hard to disentangle. Nevertheless, it is conceivable that foraging competition
482 amongst numerous aggregated individuals (several hundreds at a single FAD; personal
483 observation), within a restricted spatial sphere could favour these different behavioural
484 modes.

485 Temporal variability in associative behaviour was apparent for both species. Wavelet analysis
486 provided additional information on the persistence of diel patterns. Periods (days) when diel
487 behaviour were less distinct were apparent as gaps in the periodicity signal were observed.
488 Interestingly, periods with altered associative behaviour were sometimes synchronised
489 amongst individuals suggesting a change in behaviour that could be a response to a particular
490 stimulus of biotic or abiotic nature. In order to resolve which factors can influence the
491 associative behaviour, information on biotic and abiotic variables should be collected
492 simultaneously during experiments. More specifically, biotic factors, such as prey and
493 predator density and details on the species assemblage, and abiotic factors, such as thermal
494 structure of water column, FAD densities, would aid in understanding how such factors that
495 can influence associative behaviour.

496 **Conclusion**

497 Oceanic triggerfish and rainbow runner have remarkably similar behavioural patterns in their
498 association with FADs. This suggests that the convergence of their behaviour has risen from
499 similar selective pressures and, hence, the two species are likely to have similar motives in
500 associating with floating objects. More data on the ecology of the two species are required to
501 pinpoint the exact motivations driving their behaviour. The long residence times observed for
502 the two species implies that they are susceptible to high fishing effort on FADs. As such, key
503 biological parameters and data to determine their ecological role in the pelagic ecosystem are
504 need to model increased fishing mortality linked to the FAD based tuna fishery.

505 It must however be noted that obtaining a metric of natural departure from FADs is
506 challenging as it requires large effort, but, nevertheless, it remains a key parameter for
507 modelling approaches to estimate direct and indirect impacts of FADs on the pelagic
508 ecosystem.

509

510 **Acknowledgments**

511 This study was carried out with financial support from the Commission of the European
512 Communities, specific RTD programme of Framework Programme 7, 'Theme 2 – Food,

513 Agriculture, Fisheries and Biotechnology', through the research project MADE (Mitigating
514 adverse ecological impacts of open ocean fisheries), contract #210496. This work does not
515 necessarily reflect the Commission's views and in no way anticipates its future policy in this
516 area. The work was also financially supported by the International Seafood Sustainability
517 Foundation (www.iss-foundation.org) under its Bycatch Mitigation Project.

518

519 **Compliance with ethical standards**

520

521 *Conflict of interest*

522 The authors declare that they have no conflicts of interest.

523

524 *Ethical approval*

525 All applicable international, national, and/or institutional guidelines for the care and use of
526 animals were followed.

527

528

529 **References**

530

531 [Afonso et al. 2012] Afonso, Pedro and Graça, Gonçalo and Berke, Gregory and Fontes,
532 Jorge, "First observations on seamount habitat use of blackspot seabream (*Pagellus*
533 *bogaraveo*) using acoustic telemetry", *Journal of Experimental Marine Biology and*
534 *Ecology* 436-437 (2012), pp. 1--10.

535

536 [Alós et al. 2011] Alós, Josep and March, David and Palmer, Miquel and Grau, Amalia
537 and Morales-Nin, Beatriz, "Spatial and temporal patterns in *Serranus cabrilla* habitat use
538 in the NW Mediterranean revealed by acoustic telemetry", *Marine Ecology Progress*
539 *Series* 427, August (2011), pp. 173--186.

540

541 [Alós et al. 2012] Alós, Josep and Cabanellas-Reboredo, Miguel and March, David,
542 "Spatial and temporal patterns in the movement of adult two-banded sea bream
543 *Diplodus vulgaris* (Saint-Hilaire, 1817)", *Fisheries Research* 115-116 (2012), pp. 82--88.

544

545 [Amande et al. 2011] Amande, Monin Justin and Ariz, Javier and Chassot, Emmanuel and
546 de Molina, Alicia Delgado and Gaertner, Daniel and Murua, Hilar..., "Bycatch of the
547 European purse seine tuna fishery in the Atlantic Ocean for the 2003-2007 period",
548 *Aquatic Living Resources* 23, 4 (2011), pp. 353--362.

549

550 [Amandè et al. 2011] Amandè, J and Ariz, Javier and Chassot, Emmanuel and Chavance,
551 Pierre and Molina, Alicia Delgado De and Gaertner, Daniel ..., "By-catch and discards of
552 the European purse seine tuna fishery in the Atlantic Ocean: estimation and
553 characteristics for 2008 ...", *Collect. Vol. Sci. Pap. ICCAT* 66 (2011), pp. 2113--2120.

554

555 [Bakun 2006] Bakun, Andrew, "Frentes y remolinos como estructuras clave en el habitat
556 de las larvas de peces marinos: oportunidad, respuesta adaptativa y v...", *Scientia*
557 *Marina* 70, S2 (2006), pp. 105--122.

558

- 559 [Barnett et al. 2012] Barnett, Adam and AbrantesKá, Kátya G. and Seymour, Jamie and
560 Fitzpatrick, Richard, "Residency and spatial use by reef sharks of an isolated seamount
561 and its implications for conservation", *PLoS ONE* 7, 5 (2012), pp. 1--12.
562
- 563 [Capello et al. 2015] 1. Capello M, Robert M, Soria M, Potin G, Itano D. A Methodological
564 Framework to Estimate the Site Fidelity of Tagged Animals Using Passive Acoustic
565 Telemetry. 1-19 (2015).
566
- 567 [Castro et al. 2002] Castro, José J. and Santiago, José A. and Santana-Ortega, Ana T., "A
568 general theory on fish aggregation to floating objects: An alternative to the meeting
569 point hypothesis", *Reviews in Fish Biology and Fisheries* 11, 3 (2002), pp. 255--277.
570
- 571 [Dagorn and Fréon 1999] Dagorn, Laurent and Fréon, Pierre, "Tropical tuna associated
572 with floating objects: a simulation study of the meeting point hypothesis", *Canadian
573 Journal of Fisheries and Aquatic Sciences* 56, 6 (1999), pp. 984--993.
574
- 575 [Dagorn et al. 2000] Dagorn, Laurent and Josse, Erwan and Bach, Pascal, "Individual
576 differences in horizontal movements of yellowfin tuna (*Thunnus albacares*) in nearshore
577 areas in French Polynesia, d...", *Aquatic Living Resources* 13, 4 (2000), pp. 193--202.
578
- 579 [Dagorn et al. 2007a] Dagorn, Laurent and Holland, Kim N. and Itano, David G.,
580 "Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of
581 fish aggregating devices (FADs)", *Marine Biology* 151, 2 (2007), pp. 595--606.
582
- 583 [Dagorn et al. 2007b] Dagorn, Laurent and Pincock, Doug and Girard, Charlotte and
584 Holland, Kim and Taquet, Marc and Sancho, Gorka and Itano, David an..., "Satellite-
585 linked acoustic receivers to observe behavior of fish in remote areas", *Aquatic Living
586 312*, 2007 (2007), pp. 307--312.
587
- 588 [Dagorn et al. 2013] Dagorn, Laurent and Holland, Kim N. and Restrepo, Victor and
589 Moreno, Gala, "Is it good or bad to fish with FADs? What are the real impacts of the use
590 of drifting FADs on pelagic marine ecosystems?", *Fish and Fisheries* 14, 3 (2013), pp.
591 391--415.
592
- 593 [Dempster and Kingsford 2003] Dempster, Tim and Kingsford, Michael J. Mj, "Homing of
594 pelagic fish to fish aggregation devices (FADs): the role of sensory cues", *Marine Ecology
595 Progress Series* 258, Kingsford 1999 (2003), pp. 213--222.
596
- 597 [Filmlalter et al. 2015] Filmlalter, J and Cowley, P and Forget, F and Dagorn, L, "Fine-scale
598 3-dimensional movement behaviour of silky sharks *Carcharhinus falciformis* associated
599 with fish aggregating devices ...", *Marine Ecology Progress Series* 539, November (2015),
600 pp. 207--223.
601
- 602 [Fiorellato et al. 2019] Fiorellato F, Pierre L, Geehan J. Review of the statistical data and
603 fishery trends tropical tunas. 2019.

- 604
605
606 [Fonteneau et al. 2000] Fonteneau, Alain and Pallarés, Pilar and Pianet, Renaud, "A
607 worldwide review of purse seine fisheries on FADs", in *Pêche thonière et dispositifs de*
608 *concentration de poissons, Caribbean-Martinique, 15-19 Oct 1999* (, 2000), pp. 15--35.
609
- 610 [Fonteneau et al. 2013] Fonteneau, Alain and Chassot, Emmanuel and Bodin, Nathalie,
611 "Global spatio-temporal patterns in tropical tuna purse seine fisheries on drifting fish
612 aggregating devices (DFADs): Taking a ...", *Aquatic Living Resources* 26, August (2013),
613 pp. 37--48.
614
- 615 [Forget et al. 2015] Forget, Fabien G. and Capello, Manuela and Filmlalter, John David
616 and Govinden, Rodney and Soria, Marc and Cowley, Paul D and Da..., "Behaviour and
617 vulnerability of target and non-target species at drifting fish aggregating devices (FADs)
618 in the tropical tuna ...", *Canadian Journal of Fisheries and Aquatic Sciences* 72, 9 (2015),
619 pp. 1398--1405.
620
- 621 [Fréon and Dagorn 2000] Fréon, Pierre and Dagorn, Laurent, "No Title", *Reviews in Fish*
622 *Biology and Fisheries* 10, 2 (2000), pp. 183--207.
623
- 624 [Gilman 2011] Gilman, Eric L., "Bycatch governance and best practice mitigation
625 technology in global tuna fisheries", *Marine Policy* 35, 5 (2011), pp. 590--609.
626
- 627 [Girard et al. 2007] Girard, Charlotte and Dagorn, Laurent and Taquet, Marc and
628 Aumeeruddy, Riaz and Peignon, Christophe and Benhamou, Simon, "Homing abilities of
629 dolphinfish (*Coryphaena hippurus*) displaced from fish aggregating devices (FADs)
630 determined using ultras...", *Aquatic Living Resources* 20, 4 (2007), pp. 313--321.
631
- 632 [Gooding and Magnuson 1967] Gooding, Reginald M. and Magnuson, John J., "Ecological
633 Significance of a Drifting Object to Pelagic Fishes", *Pacific Science* 21 (1967), pp. 486--
634 497.
635
- 636 [Hall 1992] Hall, Martin A., "The association of tunas with floating objects and dolphins
637 in the Eastern Pacific Ocean", in Part VI. Association of fauna with floating objects.
638 Background document for the International Workshop on the Ecology and Fish... (,
639 1992), pp. 7.
640
- 641 [Hall 1996] Hall, Martin A., "On bycatches", *Reviews in Fish Biology and Fisheries* 6, 3
642 (1996), pp. 319--352.
643
- 644 [Hall et al. 2000] Hall, Martin A. and Alverson, Dayton L. and Metuzals, Kaija I., "By-catch:
645 Problems and solutions", *Marine Pollution Bulletin* 41, 1-6 (2000), pp. 204--219.
646
- 647 [Hallier and Gaertner 2008a] Hallier, J and Gaertner, D, "Drifting fish aggregation devices
648 could act as an ecological trap for tropical tuna species.", *Marine Ecology Progress Series*
649 353 (2008), pp. 255--264.
650

- 651 [Hallier and Gaertner 2008b] Hallier, J and Gaertner, D, "Drifting fish aggregation devices
652 could act as an ecological trap for tropical tuna species", Marine Ecology Progress Series
653 353 (2008), pp. 255--264.
654
- 655 [Holland et al. 1990] Holland, K. N. and Brill, R. W. and Chang, R. K C, "Horizontal and
656 vertical movements of yellowfin and bigeye tuna associated with fish aggregating
657 devices", Fishery Bulletin 88, 3 (1990), pp. 493--507.
658
- 659 [Hunter and Mitchell 1967] Hunter, J. R. and Mitchell, C. T., "Association of fishes with
660 flotsam in the offshore waters of Central America", Fishery Bulletin 66 (1967), pp. 13--
661 29.
662
- 663 [Ibrahim et al. 1990] Ibrahim, S. and Kawamura, G. and Ambak, MA, "Effective range of
664 traditional Malaysian FAD as determined by fish-releasing method", Fisheries research 9
665 (1990), pp. 299--306.
666
- 667 [ISSF 2019] Status of the world fisheries for tuna. Oct. 2019. ISSF Technical Report 2019-
668 12. International Seafood Sustainability Foundation, Washington, D.C., USA.
669
670
- 671 [Kerr et al. 2009] Kerr, Lisa A. and Secor, David H. and Piccoli, Philip M., "Partial
672 Migration of Fishes as Exemplified by the Estuarine-Dependent White Perch", Fisheries
673 34, 3 (2009), pp. 114--123.
674
- 675 [Kingsford 1993] Kingsford, MJ J, "Biotic and abiotic structure in the pelagic
676 environment: importance to small fishes", Bulletin of Marine Science 53, 2 (1993), pp.
677 393--415.
678
- 679 [Klima and Wickham 1971] Klima, Edward F and Wickham, Donald A, "Attraction of
680 Coastal Pelagic Fishes with Artificial Structures", Transactions of the American Fisheries
681 Society 100, 1 (1971), pp. 86--99.
682
- 683 [Koeck et al. 2014] Koeck, Barbara and Pastor, Jérémy and Saragoni, Gilles and Dalias,
684 Nicolas and Payrot, Jérôme and Lenfa..., "Diel and seasonal movement pattern of the
685 dusky grouper *Epinephelus marginatus* inside a marine reserve.", Marine environmental
686 research 94 (2014), pp. 38--47.
687
- 688 [Kojima 1956] Kojima, Shumpei, "Fishing for Dolphins in the western part of the Japan
689 Sea II- Why do fish take shelter under floating materials?", Bulletin of the Japanese
690 Society for Scientific Fisheries 21, 10 (1956), pp. 1049--1052.
691
- 692 [Kojima 1960] Kojima, Shumpei, "Fishing for dolphins in the western part of Japan Sea VI
693 - Behaviours of fish gathering around bamboo rafts", Bulletin of the Japanese Society of
694 Scientific Fisheries 26, 4 (1960), pp. 383--388.
695
- 696 [Lezama-Ochoa et al. 2015] Lezama-Ochoa, N. and Murua, H. and Chust, G. and Ruiz, J.
697 and Chavance, P. and de Molina, A. Delgado and Caballero, A. and Sanc..., "Biodiversity

- 698 in the by-catch communities of the pelagic ecosystem in the Western Indian Ocean",
699 Biodiversity and Conservation 24, 11 (2015), pp. 2647--2671.
700
- 701 [Lopez et al. 2014] Lopez, Jon and Moreno, Gala and Sancristobal, Igor and Murua,
702 Jefferson, "Evolution and current state of the technology of echo-sounder buoys used by
703 Spanish tropical tuna purse seiners in the Atlanti...", Fisheries Research 155 (2014), pp.
704 127--137.
705
- 706 [Lédée et al. 2015] Lédée, Elodie Ji and Heupel, Michelle R and Tobin, Andrew J and
707 Simpfendorfer, Colin A, "Movements and space use of giant trevally in coral reef
708 habitats and the importance of environmental drivers", Animal Biotelemetry 3, 1
709 (2015).
710
- 711 [March et al. 2010] March, D. and Palmer, M. and Alós, J. and Grau, a. and Cardona, F.,
712 "Short-term residence, home range size and diel patterns of the painted comber
713 Serranus scriba in a temperate marine reserve", Marine Ecology Progress Series 400
714 (2010), pp. 195--206.
715
- 716 [Marsac and Cayré 1998] Marsac, Francis and Cayré, Patrice, "Telemetry applied to
717 behaviour analysis of yellowfin tuna (*Thunnus albacares*, Bonnaterre, 1788) movements
718 in a network of fish...", Hydrobiologia 371-372, 0 (1998), pp. 155--171.
719
- 720 [Marsac et al. 2000] Marsac, F. and Fonteneau, A. and Ménard, F., "Drifting FADs used in
721 tuna fisheries: an ecological trap?", Proceedings of the 1st Symposium on Tuna fisheries
722 and FADs, Martinique, October 1999 (2000), pp. 537--552.
723
- 724 [Mason and Lowe 2010] Mason, Tom J. and Lowe, Christopher G., "Home range, habitat
725 use, and site fidelity of barred sand bass within a southern California marine protected
726 area", Fisheries Research 106, 1 (2010), pp. 93--101.
727
- 728 [Matsumoto et al. 2014] Matsumoto, Takayuki and Satoh, Keisuke and Toyonaga, Mikio,
729 "Behavior of skipjack tuna (*Katsuwonus pelamis*) associated with a drifting FAD
730 monitored with ultrasonic transmitters in the eq...", Fisheries Research 157 (2014), pp.
731 78--85.
732
- 733 [Menard 2000] Menard, F, "Exploitation of small tunas by a purse-seine fishery with fish
734 aggregating devices and their feeding ecology in an eastern tro...", ICES Journal of
735 Marine Science 57, 3 (2000), pp. 525--530.
736
- 737 [Moreno et al. 2007] Moreno, Gala and Josse, Erwan and Brehmer, Patrice and
738 Nøttestad, Leif, "Echotrace classification and spatial distribution of pelagic fish
739 aggregations around drifting fish aggregating devices (DFAD)", Aquatic Living Resources
740 20, 4 (2007), pp. 343--356.
741
- 742 [O'Toole et al. 2011] O'Toole, Amanda C. and Danylchuk, Andy J. and Goldberg, Tony L.
743 and Suski, Cory D. and Philipp, David P. and Brooks, Edd and Co..., "Spatial ecology and

- 744 residency patterns of adult great barracuda (*Sphyraena barracuda*) in coastal waters of
745 The Bahamas", *Marine Biology* 158 (2011), pp. 2227--2237.
- 746
- 747 [Ohta and Kakuma 2005] Ohta, I. and Kakuma, S., "Periodic behavior and residence time
748 of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa
749 Isla...", *Marine Biology* 146, 3 (2005), pp. 581--594.
- 750
- 751 [Parin and Fedoryako 1992] Parin, N V and Fedoryako, B I, "Pelagic fish communities
752 around floating objects in the open ocean", in *Proceedings of the international
753 Workshop on the Ecology and Fisheries for Tunas Associated with Floating Objects* (
754 1992), pp. 447--458.
- 755
- 756 [Percival and Walden 2000] Percival, Donald B and Walden, Andrew T, *Wavelet Methods
757 for Time Series Analysis* (, 2000).
- 758
- 759 [RCoreTeam 2014] RCoreTeam, "A Language and Environment for Statistical Computing.
760 R Foundation for Statistical Computing, Vienna, Austria" (2014).
- 761
- 762 [Raimondi and Keough 1990] Raimondi, Peter T and Keough, Michael J, "Behavioural
763 variability in marine larvae", *Australian Journal of Ecology* 15, 4 (1990), pp. 427--437.
- 764
- 765 [Robert et al. 2012] Robert, Marianne and Dagorn, Laurent and Deneubourg, Jean Louis
766 and Itano, David and Holland, Kim, "Size-dependent behavior of tuna in an array of fish
767 aggregating devices (FADs)", *Marine Biology* 159 (2012), pp. 907--914.
- 768
- 769 [Robert et al. 2014] Robert, Marianne and Dagorn, Laurent and Bodin, Nathalie and
770 Pernet, Fabrice and Arsenault-Pernet, Eve-Julie and Deneubourg, Je..., "Comparison of
771 condition factors of skipjack tuna (*Katsuwonus pelamis*) associated or not with floating
772 objects in an area known...", *Canadian Journal of Fisheries and Aquatic Sciences* 71, 3
773 (2014), pp. 472--478.
- 774
- 775 [Romanov 2002] Romanov, Evgeny V, "Bycatch in the tuna purse-seine fisheries of the
776 western Indian Ocean", *Fishery Bulletin* 100, 1 (2002), pp. 90--105.
- 777
- 778 [Rountree 1989] Rountree, Rodney A, "Association of fishes with aggregation devices:
779 effects of structure size on fish abundance", *Bulletin of Marine Science* 44, 2 (1989), pp.
780 960--972.
- 781
- 782 [Schaefer and Fuller 2005] Schaefer, K. M. and Fuller, D. W., "Behavior of bigeye
783 (*Thunnus obesus*) and skipjack (*Katsuwonus pelamis*) tunas within aggregations
784 associated with floating objec...", *Marine Biology* 146, 4 (2005), pp. 781--792.
- 785
- 786 [Schaefer and Fuller 2013] Schaefer, Kurt M. and Fuller, Daniel W., "Simultaneous
787 behavior of skipjack (*Katsuwonus pelamis*), bigeye (*Thunnus obesus*), and yellowfin (*T.
788 albacares*) tunas, within l...", *Marine Biology* 160, 11 (2013), pp. 3005--3014.
- 789

- 790 [Soria et al. 2009] Soria, Marc and Dagorn, Laurent and Potin, Gaël and Fréon, Pierre and
791 Fre, Pierre and Soria, Marc and Dagorn, Laure..., "First field-based experiment
792 supporting the meeting point hypothesis for schooling in pelagic fish", *Animal Behaviour*
793 78, 6 (2009), pp. 1441--1446.
794
- 795 [Stehfest et al. 2013] Stehfest, Kilian M. and Patterson, Toby A. and Dagorn, Laurent and
796 Holland, Kim N. and Itano, David and Semmens, Jayson M., "Network analysis of acoustic
797 tracking data reveals the structure and stability of fish aggregations in the ocean",
798 *Animal Behaviour* 85, 4 (2013), pp. 839--848.
799
- 800 [Taquet 2004] Taquet, Marc, *Le comportement agrégatif de la dorade coryphène (*
801 *Coryphaena hippurus) autour des objets flottants (Universite Paris 6, 2004).*
802
- 803 [Taquet et al. 2007a] Taquet, Marc and Dagorn, Laurent and Gaertner, Jean-Claude and
804 Girard, Charlotte and Aumerruddy, Riaz and Sancho, Gorka and Ita..., "Behavior of
805 dolphinfish (*Coryphaena hippurus*) around drifting FADs as observed from automated
806 acoustic receivers", *Aquatic Living Resources* 20, 3 (2007), pp. 263--270.
807
- 808 [Taquet et al. 2007b] Taquet, Marc and Sancho, Gorka and Dagorn, Laurent and
809 Gaertner, Jean-Claude and Itano, David and Aumeeruddy, Riaz and Wendling...,
810 "Characterizing fish communities associated with drifting fish aggregating devices (FADs)
811 in the Western Indian Ocean using und...", *Aquatic Living Resources* 20, 4 (2007), pp.
812 331--341.
813
- 814 [Yuen 1970] Yuen, Heeny S. H., "Behavior of skipjack tuna, *Katsuwonus pelamis*, as
815 determined by tracking with Ultrasonic Devices", *Journal of Fisheries Research Board of*
816 *Canada* 27, 2 (1970), pp. 2071--2079.
817

Highlights:

The associative behaviour of oceanic triggerfish (*Canthidermis maculata*) and rainbow runner (*Elagatis bipinnulata*) were investigated using acoustic telemetry satellite linked receivers at floating objects in the western Indian Ocean.

Both species remained associated with the same floating object for extended periods with mean residency estimated at 94 days for rainbow runner and 65 days for oceanic triggerfish.

A strong diel pattern was observed for both species with short excursions (< 2 hrs) away from the floating objects observed during the day.

Ambient light intensity appears to be the stimulus triggering the onset and end of the associative modes

The observed prolonged residency of these two major bycatch species suggests that they are more vulnerable to the tropical tuna purse seine gear than the targeted tuna species

Conflict of interest

The authors declare that they have no conflicts of interest.

Journal Pre-proof