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# Two's company, three's a crowd: fine-scale habitat partitioning by depth among sympatric species of marine mesopredator

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ABSTRACT: A sympatric assemblage of morphologically similar predators is expected to exhibit fine-scale habitat segregation, or resource partitioning, to reduce the effects of direct competition. This principle has been well studied for predators in terrestrial ecosystems. In the marine environment, the fine-scale spatial segregation of sympatric species of large predators is poorly understood because detailed movement and behavioural data are often not available across multiple species within the same timeframe. The ways in which co-occurring congeneric predators separate spatially is even less well understood. Medium-sized species of skates (genus *Raja*) co-occur in temperate habitats of the north-east Atlantic Ocean, share similar morphologies and have distributional ranges that overlap significantly in the western English Channel ecosystem. In the present study, detailed depth time series retrieved from 89 electronic data storage tags attached to 4 species of skate were analysed to determine preferred depth ranges. The 4 species were found to segregate spatially into 2 groups, with one group having a significantly shallower core annual depth range than the other. To our knowledge, fine-scale segregation by depth has not been observed previously. Interestingly, the members of each species group appeared complementary, each group comprising species with different dietary preferences and with a larger and smaller body size. An understanding of how core depth ranges differ and how these species utilise vertical habitat could potentially enable geographic ranges around the coast to be predicted, with important implications for how these species interact with fisheries and Marine Protected Areas.

KEY WORDS: Segregation · Resources · Marine · *Raja* · Ray · Skate · Niche

## INTRODUCTION

The mechanisms that animals with similar resource requirements use to avoid direct competition is an important ecological question, which, at least in the terrestrial realm, has received much attention. Concepts such as niche partitioning have been developed to further our understanding of the morphological and behavioural adaptations seen in co-existing animals with competitive overlap, such as African feline predators. For example, lions, cheetahs, leopards, caracals and servals coexisting in and around the African savannah exhibit a complex array of adaptations such as differing prey specialities, morphologies and life history traits, resulting in resource partitioning and, consequently, reduced direct competition (Hayward & Kerley 2008, Owen-Smith & Mills 2008). Niche partitioning can also in-

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volve behavioural adaptations, for example differing thermoregulatory behaviour in tiger beetles (Brosius & Higley 2013) or activity patterns in lizards (Vitt & Zani 1996). In sympatric assemblages of birds, niche partitioning is evident in the location of nesting sites, where clear habitat preferences have been observed with elevation, aspect and slope position being important habitat features (Dellinger et al. 2007), in addition to tree species and ground cover (Martin 1998).

In marine ecosystems and for elasmobranchs in particular, several drivers of resource partitioning have been identified. Where spatial overlap occurs, for example in reef sharks or stingrays, temporal or dietary differences have been found that allow coexistence (Cartamil et al. 2003, Speed et al. 2012). In an assemblage of reef sharks, while there was considerable overlap in the areas occupied, differences were found between the species in the times of peak abundance (Speed et al. 2011). *Carcharhius melanopterus* abundance peaked between 13:00 and 14:00 h, while *C. amblyrhnchos* abundance peaked earlier, at 10:00 h, suggesting a temporal partitioning of resources and diel movement patterns. In an Australian assemblage of stingrays, resource partitioning was found to comprise a complex of habitat preferences and dietary differences, with ontogenetic changes in diet resulting in narrowing diet breadth and reduced dietary overlap with increasing age (Platell et al. 1998). Stomach content and stable isotope studies have found diet to be an important component of resource partitioning (Speed et al. 2012), with trophic structure often based on teleost/crustacean divisions (Espinoza et al. 2015, Hussey et al. 2015b). Where dietary overlap has been identified, for example in pelagic sharks in the Hawaiian Islands, USA, niche partitioning has been achieved through spatial (geographic) segregation (Papastamatiou et al. 2006). Skates, such as *Raja* spp., generally have broad diets (Farias et al. 2006, Šantič et al. 2012), and there can be significant dietary overlap (Valls et al. 2011), despite individual specialisations. For *Raja* spp. therefore, spatial segregation, or habitat preferences, could be an important driver of resource partitioning.

Habitat partitioning is perhaps one of the clearer indications of niche separation, being easier to observe than prey preferences or behavioural adaptations, especially in cryptic ecosystems such as marine or freshwater habitats. Indeed habitat preferences have been observed in many different taxa in aquatic ecosystems, for example, freshwater fish in chalk streams (Prenda et al. 1997), in marine fish such as gurnards (Lopez-Lopez et al. 2011), pipefish (Malavasi et al. 2007) and sharks (Ceccarelli et al. 2014, Legare et al. 2015), and in copepods (Mackas et al. 1993).

Habitat preferences, for example for particular substrates, temperatures or depths, are fundamental drivers of species distributions, migrations and fine-scale movements in the marine environment (Speed et al. 2010, Gouraguine et al. 2011, Queiroz et al. 2016). Consequently, an understanding of habitat preferences is essential when considering conservation strategies (Kaiser 2005, Speed et al. 2010, Queiroz et al. 2016). This is particularly relevant to marine ecosystems, where many species have been overexploited and regulations to control or limit harvesting have resulted in reduction measures such as Marine Protected Areas (MPAs) that exclude or partially exclude fisheries (McCauley et al. 2015). However, in contrast to terrestrial ecosystems, fine-scale information concerning the movements and habitat preferences of multiple species of marine predators within the same geographical region is generally lacking (Block et al. 2011), making reliable conservation planning difficult, despite the pressing need to reduce overexploitation (Thurstan et al. 2010).

Historically, commercial fishing or research trawl survey data have been used to examine large-scale patterns in species distributions, including differences in depth range occupation among sympatric species (Gouraguine et al. 2011). However, it is not possible to examine fine-scale differences in the habitats occupied by many individuals of multiple species continuously through time with these coarse sampling approaches. Recent advances in electronic data-logging devices (tags) have opened a window on the complex behaviour of marine predators, providing insights into foraging and migratory patterns (both horizontal and vertical) of commercially important species including cod, skates, tunas, sharks and billfish (Hunter et al. 2006, Hobson et al. 2007, Sims et al. 2008, Humphries et al. 2010, Block et al. 2011, Hussey et al. 2015a). Tracking the movements of individual fish of sympatric species offers a way to investigate habitat partitioning. For example, the large-scale movements of 3 wide-ranging species of pelagic shark from the family Lamnidae (salmon shark *Lamna ditropis*; shortfin mako *Isurus oxyrinchus*; white shark *Carcharodon carcharias*) have been tracked simultaneously in the eastern Pacific Ocean (Block et al. 2011). Spatial separation was demonstrated between the 3 species over a large scale, encompassing 40° of latitude and more than 30° of longitude. This was consistent with their active behaviours and wide-ranging distributions, with the species essentially exhibiting latitudinal zonation rather than fine-scale niche separation. While fine-scale habitat partitioning might be difficult to identify in active, wide-ranging pelagic species, it might be found in the study of less active, benthic mesopredators, such as skates.

Skates are marine mesopredators strongly adapted for the benthic environment and with a worldwide distribution in all oceans. These elasmobranchs differ from their benthic teleost counterparts in this local assemblage, such as plaice *Pleuronectes platessa* or turbot *Psetta maxima*, principally by being dorsoventrally, rather than laterally, flattened and by having ventrally positioned mouths. Unlike most teleosts, including plaice, skates are *K*-selected species with a late age at maturity and low fecundity, making them vulnerable to overexploitation (Field et al. 2009, Dulvy et al. 2014). They also lack a planktonic life history stage, resulting in reduced dispersal and low re-colonisation potential compared to teleost benthic predators (van der Molen et al. 2007, Frisk et al. 2014). Studies using research trawl data have found depth to be an important factor in the segregation of the 4 elasmobranch species studied here (Gouraguine et al. 2011), and complex patterns of spatial segregation and apparent differential habitat preferences have also been identified in the eastern North Pacific (Bizzarro et al. 2014). The aforementioned study found depth to be the primary axis of segregation although it was suggested that the driver could be temperature, which was strongly correlated with depth. Interestingly, where species overlapped, the coexisting species were found to differ in size, which suggests some further level of niche partitioning. Segregation, or zonation, by depth has also been found in the South African assemblage of skates (Compagno et al. 1991, Compagno & Ebert 2007) and would therefore appear to be a common occurrence among skates over the large scales at which these studies were performed. However, all these studies were large (geographic) scale and investigated separation at a species level into different populations with different habitat preferences. Less is known about fine-scale habitat segregation in sympatric assemblages of skates, where the species co-exist over a relatively small geographical extent. This significant gap in our understanding is unsurprising given that the cryptic nature of benthic predators makes direct observation impractical and that the majority of data concerning habits and diet are derived from fisheries or trawl surveys (Bizzarro et al. 2014). Data from both fisheries and trawl surveys are inevitably sparse and the distribution of fishing effort can result in a significant bias (Bolle et al. 2005), making any conclusions regarding ecological concepts such as habitat preferences or resource partitioning somewhat speculative. Further, temperate marine benthic environments very rarely benefit from *in situ* observations that can prove so useful in elucidating behaviour and habitat preferences (Eggleston et al. 2013).

There are 4 species of skate that are commonly found in southern UK waters in the western English Channel (WEC) ecosystem: *Raja brachyura* (blonde ray; LaFont, 1871), *R. clavata* (thornback ray; Linnaeus, 1758), *R. microocellata* (small-eyed ray; Montagu, 1818) and *R. montagui* (spotted ray; Fowler, 1910). These species have been common and widespread since the last glacial maximum some 20 000 yr ago (Chevolot et al. 2006b) with distributional ranges that overlap significantly in the WEC (Ellis et al. 2005b), although abundance has declined since the 1950s as a result of fishing pressure (Chevolot et al. 2006a, Genner et al. 2010). In order to reduce direct competition, it might be expected that these 4 sympatric species would exhibit significant differences in morphology and life history (Hardin 1960). However, the members of this closely related congeneric group (McEachran & Dunn 1998, Ebert & Compagno 2007) show considerable morphological similarity and until recently were simply classified as 'skates and rays' in fisheries landings data (Dulvy et al. 2000). The most obvious difference between the 4 species is an interspecies maximum recorded size range of around 1.5 times between the smallest (*R. montagui*) and the largest species (*R. brachyura*). Further, their dietary requirements are also broadly similar, being generalist predators of crustaceans and fish with considerable overlap, especially between juvenile individuals (Ellis et al. 1996). Consequently, it is not currently known how resources are partitioned among these species in order to enable their apparent close coexistence.

To address this knowledge gap, we investigated the fine-scale habitat use of the 4 sympatric skates with tracking data collected simultaneously throughout the study area. This study analyses datasets for 4 species of skate (*R. brachyura, R. clavata, R. microocellata, R. montagui*), from 179 tags deployed from July 2007 to May 2013 off Plymouth, UK. The long-term depth time-series were analysed to determine (1) whether core depth preferences can be identified in each species; (2) whether preferred depths differ sufficiently to indicate habitat segregation, and (3) how preferences change over seasonal timescales.

To identify core depth preferences, the study used weekly mean depths for each species. To determine differences in depth preferences, the overlap in weekly time at depth occupancy between the species and how this overlap changes on seasonal timescales was examined, providing a first step in understanding the complex behaviours underlying coexistence and niche partitioning.

## MATERIALS AND METHODS

### Tags and tagging

Adult or sub-adult fish were captured during routine research survey trawls in inshore waters of the WEC between Whitsand Bay (50.34° N, 4.28° W) and Bigbury Bay (50.26° N, 3.89° W). Fish were tagged using data storage tags (DST), either CTL G5 (www.cefastechnology.co.uk) or Star Oddi (star-oddi.com). Standard G5 DSTs were 31 mm long, 8 mm in diameter and weighed 1 g in water, whereas long-life G5 DSTs were 35.5 mm long with a diameter of 11.5 mm and weighed 2.1 g in water. Star Oddi DSTs were 39.4 long with a diameter of 13 mm and weighed 5 g in water. DSTs monitor temperature from 2 to 34°C (accuracy 0.1°C, resolution 0.03°C) and pressure to a depth of 100 or 200 m (accuracy 1 %, resolution 0.04 %) depending on tag type (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m561p173_supp.pdf). All DSTs were programmed to record depth at 20 s, 30 s or 1 min intervals. All tags also recorded temperature every 10 min. DSTs were attached to skates via Peterson disc tagging using the methods described by Wearmouth & Sims (2009). Briefly, tags were mounted in a stainless steel wire cradle with a long, pointed stainless steel wire attachment. This wire was passed through a Peterson disc and then dorsoventrally through the pectoral fin, taking care to avoid the abdominal cavity. A second Peterson disc was then placed onto the length of wire on the opposite (ventral) side of the animal before securing the attachment by turning a series of rounds into the length of wire remaining. Tagging was typically accomplished in less than 2 min, including the measurement of total length and body width. Animals were immediately transferred to on board aquaria with fresh running sea water for observation prior to release within the hour. All tagging procedures were approved by the Marine Biological Association Animal Welfare and Ethical Review Body (AWERB) and licensed by the UK Home Office under the Animals (Scientific Procedures) Act 1986. DSTs were returned through the commercial net and trawl fisheries operating in the WEC with a reward of £50 given for return of the DST and the fish, or for information about the size of the fish and where it was captured.

### Data analysis

Several approaches were taken to determine core depth occupancy, separation and the degree of overlap in vertical habitat use. To determine core depth preferences and how depth usage changed over time at seasonal timescales, weekly mean depths were computed from all pooled individuals and plotted for each species. To examine depth preferences at a finer temporal scale, diel depth profiles were computed, whereby the mean depth in hourly depth bins was computed for all individuals in each species. Additionally, to investigate possible drivers of habitat preferences, weekly mean temperatures were also computed from the time-series data.

To investigate overall depth occupancy and the extent of the vertical habitat exploited, time at depth (TAD) plots were built by computing percentage time at depth for all individuals. The depth time-series data returned by the tags are complex and represent movements encompassing a rich behavioural repertoire with considerable variability both between and within species and individuals. To reveal this fine-scale detail, the datasets were used to populate TAD matrices, constructed with 4 m depth bins (rows) and weekly time bins (columns), whereby all the data for each species could be accumulated into a single matrix. The matrices were constructed with a maximum depth of 80 m, which was sufficient to encompass the recorded depths and a 4 m depth bin was consequently chosen as this provided 20 depth bins.

To reduce bias introduced by the datasets having differing durations and extents, computed TAD values were normalised by dividing by the number of datasets contributing to each grid cell to give a mean TAD value. The resulting TAD matrices were initially compared visually by producing contour plots. To further investigate shared depth occupancy between pairs of matrices, a shared TAD occupancy matrix ($S$) was computed with values for each grid cell calculated using:

$$S = \begin{cases} 0, \text{ if } p1 \text{ or } p2 = 0 \\ (1+p1) \times (1+p2), \text{ otherwise} \end{cases} \tag{1}$$

where $p1$ is the occupancy value from one species and $p2$ the value of the other. This equation is used as the normalised TAD values can be <1.0. To provide a numerical comparison of the matrices, an overlap coefficient ($O$) was computed using the following equation (Horn 1966, Rijnsdorp et al. 1998):

$$O = 2\sum_j (P_{aj} \times P_{bj}) \Big/ \left(\sum_j P_{aj}^2 + P_{bj}^2\right) \tag{2}$$

where $P_{aj}$ represents the TAD value for species $a$ in grid cell $j$ and $P_{bj}$ the corresponding value for species $b$. Using this equation, it is possible to compute an $O$ for either the entire matrix, or for sub-sets of grid cells, such as all cells in each column to provide a week by week coefficient, or for all grid cells in each row to give $O$s for each depth range. These coefficients range in value from 0.0 (no overlap) to 1.0 (matching occupancy) and provide a straightforward way in which to determine similarity between TAD matrices constructed for different species. To determine the statistical significance of the $O$s, a null model was used with a Monte-Carlo approach in a 2-step process. First, for each pair of matrices (**M1** and **M2**) being analysed, a null value was computed using a randomised **M1** matrix and the original **M2** matrix, with this being repeated 5000 times. For each iteration a count was maintained of the number of the times the randomised overlap coefficient value ($O_r$) was less than the observed overlap coefficient value ($O_o$). The process was then repeated a further 5000 times with **M2** being randomised and **M1** being the original, to give a total number of randomisations ($R$) of 10000. A mean random overlap coefficient value ($O_{rm}$) was calculated for all randomisations.

The randomisation process was a conservative approach based on the RA4 option in EcoSim (Gotelli & Ellison 2013), whereby each non-zero value was swapped with a randomly selected non-zero value. This approach preserves the overall TAD structure but modifies the distribution of 'hot' and 'cold' spots. Examples of randomised matrices are given in Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m561p173_supp.pdf.

A value greater than the $O_o$ value suggested that the observed overlap was less than expected by chance, and therefore the count of $(O_r < O_o)/R$ provides a p-value. Conversely, $O_{rm} > O_o$ suggests that the observed overlap is greater than expected by chance and then $10000 - (O_r > O_o)/R$ provides the p-value. For example, if the $O_o$ was 0.26, the $O_{rm}$ was 0.32 and 9793 of the randomisations produced a coefficient greater than observed, then the observed overlap can be said to be significantly less than expected by chance, with a p-value of 10000 − 9793/10000 = 0.0207.

The long timescale of the tagging activities/deployments and the short length of some of the datasets (range 2 to 419 d; mean = 140 d ±116 SD, n = 89) inevitably resulted in some gaps between individuals across seasons and years. To account for the gaps, we overlaid all data to a single year in all the analyses, making the assumption that on an annual scale, individual species within the study area likely exhibit similar behaviours and activities between years.

To determine the statistical significance of the separation by depth and to account more fully for individual variation, a mixed effects linear model was run using the R lmer function (Winter 2013, Bates et al. 2015, R Development Core Team 2015). The model used was Mean Depth ~ Species + Week + (1 | Individual) with a null model of Mean Depth ~ Week + (1 | Individual). The models were run using weekly mean depth data from all individuals and were compared using 1-way ANOVA to determine whether Species had a significant effect.

## RESULTS

### Tag returns and available datasets

Of the 179 tags deployed, 92 (51.4%) were returned, and 89 had useable data with a total of 35 × $10^6$ data points totalling 12585 d. A summary of the datasets available is given in Table 1, further details are given in Table S1 in the Supplement. Recapture locations were recorded for 64 tags, giving a mean displacement of 12.09 km ±13.26 SD (range 0.33 to 63.96; n = 64). Median displacements for each species are given in Table S2 in the Supplement. For 59 animals (92%), the displacement was <30 km, suggesting that these animals tended to remain in the area (Fig. 1), in agreement with previous tagging studies (Hunter et al. 2005a, Chevolot et al. 2006a). No correlation was found between days at liberty

Table 1. Datasets available for study of *Raja brachyura*, *R. clavata*, *R. microocellata* and *R. montagui*. IUCN status: NT, Near Threatened; LC, Least Concern

| Species | Days of data | No. of data points | No. of ind. | IUCN status |
|---|---|---|---|---|
| *R. brachyura* | 1240 | 4331839 | 12 | NT |
| *R. clavata* | 5949 | 15096439 | 43 | NT |
| *R. microocellata* | 3501 | 11084059 | 24 | NT |
| *R. montagui* | 1895 | 4927843 | 10 | LC |
| Total | 12585 | 35440180 | 89 | |

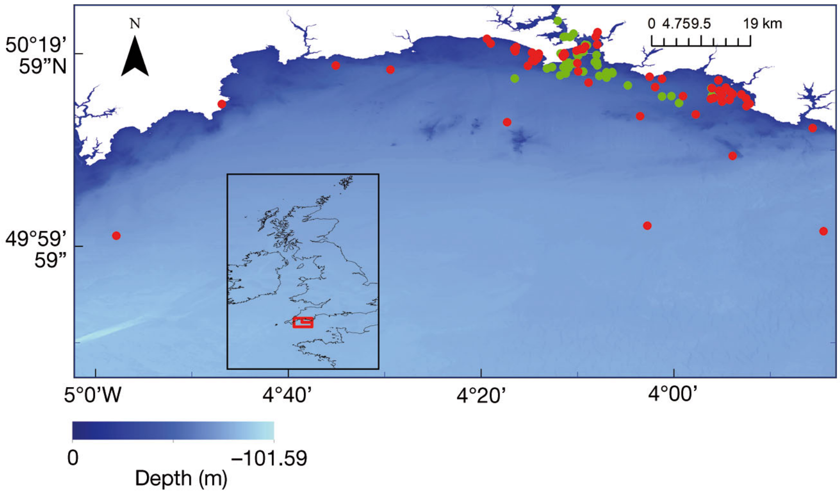

Fig. 1. Tag (green dot) release and (red dot) recapture locations of tagged *Raja brachyura*, *R. clavata*, *R. microocellata* and *R. montagui* captured in inshore waters of the western English Channel. The majority of animals for which tags were returned remained close to the release location. Inset shows the study area in relation to the UK

and displacement (Pearson Product Moment Correlation = 0.0528, p = 0.678, n = 64), indicating that the skates were not simply in transit through the area, but instead represent part of a more localised assemblage. As we do not have geographic locations, other than the release and recapture points, it is not possible to confirm whether the animals are permanent residents or are simply exhibiting site fidelity. However, if animals were migrating away then returning to the site after significant periods away, then it would be more likely for captures to have occurred further afield. Consequently, although site fidelity cannot be ruled out, residency, at least for the animals for which tags were returned, seems more likely. The animals in the study can therefore be considered to be within the same spatial frame of reference, with this level of residency being likely in other locations around coastal areas.

Although the differences in length and body width between species of the tagged animals were found to be significant (Kruskal-Wallis 1-way ANOVA on ranks, p = 0.031 and p = 0.034, respectively), with *Raja clavata* being slightly longer and *R. brachyura* slightly wider than the other 3 species (see Table S3 in the Supplement), there was in fact considerable overlap (Fig. S3 in the Supplement) and the differences were very small. The tagged animals also had very similar masses, and while *R. brachyura* and *R. clavata* were slightly heavier, this was not found to be significant (Kruskal-Wallis 1-way ANOVA on ranks, p = 0.16, Fig. S3). Consequently, for the animals tagged in this study, there was no support for the general assumption that this sample of individuals would exhibit size-driven segregation. Within species, size and weight ranges were greatest for *R. clavata* and smallest for *R. montagui*, with the ranges for *R. clavata* exceeding the range across species. These ranges are likely due to the larger sample size for this species. Some evidence for depth segregation by size might therefore be expected within *R. clavata*.

### Mean depth profiles

The TAD profiles (Fig. 2) showed strong similarities, with *R. clavata* and *R. microocellata* having very similar profiles and a peak depth occupancy of around 10 m. *R. brachyura* and *R. montagui* were also similar, both being much deeper than the other 2, with *R. brachyura* having a mean depth occupancy of around 35 m and *R. montagui* around 45 m. Although the preferred depth for *R. microocellata* was relatively shallow, this species exhibited a slightly greater range of depth use than either *R. clavata* or *R. montagui*. Differences between the median values for the 2 groups were significant (p < 0.001, Kruskal-Wallis 1-way ANOVA on ranks).

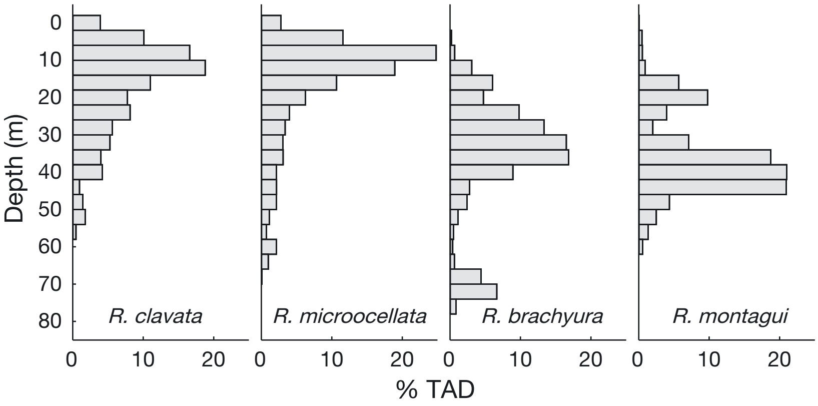

Fig. 2. Time at depth (TAD) profiles. Similarities between *Raja clavata* and *R. microocellata* and between *R. brachyura* and *R. montagui* are clear. For *R. brachyura*, n = 12; *R. clavata*, n = 43; *R. microocellata*, n = 24; *R. montagui*, n = 10

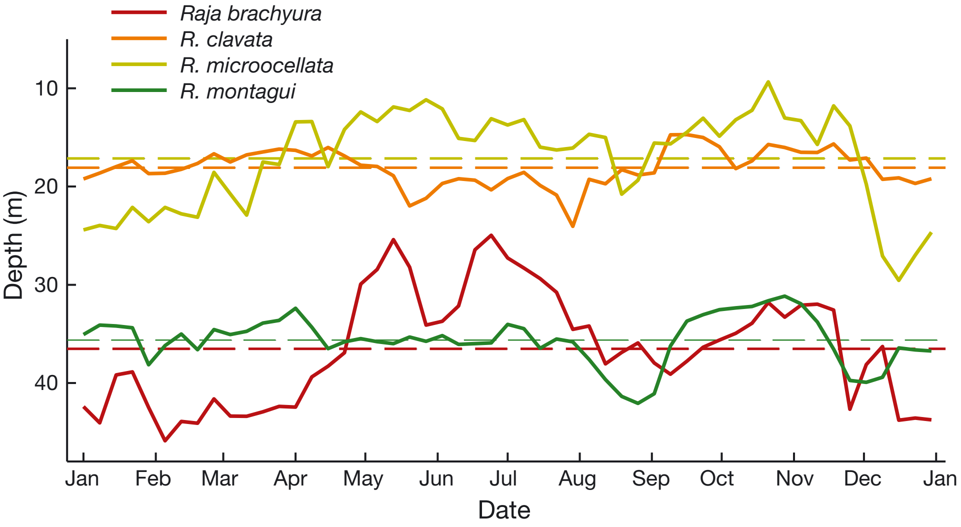

Fig. 3. Weekly mean depths computed from the depth time series. Dashed horizontal reference lines show the overall mean depth for each species, indicating a very clear separation into 2 pairs

## Weekly mean depths

A plot of weekly mean depths computed from all time-series for each species showed clear separation into the same 2 groups as the TAD profiles described above (Fig. 3). As each group comprises a 'pair' of species we will, for convenience, henceforth refer to these groups as species pairs; however, we are not implying any other connection or relationship between the species in each pair. Seasonal patterns were also evident within species pairs: *R. microocellata* changed depth to occupy shallower waters than *R. clavata* during the summer and autumn then deeper water in winter and spring. Of these 2 species, *R. microocellata* exhibited the greater range of mean depth, in agreement with the depth profiles shown in Fig. 2. A similar pattern was apparent between *R. brachyura* and *R. montagui*, with *R. brachyura* initially in deeper water until late April, when it moved to shallower waters for most of the summer. From September to December, *R. brachyura* and *R. montagui* shared similar depths and showed a similar movement to slightly shallower waters. Interestingly, the overall mean depths (indicated by the horizontal dashed lines in Fig. 3) were remarkably similar for each of the 2 pairs with clear separation between them: *R. clavata* and *R. microocellata* exhibited shallower occupancy, with mean depths of 18 and 17 m, while *R. brachyura* and *R. montagui* occupied deeper depths with mean values of 36.4 and 35.6 m.

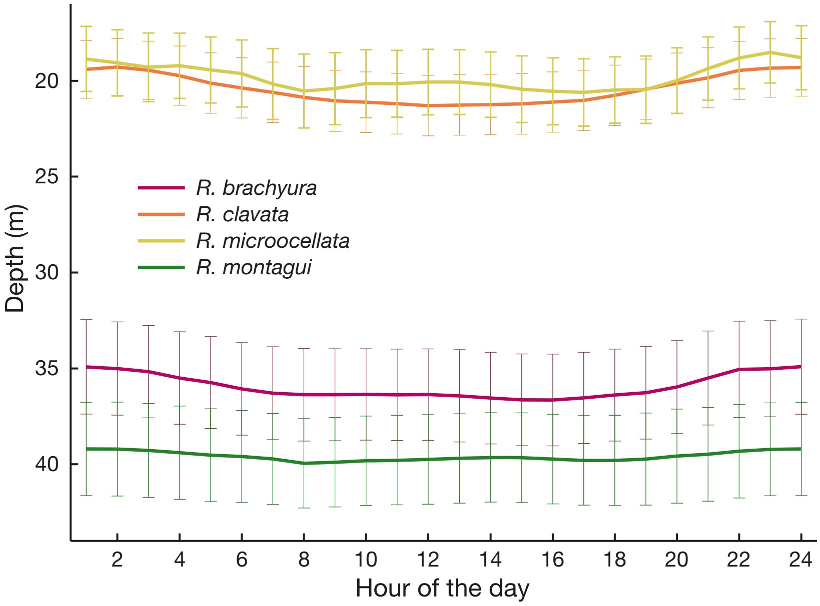

Fig. 4. Diel depth profiles using hourly depth bins for tagged *Raja brachyura*, *R. clavata*, *R. microocellata* and *R. montagui*. Error bars show ±SD

## Diel depth profiles

Diel depth profiles computed using hourly depth bins for each species (Fig. 4) showed very little difference in depths occupied and corresponded well to the mean depths computed from the weekly mean depths analysis. The error bars on this plot confirm the greater overlap between *R. clavata* and *R. microocellata* suggested in Fig. 3

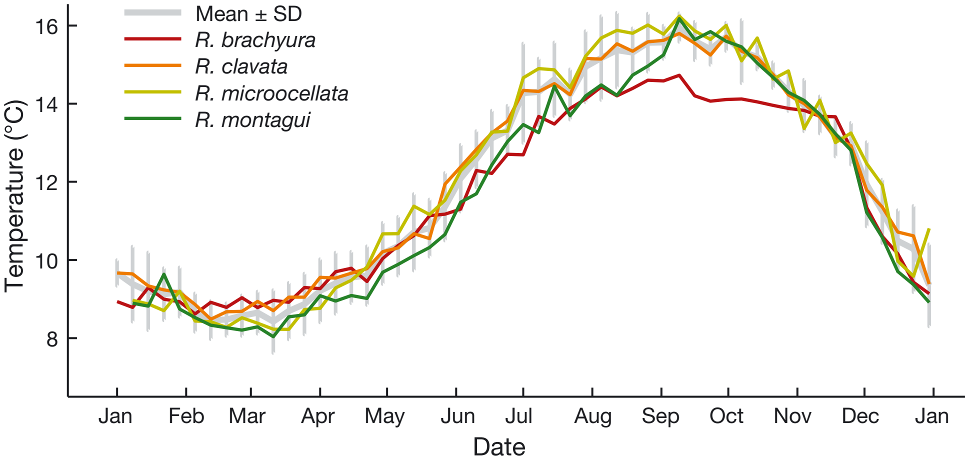

Fig. 5. Weekly mean temperatures for tagged *Raja brachyura*, *R. clavata*, *R. microocellata* and *R. montagui*. Unlike mean depths, weekly mean temperatures do not differ significantly between species

### Weekly mean temperatures

In contrast to the differences found in weekly mean depths, no significant differences were found in weekly mean temperatures (p = 0.484 Kruskal-Wallis 1-way ANOVA on ranks) in habitats occupied by skates, with temperatures for all species varying similarly with season (Fig. 5). The only species where the temperature departed noticeably from the overall mean was *R. brachyura* during August to November. The largest temperature difference between any pair of species was 1.97°C, whereas the largest mean seasonal range was considerably greater at 7.25°C.

### TAD matrix analysis

The contour plots produced from the TAD matrices illustrate the considerable range of depths occupied throughout the year (Fig. 6). However, despite this wide range, a narrow band of highest depth occupancy was apparent in all cases, suggesting a preferred depth range for each species. Comparison of the TAD matrices confirms similarities in core depth occupancy identified in the weekly mean depth analysis that suggest that the species form 2 species pairs with respect to depth occupancy, with the bands of highest occupancy corresponding well to the mean

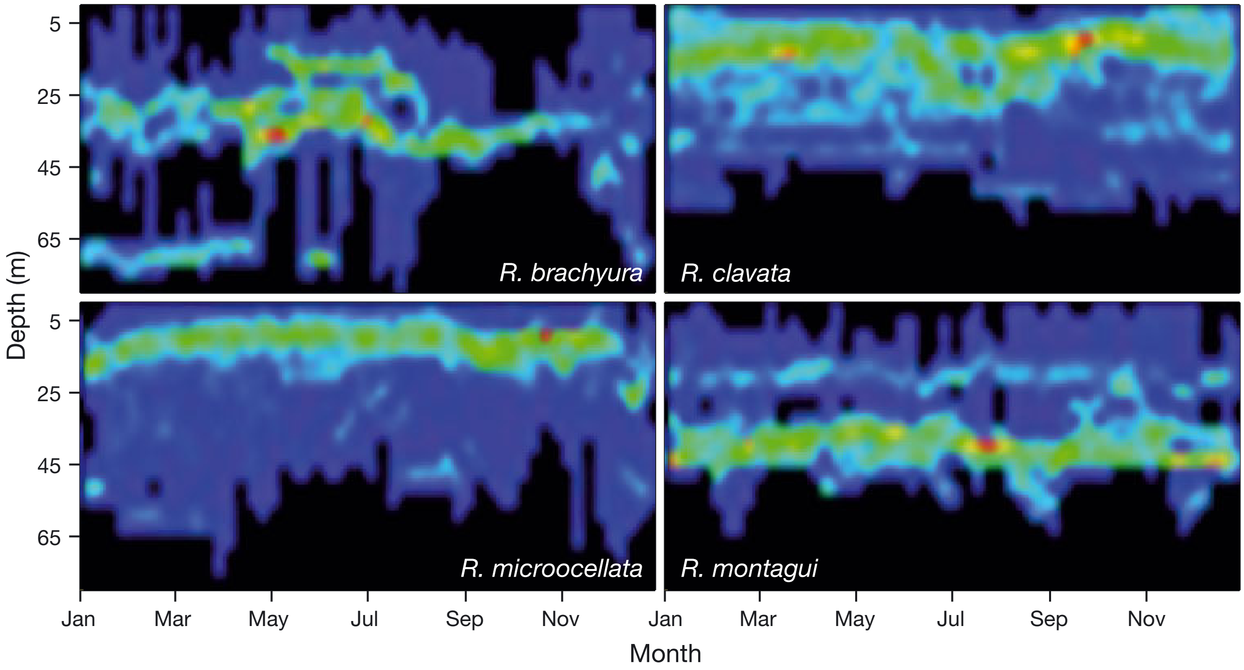

Fig. 6. Time at depth (TAD) plots for each of the 4 species. Warmer colours represent higher occupancy values. Similar core depth ranges are apparent for *Raja brachyura* and *R. montagui*, and for *R. clavata* and *R. microocellata*

values shown in Fig. 3. The considerable range of depth use suggests a high degree of within-species variability. Interestingly, despite having a consistently greater overall depth range, *R. microocellata* has the narrowest band of high occupancy, consistent with a stronger preference for the narrow depth range occupied.

The analysis showed clear hotspots of within-species shared occupancy for both *R. clavata* and *R. microocellata*, suggesting that in this data there are well-defined preferred depth ranges for both species between 5 and 20 m. There is some evidence of a seasonal shift for *R. clavata*, with deeper depths occupied during summer months; however, seasonal changes in core depth use are not evident for the other species. The deeper depths evident in the plot for *R. brachyura* resulted from the movements of just 3 individuals (A01846, A05950 and A05962). A01846 was in shallow water (7 to 27 m) from the start of the track in April, moved to deeper water (78 m) at the end of May and remained at that depth until the end of the 60 d track in mid-June. A05950 spent most of the 365 d track at depths of around 45 m but descended to around 74 m in December, returning to 45 m by the end of May. A05962 spent the majority of the 260 d track at around 40 m but performed a brief excursion (18 d) to much deeper water (maximum depth 129 m) at the end of July. Despite the variability between these individuals, the persistent core depth range is still clearly evident from the TAD plot.

Table 2. Statistical analysis of the overlap coefficient for tagged *Raja brachyura*, *R. clavata*, *R. microocellata* and *R. montagui*. Significant values in **bold**. ↓ indicates an overlap coefficient that is significantly less than expected by chance; ↑ indicates a value that is significantly greater

| | *R. clavata* | *R. microocellata* | *R. montagui* |
|---|---|---|---|
| *R. brachyura* | | | |
| Overlap coefficient | **0.26119** ↓ | **0.14104** ↓ | **0.41701** ↑ |
| Mean randomised coefficient | 0.31868 | 0.26438 | 0.29828 |
| p-value | 0.0016 | <0.0001 | 0.0001 |
| *R. clavata* | | | |
| Overlap coefficient | | **0.78546** ↑ | **0.27885** ↓ |
| Mean randomised coefficient | | 0.44463 | 0.43975 |
| p-value | | <0.0001 | <0.0001 |
| *R. microocellata* | | | |
| Overlap coefficient | | | **0.19325** ↓ |
| Mean randomised coefficient | | | 0.35803 |
| p-value | | | <0.0001 |

## Analysis of overlap coefficients

Overlap coefficients calculated between all pairs of species using the TAD matrices described in the above section further confirmed the putative grouping of the species into 2 pairs. *R. clavata* and *R. microocellata* had a coefficient of 0.785, representing more than 78% overlap in the TAD matrices. *R. brachyura* and *R. montagui* had the next highest measure of overlap (0.42), and *R. microocellata* and *R. montagui* had the lowest (0.14). Results of the statistical analysis are given in Table 2. In all cases the observed overlap (or separation) was found to be statistically significant.

The overlap coefficients for single columns (i.e. weeks) of the TAD matrices were computed for each pair of species to determine how the overlap in depth use changed throughout the year. These plots (Fig. 7) show peaks when shared depth use between a pair of species was high; for example, in Fig. 7a, shared occupancy between *R. brachyura* and *R. clavata* peaked during the summer months. Shared occupancy between *R. brachyura* and both *R. clavata* (Fig. 7a) and *R. microocellata* (Fig. 7b) was at a minimum during autumn, most likely reflecting the movement of *R. brachyura* into deeper water at this time. *R. brachyura* had, as expected, greater association with *R. montagui* (Fig. 7c) but with marked oscillatory peaks and troughs suggesting brief excursions into either deeper or shallower water by one or other of the pair. *R. clavata* clearly had a greater association with *R. microocellata* (Fig. 7d) throughout the year, apart from in late summer and winter, although even then the association was greater than many of the other pairs at any time. As expected from the analysis described above, *R. microocellata* showed generally very little overlap with *R. brachyura* or *R. montagui* (Fig. 7f). Seasonal trends were observed between *R. brachyura* and *R. clavata* (Fig. 7a) with a clear peak in summer and a low point in autumn. A similar but weaker pattern was evident between *R. brachyura* and *R. microocellata* (Fig. 7b).

## Using a mixed effect model to account for individual variation

Linear modelling showed Species to have a significant effect on mean depth ($\chi^2(3) = 47.755$, $p < 0.001$). The intercepts computed by the model, which are in

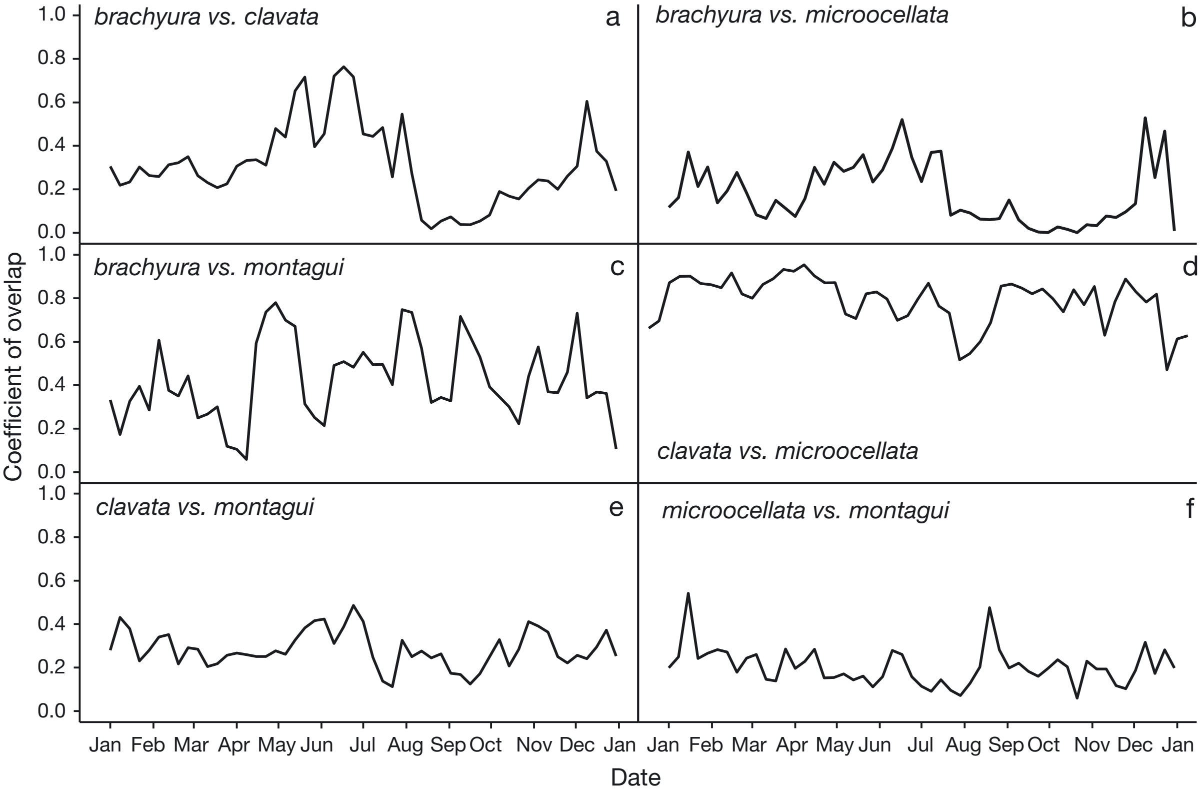

Fig. 7. Weekly paired overlap coefficients. Panels show the paired, weekly overlap coefficients for the 4 species, i.e. the 6 possible pairings of the 4 species: (a) *Raja brachyura* vs. *R. clavata*; (b) *R. brachyura* vs. *R. microocellata*; (c) *R. brachyura* vs. *R. montagui*; (d) *R. clavata* vs. *R. microocellata*; (e) *R. clavata* vs. *R. montagui*; (f) *R. microocellata* vs. *R. montagui*. While overlap is consistently low for *R. clavata* vs. *R. montagui* and *R. microocellata* vs. *R. montagui*, it is consistently high for *R. clavata* vs. *R. microocellata*. Spatial overlap for *R. brachyura* vs. both *R. clavata* and *R. montagui* shows more complex behaviour with seasonal differences reflecting inshore and offshore movements

relation to *R. brachyura* (the first species alphabetically), correspond well to the mean values computed in the weekly mean depth and diel depth profile analyses: mean depth was 15.57 and 16.24 m shallower for *R. clavata* and *R. microocellata*, respectively, and 3.8 m deeper for *R. montagui*. Week was seen to have a very small effect of only −0.046, suggesting that there is no simple linear relationship between the week and the mean depth, as suggested previously by the seasonal changes in weekly mean depth. Full results from the output are given in the Supplement ('Supplementary methods and results', Fig. S4).

## DISCUSSION

Habitat use and resource partitioning is poorly understood in temperate, benthic elasmobranchs, but is of considerable importance given the recent declines in some populations (Brander 1981, Casey & Myers 1998) and especially given the lack of global reduction in fishing pressure (Botsford et al. 1997, Worm & Branch 2012). Indeed globally, the number of skates and rays landed has been higher than landings of sharks since about 1975, suggesting skate populations may be at greater risk of overexploitation than in prior decades (Field et al. 2009, Dulvy et al. 2014). Previous research into species distributions and habitat preferences in the Rajidae is sparse and has relied principally on trawl data, either from fisheries (Serra-Pereira et al. 2014) or from fishery-independent surveys (Compagno et al. 1991, Dulvy et al. 2000, Hunter et al. 2005b, 2006, Compagno & Ebert 2007, Maravelias et al. 2012, Martin et al. 2012). Studies such as these are typically very large scale and lack information about fine-scale movements and behaviours which can significantly affect species interactions and distributions (Hussey et al. 2015a). It is known, for example, that *Raja clavata* in the eastern English Channel perform spawning migrations to estuarine environments (Hunter et al.

2005b, 2006), which differ from the habitat in which they are generally found. Ontogenetic differences in habitat use have also been identified in *R. clavata*, with younger individuals occurring in shallower areas over fine sand or mud, while older individuals are more widely dispersed and inhabit deeper waters (Martin et al. 2012). However, a study by Ellis et al. (2011) showed that, around Jersey (Channel Islands, UK), *R. clavata* show greater site fidelity than in other locations and, therefore, these animals seem to exhibit considerable behavioural plasticity. Thus it is likely that the complex movements and migrations of these animals could lead to fine-scale distributions, habitat preferences or segregations that have not been detected by trawl surveys or other large-scale studies.

We hypothesised that mechanisms for reducing competition for resources, such as those studied extensively in terrestrial ecosystems (e.g. Feinsinger 1976, Martin 1998, Brosius & Higley 2013) would also be found in benthic marine ecosystems. Consequently, it was expected that some form of fine-scale segregation would be identified in a group of congeneric and morphologically similar species living in apparent close coexistence, such as the 4 species of skate studied here. One of the most obvious strategies to reduce competition that these skates might exhibit is differential habitat occupancy. By occupying different habitats, animals have access to separate resources and can avoid contact with potential competitors.

Using a range of analysis methods, core depth occupancy ranges were identified for all species. The preferred ranges in depth occupancy were found to segregate the 4 species into 2 pairs: *R. clavata* and *R. microocellata* occupied shallower waters, while *R. brachyura* and *R. montagui* occupied deeper water throughout the year. The persistent and significant differences in depths occupied suggest preferences for specific depths for each species pair. This apparent segregation was supported by all the analyses performed, and in all cases, the differences were found to be clear and unambiguous.

Depth ranges for these species in the literature are typically very broad, reflecting the range of depths in which the animals have been found rather than depth preferences; however, there is broad agreement with our findings. For example, *R. microocellata* is reported as an inshore species rarely found at depths >100 m (Ellis et al. 2005a) and here is shown to have a depth range of 10 to 30 m and a mean depth of 17 m. *R. clavata* is considered to be most abundant at 10 to 60 m (Wheeler 1969), which agrees well with the range found here of 14 to 24 m. Both *R. brachyura* and *R. montagui* are considered to occur more deeply, with maximum depths of 150 and 283 m, respectively, in the north-east Atlantic (Ellis et al. 2005a), which although considerably deeper than the 45 and 42 m maximum depths observed here, still supports the opinion that these species occur in deeper water than the 2 other species.

It is particularly interesting that such clear segregation in depth preferences was identified in the present study because there are good reasons why it might not have been possible to detect depth segregation between these species. For example, if depth segregation is driven by competitive exclusion then, given recent population declines in most of these species including in the region where they were tracked (Genner et al. 2010), it is possible that current population densities are too low for sufficient inter-species competition. Under such conditions, interactions between individuals may be too rare to trigger avoidance behaviour, and consequently segregation might not be evident (Prenda et al. 1997). Alternatively, if partitioning is driven by physical habitat (i.e. substrate preference), then depth preferences will reflect the geographic distribution of preferred habitats (e.g. mud, sand or gravel). Given that the study area is a complex mosaic of seabed physical habitats with heterogeneous spatial distribution (see 'Natural habitat heterogeneity' in the Supplement at www.int-res.com/articles/suppl/m561p173_supp.pdf), segregation by depth would not be evident in the depth time series. Further, spatially complex habitats have been shown to support the coexistence of competitive species by allowing fine-scale spatial segregation (Boeye et al. 2014), consequently allowing shared occupation of similar depth ranges. Therefore, the segregation by depth observed here may more likely represent inherent species preferences.

Further evidence to support an inherent preference as the driver of segregation is that, in the sample of animals used in this study, no correlation was found between either the weight or the length and the maximum recorded depth, as would be expected if size were a factor in the observed depths (weight, $R^2$ = 0.001, p = 0.72; length $R^2$ = 0.005, p = 0.52; SigmaPlot linear regression [Systat Software]; see Figs. S5 & S6 in the Supplement). There is therefore no simple relationship between size and depth with perhaps larger animals being deeper and smaller animals being shallower. It seems likely, therefore, that the depth segregation observed here reflects actual preferred depth ranges in these species. In addition, it seems unlikely that temperature is a driver for the observed segregation, as the mean seasonal temperature range (7.25°C) is significantly greater than differences between the species (mean 1.97°C; 1-sample *t*-test, $p < 0.001$). It might be expected that a temperature difference would result simply from the different depths the species occupy. However, the study area comprises well-mixed coastal waters which do not exhibit the more general marked reduction of temperature with depth observed in other locations, such as well-stratified pelagic environments (Pingree & Griffiths 1978). The thermal mixing of the waters occupied by the skates tracked in this study is further illustrated in Fig. S7 in the Supplement, which shows mean temperatures computed from all individuals at a range of depths throughout the year and indicates no clear relationship between depth and temperature. For these animals, therefore, temperature would seem to be neither a driver nor a consequence of habitat preference.

The analysis of overlap coefficients again confirmed the segregation into 2 pairs and revealed seasonal changes in the extent of shared vertical occupancy. These changes suggest seasonal movements, for example the degree of overlap between *R. brachyura* and both *R. clavata* and *R. microocellata* diminished considerably in the autumn, whereas overlap between *R. montagui* and both *R. clavata* and *R. microocellata* was consistently low. These observations suggest that *R. brachyura* moves offshore during the latter part of the year, whereas both *R. clavata* and *R. microocellata* remain inshore. The continued low level of overlap between *R. montagui* and both *R. clavata* and *R. microocellata* suggests that *R. montagui* resides in deeper water throughout the year.

An interesting finding is that the species composition of each of the 2 pairs into which the species in this study are found to segregate are complementary. Firstly, while previous work has identified *Raja* spp. as generalist feeders, with considerable overlap in prey identified from stomach content analyses (Ellis et al. 1996, Farias et al. 2006), there are significant differences in the most important prey items for each species (Pinnegar 2014). For example, *R. brachyura* and *R. microocellata* have a similar dietary preference, with a slightly greater proportion of teleost prey (54 and 56% of the diet, respectively), while *R. clavata* and *R. montagui* are similar in having considerably more crustaceans in their diet (79 and 81%, respectively) (Ellis et al. 1996, Šantič et al. 2012, Pinnegar 2014). One species from each pair therefore has a greater preference for crustaceans in the diet (*R. clavata* and *R. montagui*), rather than fish. This represents further fine-scale segregation of resources beyond the occupancy of different depths initially explored here. The presence of species with differing diets at the 2 depths is further strong evidence that the segregation by depth is driven more by inherent depth preferences, as otherwise the patterns of segregation would be predicted to more closely match expected occupancy patterns of prey items. Secondly, each of the pairs contains a larger bodied species (*R. brachyura* and *R. clavata* have maximum recorded lengths of 1200 and 1050 mm, respectively, compared to *R. microocellata* and *R. montagui* with maximum lengths of 910 and 800 mm). Therefore, while the animals tracked in this study showed no clear relationship between size and depth, the maximum size differences between species might play a role in finer-scale resource partitioning.

The mechanism through which the pattern of habitat preference observed here was formed cannot be determined from this study, and many different processes might be involved (Wisheu 1998). It is not known, for example, whether the observed niches represent fundamental preferences or are the result of competitive interactions. Microhabitat characteristics of the study area are poorly understood at present, except for temperature, which has been shown to vary little. Consequently, there are no clear environmental drivers for the segregation at present. Further research into depth and habitat preferences of the other sympatric benthic mesopredators common in the region (e.g. plaice *Pleuronectes platessa*, turbot *Psetta maxima* or catshark *Scyliorhinus canicula*) is required to build a more complete picture of how the assemblage is structured and may have formed.

The current study relies on the depth record and cannot therefore provide the geographic location of the animals. It is possible that there is further geographic separation or coastal migration that could not have been detected by the analysis in the present study. While the location of the animals is not known, the core depth preferences can be used with local bathymetry to infer likely spatial extents. Fig. 8 shows spatial extents determined using the core mean depth ±1 SD. It is clear from these maps that the core depth preferences result in very different spatial extents and likely geographic segregation. Combining these predicted ranges with the boundaries of known or proposed MPAs or Marine Conservation Zones (MCZs) might help to give some indication of the extent to which these areas might offer protection from pressures such as fishing with mobile gear and how the different ranges might affect interactions with fisheries.

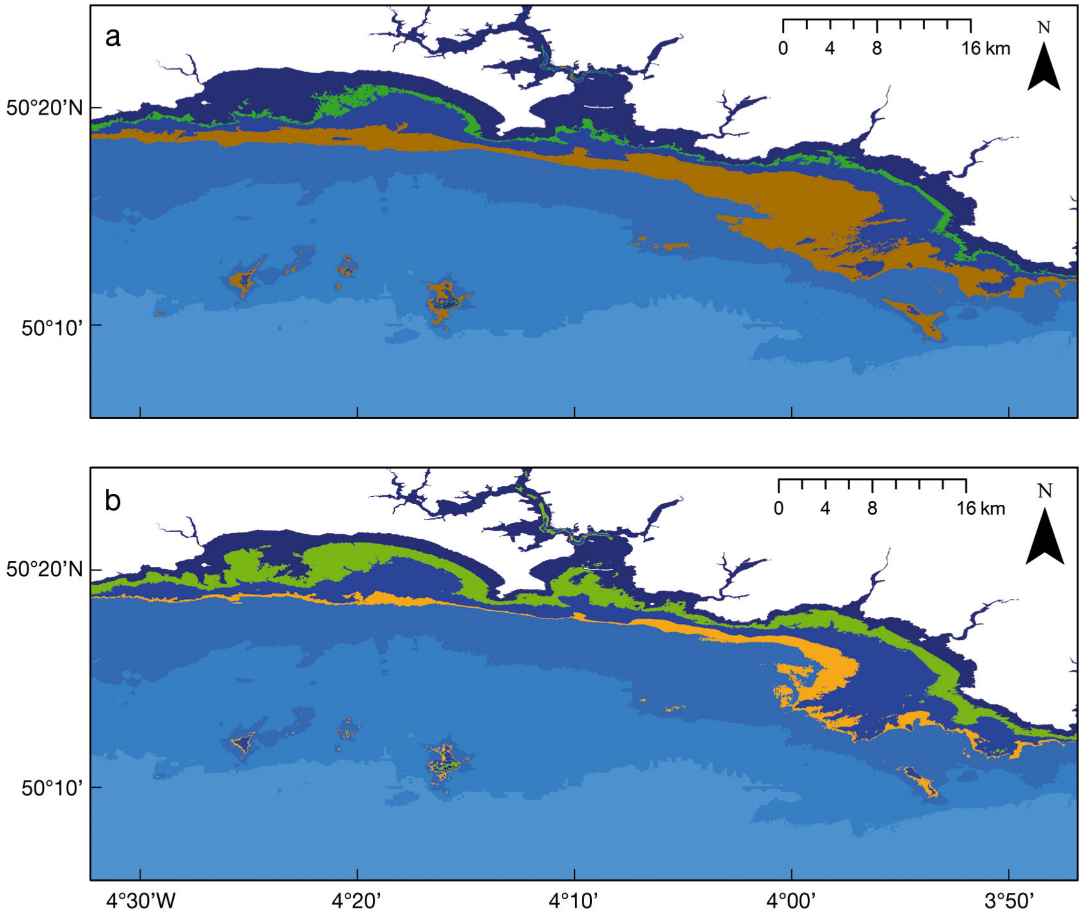

Fig. 8. Spatial extents determined from core depth preferences. (a) *Raja clavata* (dark green), *R. brachyura* (brown). (b) *R. microocellata* (light green), *R. montagui* (orange). Differences in core depth preferences result in clearly segregated core spatial extents, given the local bathymetry

In summary, while depth preferences indicate an interesting segregation into 2 pairs of species, with further separation by diet and size, the context of the segregation within the wider species assemblage cannot be understood without similar investigations into the other species common to the area. Studies into depth and habitat preferences of teleosts, such as flatfish (plaice *Pleuronectes platessa*, turbot *Psetta maxima*, common sole *Solea solea* L.) or other demersal elasmobranchs (catshark *Scyliorhinus canicula*), are needed to fully understand the patterns of habitat preference reported here.

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## LITERATURE CITED

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1–48

Bizzarro JJ, Broms KM, Logsdon MG, Ebert DA, Yoklavich MM, Kuhnz LA, Summers AP (2014) Spatial segregation in eastern North Pacific skate assemblages. PLOS ONE 9:e109907

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Boeye J, Kubisch A, Bonte D (2014) Habitat structure mediates spatial segregation and therefore coexistence. Landsc Ecol 29:593–604

Bolle LJ, Hunter E, Rijnsdorp AD, Pastoors MA, Metcalfe JD, Reynolds JD (2005) Do tagging experiments tell the truth? Using electronic tags to evaluate conventional tagging data. ICES J Mar Sci 62:236–246

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277: 509–515

Brander K (1981) Disappearance of common skate *Raja batis* from Irish Sea. Nature 290:48–49

Brosius TR, Higley LG (2013) Behavioral niche partitioning in a sympatric tiger beetle assemblage and implications for the endangered Salt Creek tiger beetle. PeerJ 1:e169

Cartamil DP, Vaudo JJ, Lowe CG, Wetherbee BM, Holland KN (2003) Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. Mar Biol 142:841–847

Casey JM, Myers RA (1998) Near extinction of a large, widely distributed fish. Science 281:690–692

Ceccarelli DM, Frisch AJ, Graham NAJ, Ayling AM, Beger M (2014) Habitat partitioning and vulnerability of sharks in the Great Barrier Reef Marine Park. Rev Fish Biol Fish 24:169–197

Chevolot M, Ellis JR, Hoarau G, Rijnsdorp AD, Stain WT, Olsen JL (2006a) Population structure of the thornback ray (*Raja clavata* L.) in British waters. J Sea Res 56: 305–316

Chevolot M, Hoarau G, Rijnsdorp AD, Stam WT, Olsen JL (2006b) Phylogeography and population structure of thornback rays (*Raja clavata* L., Rajidae). Mol Ecol 15: 3693–3705

Compagno LJV, Ebert DA (2007) Southern African skate biodiversity and distribution. Environ Biol Fishes 80: 125–145

Compagno LJV, Ebert DA, Cowley PD (1991) Distribution of offshore demersal cartilaginous fish (class Chondrichthyes) off the west-coast of southern Africa, with notes on their systematics. S Afr J Mar Sci 11:43–139

Dellinger RL, Wood PB, Keyser PD, Seidel G (2007) Habitat partitioning of four sympatric thrush species at three spatial scales on a managed forest in West Virginia. Auk 124:1425–1438

Dulvy NK, Metcalfe JD, Glanville J, Pawson MG, Reynolds JD (2000) Fishery stability, local extinctions, and shifts in community structure in skates. Conserv Biol 14:283–293

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. eLife 3:e00590

Ebert DA, Compagno LJV (2007) Biodiversity and systematics of skates (Chondrichthyes: Rajiformes: Rajoidei). Environ Biol Fishes 80:111–124

Eggleston DB, Herrnkind WE, Hines AH (2013) Behavioral ecology of mobile animals: insights from in situ observations. Smithson Contrib Mar Sci 39:99–114

Ellis JR, Pawson MG, Shackley SE (1996) The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. J Mar Biol Assoc UK 76:89–106

Ellis J, Dulvy NK, Jennings S, Parker-Humphreys M, Rogers SI (2005a) Assessing the status of demersal elasmobranchs in UK waters: a review. J Mar Biol Assoc UK 85: 1025–1047

Ellis JR, Cruz-Martinez A, Rackham BD, Rogers SI (2005b) The distribution of chondrichthyan fishes around the British Isles and implications for conservation. J Northwest Atl Fish Sci 35:195–213

Ellis JR, Morel G, Burt G, Bossy S (2011) Preliminary observations on the life history and movements of skates (Rajidae) around the Island of Jersey, western English Channel. J Mar Biol Assoc UK 91:1185–1192

Espinoza M, Munroe SEM, Clarke TM, Fisk AT, Wehrtmann IS (2015) Feeding ecology of common demersal elasmobranch species in the Pacific coast of Costa Rica inferred from stable isotope and stomach content analyses. J Exp Mar Biol Ecol 470:12–25

Farias I, Figueiredo I, Moura T, Gordo LS, Neves A, Serra-Pereira B (2006) Diet comparison of four ray species (*Raja clavata*, *Raja brachyura*, *Raja montagui* and *Leucoraja naevus*) caught along the Portuguese continental shelf. Aquat Living Resour 19:105–114

Feinsinger P (1976) Organization of a tropical guild of nectarivorous birds. Ecol Monogr 46:257–291

Field IC, Meekan MG, Buckworth RC, Bradshaw CJA (2009) Susceptibility of sharks, rays and chimaeras to global extinction. Adv Mar Biol 56:275–363

Frisk MG, Jordaan A, Miller TJ (2014) Moving beyond the current paradigm in marine population connectivity: Are adults the missing link? Fish Fish 15:242–254

Genner MJ, Sims DW, Southward AJ, Budd GC and others (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. Glob Change Biol 16:517–527

Gotelli NJ, Ellison AM (2013) EcoSimR 1.00. www.uvm.edu/~ngotelli/EcoSim/EcoSim.html

Gouraguine A, Hidalgo M, Moranta J, Bailey DM and others (2011) Elasmobranch spatial segregation in the western Mediterranean. Sci Mar 75:653–664

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297

Hayward MW, Kerley GIH (2008) Prey preferences and dietary overlap amongst Africa's large predators. S Afr J Wildl Res 38:93–108

Hobson VJ, Righton D, Metcalfe JD, Hays GC (2007) Vertical movements of North Sea cod. Mar Ecol Prog Ser 347: 101–110

Horn HS (1966) Measurements of 'overlap' in comparative ecological studies. Am Nat 100:419–424

Humphries NE, Queiroz N, Dyer JRM, Pade NG and others (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465: 1066–1069

Hunter E, Blickley AA, Stewart C, Metcalf JD (2005a) Repeated seasonal migration by a thornback ray in the southern North Sea. J Mar Biol Assoc UK 85:1199–1200

Hunter E, Buckley AA, Stewart C, Metcalfe JD (2005b) Migratory behaviour of the thornback ray *Raja clavata*, in the southern North Sea. J Mar Biol Assoc UK 85: 1095–1105

Hunter E, Berry F, Buckley AA, Stewart C, Metcalfe JD (2006) Seasonal migration of thornback rays and implications for closure management. J Appl Ecol 43:710–720

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ and others (2015a) Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642

Hussey NE, MacNeil MA, Siple MC, Popp BN, Dudley SFJ, Fisk AT (2015b) Expanded trophic complexity among large sharks. Food Webs 4:1–7

Kaiser MJ (2005) Are marine protected areas a red herring or fisheries panacea? Can J Fish Aquat Sci 62:1194–1199

Legare B, Kneebone J, DeAngelis B, Skomal G (2015) The spatiotemporal dynamics of habitat use by blacktip (*Carcharhinus limbatus*) and lemon (*Negaprion brevirostris*) sharks in nurseries of St. John, United States Virgin Islands. Mar Biol 162:699–716

Lopez-Lopez L, Preciado I, Velasco F, Olaso I, Gutierrez-Zabala JL (2011) Resource partitioning amongst five coexisting species of gurnards (Scorpaeniforme: Triglidae): role of trophic and habitat segregation. J Sea Res 66:58–68

Mackas DL, Sefton H, Miller CB, Raich A (1993) Vertical habitat partitioning by large calanoid copepods in the oceanic sub-arctic pacific during spring. Prog Oceanogr 32:259–294

Malavasi S, Franco A, Riccato F, Valerio C, Torricelli P, Franzoi P (2007) Habitat selection and spatial segregation in three pipefish species. Estuar Coast Shelf Sci 75:143–150

Maravelias CD, Tserpes G, Pantazi M, Peristeraki P (2012) Habitat selection and temporal abundance fluctuations of demersal cartilaginous species in the Aegean Sea (eastern Mediterranean). PLOS ONE 7:e35474

Martin TE (1998) Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656–670

Martin CS, Vaz S, Ellis JR, Lauria V, Coppin F, Carpentier A (2012) Modelled distributions of ten demersal elasmobranchs of the eastern English Channel in relation to the environment. J Exp Mar Biol Ecol 418–419:91–103

McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR (2015) Marine defaunation: animal loss in the global ocean. Science 347:1255641

McEachran JD, Dunn KA (1998) Phylogenetic analysis of skates, a morphologically conservative clade of elasmobranchs (Chondrichthyes: Rajidae). Copeia 271–290

Owen-Smith N, Mills MGL (2008) Predator-prey size relationships in an African large-mammal food web. J Anim Ecol 77:173–183

Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Mar Ecol Prog Ser 320:239–251

Pingree RD, Griffiths DK (1978) Tidal fronts on the shelf seas around the British Isles. J Geophys Res 83:4615–4622

Pinnegar JK (2014) DAPSTOM — an integrated database & portal for fish stomach records. Version 4.7. Centre for Environment, Fisheries & Aquaculture Science, Lowestoft

Platell ME, Potter IC, Clarke KR (1998) Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. Mar Biol 131:719–734

Prenda J, Armitage PD, Grayston A (1997) Habitat use by the fish assemblages of two chalk streams. J Fish Biol 51:64–79

Queiroz N, Humphries NE, Mucientes G, Hammerschlag N and others (2016) Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. Proc Natl Acad Sci USA 113:1582–1587

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES J Mar Sci 55:403–419

Šantič M, Rađa B, Pallaoro A (2012) Diet and feeding strategy of thornback ray *Raja clavata*. J Fish Biol 81:1070–1084

Serra-Pereira B, Erzini K, Maia C, Figueiredo I (2014) Identification of potential essential fish habitats for skates based on fishers' knowledge. Environ Manag 53:985–998

Sims DW, Southall EJ, Humphries NE, Hays GC and others (2008) Scaling laws of marine predator search behaviour. Nature 451:1098–1102

Speed CW, Field IC, Meekan MG, Bradshaw CJA (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408:275–293

Speed CW, Meekan MG, Field IC, McMahon CR and others (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. Mar Ecol Prog Ser 429:261–275

Speed CW, Meekan MG, Field IC, McMahon CR, Abrantes K, Bradshaw CJA (2012) Trophic ecology of reef sharks determined using stable isotopes and telemetry. Coral Reefs 31:357–367

Thurstan RH, Brockington S, Roberts CM (2010) The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat Commun 1:15

Valls M, Quetglas A, Ordines F, Moranta J (2011) Feeding ecology of demersal elasmobranchs from the shelf and slope off the Balearic Sea (western Mediterranean). Sci Mar 75:633–639

van der Molen J, Rogers SI, Ellis JR, Fox CJ, McCloghrie P (2007) Dispersal patterns of the eggs and larvae of spring-spawning fish in the Irish Sea, UK. J Sea Res 58:313–330

Vitt LJ, Zani PA (1996) Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. Can J Zool 74:1313–1335

Wearmouth VJ, Sims DW (2009) Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. J Exp Mar Biol Ecol 380:77–87

Wheeler A (1969) The fishes of the British Isles and northwest Europe. Macmillan, London

Winter B (2013) Linear models and linear mixed effects models in R with linguistic applications. arXiv: 1308.5499. http://arxiv.org/pdf/1308.5499.pdf

Wisheu IC (1998) How organisms partition habitats: different types of community organization can produce identical patterns. Oikos 83:246–258

Worm B, Branch TA (2012) The future of fish. Trends Ecol Evol 27:594–599

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