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Fabien Forget, Paul Cowley, Manuela Capello, John D. Filmalter, Laurent Dagorn. Drifting along in the open-ocean: The associative behaviour of oceanic triggerfish and rainbow runner with floating objects. *Marine Environmental Research*, 2020, 161, pp.104994. 10.1016/j.marenvres.2020.104994 . hal-03410880

HAL Id: hal-03410880

<https://hal.umontpellier.fr/hal-03410880>

Submitted on 22 Aug 2022

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# 1 Drifting along in the open-ocean: the associative behaviour of 2 oceanic triggerfish and rainbow runner with floating objects

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10

## 11 Abstract

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

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## 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: intranant (< 50 cm  
60 from the object), extranant (50 cm to 2 m from the object) and circumnatan (> 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

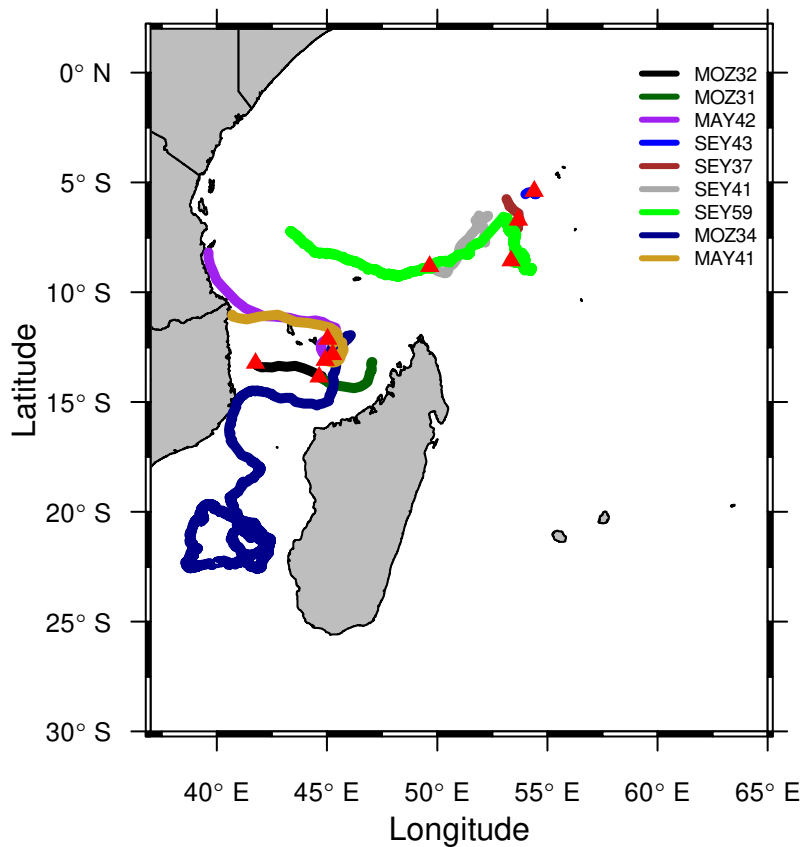
86 of FAD sets by purse seine fleets now represents between 90-96% (fleet dependent) of total  
87 sets [Fiorellato et al. 2019]. The multispecies nature of aggregations around floating objects  
88 means that this practice generates 2.8–6.7 times (ocean dependant) more bycatch than when  
89 fishing 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  $\geq 5$  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

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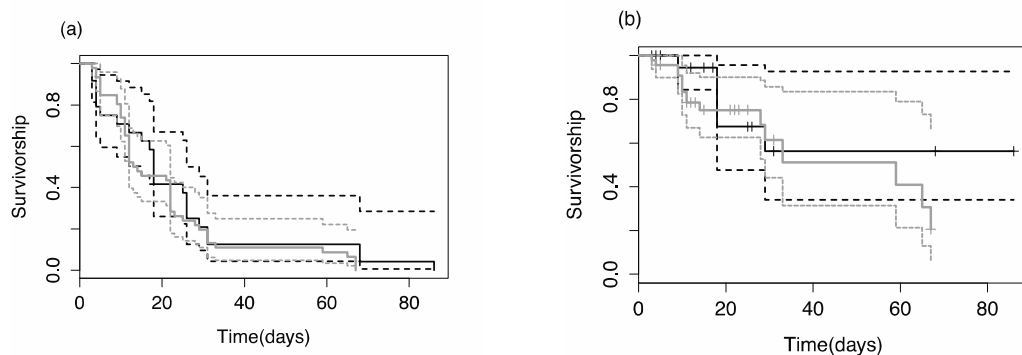
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## 230 Residency

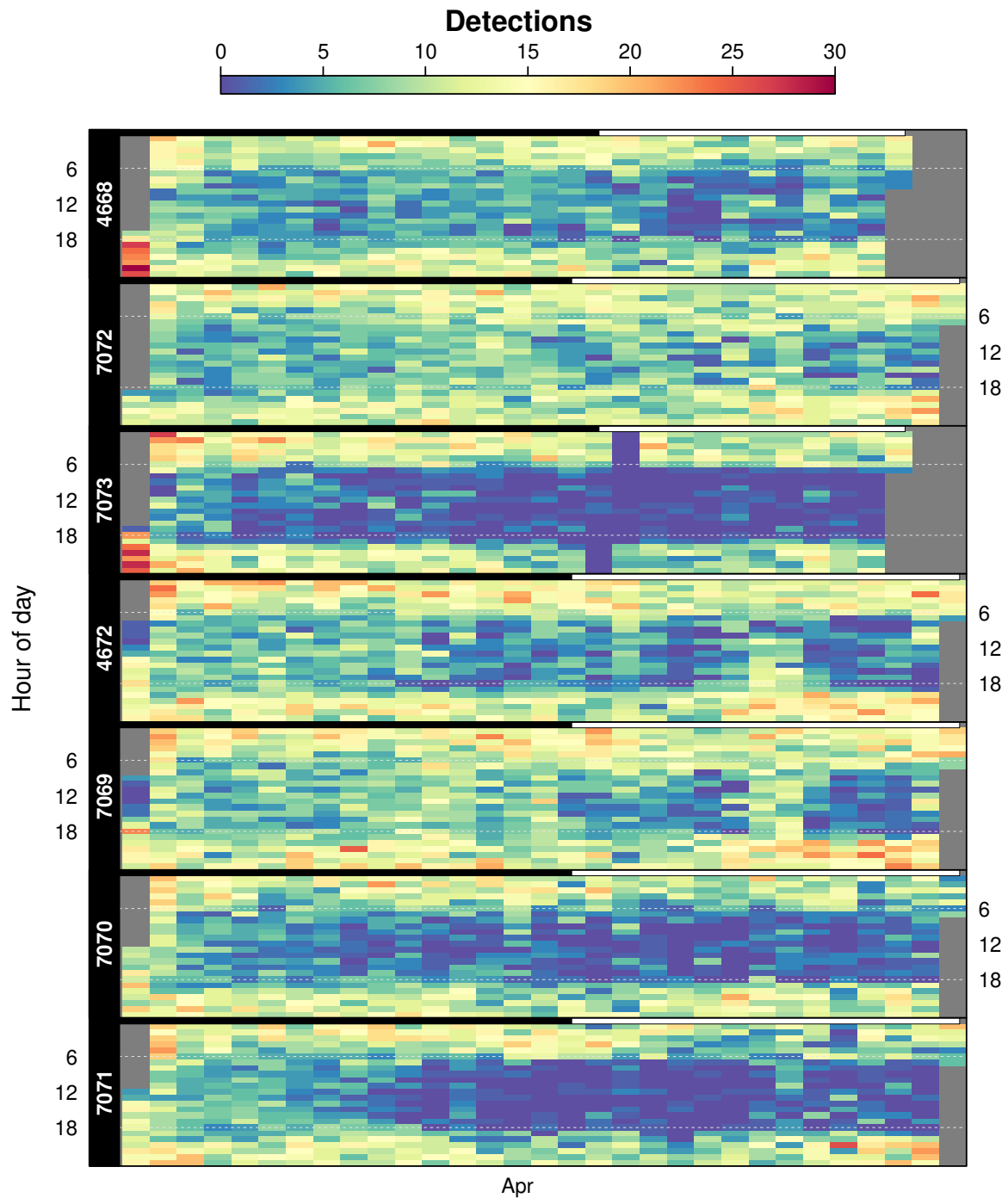
231 TRT at FADs for the rainbow runner ranged between 1.9 to 84.9 days and 2.8 and 66.4 days  
232 for the oceanic triggerfish. The large range in residency was not always indicative of natural  
233 behaviour as observations were often terminated prematurely due to either fishing operations,  
234 which 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 ( $0.75 \pm 0.28$ , mean  $\pm$   
236 SD) and rainbow runner ( $0.75 \pm 0.25$ , 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 ( $\pm 17.59$  SD) for oceanic triggerfish and 23.5 days ( $\pm 21.80$  SD) for rainbow  
254 runner



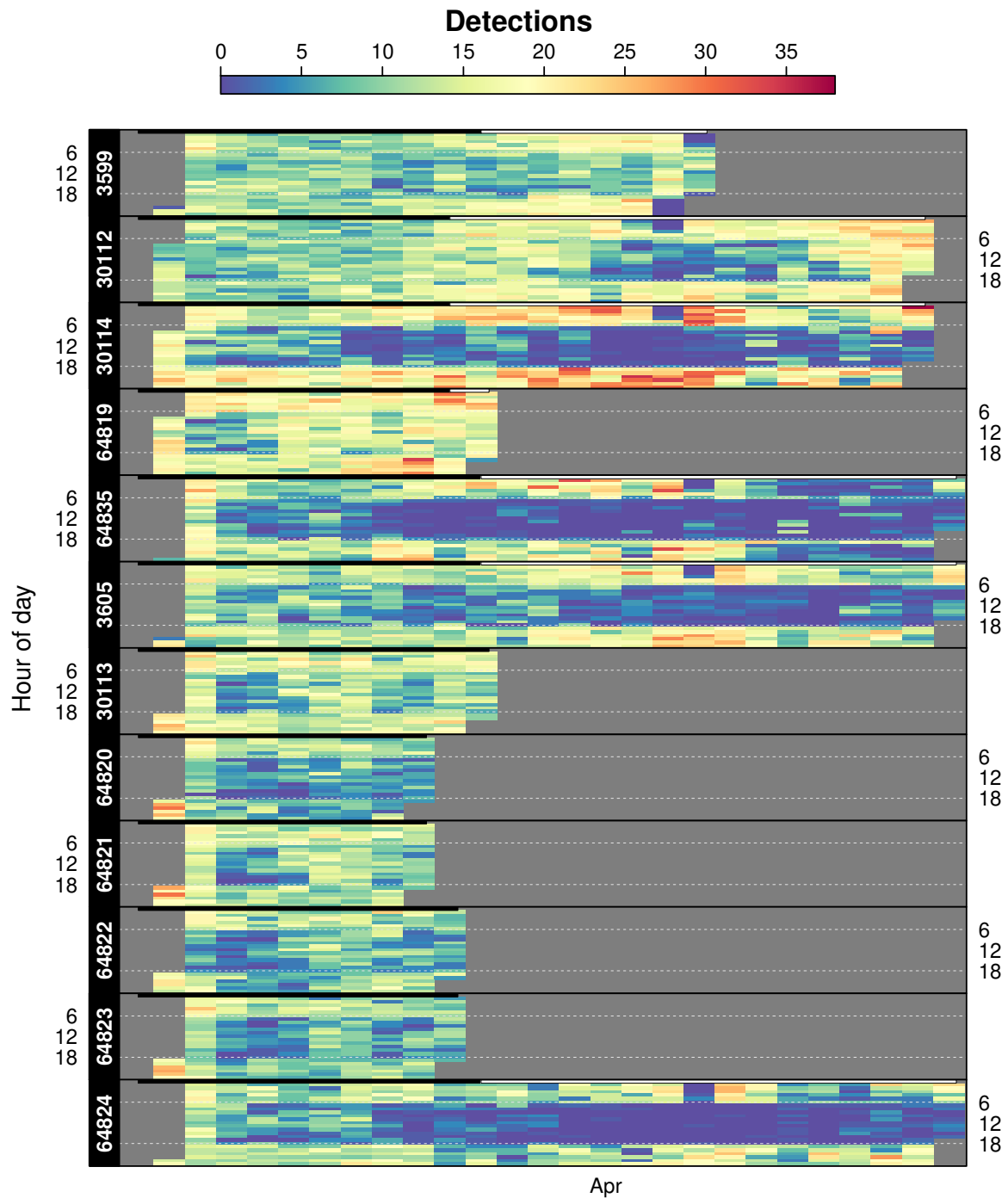
255  
256 Figure 2: Kaplan-Meier survival functions for oceanic triggerfish (grey line) and rainbow  
257 runner (black line) for (a) all TRTs and (b) natural departure TRTs and censored TRTs.  
258 Horizontal ticks indicate censored data points. Dotted lines represent 95% confidence  
259 interval.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

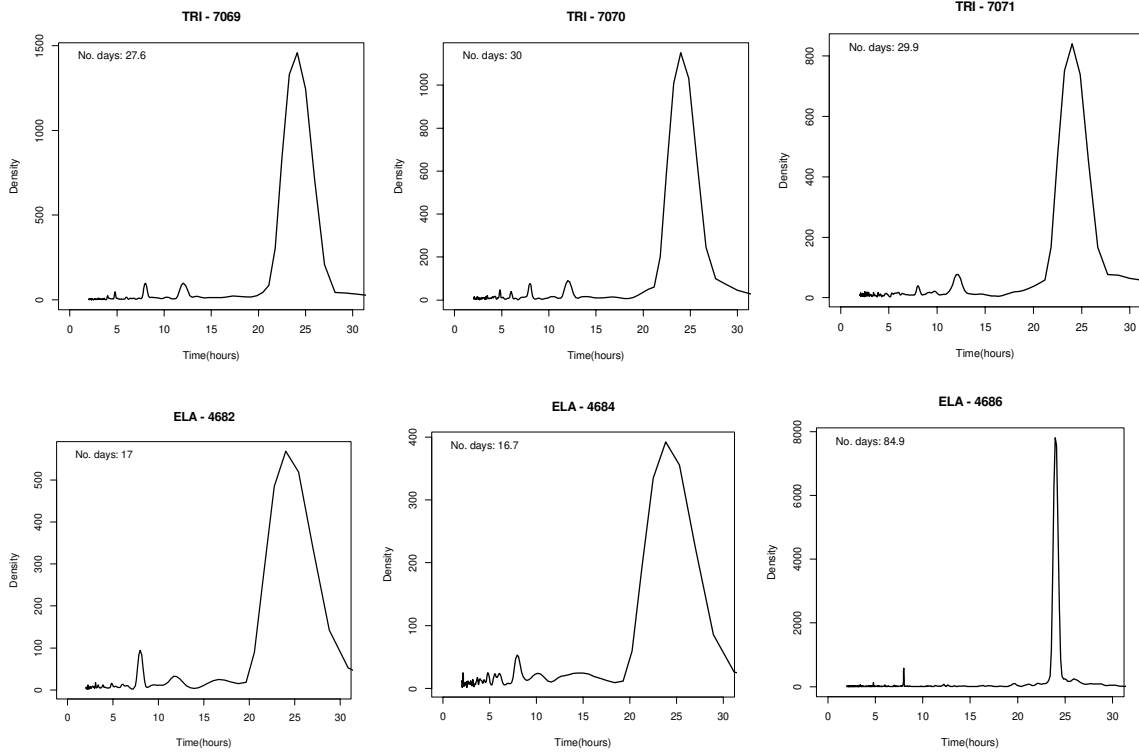


267  
 268 Figure 3: Examples of hourly detection chronogram for rainbow runner (ID# 4668, 7072,  
 269 7073) and oceanic triggerfish (ID# 4672, 7069, 7070, 7071) at FAD SEY41. Each strip  
 270 illustrates the hourly detections of an individual (ID# on the left). Hour of the day is on the y-  
 271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



272  
 273 Figure 4: Examples of hourly detection chronogram for oceanic triggerfish (ID# 3605, 30113,  
 274 64820, 64823, 64824, 64822, 64821) and rainbow runner (ID# 30112, 64835, 64819, 30114,  
 275 3599) at FAD MAY42. Each strip illustrates the hourly detections of an individual (ID# on  
 276 the right). Hour of the day is on the y-axis and time (days) on the x-axis. The scale denotes  
 277 the corresponding number of detections.  
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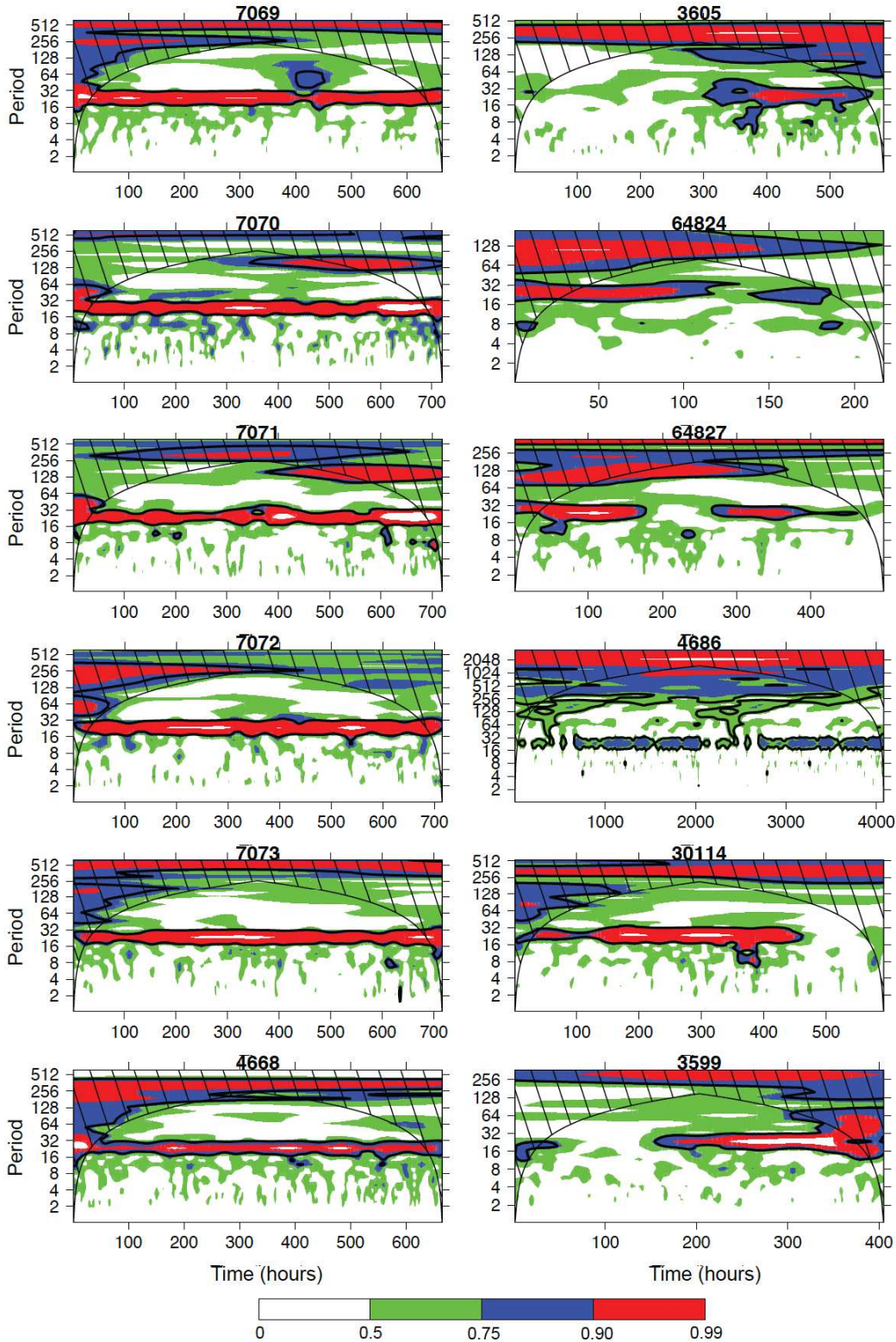
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Figure 5: Examples of fast fourier transform (FFT) spectral densities for three oceanic triggerfish (top) and three rainbow runner (bottom) at drifting FADs.



288  
 289 Figure 6: Wavelet spectrum examples of oceanic triggerfish (Top; ID# 7069, 7070, 7071,  
 290 3605, 64824, 64827) and rainbow runner (bottom; ID# 7072, 7073, 4668, 4686, 30114, 3599)  
 291 using Morlet wavelet of hourly detections showing persistent diel behaviour (left) and  
 292 intermittent diel behaviour (right). Barred area represents the cone of influence (COI). Values  
 293 inside the COI cannot be interpreted due to edge effects. The thick black contour lines  
 294 represent 95% confidence level and the scale bar represents the intensity of the time-  
 295 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.

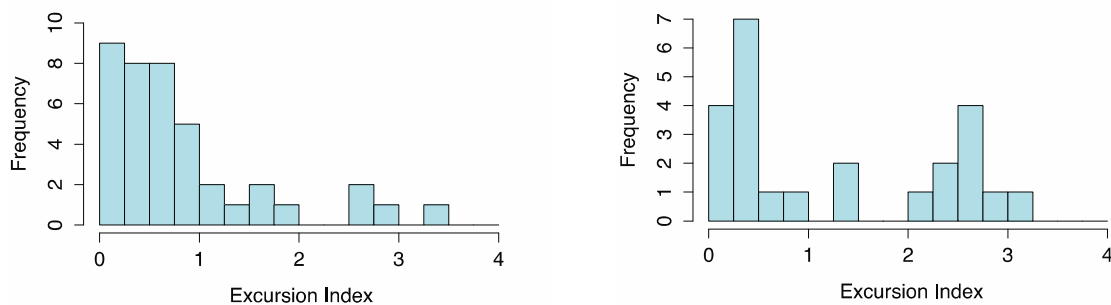
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303 Moreover, the 24 h periodicity was clear on the wavelet spectrograms with a significant  
304 signal (Fig. 6). However, intraspecific variability in the persistence of the 24 h periodicity  
305 was apparent (Fig. 6). Examples in Fig. 6 illustrates 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

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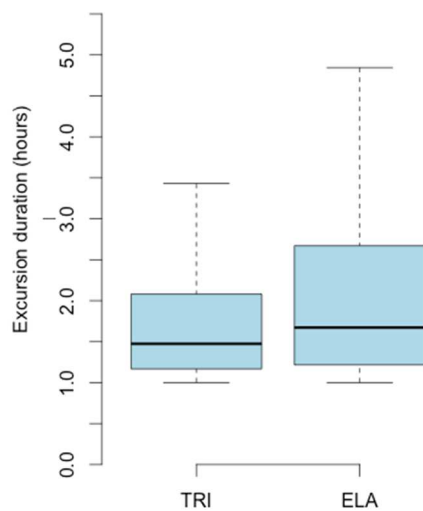
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323 Figure 7: Frequency histogram distributions of excursion index for oceanic triggerfish (left)

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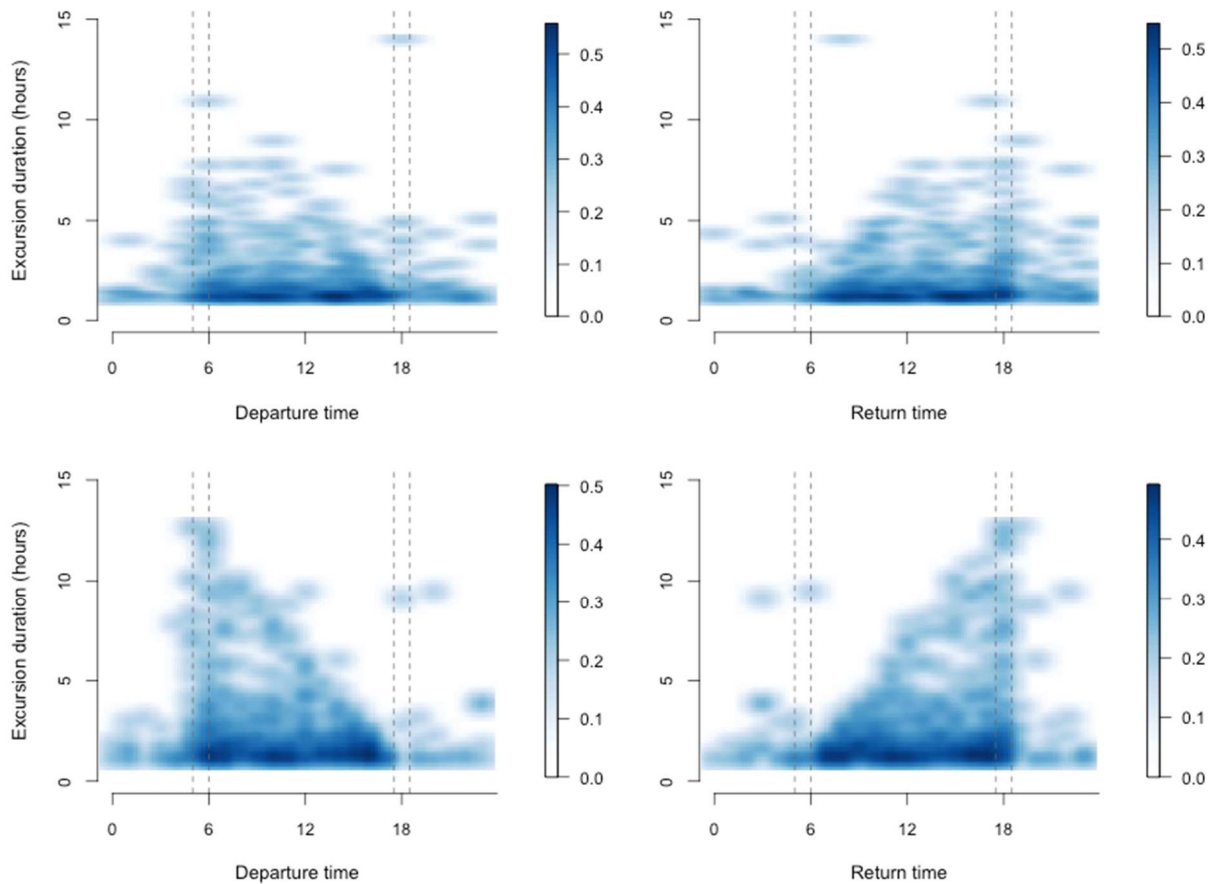
and rainbow runner (right)

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

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 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).

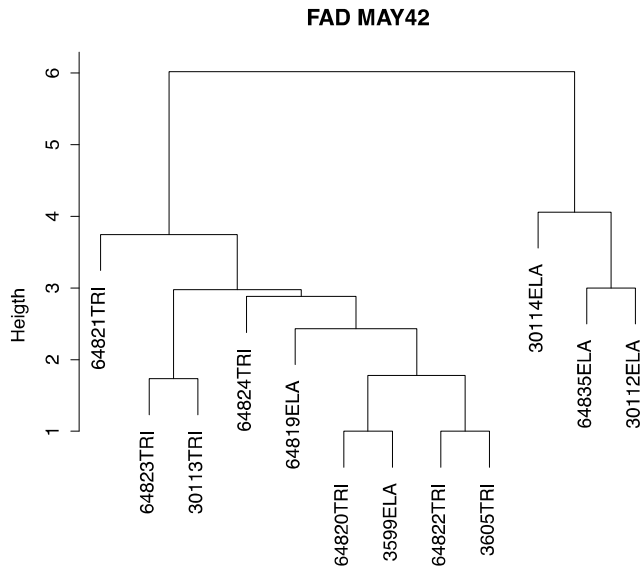


340  
 341 Figure 9: Heatmap of departure and return time (local time) of excursions with corresponding  
 342 durations for oceanic triggerfish (top) and rainbow runner (bottom) at all the FADs. Densities  
 343 are represented on the scale bars. Areas between dotted lines represent sunrise and sunset  
 344 hours.

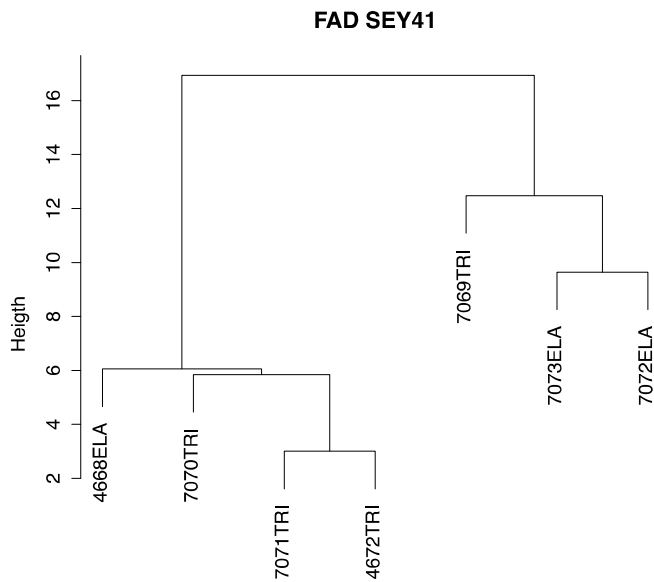
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347 The variability in the associative behaviour amongst individuals of the two species as well as  
 348 temporal variability of individuals during their association is depicted in Figs. 3,4 and 6.  
 349 While some detection gaps may appear to be 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).  
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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).

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## 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](http://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

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