



Habitat selection, fine-scale spatial partitioning and sexual segregation in Rajidae, determined using passive acoustic telemetry

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ABSTRACT: Habitat selection is the process by which an individual makes an active decision to make use of a particular habitat when others are available. The ability to infer habitat selection therefore requires observations of movement through space and time which can be particularly challenging for marine species that are cryptic and do not regularly visit the sea surface. Rajidae (skates) are benthic mesopredators that inhabit turbid coastal waters and exhibit site fidelity, making them an ideal group for studying habitat selection and resource partitioning using a fixed, passive acoustic receiver array in the western English Channel, UK. Using network analysis, significant differences were found in the way 4 species of Rajidae occupied different parts of the array; for example, *Raja microocellata* and *R. clavata* occupied shallower habitat than *R. brachyura* and *R. montagui*. *R. montagui* and *R. brachyura* were further separated, with each species detected more frequently at different receivers. Males and females of all 4 species were also detected at different receivers and at different times. These results demonstrate habitat selection, resource partitioning among species and sexual segregation in these 4 species of Rajidae. Our findings are important evidence for management of fisheries, such as the designation of marine protected areas, and further highlight the potential of this method for tracking other mobile marine species in temperate, open coastal regions.

KEY WORDS: Tagging · Skate · Biologging · *Raja* · Ray

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1. INTRODUCTION

Mobile species have the capacity to shift their spatial occurrence and habitat associations within an individual's lifetime and make behavioural decisions to make use of habitats that are optimal at a particular time (Hutto 1985, Krausman 1999). This process is known as habitat selection (Kramer et al. 1997). Habitat preference is defined as the consequence of habitat selection, which results in the disproportional use of one habitat over another (Johnson 1980, Hall et al. 1997). Tracking the movement

of species through space and time in order to investigate habitat selection is particularly challenging in the marine environment. Constraints result from difficulties in monitoring movements of animals that spend their entire lives submerged and which, consequently, limit the use of technology that can otherwise be deployed in terrestrial systems or on species that breach the sea surface (Cooke et al. 2013, Hussey et al. 2015). Further limitations arise from limited knowledge of habitat variables, such as the fine-scale structure and composition of the seabed.

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Historically, the spatial occurrence of where and when aquatic organisms were caught (e.g. in commercial fisheries), or the use of mark and recapture, were the only available measure of the movement patterns of a species (Hussey et al. 2015, Simpson et al. 2020). This knowledge has provided low-resolution movement patterns, but does not necessarily indicate whether an individual is actively moving towards a particular habitat (Kramer et al. 1997). However, the development of various electronic tags has enabled some insight into habitat selection. For example, in one of the first reports on habitat selection in elasmobranchs, lemon sharks *Negaprion brevirostris* actively tracked with acoustic transmitters selected shallow (0–50 cm), warm ($\geq 30^{\circ}\text{C}$) waters with a rocky or sandy substrate (Morrissey & Gruber 1993), probably to avoid predators.

The Rajidae (skates) are cryptic species that bury in the sediment for extended periods of time (Greenway et al. 2016) and inhabit turbid coastal waters (Steven 1936). Despite being commercially important species in the UK (Enever et al. 2009), little is known about their fine-scale distributions, with most detailed studies focussing on the thornback ray *Raja clavata*, the most common of the 14 species in UK coastal waters (Hunter et al. 2006). These 14 species have varied distributions in coastal waters around the UK, with some species such as the blonde ray *R. brachyura* occupying southern UK waters, whereas other species, such as *R. clavata*, occupy all coastal waters around the UK, overlapping the distribution of *R. brachyura* (Walker & Heessen 1996, Walker & Hislop 1998, Ellis et al. 2005, Martin et al. 2010). Depth ranges have been established for some species, with the most common species found between 0 and 283 m and with a high degree of overlap among the species (Ellis et al. 2005). Fulton (1893) may have published one of the earliest studies to question the movements of *R. clavata* and used a method of marking and recapturing to assess the distance travelled whilst at liberty. Fulton found that after 278 days at liberty, skates were recaptured relatively close to where they were released. The majority of studies since, which have included various species and different locations around the UK and worldwide, conclude, like Fulton (1893), that generally, skate species show high site fidelity and rarely move far (10s of km) from where they were released (Steven 1936, Templeman 1984, Walker et al. 1997, King & McFarlane 2010, Ellis et al. 2011). However, some studies have suggested that occasionally individuals are capable of moving larger distances (e.g. 2340 km, King & McFarlane 2010, Bird et al. 2020). Seasonal patterns in movement have also

been shown for Rajidae; *R. clavata* is known to make seasonal migrations from the Thames Estuary area to deeper offshore locations in the winter, before returning to shallower inshore areas in the spring and summer (Hunter et al. 2005, 2006). Species of Rajidae (Ellis et al. 2011) create sympatric assemblages in coastal regions (Steven 1936). Nevertheless, there is a paucity of studies that explicitly investigate fine-scale spatial occurrence, habitat selection and habitat partitioning in the UK Rajidae.

In addition, studies have also identified a biased sex ratio towards females in catches, which suggests the occurrence of sexual segregation (Steven 1933). Sexual segregation is ubiquitous across the animal kingdom and is defined as the separation of a species by sex, either as individuals or in groups (Wearmouth & Sims 2008). Sexual segregation in elasmobranchs is well documented in a number of species, including white sharks *Carcharodon carcharias* (Domeier & Nasby-Lucas 2012), catsharks *Scyliorhinus canicula* (Wearmouth et al. 2012) and blacktip reef sharks *Carcharhinus melanopterus* (Mourier et al. 2013). However, there is conflicting evidence for sexual segregation in Rajidae (Steven 1933, Rousset 1990, Martin et al. 2010). Previous studies used fishing surveys to investigate distribution, which limits the presence or absence to one location in time. Therefore, the spatial movements underpinning patterns of sexual segregation remain to be determined.

In previous studies, habitat associations and apparent partitioning among 4 species of Rajidae from biogeochemical tracers (Simpson et al. 2019), research surveys (Martin et al. 2010), archival tags (Humphries et al. 2016) and recapture data (Simpson et al. 2020) were identified. Many of these findings were limited to establishing habitat associations because research survey data, for instance, can only provide 1 known location in time, whilst mark and recapture provides only 2 location points in time. Humphries et al. (2016) used archival depth time-series data to demonstrate differences in depth preferences among species, with *R. clavata* and the small-eyed ray *R. microcellata* spending more time at shallower depths than *R. brachyura* and the spotted ray *R. montagui*. However, there may be finer-scale, geographic partitioning between and within species that cannot be detected by depth-recording tags alone. Hence, with these low-resolution data alone it is difficult to demonstrate active habitat selection or, importantly, to identify differences in habitat selection between species or sexes.

Passive acoustic monitoring using a spatial array of acoustic receivers can record relatively fine spatial

scale (100s of m) movement data in the long term (years) without the need for the physical recovery of the tags. Stationary hydrophone receivers placed on the seabed or suspended in the water column detect the presence of animals tagged with acoustic transmitters within the detection range of a receiver. This range varies depending on the power output of the tag, environmental conditions surrounding the receiver, including water depth, water flow and even biofouling on the receiver, but is typically between 120 and 900 m (Kessel et al. 2014, Lea 2017, Setyawan et al. 2018). Acoustic arrays can potentially provide a higher spatial resolution of the changing distribution of a fish through time than conventional tagging and are only limited in resolution by the number of receivers placed in the study area. Arrays also enable the simultaneous tracking of multiple individuals (Sims & Quayle 1998, Heupel et al. 2006).



Fig. 1. One of 12 receiver deployments on large tripod landers off the coast of Plymouth, UK. The data-logging acoustic receiver is arrowed. Photo: Marine Biological Association, Plymouth

Previous studies have successfully demonstrated the use of passive acoustic receiver arrays to identify habitat selection in multiple mobile species. For example, tiger sharks *Galeocerdo cuvier* occupied shallow lagoons more than Galapagos sharks *Carcharhinus galapagensis* (Meyer et al. 2010) and in another study, over half of the tagged flapper skates *Dipturus intermedius* were resident at the study site over a period of months (Neat et al. 2015). Acoustic tracking has also been used to determine the space use of reef-associated sharks and turtles to determine the efficacy of a proposed marine protected area (MPA) (Lea et al. 2016).

The cryptic nature of Rajidae (Greenway et al. 2016), in addition to the site fidelity they exhibit and the success of other acoustic arrays (Neat et al. 2015), suggests that these species may be ideal for using passive acoustic telemetry to help understand spatial dynamics, fine-scale habitat selection and resource partitioning.

Here we used passive acoustic telemetry to investigate habitat selection and spatial partitioning among 4 species of Rajidae off the southwest coast of the UK (western English Channel). We investigated whether movement patterns differed from expectations if no habitat selection or sexual segregation occurred. We also compared movements between species and sexes to identify spatial or habitat partitioning, as well as temporal spatial partitioning and examined where and when associations between individuals occurred.

2. MATERIALS AND METHODS

2.1. Tagging and tracking

During the study period between 2010 and 2017, 2 deployments were made of 6 Vemco hydrophone receivers ($n = 6$ VR3 and 6 VR4). All receivers were deployed by the Marine Biological Association (MBA) using its research vessels onto the seabed attached to large, weighted metal tripods ('landers', Fig. 1). Six VR3 receivers were deployed in close formation (610 m between the 2 closest receivers) within the Whitsand Bay area in 2010 at depths between 19 and 25 m (hereafter the Whitsand array); the 6 VR4 receivers were deployed in 2014, spread across an area ranging from the Eddystone to Bigbury Bay, at depths between 29 and 53 m (the Plymouth array) (Table 1, Fig. 2). Receiver locations were selected where there was flat substrate to ensure maximum detection ranges and within the boundary of an MPA (a special

Table 1. Receiver array depths and names

Whitsand Bay array					Plymouth array				
ID	Depth (m)	Salinity (‰)	Substrate	Energy	ID	Depth (m)	Salinity (‰)	Substrate	Energy
L1	19.4	34.846	Fine sand or muddy sand	High	M1	53.3	35.075	Coarse sediment	Moderate
L2	20.2	34.846	Fine sand or muddy sand	High	M2	30.1	34.794	Coarse sediment	High
L3	19.4	34.846	Fine sand or muddy sand	High	M3	46.6	34.898	Coarse sediment	Moderate
L4	24.7	34.846	Fine sand or muddy sand	High	M4	29.7	34.852	Coarse sediment	Moderate
L5	24.5	34.846	Fine sand or muddy sand	High	M5	52.2	35.002	Circalittoral sediment	Moderate
L6	20.8	34.846	Fine sand or muddy sand	High	M6	30.4	34.797	Coarse sediment	Moderate

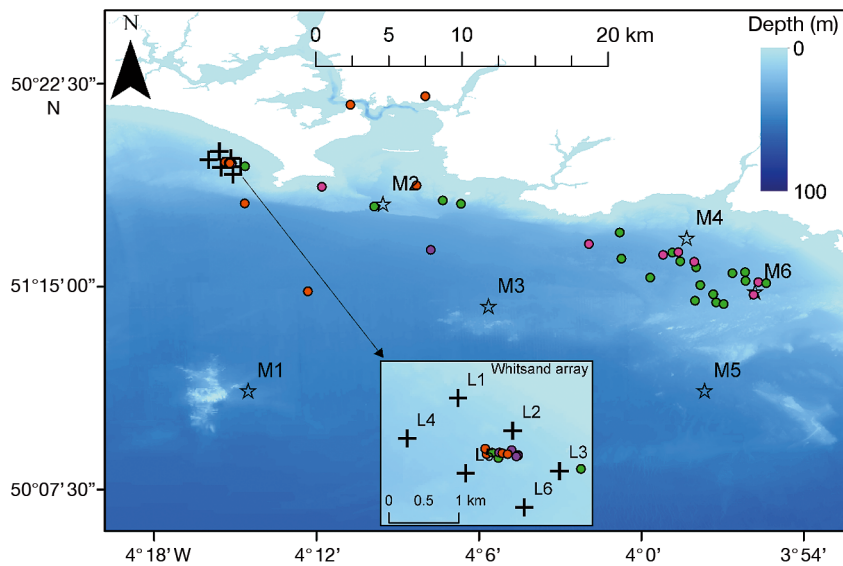


Fig. 2. Location of the Whitsand (crosses and L labels) and Plymouth arrays (stars and M labels) off the coast of Plymouth, UK. Inset highlights the Whitsand array in more detail. Circles show release positions: pink = *Raja brachyura*, orange = *R. clavata*, purple = *R. microocellata*, green = *R. montagui*

area of conservation), primarily to avoid potential damage from mobile fishing gear used commonly in adjacent areas. The Whitsand array was designed to cover a specific area of the bay, between rocky reef habitats, whereas the later deployments of VR4 receivers were designed to cover a very large area and differing habitats and depths. Receivers recorded the identification number and time stamp of coded transmitters which were later transmitted to a surface modem on demand (Vemco 2013). Surface range drift testing with a V9-2L tag in the Whitsand array indicated that receivers in that array had a detection range between 408 and 648 m (mean \pm SD, 502.5 \pm 105.62 m) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m666p115_supp.pdf).

Four Rajidae species (*Raja brachyura*, *R. clavata*, *R. microocellata* and *R. montagui*) were caught, tagged and released (Fig. 2) from 2014 to 2016 using beam or

otter trawls off the coast of Plymouth, southwest UK. Vessels were either the RV 'MBA Sepia' or RV 'Plymouth Quest', and all tows lasted less than 40 min. The acoustic tags, together with serially numbered 10 mm Peterson discs, were attached to skates using the methods described by Wearmouth & Sims (2009). Briefly, tags were secured in place with a pointed stainless-steel wire attachment that was passed through a Peterson disc and then through the centre of the pectoral fin. A second Peterson disc was placed onto the length of wire on the opposite (ventral) side of the skate before turning a series of rounds into the length of wire remaining to secure it. Tagging took less than 2 min, including the measurement of total length and disc width of the individual. Skates were immediately transferred to aquaria with fresh running

seawater for visual observation of vitality and tag attachment site prior to release. Release occurred typically within 1 h of capture. A total of 201 Rajidae were released with Vemco V13 (147 dB re 1 μ Pa @ 1 m) tags during the study period (Table 2). The tags used for all fish were V13 69 kHz transmitters that were 36 mm long, weighing 11 g in air and 6 g in water and were programmed with a 180 s nominal random delay to give an estimated maximum lifespan of 1520 d.

Table 2. Number of acoustic tags released by species and sex

Species	Male	Female
<i>Raja brachyura</i>	15	16
<i>R. clavata</i>	28	26
<i>R. microocellata</i>	10	34
<i>R. montagui</i>	30	42

2.2. Data analysis

Data recorded by the 12 receivers were uploaded remotely with a Vemco deck box and surface modem. Uploaded detections were imported into a Microsoft Access database, which assigned transmitter detections to the appropriate individuals and receiver locations, while filtering out detections that did not match an active tag or receiver. Due to the widely spaced array and relative low number of tags, collisions between tag detections and the subsequent chance of ghost detections was considered very unlikely. Detection time corrections were computed during the import process and were calculated from the difference between the receiver and PC clock at the time of download, assuming linear receiver clock drift, as recommended by the manufacturer. Days at liberty were calculated as the number of days between the release date and either the day of the last detection or the recapture date. The residency index (R_i) was calculated as the percentage of days on which the individual skate was detected in the array:

$$R_i = \frac{D_d}{D_{al}} \times 100 \quad (1)$$

where D_d is number of days detected and D_{al} is the number of days at liberty.

2.3. Acoustic networks

In network theory, connected systems are comprised of nodes connected by edges. Nodes can represent mobile individual organisms or static physical locations, while edges represent the associations between those nodes creating a network (Jacoby et al. 2012, Finn et al. 2014). In the present study, nodes represent the 12 static acoustic receivers and edges represent the movement of individuals between pairs of receivers within the array.

Movements between receivers were used to construct a network displaying the movement of animals through space that can be used to test for preferential habitat use within the array. There were no time frame restrictions set on connections due to these species moving relatively slowly throughout the wide spacing of the Plymouth array.

To test whether the observed movements of the 4 species differed from random expectation, randomised networks were generated by performing multiple random walks through the array. Due to the inherent spatial restrictions of the nodes in the network, connections between nearby receivers are more likely than

between more distant receivers. Randomised networks therefore accounted for this spatial bias in the network structure as follows: for each individual, the first detection at the first receiver was used as the starting location, and then a maximum swimming distance was calculated based on the time between detections and the average swim speed of that individual. An average swim speed was calculated for each individual from the time between detections and the distance between receivers for all pairs of detections identified as representing real movements. Receivers were then selected at random until 2 had been found within the maximum swimming distance; the closer of the 2 was then assigned as the next location. If no receiver was found in range then the current receiver was assigned (i.e. no movement occurred). This was repeated for each detection in the track, and 100 times for each individual to provide the mean randomised network metrics. Network metrics include 'node density', which measures the extent of the array occupied, and 'edge density', which provides a measure of mobility within the network (where edges are the connections between nodes). The values of both metrics ranged on an index from 0 to 1. These random networks were compared with the observed networks using a Wilcoxon matched pairs signed-rank test. Species where the observed network differed from random were compared to identify differences in receiver occupancy and identify potential habitat partitioning in the 4 Rajidae species.

To identify whether species used space within the total array extent equally, the total number of detections and connections were compared between species within the Whitsand array, the Plymouth array and between arrays with a chi-squared goodness of fit test. Expected values were based on the total number of days where there was at least 1 detection per species. The number of connections between the 2 arrays were also investigated with the same test, but with the expected values based on the total number of ping days across the entire array. In addition, the same analysis was applied to investigate the difference in the number of detections by males and females within a species, with expected values based on total number of ping days for each sex.

2.4. Spatial overlap analysis

To further investigate shared occupancy between pairs of species, a shared occupancy matrix was computed with counts of detections for each 0.25 km². To generate the occupancy matrices, the recorded de-

tections for each individual were converted to a time series of geographical locations, with coordinates taken from the receiver locations. These time series were linearly interpolated to daily locations and used to populate a 0.5 km scale grid that encompassed the study area (see Lea et al. 2016). Occupancy for each grid cell was computed as a count of detections, with all detections given equal weight, as all tags were programmed with the same nominal transmission interval of 180 s. To provide a numerical comparison of the matrices, an overlap coefficient (O) was computed using the following equation (Horn 1966, Rijnsdorp et al. 1998):

$$O = 2 \sum_j (P_{aj} \cdot P_{bj}) / \left(\sum_j P_{aj}^2 + P_{bj}^2 \right) \quad (2)$$

where P_{aj} is the occupancy value (count of detections) for species a in grid cell j , and P_{bj} is the corresponding value for species b . These coefficients range from 0.0 (no overlap) to 1.0 (matching occupancy) and provide a way to determine similarity between grid occupancy maps constructed for the 4 different species. To investigate the statistical significance of the overlap coefficients, a null model was used with a Monte-Carlo approach summarised by Humphries et al. (2016). Briefly, each occupied grid cell has a value for the P_a occupancy and a value for the P_b occupancy. The randomisation has 2 stages. In the first step, the program swaps every P_a value for a randomly selected non-zero P_a value, leaving the P_b occupancy values as they are. After each set of swaps, the program calculates O , as shown above, then restores the original values. This is repeated, but swapping the P_b values, leaving the P_a values as they are. This relatively conservative approach should not generate extreme randomisations that are guaranteed to be very different from the observed pattern. A p-value is calculated as the proportion of times O (random) is $> O$ (observed).

To investigate the extent of spatial overlap through time and to identify possible temporal segregation, the occupancy analysis was repeated using monthly time intervals. To further examine the temporal (seasonal) and spatial aspects of when species do overlap, the number of habitat associations between species pairs was calculated as the number of times both species were detected at the same receiver in the same month (regardless of year). Years were disregarded to reduce gaps in the data and improve the seasonal analysis, assuming that seasonal behaviour would not change significantly between years. The same habitat associations were calculated for sex. These associations were plotted in QGIS (3.12.0-București), as the receiver locations with the number

of habitat associations between the species, with a pie chart to illustrate the proportion of habitat associations over seasons.

3. RESULTS

During the study period, a total of 201 skates were released with acoustic transmitters, of which 134 (66.7%, Table 2) were subsequently detected in the array (Table 3; Table S1 in the Supplement), providing a total of 17 288 tracking days. The median track length was 71 d, and the longest track was recorded for an individual *Raja montagui* that was never recaptured but was detected in the array after 831 d (Table 3). Most tags (124) were deployed during 2015, and this is reflected in the number of detections within the acoustic array (Fig. 3).

3.1. Species detections

For each species, the observed network patterns (both node and edge metrics) were significantly different from the randomised acoustic networks (Fig. 4, $p < 0.001$, Wilcoxon signed-rank matched pairs t -test, Tables S2 & S3).

Considering each array separately, the number of detections in each array was not equally distributed between species [Whitsand $\chi^2_3(N = 42\,512) = 16\,894.8$, $p < 0.001$; Plymouth array $\chi^2_3(N = 22\,180) = 36\,267.8$, $p < 0.001$]. For the Whitsand array, *R. clavata* were detected more than expected by the randomised networks, but both *R. montagui* and *R. brachyura* were detected less often. Conversely, in the Plymouth array, *R. montagui* and *R. brachyura* were detected more frequently than expected, while *R. clavata* and *R. microocellata* were detected less often (Fig. 5).

Within the Whitsand array, species differed in the number of network connections observed between any 2 receivers [$\chi^2_3(N = 4184) = 2232.68$, $p < 0.001$],

Table 3. Number of days at liberty, residency index (percentage of days on which an individual skate was detected in the array) and number detected for each species

Species	Residency index (mean \pm SD)	Days at liberty (mean \pm SD)	Number detected
<i>Raja brachyura</i>	21.86 \pm 48.79	124.68 \pm 92.81	21
<i>R. clavata</i>	26.09 \pm 32.15	96.68 \pm 131.93	37
<i>R. microocellata</i>	38.15 \pm 46.51	103.44 \pm 141.78	36
<i>R. montagui</i>	21.21 \pm 36.55	182.23 \pm 208.52	40

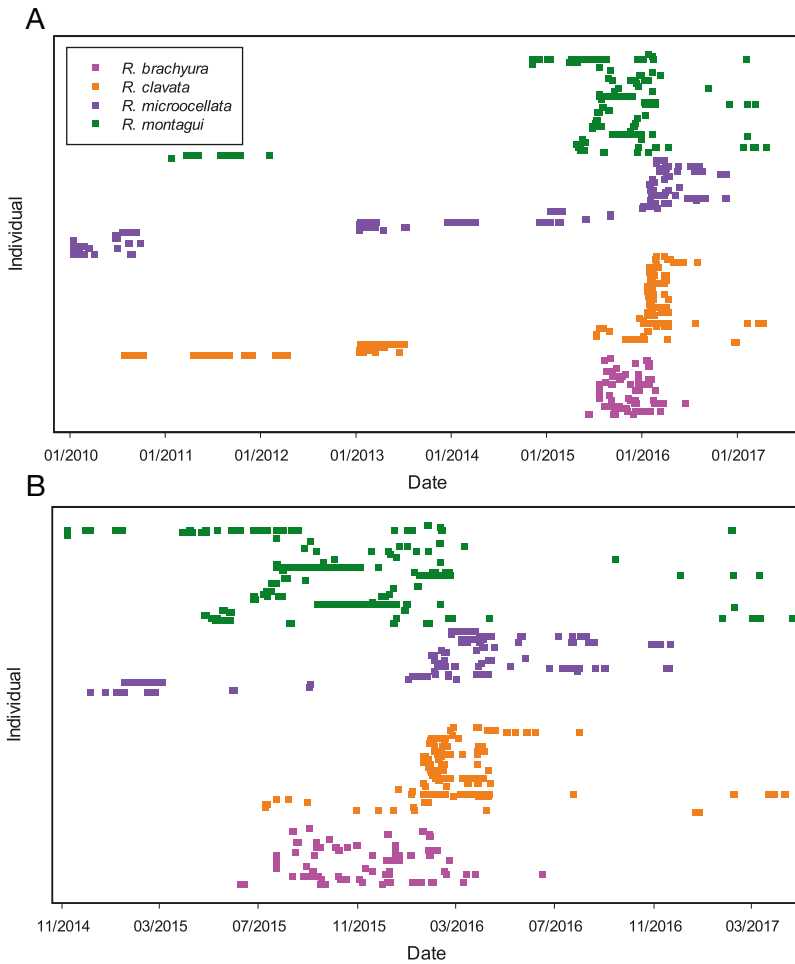


Fig. 3. (A) *Raja* spp. tag detections over time from 2010 to 2017. (B) Tag detections over time from 2014 to 2017, representing the period when most tags were released. The y-axis represents each individual released

i.e. in the number of movements made between receivers. *R. microocellata* and *R. clavata* both had more connections than the expected values, while *R. brachyura* and *R. montagui* had fewer. In the Plymouth array, species again did not show equal numbers of connections between receivers [$\chi^2_3(N = 39) = 257.876$, $p < 0.001$]. *R. brachyura* had significantly more connections than expected, while the other 3 species connected less than indicated with random networks (Figs. 5 & 6).

Detections were not evenly distributed amongst receivers, and those with the most detections differed between species. For *R. brachyura*, 87.8% of detections occurred at M4 in the Bigbury Bay area, while for *R. montagui*, 60% of detections were at M3 and 22% at M6. In *R. clavata*, 31% of detections occurred at L3 and another 31% of detections at L6. Finally, in *R. microocellata*, 41% were detected at L6 and 29% at L1 (Fig. 6).

3.2. Spatial overlap

The species pairs with a significantly lower overlap coefficient than the randomised coefficient were *R. clavata* versus *R. brachyura*, *R. microocellata* versus *R. brachyura*, and finally *R. montagui* versus *R. clavata*; these species pairs overlapped less than expected by random chance (Table 4). Conversely, *R. montagui* overlapped *R. brachyura*, and *R. microocellata* overlapped *R. clavata*, significantly more than expected by chance (Table 4). Finally, the overlap between *R. montagui* and *R. microocellata* was not significantly different (Table 4) from the randomised overlap coefficient.

3.3. Temporal spatial overlap

Although some spatial overlap was observed between species, there was often temporal variation in the overlap (Fig. 7). *R. brachyura* and *R. microocellata* had relatively low overlap throughout the year except for June (Fig. 7A). This summer overlap primarily occurred in the Whitsand array (Fig. 8A), which is interesting given that *R. brachyura* was detected predominantly in the Plymouth array.

There was higher overlap between *R. montagui* and *R. brachyura*, but less so in spring. Associations were highest in winter (Fig. 7B) and predominantly occurred in the east of the Plymouth array (Fig. 8B). *R. microocellata* and *R. montagui* had relatively low overlap coefficients across the year (Fig. 7C), the highest (0.3) occurring in September. Associations were split between the Whitsand array and receiver M6 in the Plymouth array (Fig. 8C). *R. clavata* and *R. montagui* had low overlap all year, but overlap was highest from July to December (Fig. 7D); these associations occurred across both arrays, with 7 associations occurring at the further offshore receiver M5, the highest for any species pair (Fig. 8D). As expected from the previous results, *R. clavata* and *R. brachyura* rarely overlapped, but when they did, it tended to be in summer (Fig. 7E). Associations occurred across the array in low numbers (Fig. 8E). Finally, the overlap pattern across time for *R. microocellata*

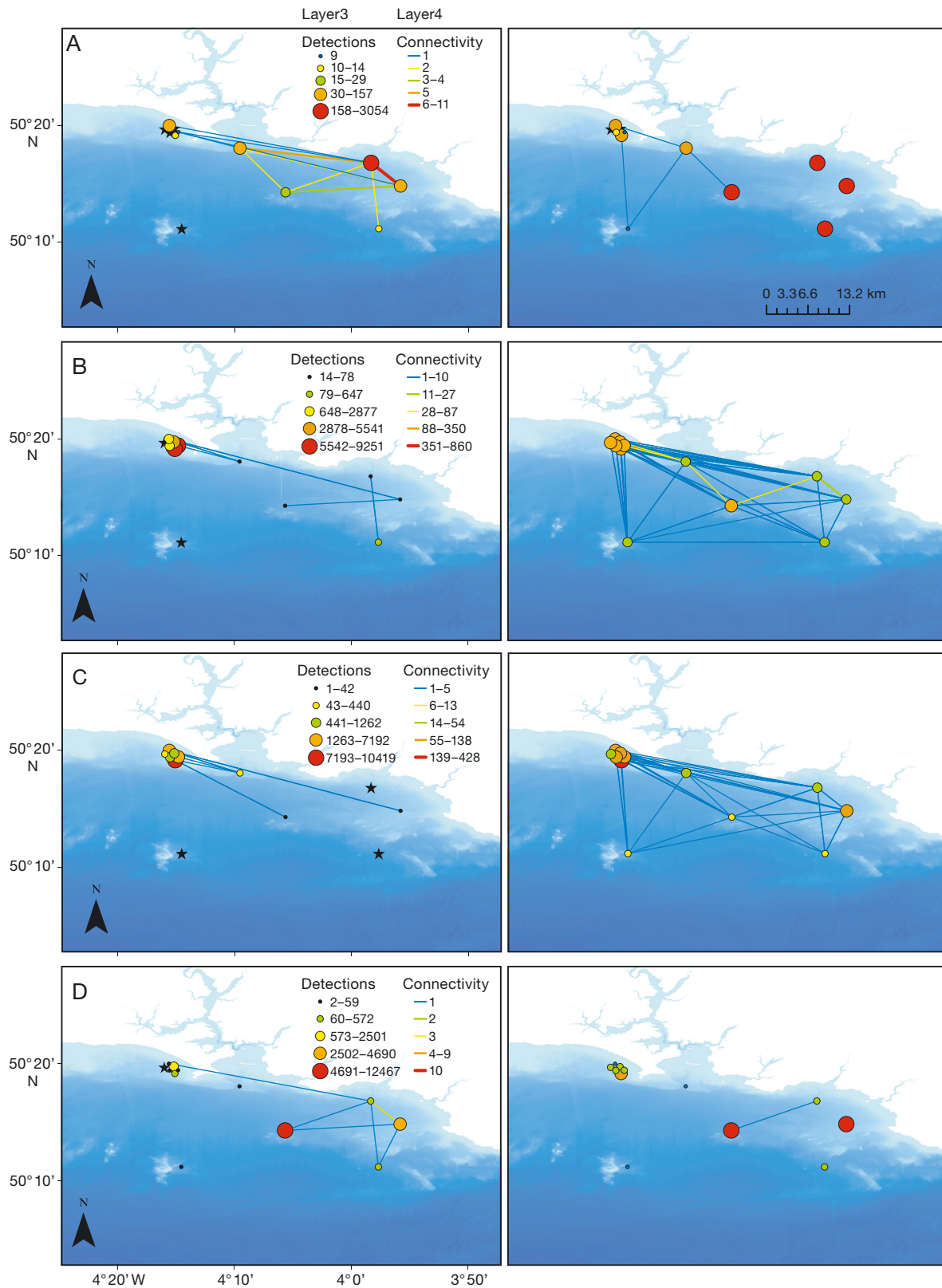


Fig. 4. Observed networks (left column) and example randomised networks (right column) for (A) *Raja brachyura*, (B) *R. clavata*, (C) *R. microocellata* and (D) *R. montagui*. Warmer colours indicate more connections/detections (note the different bin ranges for each species). Stars indicate nodes with zero detections

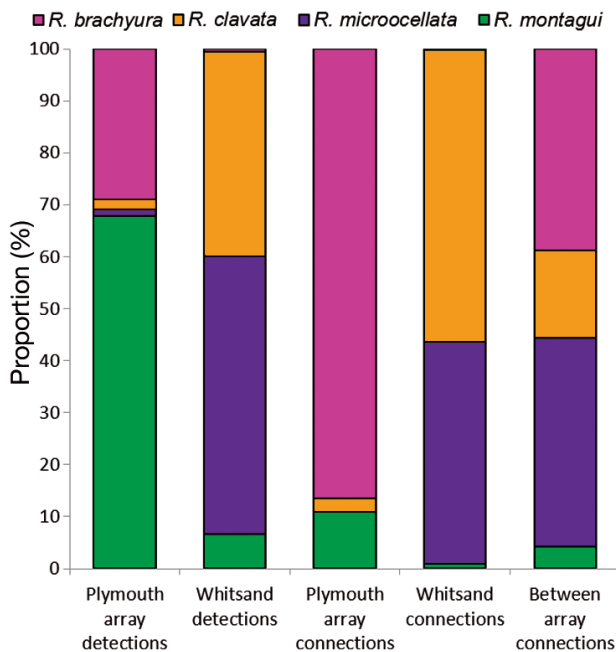


Fig. 5. Proportion of detections and connections for *Raja* spp. at the Plymouth and Whitsand arrays and connections between the 2 arrays

and *R. clavata* peaked in the winter months (Fig. 7F), primarily in the southeastern end of the Whitsand array (Fig. 8F).

3.4. Differences in the detection of sexes

Every species showed significant differences in the number of detections between males and females (Fig. 9). For *R. brachyura*, males were detected more frequently than the equality expected from the number of 'ping days' for the species, and females less [$\chi^2_1(N = 3348) = 179.61, p < 0.001$]. In *R. clavata*, females were detected more than expected and males less [$\chi^2_1(N = 29541) = 2226.4, p < 0.001$]. In *R. microocellata*, females were detected more frequently than males [$\chi^2_1(N = 24634) = 747.05, p < 0.01$]. Finally, in *R. montagui*, females were detected more than expected and males less [$\chi^2_1(N = 17793) = 6305.93, p < 0.001$].

R. brachyura males were recorded predominantly in the east and south of the Plymouth array, and while females overlapped males in the east, they also made connections to the Whitsand array in the west (Fig. 10A). While there were only a few detections of *R. clavata* males, when they were detected they overlapped the females in the west end of the Whitsand array (Fig. 10B). In *R. microocellata*, both sexes were

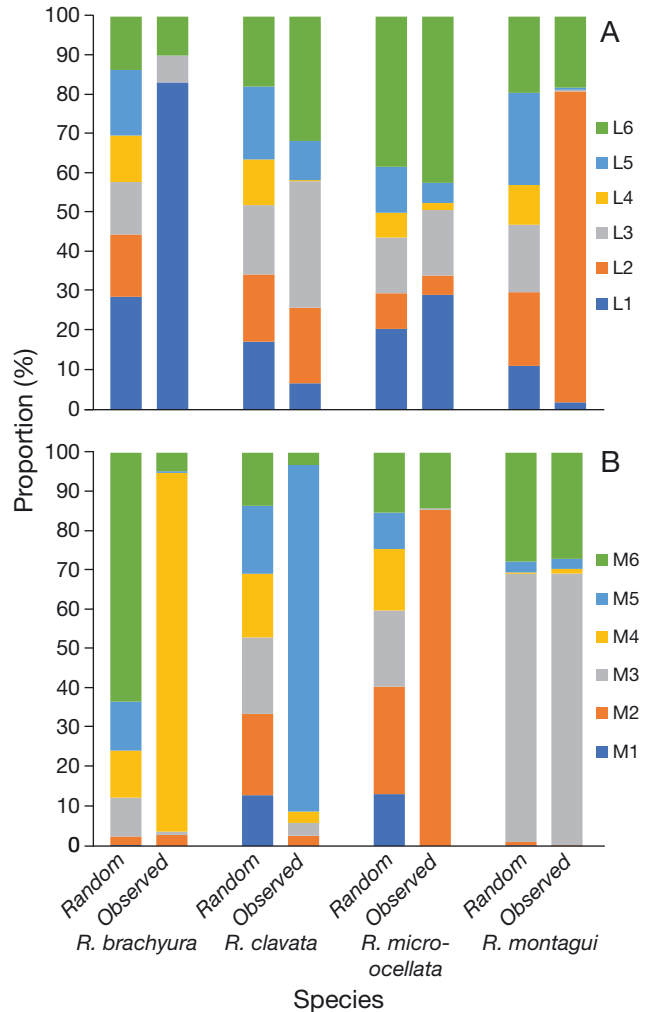


Fig. 6. Observed and average random detections. Proportions of detections for *Raja* spp. at the 12 different receivers: (A) Whitsand array, (B) Plymouth array

detected predominantly in the Whitsand array (Fig. 10C). For *R. montagui*, both sexes were detected predominantly in the Plymouth array to the east (Fig. 10D).

For *R. clavata*, *R. microocellata* and *R. brachyura*, the sexes displayed high spatial overlap (Table 5). However, this varied temporally, and there were times when females were detected, but males were not, as expected from the significantly lower number of male detections. *R. brachyura* overlaps of males and females were highest in summer and into winter but absent in spring (Fig. 11A), and associations occurred at receivers M4 and M6 (Fig. 12A). *R. montagui* males and females overlapped during the summer months (May–August), but there were times when both males and females were detected, with an overlap coefficient of zero (spring and autumn)

Table 4. Observed versus randomised overlap coefficient. ↓: Overlap coefficient was lower than expected by chance; →: not significantly different than expected by chance; ↑: higher than expected by chance

	<i>R. clavata</i>	<i>R. microocellata</i>	<i>R. montagui</i>
<i>Raja brachyura</i>			
p	0.006	0.046	0.035
Overlap coefficient	↓0.176	↓0.144	↑0.854
Mean randomised coefficient	0.457	0.359	0.453
<i>R. clavata</i>			
p		<0.001	0.034
Overlap coefficient		↑0.979	↓0.231
Mean randomised coefficient		0.544	0.458
<i>R. microocellata</i>			
p			0.073
Overlap coefficient			→0.197
Mean randomised coefficient			0.408

(Fig. 11B). Associations occurred primarily at M6 and to a lesser extent M4 (Fig. 12B). *R. microocellata* sexes had relatively low overlap coefficient over time but peaked in January (Fig. 11C) and associations only occurred in the Whitsand array, primarily at receiver L1 (Fig. 12C). Finally, *R. clavata* sexes only overlapped in January–April, and males had very low to zero occupancy within the array after April (Fig. 11D), with these interactions occurring primarily in the Whitsand array (Fig. 12D).

4. DISCUSSION

4.1. Habitat selection by Rajidae

Habitat selection is defined as space use that is non-random due to voluntary movements by a species (Kramer et al. 1997, Morris 2003, Sims 2003). The networks analysed in this study represent the voluntary movements of 4 species and, in every species, observed network metrics differed significantly from random expectations. For example, in the Plymouth array, receiver M1 was never visited, M5 very occasionally, while M4 and M6 and most of the Whitsand array received a higher number of detections,

which differs from what would be expected if individuals moved randomly. For example, on average 13% of the randomised detections for *Raja clavata* were at M1, but no detections were actually observed. In a recent study, depth was a factor for habitat preference in Rajidae; indeed, the maximum mean depth for any of these 4 species was 36 m, suggesting preference for shallow coastal habitats (Humphries et al. 2016). This may explain why receivers M1 (53 m) and M5 (52 m) were rarely visited,

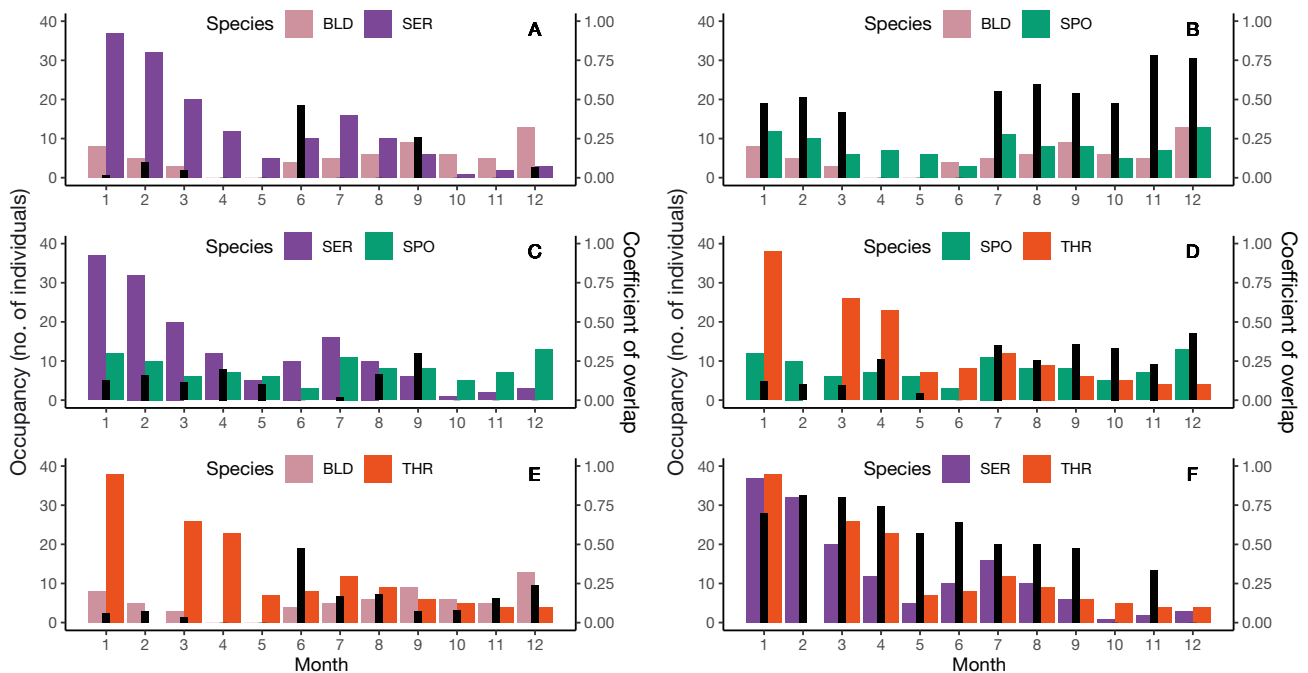


Fig. 7. Spatial overlap between species pairs over time. Black bars indicate the timing and extent of overlap between species (overlap coefficient). Coloured bars show occupancy. Pink = blonde ray *Raja brachyura* (BLD), orange = thornback ray *R. clavata* (THR), purple = small-eyed ray *R. microocellata* (SER), green = spotted ray *R. montagui* (SPO)

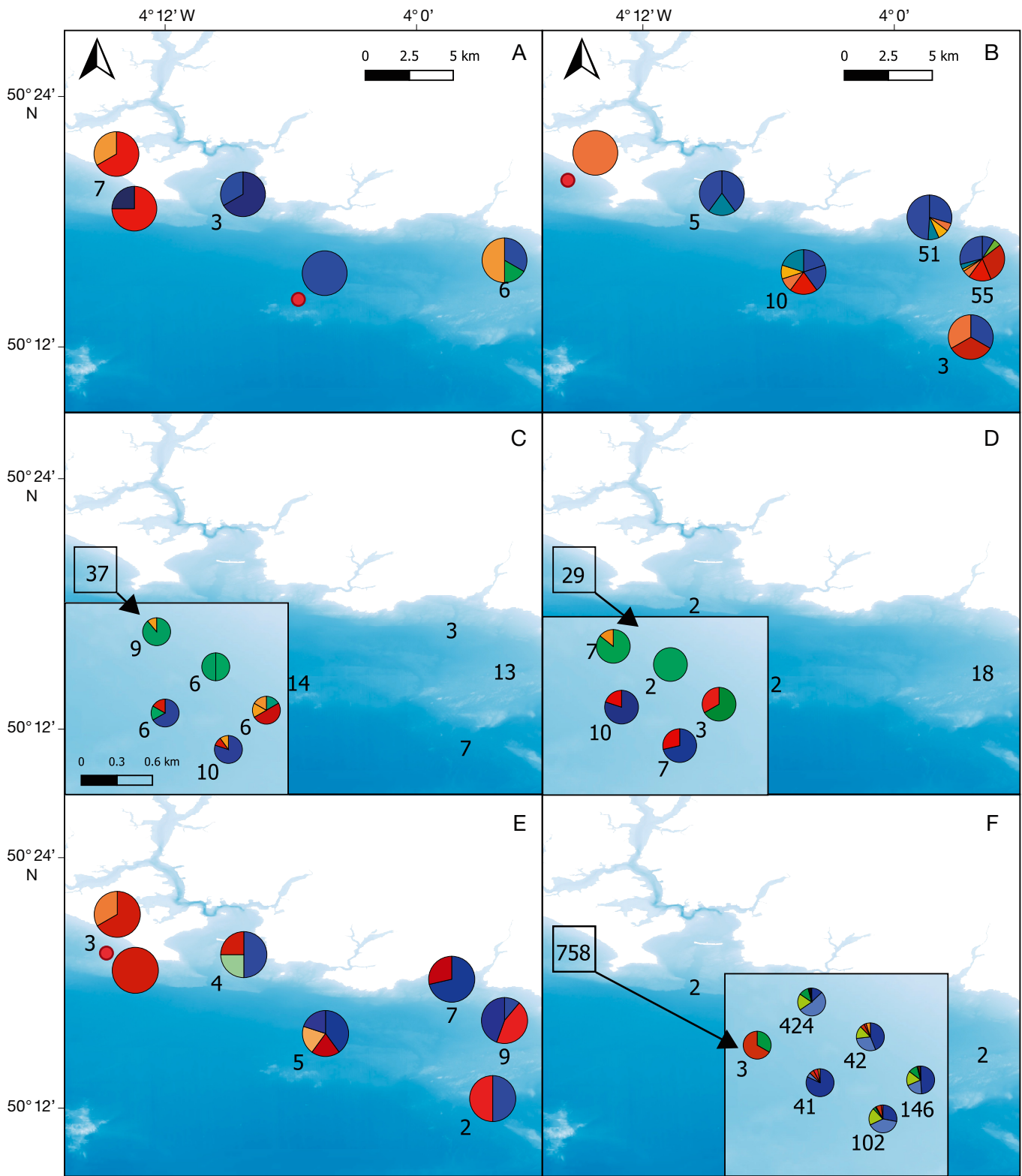


Fig. 8. Species associations. (A) *Raja microocellata* and *R. brachyura*, (B) *R. montagui* and *R. brachyura*, (C) *R. microocellata* and *R. montagui*, (D) *R. clavata* and *R. montagui*, (E) *R. clavata* and *R. brachyura*, (F) *R. clavata* and *R. microocellata*. Black numbers indicate the number of associations made between the species. Pie charts indicate the timing of the associations (reds = warmer summer months, blues = winter, orange = autumn, greens = spring)

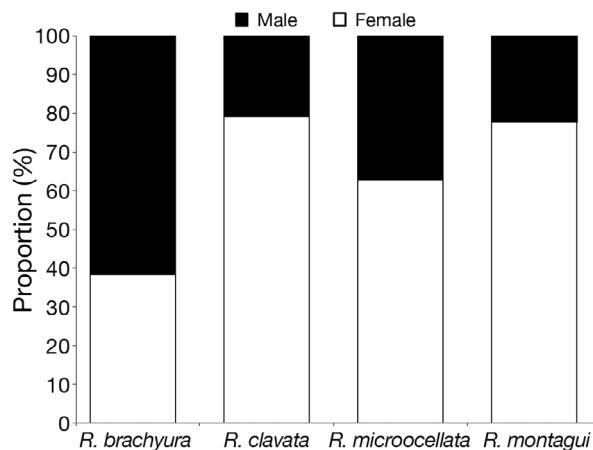


Fig. 9. Proportion of detections by sex for *Raja* spp., normalised by total number of days with at least 1 ping to account for tagging bias

although Rajidae can be found at considerably deeper depths (Ellis et al. 2005). We also found that species had preferences for particular locations, with *R. brachyura*, for example, having 88% of detections at M4, at 29.7 m depth and a coarse sand substrate.

Our findings demonstrate collectively that the distribution of Rajidae is non-random and infers active selection towards particular areas (receiver nodes), consistent with habitat selection on a fine scale. Several hypotheses may explain the occurrence of habitat selection by Rajidae. First, the study area is a complex ecosystem, influenced by an estuary and having varying habitat types, including sandy to rocky substrates (European Environment Agency 2018), which may play a role in habitat selection by these species. Substrate has been reported as an important driver of Rajidae distribution, with many species associated with sandy or muddy sea beds (Martin et al. 2010, Damalas et al. 2016) which they may be actively selecting when moving within their preferred areas of the acoustic array. Our receiver arrays were positioned over differing substrate: the Whitsand array over fine sand or mud and the Plymouth array over coarser substrate. Rajidae often bury into sediment for extended periods of time (Wallace et al. 2014), which may explain the importance of the sandy or coarse sediments selected by the individuals tagged in this study over other habitats that were available within the area covered by the receiver array.

Second, prey availability can drive habitat selection. For example, tiger sharks have been shown to preferentially occupy shallower seagrass habitats where their prey is most abundant (Heithaus et al. 2002). Similarly, the distribution of the small spotted

catshark in the Mediterranean was associated with the availability (abundance) of finfish and cephalopod prey (Navarro et al. 2016). The size of the tags used (36 mm long for V13s) and ethical considerations placed limits on the size of skates we were able to tag. Consequently, most of the skates were either adults or sub-adults and were therefore all considered to have adult diets, so it was not possible to determine any ontogenetic change in behaviour. Rajidae are broadly opportunistic feeders, and while every species is capable of eating both crustaceans and fish, some species appear to exhibit preferences. *R. clavata* and *R. montagui* show preference for crustaceans, while *R. microocellata* and *R. brachyura* prefer teleost fish (Ellis et al. 1996, Forman & Dunn 2012). It is likely that the sandy or coarse sediment habitats within the study site are more likely to contain a greater abundance of preferred prey items, such as sand eels (Ammodytidae) or swimming crabs (Portunidae) (Kaiser et al. 2004), and this may account for the observed habitat selection.

A third possibility is that reproductive state is important, as it can be another known driver of habitat selection in elasmobranchs. Nurse sharks, for example, use specific sites for mating and parturition behaviour (Carrier & Pratt 1998). Rajidae are oviparous species and are thought to use shallower nursery grounds for oviposition (Ellis et al. 2005); this may explain movements between specific habitats found in the current study, such as female *R. brachyura* moving between landers M4 (29.7 m) and M6 (30.4 m). More information on the maturity status of the individuals would be required to assess this further. Finally, competition from other benthic predators, including plaice *Pleuronectes platessa* or other skate species may lead to each species having a different habitat selection (Papasmatiou et al. 2006). It is possible that a combination of suitable soft substrates for burying, the availability of prey and the need to find mates and deposit eggs drive the habitat selection observed in the current study, but more research into possible nursery grounds and foraging patterns in Rajidae may help to elucidate which of these factors primarily drives habitat selection.

4.2. Spatial partitioning in Rajidae

A major driver of habitat partitioning between species is competitive exclusion, that is, by occupying different habitat, sympatric species can separate resources and avoid potential competitors (Papasmatia-

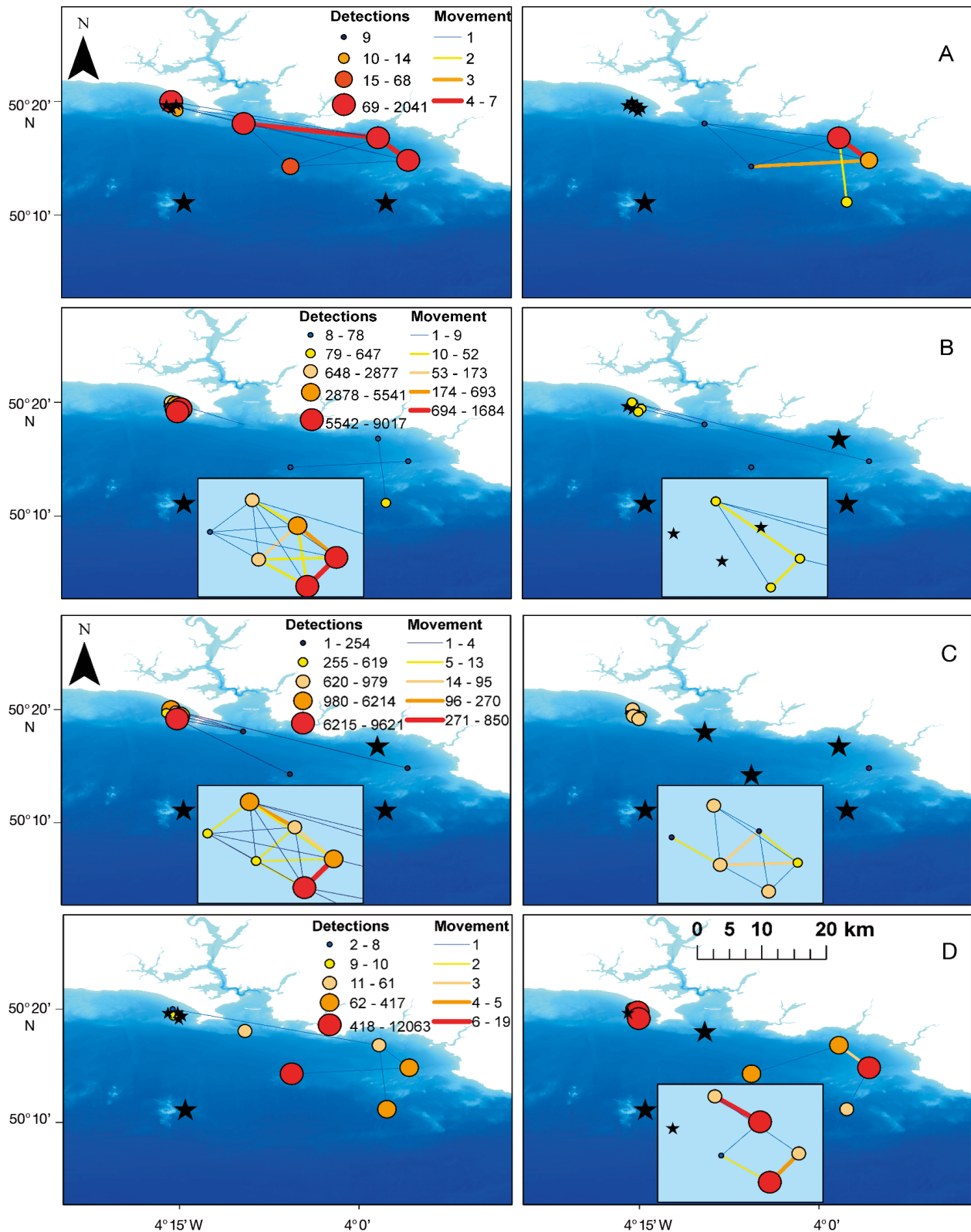


Fig. 10. Acoustic networks comparing sexes (females in left column; males in right column) of (A) *Raja brachyura*, (B) *R. clavata*, (C) *R. microocellata* and (D) *R. montagui* Insets highlight the Whitsand array in more detail where required. Warmer colours indicate more connections/detections (note the different bin ranges for each species). Stars indicate receivers with zero detections

Table 5. Observed versus randomised sex overlap coefficient. Arrow symbols as in Table 4

Species	p	Overlap coefficient	Randomised coefficient
<i>Raja brachyura</i>	<0.001	0.956↑	0.610
<i>R. microocellata</i>	0.0456	0.845↑	0.634
<i>R. montagui</i>	0.1277	0.643→	0.384
<i>R. clavata</i>	0.0026	0.757↑	0.410

tiou et al. 2006). The sympatric Rajidae species at the focus of the current study are morphologically similar, and although there are some maximum size differences among species (McCully et al. 2012), they are also broadly considered to be opportunistic generalist feeders (Ellis et al. 1996), which may mean they exhibit habitat partitioning to reduce competition.

We found that detections at receiver locations differed between species. There were differences between species networks and the proportion of time

spent at receivers. *R. clavata* and *R. microocellata* were detected at the shallower receivers (19–25 m) in the Whitsand array, while *R. montagui* and *R. brachyura* were detected more frequently in the deeper Plymouth array (30–53 m), splitting the 4 species into 2 pairs. This species pairing has previously been demonstrated with depth-logging electronic tags (Humphries et al. 2016). However in the current study, which can pinpoint a geographic location to within a few hundred metres, *R. montagui* were more frequently detected at lander M3 (47 m, 60%), while *R. brachyura* were predominantly detected 9.9 km away at M4 (30 m, 88%), suggesting geographic spatial partitioning in this pair irrespective of depth.

Spatial overlap analysis identified species pairs with differing degrees of spatial overlap. However, when investigating space use over time, there was less overlap between species than expected based on randomisations. Variation in spatio-temporal overlap among species may be explained by the timings of

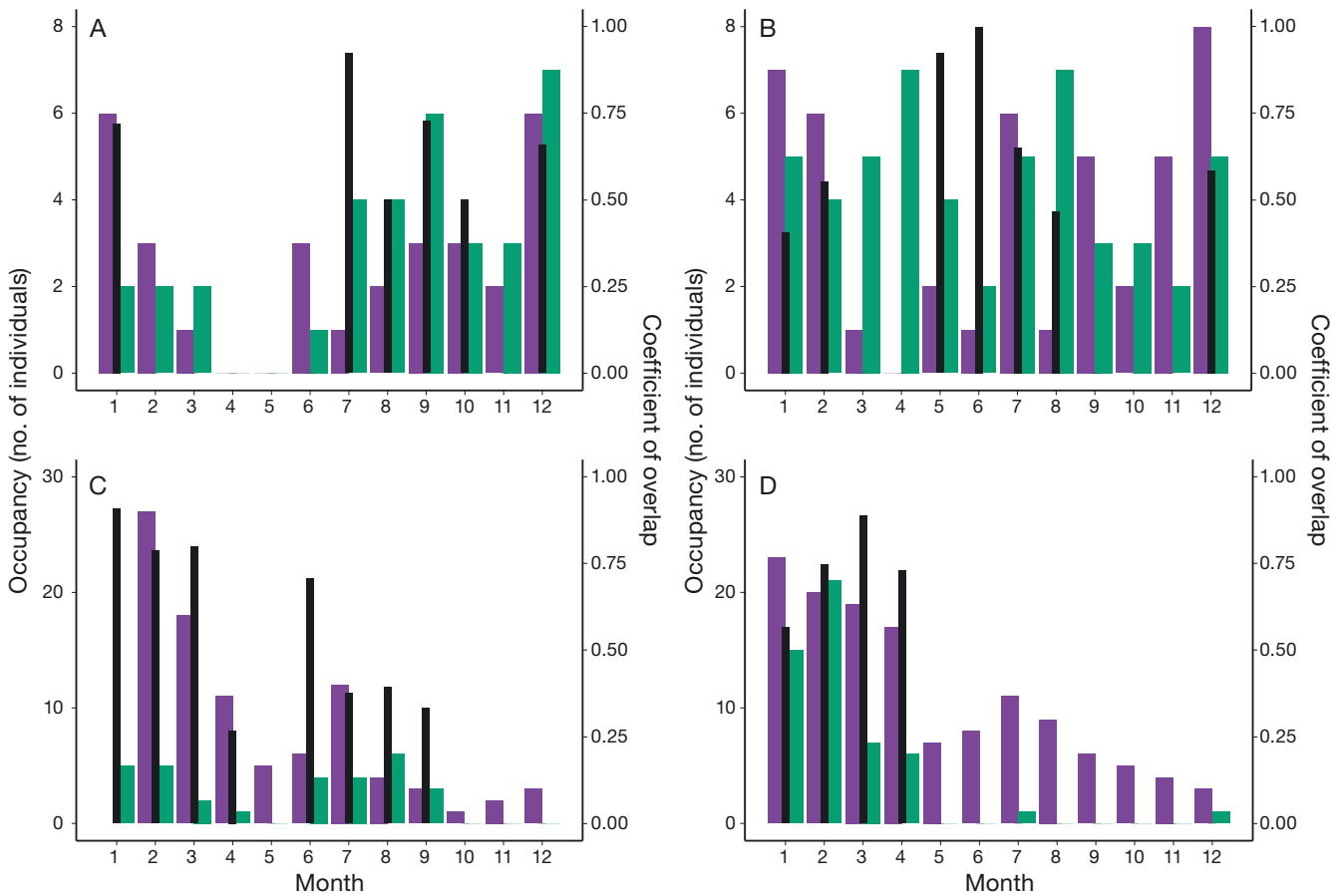


Fig. 11. Spatial overlap between sexes over time. Black bars indicate the timing and extent of spatio-temporal overlap between sexes (overlap coefficient). Coloured bars indicate sex (purple = female, green = male) for (A) *Raja brachyura*, (B) *R. montagui*, (C) *R. microocellata*, (D) *R. clavata*

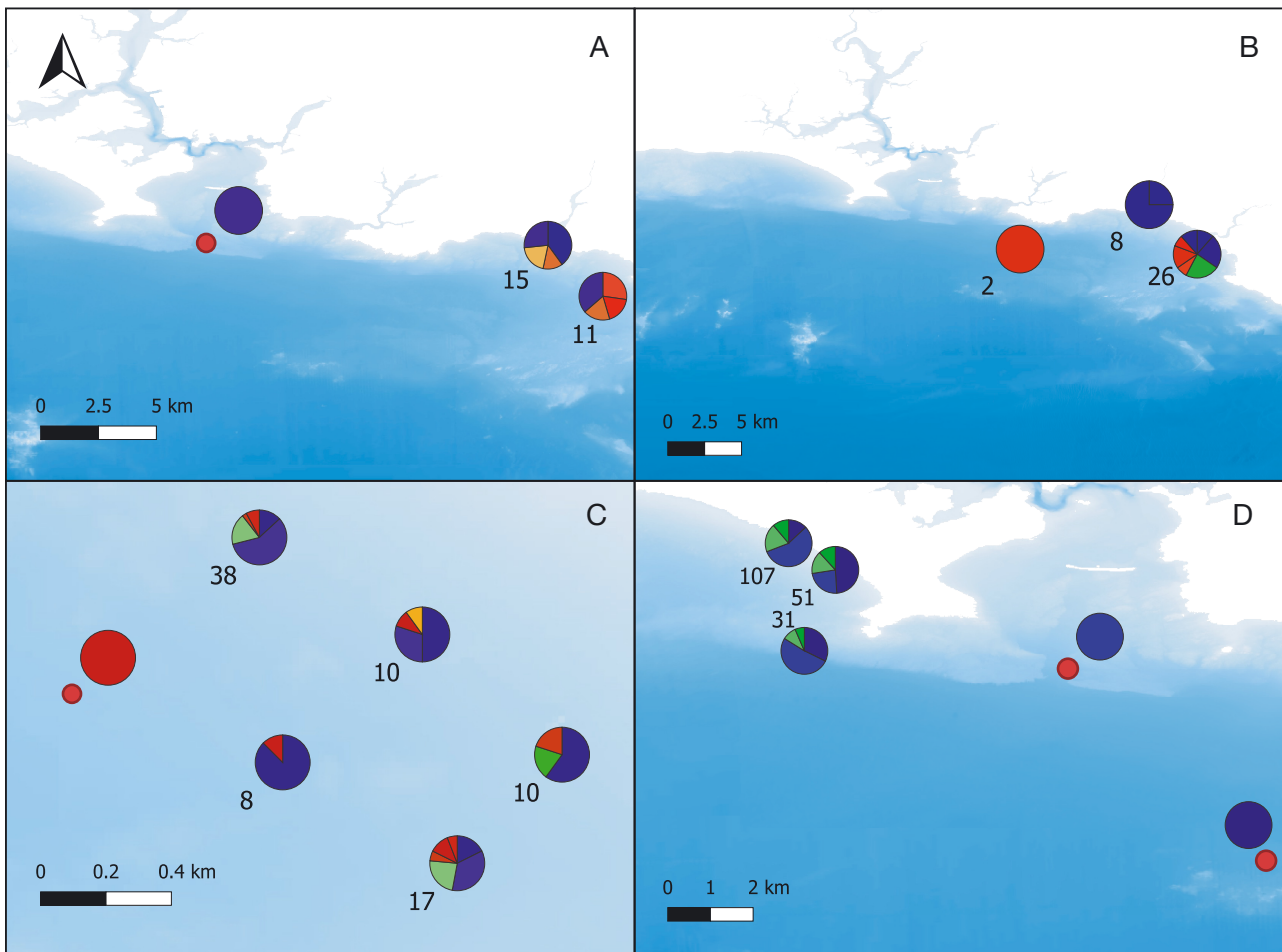


Fig. 12. Spatial associations between sexes over time. Black numbers indicate the number of associations made between the species. Pie charts indicate the timing of the associations as a proportion of the total overlap (reds = warmer summer months, blues = winter, orange = autumn, greens = spring) for (A) *Raja brachyura*, (B) *R. montagui*, (C) *R. microcellata*, (D) *R. clavata*

migrations into and out of different habitats. *R. brachyura* and *R. montagui*, for example, had a lower overlap coefficient in spring, *R. brachyura* had very low occupancy during these months, suggesting a movement away from the area. Previous studies in the same area off Plymouth have found similar patterns, in which *R. montagui* were captured more commonly in spring, whereas *R. brachyura* catches were higher in autumn (Simpson et al. 2020). Similarly, Humphries et al. (2016) found *R. brachyura* were deeper in winter and early spring while *R. montagui* remained at a more consistent depth all year. Taken together, it appears that *R. montagui* have more of a year-round presence in this habitat compared to *R. brachyura*, which moves away in spring.

Another example of spatio-temporal partitioning was between *R. brachyura* and *R. clavata*, 2 species with very low overlap. The month with the highest

overlap was June, the month when *R. brachyura* were shown to move shallower into the preferred depth range of *R. clavata* (Humphries et al. 2016). Overall, habitat use and associations among species found in this study differ over time and provide further evidence of spatio-temporal partitioning of shared habitats among Rajidae species.

Care must be taken when interpreting these results. Investigating timing of increased detections could be biased by a large release of tagged animals. Nonetheless, this potential bias may be mitigated by the observation that large batches of tag releases occurred at a time when skates were caught in a particular area, which may be entirely representative of the individuals' presence in space and time given that our research trawl surveys continued throughout the year in the area studied. In addition, we can only detect tags within receiver detection range, and be-

cause the array is relatively limited spatially, the lack of overlap between species may result from the constraint of only being able to sample at 12 locations. The array does not cover the entire home range of these species, so there may be more overlap outside the array. Despite these limitations, it is clear that these 4 sympatric species exhibit fine-scale temporal habitat partitioning within the study area.

It is interesting to note that density-dependent habitat selection suggests that in an expanding population, some individuals will occupy suboptimal habitat. Conversely, in a decreasing population, a species may move to occupy only the optimal part of its range (Sutherland 1983, Blanchard et al. 2005). In addition, fishing pressure may also have acted to remove skates from optimal habitats where fisheries co-occur, so that they are generally observed to occur more frequently in sub-optimal habitats. This may act further to reduce the overlap between the species. Over the last century, Rajidae populations have declined; for example, between 1956 and 1995, there was a reported 80% decline in *R. clavata* in the North Sea, and a 45% decline in the Irish Sea was recorded between 1988 and 1997 (Walker & Heessen 1996, Dulvy et al. 2000, Chevolut et al. 2006). It is possible that the habitat partitioning observed in the current study is more apparent because these Rajidae populations have declined and their distributions have contracted into areas of the highest habitat suitability. Common skates (*Dipturus batis*–*D. intermedius* complex) are an example of species that were once common but are now locally extinct due to overfishing (Brander 1981). Hence, they may now occupy refugia where areas of low fishing effort and adequate habitat co-occur (Shephard et al. 2012). On balance, it is likely that the population declines in Rajidae have exaggerated the habitat partitioning observed in the study area relative to the historic baseline ecosystem, for which there is very limited information.

Understanding habitat partitioning among Rajidae species is also important to consider in a commercial fisheries context, because habitat partitioning has an impact on the catchability and therefore the vulnerability of each species (Mucientes et al. 2009). As explored by Simpson et al. (2020), it is clear that when habitat partitioning exists, some species are caught by different gear types and different species may occupy habitats that vary in fishing pressure. Quotas for Rajidae species are still largely set by fisheries managers as a grouped quota and are not treated as individual species (MMO 2017). When particular species have higher catchability due to their habitat

selection, grouped quotas may potentially result in the further decline of those species that may go undetected.

4.3. Differences in movement among species

The connections observed in the networks are a proxy for the movements made by individuals between different geographical locations. The 4 rajid species differed in their movements within the arrays. Within the Plymouth array, movements between locations were predominantly made by *R. brachyura*, and the distances within this array are much greater than in the Whitsand array. In addition, long-distance movements between the arrays were made primarily by *R. brachyura* and *R. microocellata*. *R. montagui* were detected more frequently within the Plymouth array than *R. brachyura*, but made fewer movements, indicating that *R. montagui* exhibit a higher degree of residency than *R. brachyura*. The differences in the extent of their movement may reflect prey availability, with the preferential piscivores (*R. microocellata* and *R. brachyura*) (Ellis et al. 1996) searching over wider areas for their more mobile prey. *R. clavata* are associated with both marine and brackish waters and are considered to have the widest distribution of the 4 studied species (Ellis et al. 2005, Hunter et al. 2006, Simpson et al. 2019), yet individuals tracked in this study were not recorded to make long-distance movements within or between the arrays. Conversely, *R. brachyura* are considered to have a patchy and narrower range in UK waters (Martin et al. 2010), but were observed here to make relatively long-distance movements within the array. The wider habitat tolerances of *R. clavata* may allow this species to exploit a range of habitats in close proximity and therefore, it may only need to move short distances to find suitable habitat. In contrast, *R. brachyura*, with its narrower habitat preference, may therefore have to move greater distances to find these preferred (less generalised) habitats. *R. microocellata* has previously been demonstrated to move greater distances than the other 3 species with mark-and-recapture tagging (Simpson et al. 2020), perhaps to reach preferred patchy habitats. The lower degree of movement found in *R. montagui* may also be a reflection of their smaller body size relative to the other species (total lengths, mean \pm SD: *R. montagui* 583 \pm 74 mm, *R. clavata* 731 \pm 105 mm, *R. microocellata* 678 \pm 102, *R. brachyura* 760 \pm 145 mm); smaller body sizes have been shown to reduce activity space (McNab 1963). Overall, the

results indicate a clear difference in the movement strategies of these 4 species.

4.4. Sexual segregation in Rajidae

In every species, there were biases between sexes in the proportion of detections made within the array. In *R. microocellata*, *R. montagui* and *R. clavata*, significantly more detections were made of females, while in *R. brachyura* more males were detected. Associations between the sexes occurred at different times of the year.

Importantly, there were months when one sex was detected and another was not; for example, *R. montagui* males have peak occupancy in spring, while females were absent. These temporal differences in habitat uses between sexes may reflect males or females (or both) migrating between shared habitat use (months with high overlap) and segregated habitat (months where only one sex is present or spatial overlap is low).

Evidence for sexual segregation has been implied previously by studies that found a tendency to capture females in trawls (Steven 1933). Sex ratio bias in trawls was also demonstrated in *R. clavata* in the Bay of Douarnenez, France, where trawl catches for this species were predominantly male-biased inside the bay and female-biased outside the bay (Rousset 1990). The results of the current study suggest that males and females do not consistently occupy the same fine-scale habitat, which confirms active sexual segregation in these species.

Two of 5 main hypotheses (Wearmouth & Sims 2008) are likely explanations for sexual segregation in Rajidae. The activity budget hypothesis suggests that sex differences in body size and reproductive investment result in sex-specific activity budgets resulting in different habitat requirements. As previously discussed, Rajidae are oviparous, and females grow larger and mature later than males. As females lay eggs in nursery areas, they may select different habitats than males during oviposition. Growth rate and age of maturity may also cause a separation by size of the sexes in these species. Additionally, the social factors hypothesis suggests that sexual segregation is caused by intra-sexual affinity for the purpose of cooperation of information transfer or alternatively intersexual aversion, due to aggression. Elasmobranch males tend to exhibit aggressive behaviour towards females during mating, which is likely costly to females and often results in female avoidance of males (Kimber et al. 2009, Wearmouth

et al. 2012). Female Rajidae also have the capacity to store sperm, thereby reducing the need to mate regularly and enabling females to avoid males for longer periods (Luer & Gilbert 1985). The timing of high overlap between males and females seen in this study may therefore represent the timing of mating at these sites. Currently there is not enough evidence to conclude which of these 2 main hypotheses is more likely; indeed, it is plausible that both oviposition by females and female avoidance of males play a role in the sexual segregation observed here.

4.5. Limitations

A key limitation of the acoustic array used in this study is the number of receivers in the array and therefore the spatial coverage of detection. This resulted in a third of tagged skates never being detected by the array, which reduces our ability to record fine-scale movements beyond the array and decreases the resolution of the spatial and temporal data recorded. The placement of additional receivers is possible; however, in this heavily fished region, receivers should ideally be placed within the boundaries of MPAs to reduce potential damage by mobile fishing gear. Furthermore, the detection ranges of the receivers can change depending on multiple environmental conditions such as wave noise, particulate matter, salinity and temperature (Kessel et al. 2014), likely resulting in seasonal changes in the coverage of the array. The data and conclusions from such studies must therefore be interpreted with some caution. Nevertheless, the passive acoustic array at the focus of the current study was successfully deployed and remained operational over a long period, with the Whitsand array remaining in position and detecting tags for approximately 7 yr. The array was still in place and receivers were able to communicate remotely, even after the severe winter storms of 2014–2015 (Met Office 2015), suggesting that the use of an acoustic array is possible in a high-energy, open coastal ecosystem over long periods.

4.6. Conclusions

Our findings suggest habitat selection and partitioning among the 4 investigated Rajidae species, as well as intra-species sexual segregation, revealed by long-term acoustic telemetry. The higher spatial and temporal resolution provided by the passive acoustic array relative to mark-and-recapture and fishing surveys

allows for a more robust and fine-scale picture of the spatial distribution of rajids. *R. brachyura* and *R. montagui* appeared to exhibit a greater degree of fine-scale separation than previously demonstrated (Humphries et al. 2016). The results further demonstrate that these species, which are often grouped for management, have more complex habitat use; thus our findings provide information to aid species-specific management of Rajidae. For example, the use of MPAs covering habitat selected by a particular species could aid in the conservation of this species.

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