Intra- and interspecific associations in two predatory reef fishes at a shallow seamount

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ABSTRACT: The spatial dynamics of marine populations are shaped by habitat availability, environmental variability and individual interactions, particularly when multiple species share limited habitat such as patchy offshore reefs. The yellowmouth barracuda *Sphyraena viridensis* and the almaco jack *Seriola rivoliana* are the 2 most abundant bentho-pelagic reef predators in the Azores archipelago (central North Atlantic). They aggregate at shallow offshore seamounts, and largely share diet preferences, but very little is known about how habitat and resources are shared by these predators intra- and inter-specifically. Here we use long-term (over 3 yr) passive acoustic telemetry to investigate the patterns of activity, space use and associative behaviour at an isolated, small shallow seamount. By quantifying fine-scale spatiotemporal overlaps and performing null model randomization tests, we found evidence of non-random associations, mostly between conspecifics of both species, as well as shifts in diel and seasonal patterns of space occupancy. Both species were detected more often during spring, and appear to be more active during daytime, suggesting the absence of fine-scale temporal habitat partitioning. Additionally, we found evidence of size-dependent spatial behaviour in almaco jack, with similarly sized individuals co-occurring more often and larger specimens being more infrequently detected. This study quantitatively assesses individual associations using solely presence–absence data collected through passive acoustic telemetry, showing the potential of this approach in a broader application to a significant number of past and ongoing studies, even if many were not originally designed to study this important aspect of fish ecology.

KEY WORDS: Yellowmouth barracuda · Almaco jack · Acoustic telemetry · Space use · Association dynamics · Aggregations · Spatial overlap

1. INTRODUCTION

The aggregation of individuals in space and time is a common behaviour across marine taxa, not only between conspecifics but also between individuals of different species (Ward et al. 2002, Sadovy de Mitcheson & Colin 2011). These aggregations show different spatial and temporal patterns depending on life history traits and environmental conditions. Marine animals are thought to aggregate for a variety of benefits,

from enhanced foraging efficiency to reduced predation or increased reproductive success, even if they might suffer detrimental effects such as increased competition for food resources and risk of parasitism or predation (Romey 1995, Heupel & Simpfendorfer 2005). Indeed, many co-occurring species have evolved to minimize direct competition and increase their tolerance for niche overlap, by means of either diet specialization or fine-scale spatiotemporal segregation (Carothers & Jaksić 1984, Kronfeld-Schor &

Dayan 2003, Sánchez-Hernández et al. 2011). By ultimately determining encounter rates between conspecific and interspecific individuals, these behavioural traits can profoundly impact community-wide trophic dynamics as well as species' reproductive fitness and resilience (Lowerre-Barbieri et al. 2019).

Yet, notwithstanding the ecological importance of these processes, quantitative studies of marine aggregation dynamics remain surprisingly limited and so is our understanding of the causal links between the motivations to aggregate and the observed social assortment patterns. Although marine acoustic biotelemetry has greatly expanded in the last 2 decades, only recently have studies started to investigate the dynamics of species coexistence and to account for biological interactions that may be key to a better understanding of the spatial dynamics and fitness of marine populations (e.g. Jacoby et al. 2016, Mourier et al. preprint doi:https://doi.org/10.1101/749085).

A particular case where the fitness consequences of individual interactions might be amplified is when habitat and resources are limited, such as in small, isolated reef patches. Indeed, a variety of oceanic and reef species are known to aggregate and share these particular habitats, including reefs located on the summits of shallow seamounts and atolls (e.g. Meyer et al. 2007, Afonso et al. 2014, Fontes et al. 2014, Fontes & Afonso 2017). This phenomenon is thought to be a behavioural response to profit from the increased flux of nutrients (and the prey depending on them) promoted by the jets and trapping currents originating in the steep slopes of the seamounts rising from the deep sea (Genin et al. 1986, Rogers 2004, Menezes et al. 2006, Genin & Dower 2007).

The yellowmouth barracuda *Sphyraena viridensis* (Cuvier, 1829) and the almaco jack *Seriola rivoliana* (Valenciennes, 1833) are the 2 most abundant bentho-pelagic predatory reef fishes in the Azores archipelago, central North Atlantic (Afonso et al. 2018). Despite their important ecological role on reef communities and high value for artisanal and recreational fisheries across their distribution range (Diogo & Pereira 2013, 2014), their spatial ecology remained fairly unknown until recently (see Fontes et al. 2014, Fontes & Afonso 2017). Both species are known to form large aggregations (up to hundreds of individuals) on offshore reefs and seamounts within the NE Atlantic archipelagos of Macaronesia. In the Azores, their diet is largely composed of juvenile blue jack mackerel *Trachurus picturatus* (Barreiros et al. 2002, 2003). Thus, these are 2 taxonomically distant species that share both a substantial habitat and a diet niche.

Studies have also reported a seasonal pattern in abundance and, presumably, aggregation behaviour, with both species forming larger schools during the summer, at least on shallow reefs where they can be observed underwater by divers (Terceira Island, Azores; Barreiros et al. 2002). This behaviour could be a response to baitfish prey abundance, reflecting the trade-offs of schooling for feeding purposes. These aggregations may also be motivated by reproductive activity (Heyman 2001), as both species are known to spawn during the summer (P. Afonso & T. Morato unpubl. data). Interestingly, they were found to be year-round residents on Azorean seamounts, contradicting the generalized perception that these are highly mobile seasonal visitors (based on local traditional knowledge; Fontes et al. 2014, Fontes & Afonso 2017). It is possible, though, that aggregations might still occur for spawning purposes at a much more localized scale, as in many benthic reef fishes (e.g. Afonso et al. 2008a,b). The 2 hypotheses (i.e. feeding vs. spawning aggregative behaviour) remain virtually untested on these and other ecologically similar species (but see Meyer et al. 2007, Afonso et al. 2008b, 2009b).

Our study investigates how individuals of these 2 predatory reef fishes share an isolated and limited habitat. Using long term (over 3 yr) presence–absence data from passive acoustic telemetry at a remote shallow seamount, we (1) estimate the spatiotemporal overlap between conspecifics and individuals of both species, (2) investigate the diel and seasonal temporal patterns of space use, and (3) investigate the links between associative behaviour and potential environmental drivers across the years.

2. MATERIALS AND METHODS

2.1. Study site

The Formigas Bank is an isolated, relatively small (7 × 3 km) volcanic seamount rising from the deep sea, 36 km northeast of Santa Maria Island and 60 km southeast of São Miguel Island, Azores (Fig. 1; Ávila & Azevedo 1997). Its shallow portion, i.e. the rims and centre of the extinct volcano's caldera which resulted from the subsidized primitive cone, comprises 3 major rocky reefs: (1) the Formigas islets, an emerged basaltic lava ridge forming the west rim of the seamount summit; (2) the Dollabarat reef, an ash-deposit plateau forming the east rim of the seamount summit (minimum depth 3 m); and (3) the Middle reef (25 m), an ash-deposit plateau from a later erup-
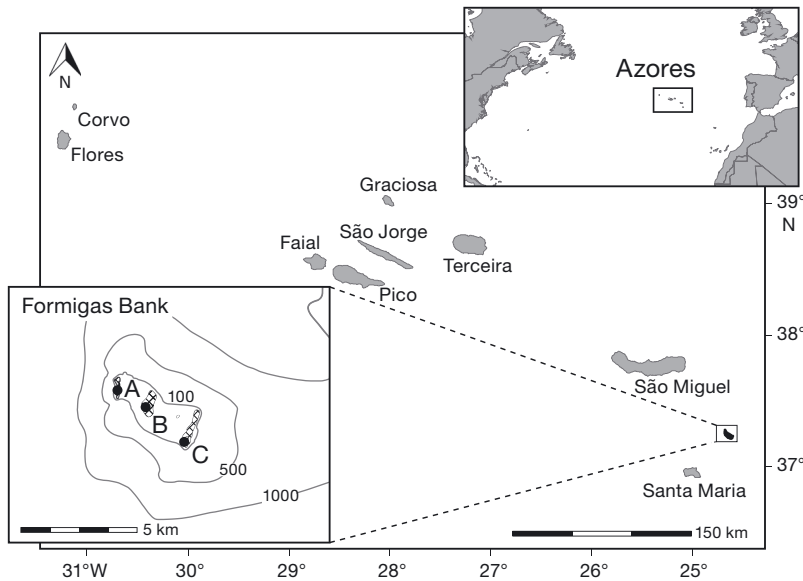
Fig. 1. Location of the Azores archipelago in the mid-north Atlantic (upper right), a detailed view of the islands (middle) and the Formigas Bank (bottom left). Gridded area denotes habitat shallower than 50 m depth; black dots indicate location of the receivers. A: Formigas islets; B: Middle reef; C: Dollabarat reef

tion in the central zone. All three reefs run along the north-south axis. The blend of oceanic, coastal and deep-sea habitats and communities of the Formigas Bank is considered unique (Afonso et al. 2018) and led to its classification as a regional marine protected area (MPA) in 1988. Initially, only partial protection was offered to the shallow portion of the seamount (<200 m), but since 2003 only pole-and-line tuna fishing is allowed down to 1800 m within a 530 km² box, including the 0.2 km² of shallow habitats (Fontes et al. 2014). The area is also classified as an international MPA by the Oslo-Paris Commission (Convention for the Protection of the Marine Environment of the North-East Atlantic).

2.2. Capture and tagging

A total of 16 almaco jack and 17 yellowmouth barracuda were acoustically tagged at the Formigas Bank. Two different fishing and tagging batches were carried out: one in September 2007 (n = 23 fish, 10 jack and 13 barracuda) using the traditional surface pole-and-line fishing with live bait (juvenile *Trachurus picturatus*) and another in August 2008 (n = 10, 6 jack and 4 barracuda) by near-bottom jigging (20 to 90 m depth) to target larger individuals. Fish captured at depth were slowly hauled (ca. 0.2 m s⁻¹) to reduce the risk of swim bladder rupture. Ultrasonic coded transmitters (Vemco V16-4H model, 69 kHz, 158 dB power

output, 60 to 180 s nominal delay and expected 1470 d of battery life) were surgically implanted into the peritoneal cavity of individuals while maintaining them in an inverted position for tonic immobility and providing them a continuous flow of seawater directly though the mouth and gills. Before release, all fish were measured and tagged with a small external spaghetti dart tag (Hallprint) for external recognition if recaptured. Handling and tagging procedures lasted less than 4 min and were carried out by trained and experienced researchers. None of the caught animals died or showed visible signs of barotrauma or abnormal behaviour (Nichol & Chilton 2006, Fontes et al. 2014).

2.3. Acoustic passive monitoring

The presence of the tagged animals (i.e. the exact date/time stamp of a given ID transmission) was continuously monitored and recorded by 3 single-frequency receivers (Vemco VR2Ws) moored 2.5 m above the sea floor (ca. 25 m depth), one at each of the 3 shallow reefs in the MPA (Fig. 1). Receivers deployed at the Formigas and Dollabarat reefs recorded data for 1410 d (from August 2007 to July 2011), which includes the whole duration of the estimated battery life of the transmitters. The middle reef receiver failed after 1039 d (in September 2010). Receivers were annually retrieved by SCUBA diving, and the stored data downloaded. Although specific listening range tests were not carried out at the study site, similar assessments had been already carried out on comparable Azorean coastal reefs (see Afonso et al. 2008a,b) and seamounts (Afonso et al. 2012) with the same equipment. Based on those tests, we assumed a maximum (average) detection range of 800 m, and simulated the effect of potential noise in detection probability between day and night periods (see Text S1 in the Supplement at www.int-res.com/articles/suppl/m654p093_supp.pdf for details).

2.4. Data analysis

The 4 yr detection dataset was exported from the manufacturer's handling database (VUE) and analysed using specific routines in R (version 3.6; R Core

Team 2019). First, the data were cleaned of the false detections which may occur whenever signals from different transmitters collide (Heupel et al. 2006). We considered false any detection from a given transmitter ID occurring isolated over 24 h in the whole 3-receiver network (Meyer et al. 2007, Afonso et al. 2009a). Detections were then plotted to provide a visual interpretation of individual detection patterns and used to compute an overall residency index (I_R) for each individual at the Formigas Bank. I_R ranges from 0 (no residency) to 1 (full time resident) and corresponds to the number of days a fish was detected (D_d) divided by the maximum possible number of days it could be detected (T_p), i.e. the period between the day of release and the fish's last detection (Abecasis et al. 2014). To investigate the existence of preferential sites within the seamount bank, we computed the Shannon entropy index (Shannon 1948, 1949) on the proportion of stations where each individual occurred. Shannon's entropy index measures the uncertainty of probability distributions, and has been commonly used as a measure of species and genetic diversity in ecology (Fuhrman et al. 2000, Ricotta & Szeidl 2006, Chao et al. 2015). This index was preferred over the more commonly used bivariate kernel utilization distributions (Worton 1989) due to the inaccuracy of estimating home range areas with a limited, non-overlapping receiver coverage.

Since the index's maximum depends on the number of receivers within the array, we normalized values to range between 0 (whenever a fish is detected at a single receiver) and 1 (when it is equally detected across all 3 receivers). Letting p_i denote the proportion of detections in receiver i during an individual's monitoring period and where n denotes the total number of receivers, normalized entropy (H) can be expressed as:

$$\text{Normalized Entropy } (H) = \frac{-\sum_{i=1}^{n} p_i \ln(p_i)}{\ln(p_i)} \quad (1)$$

Detections at a given receiver were then pooled into 30 min bins and rearranged in a time bin x individual matrix. This interval was chosen after several preliminary tests (see Text S1 and Fig. S2 for further details) and based on the estimated swimming speeds of both species (M. Gandra et al. unpubl. data). To test for the existence of temporal patterns in the associations, time bins were classified according to time of day and season. Time of day (day vs. night) was defined based on sunrise and sunset times estimated for the study site coordinates using algorithms provided by NOAA. Annual seasons were defined on a monthly basis, with spring ranging from March to May, summer from June to August, autumn from September to November and winter from December to February.

The extent of association between the individuals was assessed through multiple pairwise comparisons, assuming that joint space usage occurred whenever the individuals overlapped in space (receiver) and time (bin). Only the total shared periods of detection for a given pair were considered for this analysis, i.e. the time bins from the latest release date to the earliest last detection between each pair of individuals. This truncation step ensured that the absence of an individual in the receiver array was not due to transmitter failure or premature death. The pairwise comparison index is analogous to the simple ratio association index (Cairns & Schwager 1987, Ginsberg & Young 1992), ranging from 0% (no overlap) to 100% (complete overlap). Letting x denote the number of time bins in which a given pair was detected at the same station, y_A and y_B the number of time bins in which only 1 of the individuals of the pair was detected and y_{AB} the number of time bins where individuals were detected at different stations, it can be represented as:

$$\text{Overlap (\%)} = \frac{x}{x + y_{AB} + y_A + y_B} \times 100 \quad (2)$$

Time bins with neither of the individuals detected are not included in the denominator of the coefficient, since they do not provide information regarding spatiotemporal co-occurrence (animals could either be associated in an area not covered by the range of the receivers or be not associated at all). The resultant overlap statistics were then compared against the null hypothesis of temporally independent space use (i.e. each animal occurs independently of the other) using Monte Carlo permutation tests. As presence–absence null model tests have been a major source of controversy in community ecology (Gotelli 2000), we chose the conservative approach of only permuting entries within each column, so that the total number of detections of each individual and the relative occurrence frequencies across the receivers were kept unchanged. We also accounted for potential diel and seasonal trends in occurrences by only allowing permutations across time bins within the same diel phase and day (Castro-Arellano et al. 2010). Using this procedure, we generated 10 000 simulated datasets for each population, and tested for non-randomness by comparing the observed pairwise and population, median overlaps with the distribution of the same statistics calculated for the randomized data. Thus, p-values were obtained by calculating

the probability of obtaining a value greater or lower than the observed statistic within the null distribution. The result would therefore indicate a tendency for joint resource utilization (attraction) if significantly higher than the null distribution or indicate spatiotemporal segregation (avoidance) if significantly lower (Bejder et al. 1998, Whitehead et al. 2005).

Potential size-assortative differences in space use sharing, i.e. the effect of both individual size and size similarity in the extent of overlaps observed, were visually inspected through network plots and formally tested using a Pearson's correlation analysis. Network theory is based on the notion that interconnected systems are made up of nodes, or individual entities, connected by edges, which represent some form of relationship and can be either binary or weighted (Jacoby et al. 2012, Psorakis et al. 2012). In our analysis, nodes represent single fish and are proportionally dimensioned according to each individual's length, while edges represent the extent of spatial overlap between each fish pair.

After testing for assumptions of data distribution and normality, differences in detection frequency and overlap scores across diel and seasonal cycles were inspected through box plots and formally tested with non-parametric Wilcoxon signed rank tests (day vs. night) and Kruskal-Wallis rank sum tests (annual seasons). To further investigate potential interactions between diel and seasonal cycles, we averaged both metrics by month and hour and generated contour plots (i.e. heat maps, color-coded 2-dimensional plots).

Whenever seasonal differences were found in overlap estimates, we searched for potential environmental drivers using generalized linear mixed models. Models were estimated using the glmmTMB R package (Brooks et al. 2017), and included the following explanatory covariates: sea surface temperature (SST), surface chl *a* concentration, geostrophic current velocity and sea surface height (SSH) above sea level. SST and geostrophic current velocity data were retrieved through ERDDAP from the Multiscale Ultra-high Resolution SST Analysis and AVISO datasets, respectively. Chl *a* and SSH covariates were sourced from the Copernicus Marine and Environment Monitoring Service (http://marine. copernicus.eu). Additionally, to account for potential asynchronicities between phytoplankton and zooplankton blooms, 1 mo lagged chl *a* estimates were also included in the analysis (Druon et al. 2019). As overlap estimates were overdispersed and non-normally distributed, we used logistic regression and fitted a zero-inflated beta-binomial model, including the numerator of the overlap index (number of co-occurrences) as the response variable and the denominator as the weights component. The zero-inflation component of the model was included since the absence of overlap can arise in different cases (i.e. tagged fish were not present, not detected or registered at different receivers). All variables were averaged by month/year and previously tested for correlation and collinearity through a variance inflation factor analysis (Zuur et al. 2010). While all environmental covariates were considered as fixed factors, year and fish pair ID were treated as random factors to account for repetitive measures. Additionally, we controlled for potential temporal autocorrelations by refitting the models with an AR(1) covariance structure. The best models were selected through a backward stepwise procedure (i.e. sequentially removing covariates from a full model) based on the Akaike's information criterion, and model performance was examined using plots of residuals vs. fitted values, observed vs. predicted values and simulated residuals quantile–quantile plots (DHARMa package; Hartig 2019).

3. RESULTS

Twenty-nine of 33 (88%) tagged fish were detected by the receiver array. All 4 undetected fish were barracuda (Table 1). Despite the broad coverage of the listening acoustic array across the archipelago, including receivers in the adjacent island of Santa Maria and other major seamounts (see Fontes et al. 2014 or Fontes & Afonso 2017), none of the tagged fish were detected outside the Formigas array. Since transmitters are assumed to have low failure rates, it is likely that these individuals emigrated from the seamount or suffered post-release mortality, either as a result of the tagging procedures or due to illegal capture (known to frequently occur in the area). Most individuals were detected in multiple years, some on a daily basis, while others were periodically undetected for variable periods of time (Fig. 2, Figs. S3 & S4). Excluding the 4 undetected individuals, tagged barracuda (68.5 to 96.0 cm fork length [FL]) were detected for 41 to 1409 d (Table 1) with an average of 0.49 (0.14 to 0.83) seamount residency. Barracuda #9 was absent for over 2 yr. Jack (53.5 to 118.0 cm FL) were detected for 592 to 1410 d (Table 1) with an average of 0.79 (0.62 to 0.93) residency. Entropy averaged 0.62 (0.18 to 0.91) in barracuda vs. 0.81 (0.61 to 0.98) in jack (Table 1), indicating that jack were detected

Table 1. Summary data for yellowmouth barracuda *Sphyraena viridensis* and almaco jack *Seriola rivoliana* tagged at the Formigas Bank. FL: fork length; T_P: total period of detection (i.e. number of days between the release date and the fish's last detection); D_d: number of days with detections; I_R: residency index; H: entropy index; (−) missing values. Mean values ± SE are displayed below each species (na: not applicable)

Fish ID	FL (cm)	Tagging site	Tagging date (dd/mm/yyyy)	Last detection (dd/mm/yyyy)	T_P	D_d	I_R	H
S. viridensis								
#1	81.0	Middle	04/09/2007	24/06/2009	660	545	0.83	0.63
#2	83.0	Dollabarat	05/09/2007	14/07/2011	1409	1112	0.79	0.64
#3	83.0	Formigas	05/09/2007	02/07/2010	1032	163	0.16	0.37
−	95.0	Formigas	05/09/2007	−	−	−	−	−
#4	83.5	Middle	07/09/2007	17/10/2007	41	20	0.49	0.18
#5	84.0	Middle	07/09/2007	27/08/2008	356	256	0.72	0.69
#6	76.5	Formigas	07/09/2007	10/05/2008	247	146	0.59	0.91
#7	86.0	Formigas	07/09/2007	15/07/2011	1408	975	0.69	0.89
#8	85.5	Formigas	07/09/2007	14/07/2011	1407	407	0.29	0.67
#9	83.0	Formigas	08/09/2007	20/03/2011	1290	176	0.14	0.22
#10	72.0	Formigas	08/09/2007	10/07/2011	1402	992	0.71	0.87
−	65.0	Formigas	08/09/2007	−	−	−	−	−
−	91.5	Middle	08/09/2007	−	−	−	−	−
#11	96.0	Middle	28/08/2008	11/07/2011	1048	467	0.45	0.85
−	104	Formigas	29/08/2008	−	−	−	−	−
#12	92.5	Formigas	29/08/2008	12/07/2011	1048	219	0.21	0.58
#13	68.5	Formigas	29/08/2008	10/07/2011	1046	255	0.24	0.63
Mean	82.7	na	na	na	953 ± 133	441 ± 101	0.49 ± 0.07	0.62 ± 0.07
S. rivoliana								
#14	64.0	Dollabarat	05/09/2007	15/07/2011	1410	1251	0.89	0.61
#15	53.8	Middle	07/09/2007	12/07/2011	1405	1043	0.74	0.97
#16	53.5	Middle	07/09/2007	21/07/2009	684	542	0.79	0.89
#17	56.5	Middle	07/09/2007	11/07/2011	1404	1083	0.77	0.98
#18	60.5	Middle	07/09/2007	15/07/2011	1408	1103	0.78	0.88
#19	59.5	Middle	07/09/2007	15/07/2011	1408	1160	0.82	0.93
#20	55.5	Middle	07/09/2007	15/07/2011	1408	1111	0.79	0.83
#21	58.0	Formigas	08/09/2007	14/07/2011	1406	1038	0.74	0.64
#22	59.0	Formigas	08/09/2007	15/07/2011	1407	873	0.62	0.67
#23	58.0	Formigas	08/09/2007	15/07/2011	1407	1312	0.93	0.70
#24	92.0	Middle	28/08/2008	15/07/2011	1052	669	0.64	0.91
#25	69.5	Formigas	28/08/2008	15/07/2011	1052	898	0.85	0.78
#26	95.0	Formigas	28/08/2008	11/04/2010	592	516	0.87	0.69
#27	106.0	Formigas	29/08/2008	15/07/2011	1051	726	0.69	0.88
#28	118.0	Formigas	30/08/2008	15/07/2011	1050	763	0.73	0.78
#29	56.0	Formigas	30/08/2008	14/07/2011	1049	858	0.82	0.75
Mean	69.7	na	na	na	1200 ± 69	934 ± 61	0.78 ± 0.02	0.81 ± 0.03

more uniformly across the 3 receivers, although all fish were still detected on more than 1 station.

3.1. Intraspecific associations

Most detections and conspecific co-occurrences were recorded at the Formigas islets for both species (Fig. S5). Since barracuda #4, #5 and #6 were last detected before the tagging of barracuda #11, #12 and #13, only 69 of the possible 78 pairwise comparisons were carried out between barracuda conspecifics. Still, the average shared detection period among bar-

racuda pairs reached almost 2 yr. Barracuda pairwise overlap averaged 4.4% (ranging from 0.0 to 20.6%). After performing the null model analysis, 45 of those 69 pairwise overlap extents were found to be significantly higher than what could be expected from random space use (Fig. 3). Likewise, the median barracuda population overlap (3.1%) was significantly higher than the medians obtained for the simulated datasets (Fig. 3). As jack were detected for longer periods than barracuda, on average, their mean shared period of detection (1040 d, approximately 2.85 yr) was also larger. Individual jack did, however, overlap an average of 12.9% (0.9 to 27.9%) of the time, i.e. 3
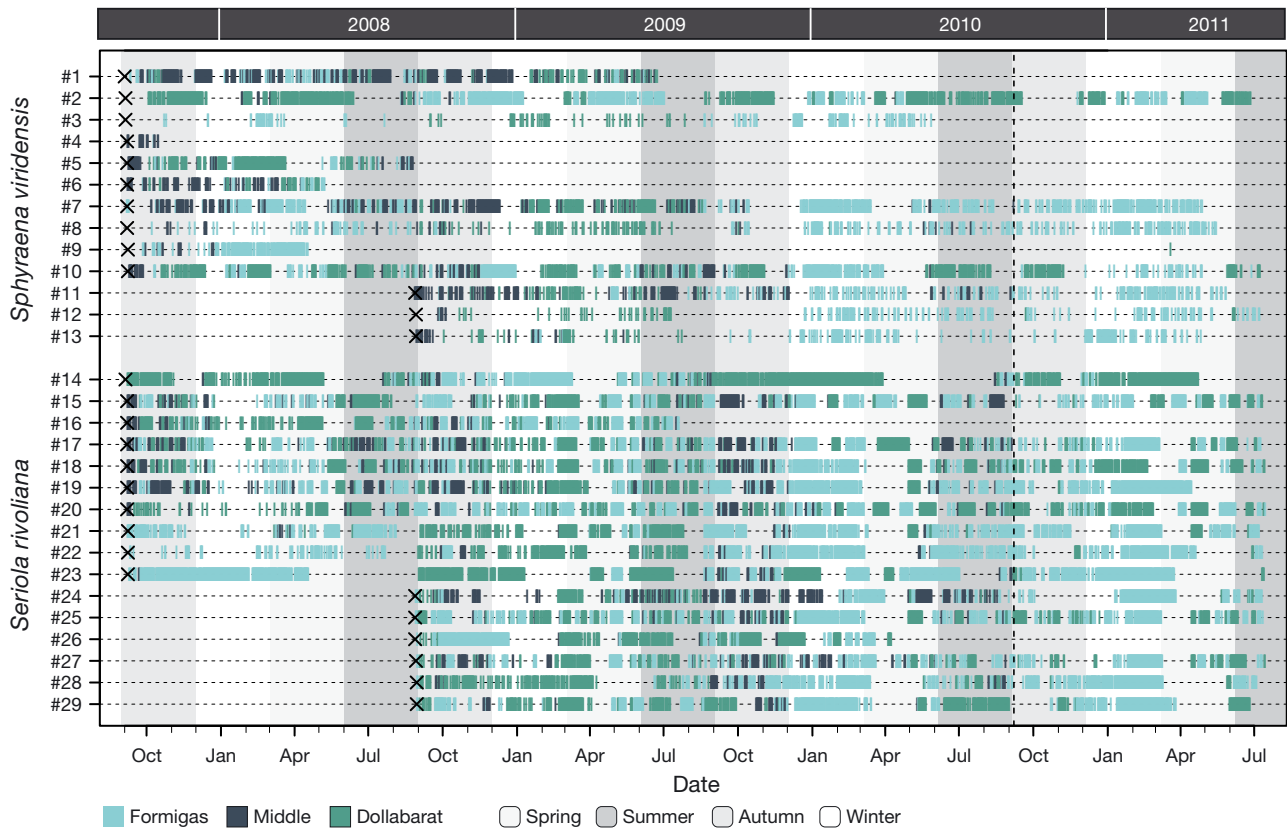
Fig. 2. Detection patterns of yellowmouth barracuda *Sphyraena viridensis* and almaco jack *Seriola rivoliana* tagged at the Formigas Bank. Colours: different receivers; vertical dashed line: day the middle reef receiver was deactivated; shaded areas: different seasons; Cross marks (×): release dates
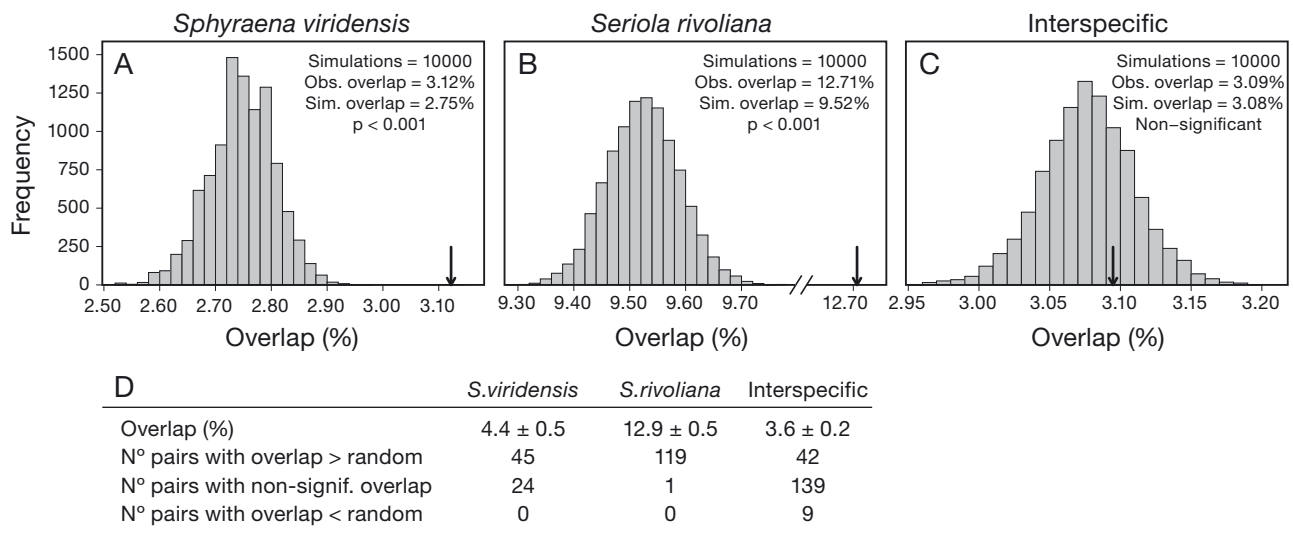

D	*S.viridensis*	*S.rivoliana*	Interspecific
Overlap (%)	4.4 ± 0.5	12.9 ± 0.5	3.6 ± 0.2
Nº pairs with overlap > random	45	119	42
Nº pairs with non-signif. overlap	24	1	139
Nº pairs with overlap < random	0	0	9

Fig. 3. Frequency distributions of median pairwise overlaps obtained through Monte Carlo permutation tests. Analysis was carried out for both intraspecific ([A] yellowmouth barracuda, [B] almaco jack) and (C) interspecific dyads, using 10 000 simulations of each dataset. Null hypotheses were tested by comparing the observed median overlaps (Obs. overlap, indicated by arrows) to the upper and lower tails of the null distributions, using α = 0.05. Distribution means (Sim. overlap) and correspondent p-values are shown on the top right corner of each plot. (D) Mean overlap (±SE) of each population, together with summary results of the same null model test run individually for each fish pair

times that of barracuda, and only 1 of 120 pairs did not exhibit significantly higher overlaps than the scores estimated through the randomization procedure (Fig. 3). Jack #21 and #23 co-occurred continuously for 18.5 h at the Formigas islets in April 2008, the maximum period of uninterrupted co-detection of 2 fishes registered in the present study. As expected, the median jack population overlap (12.7%) was also significantly larger than the randomly generated median estimates (Fig. 3).

No significant correlation was found between pairwise size differences and pairwise overlap (p = 0.798; Fig. 4A,D) or between total length and average overlap of barracuda (p = 0.984; Fig. 4A,G). Contrarily, jack appear to show stronger associations between similarly sized conspecifics, as indicated by the inverse linear relationship between pairwise size differences and overlaps (r = −0.38, p < 0.001; Fig. 4B,E). A significant correlation was also found between the individual size of tagged jack and their average overlap, with smaller specimens overlapping more frequently than larger individuals (r = −0.60, p = 0.014; Fig. 4B,H).

Both species showed a significant fluctuation in conspecific overlap across seasons, individuals being detected together more often during the spring and more rarely during the summer (Fig. 5, Fig. S6). The monthly intraspecific overlap estimates were also found to be negatively associated with SST and positively associated with geostrophic current and 1 mo lagged surface chl *a* for both species (p < 0.05; Table 2).
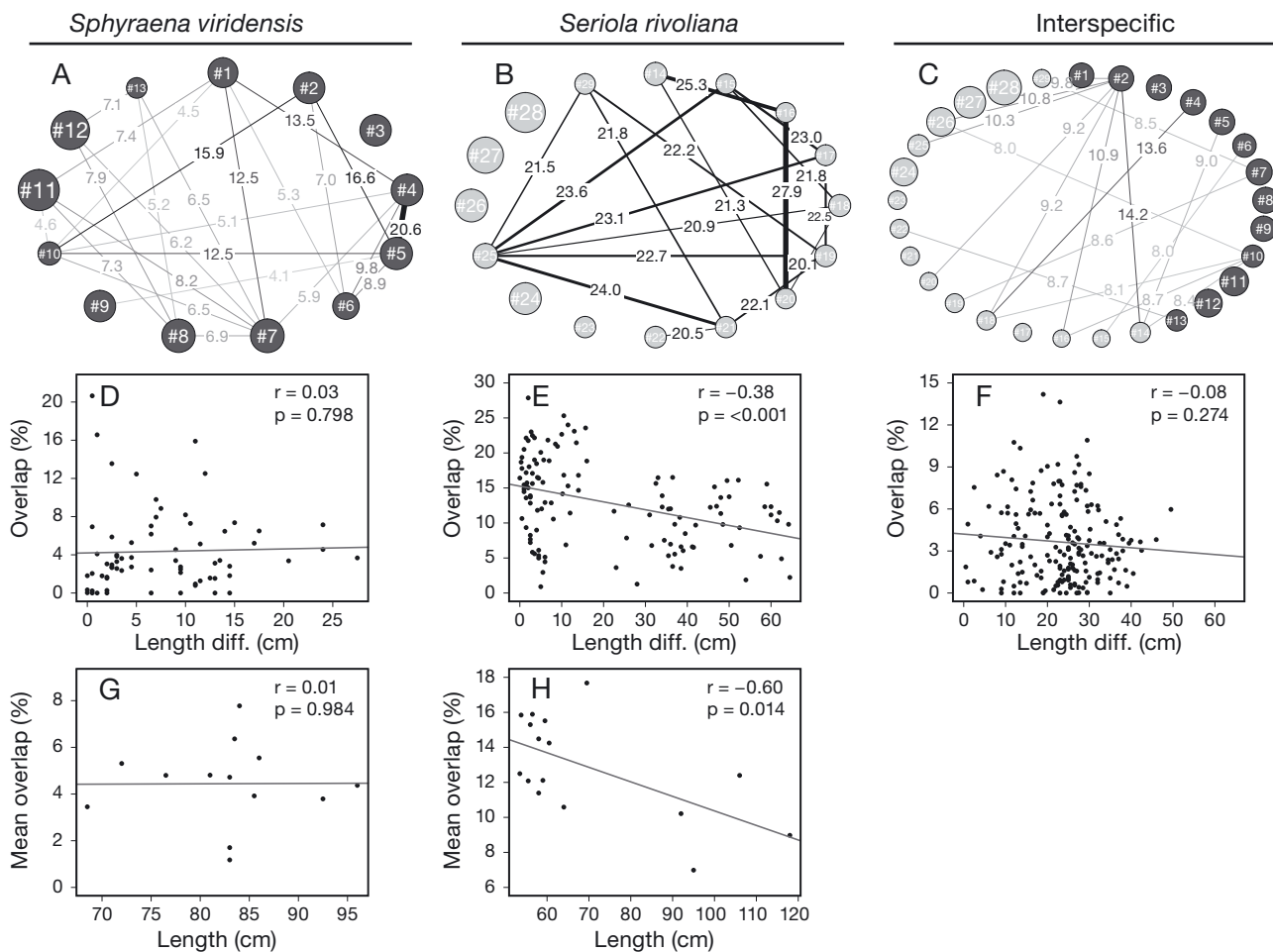

Fig. 4. Network representation of pairwise overlap scores obtained for (A) yellowmouth barracuda, (B) almaco jack and (C) interspecific dyads. Each node represents a single fish (shaded by species), and is dimensioned proportionally to its size (standardized by plot). Edges represented the extent of spatial overlap between each fish pair (i.e. greater thickness indicates a higher overlap). To simplify visual interpretation, an overlap threshold was set in each network, with only overlap scores above 4, 20 and 8% being shown for barracuda, jack and interspecific pairs, respectively. Relationships (linear regression) (D,E,F) between pairwise differences in body length and overlap scores and (G,H) between body length and average overlaps are shown, together with Pearson's correlation statistics
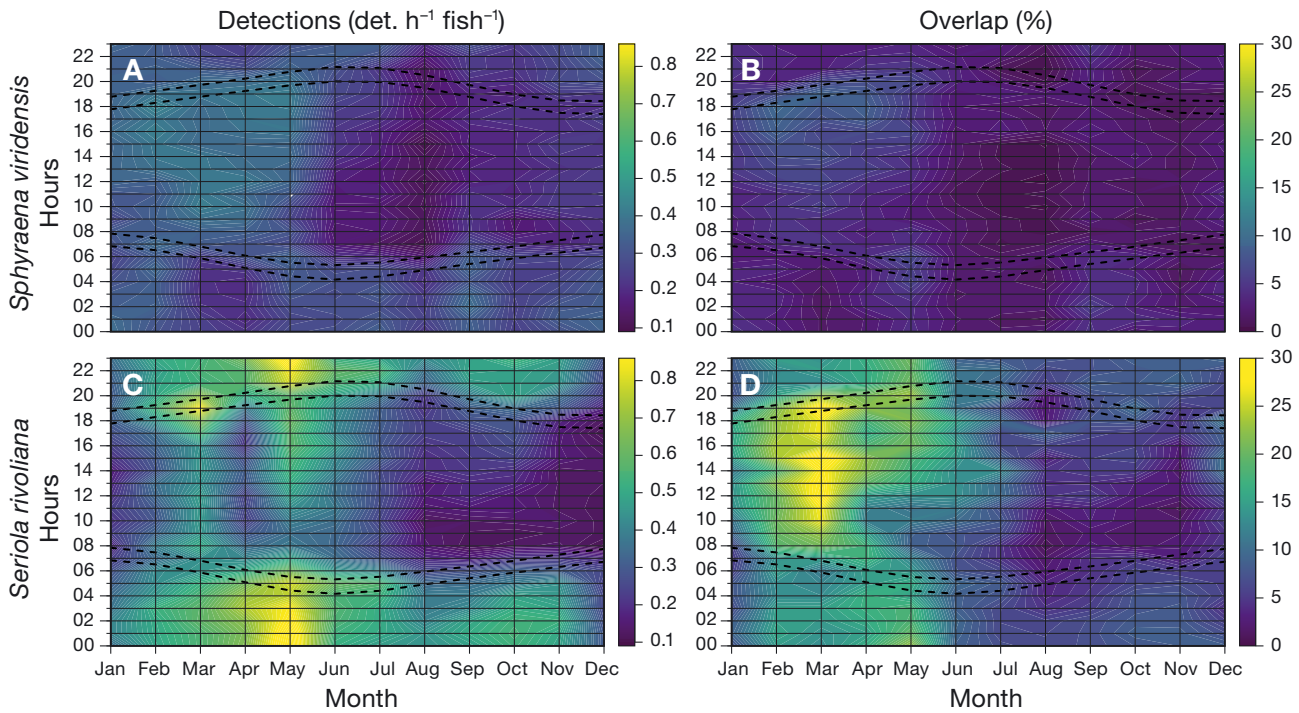
Fig. 5. Contour plots representing detection frequencies and overlap estimates averaged per hour and month. Intraspecific patterns are shown for (A,B) yellowmouth barracuda and (C,D) almaco jack. Dashed lines correspond to dawn, sunrise, sunset and dusk periods estimated for the study site location, illustrating the annual variation of daylight time. Plot scales are standardized by response variable

Table 2. Generalized linear mixed model to test the effect of environmental factors on the extent of monthly spatiotemporal overlap amongst yellowmouth barracuda *Sphyraena viridensis* and almaco jack *Seriola rivoliana* conspecifics. (−): excluded. *p < 0.05, **p < 0.01, ***p < 0.001

~ Overlap	Estimate ± SE	z	p
S. viridensis			
(Intercept)	−3.035 ± 0.597	−5.081	<0.001***
Sea surface temperature	−0.078 ± 0.024	−3.260	0.001**
Chl *a* concentration[a]	2.776 ± 0.569	4.882	<0.001***
Geostrophic current velocity	7.075 ± 2.193	3.226	0.001**
Sea surface height anomaly	−	−	−
Zero-inflation intercept	−18.760 ± 1505.04	−0.012	0.99
S. rivoliana			
(Intercept)	−2.424 ± 0.295	−8.223	<0.001***
Sea surface temperature	−0.040 ± 0.011	−3.628	<0.001***
Chl *a* concentration[a]	3.517 ± 0.313	11.264	<0.001***
Geostrophic current velocity	4.382 ± 1.200	3.651	<0.001***
Sea surface height anomaly	−	−	−
Zero-inflation intercept	−2.433 ± 0.083	−29.26	<0.001***

[a]Lagged variable (1 mo)

Regarding diel activity patterns, species displayed differing levels of intraspecific variability (Fig. 6). Although detection and overlap trends obtained for barracuda were not significant and further confounded by the simulated environmental noise (Fig. S1), jack were detected significantly more dur-

ing nocturnal hours (Fig. 6C), the period when detection efficiency is supposed to be at its lowest. Yet, they were found to overlap more often during the day (Fig. 6D).

3.2. Interspecific associations

We analysed 190 multispecific pairwise comparisons throughout the duration of the study. The mean shared detection period for each interspecific pair was approximately 418 d. The longest consecutive period was observed between barracuda #13 and jack #23, which co-occurred during 16 h at the Formigas islets on March 2009. The higher number of interspecific co-occurrences was also registered in the islets (Fig. S5). On some occasions, we detected up to 5 or 6 barracuda co-occurring with up to 12 almaco jack.

Interspecific co-occurrence was lower than intraspecific co-occurrence, with pairwise overlap scores ranging from 0 to 14.2%. Indeed, the median interspecific overlap (3.1%) did not significantly differ
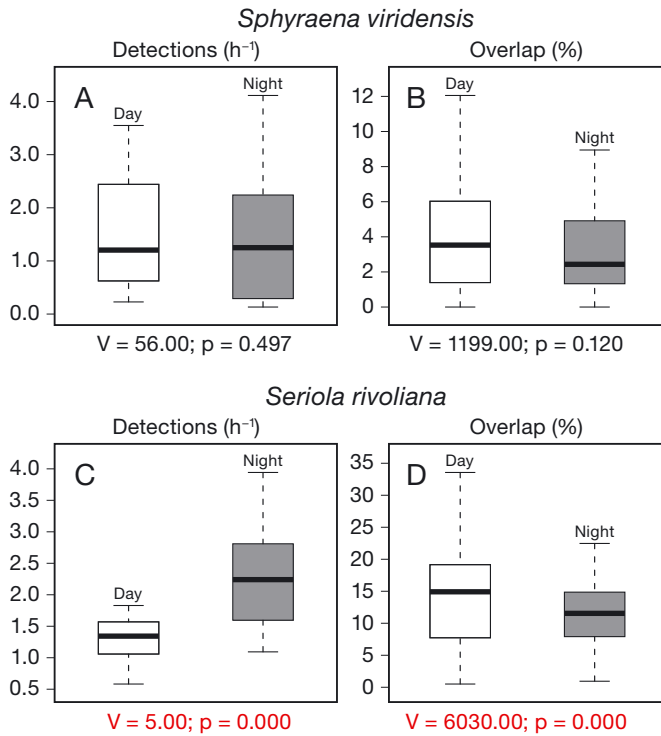
Sphyraena viridensis

Fig. 6. Detection frequencies and spatiotemporal overlap estimated across different diel phases (day vs. night) for (A,B) tagged barracuda and (C,D) jack. Upper and lower box limits represent 75th and 25th quartiles, horizontal lines represent medians and whiskers represent values within 1.5 interquartile ranges. Outlier values were not included to simplify visual interpretation. Wilcoxon signed rank test results (V statistics and p-values) are displayed below each plot (variables with significant differences highlighted in red)

from the random values generated by the null model analysis (p > 0.05; Fig. 3C), with 139 of the 190 interspecific pairs analysed lacking evidence of any strong or weak association. Of the 51 pairs with some degree of association/segregation, 42 overlapped more often and 9 less often than what could be expect by chance alone (Fig. 4). We did not find any significant correlation between interspecific pairwise size difference and overlap extent (Fig. 4C,F); yet, 7 of the 9 pairs that exhibited a tendency for spatiotemporal segregation involved at least 1 large individual (Fig. 7).

4. DISCUSSION

We investigated the patterns of space use by 2 sympatric predatory fishes of similar diet preferences to assess their potential association and fine-scale space use sharing. These hypotheses were tested for both conspecific and interspecific fish. Despite the limitations of our experimental design, this study provides some of the longest data series on the movement and behaviour of barracuda and carangid species to date, contributing to the growing body of knowledge on the movements and space use of pelagic fish species.

4.1. Analytical framework

To date, many published research studies have investigated fish aggregations using location data obtained through acoustic triangulation (e.g. Capello

Fig. 7. Results of the null model randomization test for interspecific pairwise overlaps. The null hypothesis (i.e. each animal occurs independently of the other) was tested by comparing the observed dyadic overlap indexes to the upper and lower tails of the correspondent null distributions, using α = 0.05. Real overlap estimates that were significantly higher (+) or lower (−) than the random overlaps simulated for that dyad suggest, respectively, the existence of joint resource utilization or spatiotemporal segregation; whereas non-significant results (ns) indicate that no particularly strong or weak association was observed. Individuals of each species were sorted according to their fork lengths to visually identify size-structured behavioural patterns

et al. 2013) or by estimating centre of activity positions (Simpfendorfer et al. 2002). The experimental setup used in this study was originally designed to investigate long-term residency patterns, with no overlap among receiver ranges, thus precluding us from monitoring the whole shallow habitat available. Nevertheless, it provided presence–absence data, which we used to extract novel information about space use and space sharing by implementing an adapted association index combined with a null model test approach. There are, however, some caveats associated with this approach. For example, the extent of overlap between any individual pair is dependent on the arbitrary selection of the time bin, since it defines the maximum allowable lag time between detections so that they are considered co-occurrences (Fig. S2). The time lag (or window of simultaneity) should be carefully selected considering species mobility patterns as well as the distance between receivers. Ideally, this interval should be long enough so that any fish in the vicinity of a receiver would be detected but not too prolonged to avoid the fish's detection at multiple receivers within a single time bin. Whenever this happened, we opted to keep the receiver's ID with the greatest number of occurrences. It is also important to acknowledge that any fish pair detected simultaneously may be anywhere from a few centimetres of each other to 1600 m apart, considering the maximum detection ranges for the V16 transmitters (800 m radius). Therefore, caution should be taken when interpreting the results, namely when making inferences about biotic or fish–habitat relationships.

The significance of the observed levels of spatial overlap was assessed with a null model analysis, a statistical tool commonly used to assess species co-occurrence patterns in ecological and biogeographical research (e.g. Manly 1995). Randomizing algorithms that constrain permutations so that species or individual occurrence frequencies are maintained have been recommended (Gotelli 2000). Yet, it remains subjective how detections should be distributed among receivers. While we could have considered detections to be equiprobable across the receiver's array or proportional to population totals, we decided to fix the number of each individual's occurrences at each site. This method allowed us to maintain non-random occurrence patterns with respect to the spaces used, randomizing only the temporal component of detections. Despite some claims that this procedure is redundant, as occurrence frequencies themselves may reflect biological

interactions (e.g. Presley et al. 2010), we were still able to detect strong signals of non-randomness in the original data.

4.2. Intraspecific space use sharing

Not surprisingly, the extent of spatiotemporal overlap observed among conspecifics of both species was significantly higher than what could be expected by random distribution across the suitable reef habitat. This result suggests that conspecifics exhibited a tendency to associate, possibly as a result of social-mediated behaviours or as a consequence of synchronized movements in response to short-term (hourly level) fluctuations in environmental conditions, including food availability. Importantly, it consubstantiates the aggregative and schooling behaviour known for both species (Barreiros et al. 2002, 2003).

The level of overlap between barracuda conspecifics (although significant) was considerably lower than that exhibited by jack. Together with the lower detection frequencies, this result could perhaps be attributed to differences in their foraging strategy. While carangid species are often regarded as patrolling foragers, swimming at constant speeds for several hundreds of metres (Holland et al. 1996), barracuda are ambush predators that spend most of their time swimming slowly or hovering in the water column (de Sylva 1963). Since animals are reported to be less mobile when schooling, spending 75% of the observation time drifting with currents (Barreiros et al. 2002), fewer displacements across the reef were likely to translate into lower probabilities of detection across the sparsely located stations. It is also possible that individuals caught in different years and sites did not have or form thereafter social links, in which case one would potentially expect low levels of temporal cohesion of aggregations and reduced fidelity of individuals to a particular school.

Temporal patterns in detection frequency and overlap levels were also observed, despite some individual variability. Even though we did not observe strong diel shifts in behaviour of tagged barracuda, previous studies on the congeneric *Sphyraena barracuda* (de Sylva 1963, O'Toole et al. 2010) suggest that these fish are mostly diurnal foragers, relying on visual cues to capture their prey. The same can be argued for jack, which are also visual hunters. Yet, jack detections were more common during nighttime, and percentage overlap was higher during the day. One possible explanation could be that jack forage mostly during the day, when they would be more active, preying in

groups in areas outside the listening range, and are more quiescent during the night, being more spread across the seamount reefs and remaining closer to the surface mixed layer. Indeed, this pattern is consistent with the diel vertical movements reported for other pelagic predators inhabiting seamounts (e.g. Fock et al. 2002, Musyl et al. 2003, Afonso et al. 2014). These movements are potentially associated with the migrations undertaken by mesopelagic fish, squid and other prey organisms that comprise the deep scattering layer, which ascend at night to feed in the shallow epipelagic waters and return to deeper layers of the ocean during the day (Cascão et al. 2019). It is important to note, however, that without conducting a concurrent sentinel transmitter study, these hypotheses remain merely conjectural. Additional research using active tracking, digital action cameras or pressure logging tags (satellite or acoustic) should be undertaken to confirm these hypotheses.

Seasonally, both species were detected and overlapped more frequently during the spring. All environmental predictors with the exception of SSH (i.e. SST, lagged chlorophyll concentration and geostrophic current) contributed to explain the extent of overlap between conspecific fish, both for *Sphyraena viridensis* and for *Seriola rivoliana*. These results, particularly the high correlation between overlap and 1 mo lagged chlorophyll concentration, are consistent with the occurrence of bottom-up trophic cascades driven by seasonal dynamics of ocean productivity. The surge of nutrient-rich waters from the deep originates an increase in primary production, which in turn leads to the proliferation of zooplankton that attracts forage fish (i.e. North Atlantic spring bloom; Visser et al. 2011). However, these processes are not synchronous, with changes in zooplankton biomass often lagging the upwelling by weeks to months (i.e. temporal decoupling; Thompson et al. 2012, Ward et al. 2014). A similar pattern was observed in a similar acoustic tagging study on great barracuda *Sphyraena barracuda* in coastal waters of the Bahamas, where tagged individuals were detected less frequently during periods of warmer oligotrophic water conditions (O'Toole et al. 2011). In contrast, Barreiros et al. (2002) reported large schools of barracuda aggregating during the summer on coastal reefs, the onset of the presumed spawning period for this species in the Azores (between June and September; P. Afonso & T. Morato unpubl. data). While these different results might be a consequence of the different spatial and temporal nature of short-term focal observations in that study and long term-passive acoustic telemetry, it remains possible that

telemetered individuals were aggregating beyond the listening ranges of the receivers or that many of the tagged fish did not share social links.

Our results also suggest that jack tend to associate more with individuals of similar size. While this pattern may be linked to social behaviour, such as a preference to school with similarly sized conspecifics, it may also reflect different habitat or prey preferences between smaller and larger individuals. Indeed, it is likely that larger fish exhibit broader resource exploitation or a distinct vertical behaviour as ontogenetic habitat shifts have been commonly observed in carangids (e.g. Reis-Filho et al. 2019). This hypothesis is also consistent with the fewer detections registered for the larger jack (fish #26, #27 and #28) and with the different depths at which fish were captured: larger fish were captured in the deepest water (between 80 and 100 m) and closer to the bottom, while most of the smaller fish were captured near the surface.

4.3. Interspecific associations

Ecological niche theory has long predicted temporal partitioning and habitat segregation as the major mechanisms of coexistence between competing species, alongside resource differentiation. Not surprisingly, the overlap between the 2 species in our study was lower than that observed between conspecifics. Although Paterson (1998) observed heterospecific groups including barracuda and small carangids, there is no evidence of mixed schooling for these species in the Azores (Barreiros et al. 2002). Somewhat contradictorily, we did not find strong evidence of significant spatiotemporal segregation between the 2 species within the limited reef habitat of the Formigas seamount. It is possible that occasional segregation occurred due to antagonistic behaviours (interference competition; Case & Gilpin 1974, Pianka 1981, Carothers & Jaksić 1984) or predation avoidance when larger individuals were involved, yet these hypothesized patterns were only consistent with a small fraction of the analysed pairs. Although depth stratification might also occur between interacting animals (Aspillaga et al. 2019), and thus play an important role in putative resource partitioning at a smaller scale, it is thus likely that the 2 predatory fish are able to co-exist without significant interspecific competition pressure. This hypothesis seems plausible given the local abundance of prey, but again, it is important to recall that the large detection range of the present system means that barracuda and jack

could be up to 1.6 km apart and still be detected simultaneously by the receivers, reinforcing the opportunity to conduct studies that directly evaluate the availability of prey and finer-scale patterns of co-occurrence.

5. CONCLUSIONS

Following previous findings on the ecology of pelagic reef species in the Azores, we found evidence of non-random shared-space occupancy between conspecifics of both *Sphyraena viridensis* and *Seriola rivoliana*. The contrasting lack of significant overlap between heterospecific fish together with their diel foraging habits suggests that these pelagic predators do not actively associate, nor do they avoid each other (exceptions might occur, however, for large individuals). Additionally, we also found evidence of size-structured behavioural differences between conspecific almaco jack, with similarly sized fish overlapping more often and large-sized individuals being more infrequently detected. While the present work provides new insights into the spatial ecology of yellowmouth barracuda and almaco jack, the combination of underwater visual census and finer-scale active acoustic tracking should allow us to improve our understanding of fine-scale spatial patterns, and possibly disentangle the role of social interactions from ecological processes. Recent developments in technology and increased funding opportunities have led to an increase in marine telemetry studies and the collection of unprecedented amounts of data. Although fine-scale positional telemetry systems (Espinoza et al. 2011, Biesinger et al. 2013) are already available, an extraordinary amount of presence–absence telemetry data from past and current studies exist, as these studies are much easier to deploy and allow more flexible experimental designs (Binder et al. 2016). Consequently, we think that the described framework can have a potentially wide application in behavioural studies, and we believe that its implementation may contribute to a better understanding of animal spatial dynamics.

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