FEATURE ARTICLE

Implications of using different metrics for niche analysis in ecological communities

Adam Gouraguine[1],*, Carlos J. Melián[2], Olga Reñones[3], Hilmar Hinz[4],
Heather Baxter[5], Luis Cardona[6], Joan Moranta[3]

[1]School of Biological Sciences, University of Essex, Colchester CO4 3SQ, UK

[2]Department of Fish Ecology and Evolution, Center for Ecology, Evolution and Biogeochemistry,
Swiss Federal Institute of Aquatic Science and Technology, 6047 Kastanienbaum, Switzerland

[3]Instituto Español de Oceanografía (IEO), Centre Oceanogràfic de les Balears, Ecosystem Oceanography Group (GRECO),
Moll de Ponent sn, 07015 Palma, Spain

[4]Department of Ecology and Marine Resources, Instituto Mediterráneo de Estudios Avanzados IMEDEA (CSIC-UIB),
07190 Esporles, Spain

[5]School of Geographical and Earth Sciences, University of Glasgow, Glasgow G12 8QQ, UK

[6]IRBio and Department of Evolutionary Biology, Ecology and Environmental Science, Faculty of Biology,
University of Barcelona, 08007 Barcelona, Spain

ABSTRACT: Explaining the mechanisms driving niche partitioning among species is of great importance in ecology. Unlike the fundamental niche, a species' realised niche can only be measured *in situ*, as a result of biotic and abiotic interactions defining its size. Following current methodology, the realised niche of a species is often influenced by the rare and divergent individuals of the community sampled. In this study, using fish on coral and temperate reefs as an example, behavioural empirical data were collected to estimate realised niche sizes and niche overlaps. Niche measurements were made using the total area of the convex hull (TA), but as an alternative, a metric not as strongly influenced by sample size, standard ellipse area (SEA), was also used. A comprehensive description is given, and context-dependent pros and cons of using both metrics are discussed. Additionally, an alternative sample size correction was presented for both metrics. The analyses revealed large differences in the sizes of realised niches and their overlaps between species depending on the measurement metric used. Regardless of the species, niche size and overlap were always larger for TA than SEA. Increasing sample size reduced niche size variability for both TA and SEA, but the variation was always smaller for SEA than TA. We successfully adapted the SEA metric for analysis of behavioural niche components and demonstrated that measuring niche sizes using the 2 metrics, each with their own strengths and weaknesses, can produce contradictory results, the ecological consequences of which are likely to be important.

Two fish species from the temperate reef community studied, East Atlantic peacock wrasse *Symphodus tinca* (foreground) and common two-banded seabream *Diplodus vulgaris* (background).

Photo: Adam Gouraguine

KEY WORDS: Realised niche · Niche variability · Standard ellipse area · Total area of the convex hull · Algal reefs · Coral reefs · Teleostei

1. INTRODUCTION

A species' niche can be described as an *n*-dimensional hyperspace, partitioned into environmental and trophic (resource) components representing the

*Corresponding author: adg31@aber.ac.uk

ecosystem (Hutchinson 1957). The fundamental niche is defined as the space a species occupies resulting from the combination of physiological and behavioural characteristics in the absence of intra- and inter-specific competition, when a species potentially occupies the space along all the axes of the ecosystem (Connell 1961, Begon et al. 2006). The presence of dominant competitors and predation pressure along the ecosystem axes prevents the species from fully exploiting the entire ecosystem, so the constrained space actually occupied by the species under these effects represents the realised niche (hereafter, RN) (Hutchinson 1957, Whittaker et al. 1973, Devictor et al. 2010). To measure any dimension of the RN, an interaction of the specific acting agents must be considered. Accordingly, RNs can only be assessed using data collected *in situ*, where restricting agents are operating. Unfortunately, there is a notable lack of empirical studies encompassing field measurements to determine species' RNs across communities (Hooper et al. 2005, Tingley et al. 2014).

Furthermore, despite the existence of several similar metrics, one of the common problems in the analysis of a RN is the calculation of its volume and amount of overlap between different species. Currently, RN is most commonly calculated as the total area of the convex hull (TA), where measurements tend to be characterised by the individuals with the most extreme positions within the sample (Jackson et al. 2011). The niche sizes obtained using this method are generally influenced by a small number of divergent individuals within the population, and thus measuring the TA takes into consideration intraspecific variability. More recently, a different metric based on the measurement of the standard ellipse area (SEA) has been proposed. To date, the SEA metric has only been discussed for calculations of isotopic niche overlaps (Jackson et al. 2011, Syväranta et al. 2013) but it could also be used for analysis of other components of the niche, to provide ecologically relevant information about the individual, population or community (Bearhop et al. 2004). The use of SEA has been proposed mainly because it is not as strongly influenced by sample size as the TA method. The SEA represents the mean niche values of the community in question (Jackson et al. 2011). This method does not emphasise the importance of within-species individual variability and likely represents the niche space delimited by the most frequent traits characterising the individuals sampled. As such, the SEA niche measurement method represents the niche of the majority of the individuals within the population, but not the divergent individuals.

In this study, using continuously recorded behavioural data, estimates were made of RN sizes and niche overlaps between the TA and SEA metrics for several abundant fish species with different life histories occurring in 2 distinct systems. Continuous observation allows for identification of behaviours of interest and associated habitats, followed by quantification and comparison of behaviour expression and habitat use. Consequently, multiple functional traits, rather than a single trait (e.g. diet), can be considered to determine species' niches and their overlaps (Bellwood et al. 2004, Adam et al. 2015a). Using multiple functional traits allows for better estimates of complementarity and redundancy between species, as it is possible that species that appear to be functionally redundant based on a single trait can exhibit different levels of complementarity or redundancy when multiple functional traits are considered (Cadotte et al. 2011, Adam et al. 2015b). Further, use of abundant and life-history-diverse species aids in better representation of the assemblage (numerically and behaviourally), while sampling distinct systems allows for subsequent observation of common patterns across systems. Accordingly, niche overlaps were compared by measuring the TA of each species, but as an alternative, a metric based on SEA was also used. An attempt was made to give a comprehensive comparison of measurement-method-dependent differences in RN sizes, highlighting the importance of previously unknown properties of different metrics for RN measurements, and demonstrating how past and future findings could be altered. To address the issue of adequate sample sizes commonly encountered in ecological studies, an alternative sample size correction was presented for both metrics, the pros and cons of both were discussed and recommendations for their future use in ecological studies were made.

2. MATERIALS AND METHODS

Field-based observations were conducted to measure RNs and their overlaps for several fish species on tropical coral- and temperate algal-dominated rocky reefs.

2.1. Sampling habitats and fish behaviours

Sampling took place on the coral reefs around Curieuse Island of the Seychelles in the Indian Ocean and on the algal-covered rocky reefs off the western coast of Mallorca Island in the Mediterranean Sea, in

April and June of 2015, respectively (Fig. 1). In both locations, 8 different sites were sampled, each separated by a minimum distance of 500 m.

On the coral reefs, data collection was conducted between 1 and 12.5 m depth, while on the algal-covered rocky reefs the sampling depth was between 1 and 15 m. At each site the fish community and habitat composition were initially assessed by underwater visual census (Harmelin-Vivien et al. 1985, English et al. 1997). The fish assemblage abundance and species richness were assessed in 3 replicates of 30 × 5 m transects with a horizontal gap between each transect of at least 20 m. The continuous line intercept transect technique was used to assess the benthic community along the 30 m transects (English et al. 1997). The area intercepting the transect tape was classified according to the benthic category, and the percentage cover of each category was then calculated by dividing by the total transect length and multiplying by 100. The cover was estimated for the same number of benthic categories in each location: algae, branching, massive and dead coral, rock, rub-

ble and sand for the Seychelles and *Posidonia oceanica*, erect, filamentous and turf algae, rock, rubble and sand for Mallorca.

Based on the data from the visual censuses, the most abundant families were subsequently identified. To represent a large (numerical abundance) and a diverse part of the assemblage (varied resource and habitat use), the most commonly occurring species within the families from different feeding guilds were sampled.

The following coral reef species were sampled in the Indian Ocean: *Pomacentrus caeruleus*: planktivore (47 individuals), *Ctenochaetus striatus*: herbivore (41 individuals), *Hemigymnus melapterus*: macroinvertebrate feeder (40 individuals) and *Chaetodon trifasciatus*: coralivore (49 individuals). In the Mediterranean, *Symphodus tinca*: macro-invertebrate feeder (82 individuals), *Coris julis*: micro-invertebrate feeder (82 individuals), *Sarpa salpa*: herbivore (81 individuals) and *Diplodus vulgaris*: macro-invertebrate feeder (82 individuals) were sampled (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m630p001_supp.pdf). All observations were carried
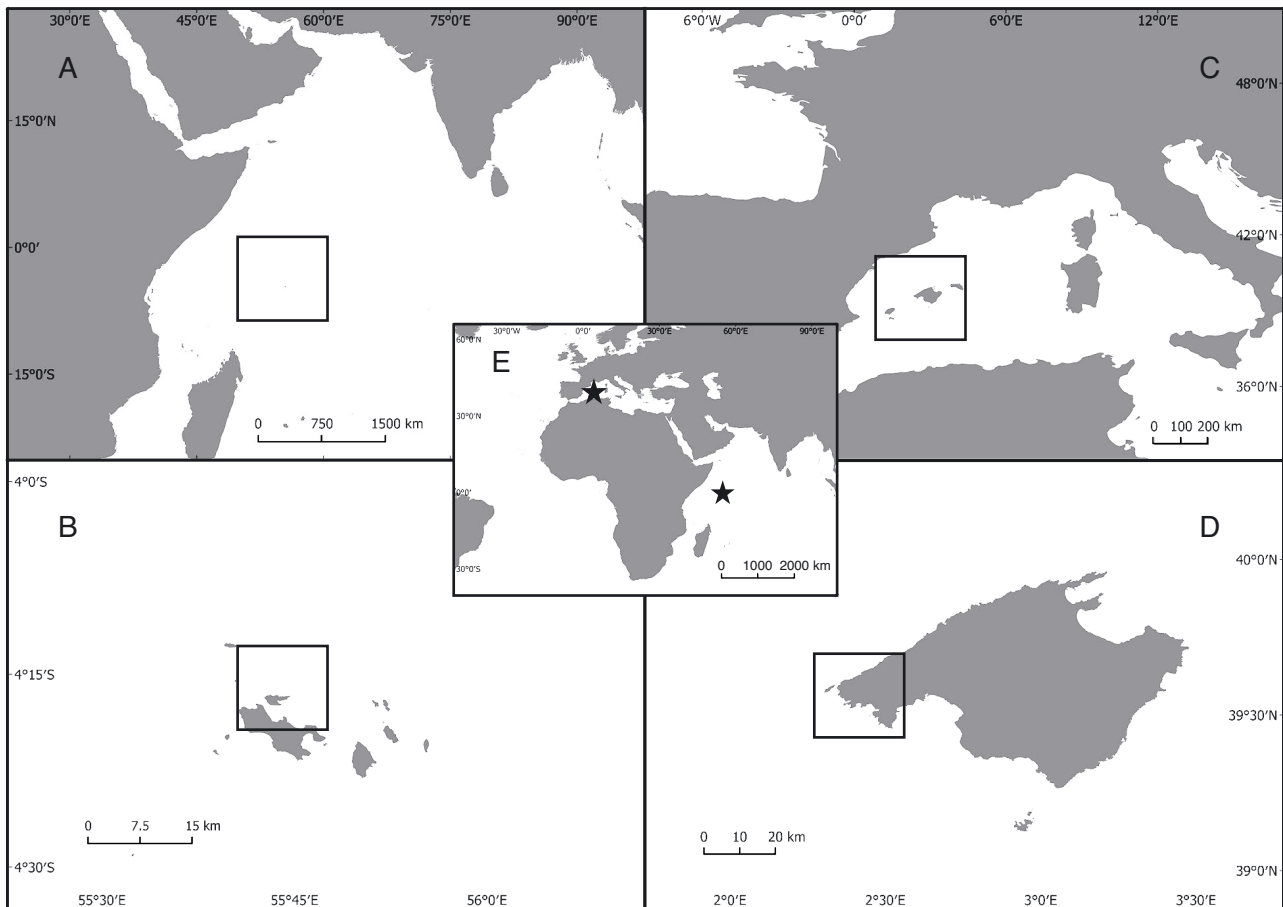

Fig. 1. Sampling locations: (A) The Seychelles, (B) Curieuse and Praslin islands' sampling area, (C) western Mediterranean, (D) western coast of Mallorca sampling area and (E) both sampling locations on the same map

out on adult individuals with full adult markings and of an adult size. If the fish exhibited a detectable response to the observer by altering its behaviour (e.g. escaping or hiding from, or being attracted to the observer), the data were discarded.

The optimum sampling time was determined by initial, continuous, 30 min observations of 4 individuals of each species. The total number of behaviours the individual demonstrated during this period was recorded in order to subsequently plot the cumulative number of observed behaviours by time and species (Lehner 1979). The total observation time was broken down into accumulating 5 min periods (Martin & Bateson 1993). Subsequently, the optimum observation time was determined by identifying the 5 min period in which ≥80% of all behaviour types were displayed, and beyond which few new behaviours were seen for each additional unit of time spent observing.

A randomly selected individual of the study species was followed underwater and all its behaviours were continuously recorded. By using the continuous recording sampling method, it was possible to document a complete account of all behaviour units of interest: occurrence, duration and sequences of events (Lehner 1979). A catalogue of observed behaviours was made and each behaviour was assigned a short abbreviation in order to make recording the data easier (Brockmann 1994). The following behaviours were identified: intraspecific (a) and interspecific aggression (b), advertising (ad), cleaning (c), diffused feeding (df), focused feeding (ff), water column feeding (wc), hovering (h), searching (s), roaming (rm) and rubbing (rb) (Table S1) (Curtis-Quick 2013). In addition, the duration (in s) of each behaviour expressed was measured. Finally, the microhabitat in which each of the behaviours occurred was characterised and recorded. The microhabitat was assigned a surface orientation (A: open horizontal; B: open vertical; C: underside or D: concealed) (Fig. S1) and a substratum type (Table S1). Except for the dead coral category found only on the coral reef sites, the abiotic substrata (r: rock; rub: rubble; s: sand) were the same in both locations. The biotic substrata types included macro-algae (alg) and 2 broad coral categories: branching (b) and massive (m) for the Indian Ocean coral reefs and seagrass (p) and algal morphotypes (et: erect; fl: filamentous; tf: turf) for the Mediterranean algal-covered rocky reefs.

2.2. TA and SEA

To assess the RN of species, a multidimensional niche space can be created using the behavioural ob-

servations collected from individuals (Brandl & Bellwood 2014). The time each behaviour was expressed during the sampling period, as well as the surface position and substratum type were recorded. Subsequently, a data matrix was created with the top row containing labels of all possible combinations of the behaviour, surface position and substratum type, and the main column containing individual fish IDs. The matrix was then populated with each individual's total time contribution to the corresponding combinations of behaviour, surface position and substratum type observed during the sampling period.

A principal component analysis (PCA) was performed on the data from the matrix using the 'PrCoord' program in CANOCO v.4.56 (ter Braak & Smilauer 2002). PCA can be used to represent patterns from pairwise distance measures, and is designed to function with multiple distance metrics (Brandl & Bellwood 2014). The data were imported into PrCoord, $\log(y + 1)$ transformed, with Euclidian distance used as the distance measure in the calculation. As a result, a data file containing sample coordinates on all PCA axes with positive eigenvalues was created. Based on the relative importance of the time for each of the combinations in the initial data set, the eigenvalues of the PCA analysis represented the position of the individuals in the multidimensional space from which individual coordinates were extracted (Laliberté & Legendre 2010). Using these individual coordinates, species' niche sizes were calculated, encompassing all individuals of a species within a given habitat (Brandl & Bellwood 2014).

To calculate the species' RNs and the niche overlaps between species (termed the RN overlap, representing redundancy or complementarity), 2 different metrics were used: the TA and the SEA. The TA is delimited by the individuals within the species of a given sample with the most extreme positions (Jackson et al. 2011). The SEA, describing some data x and y, is underpinned by its associated covariance matrix:

$$\left(\Sigma \begin{bmatrix} \sigma_x^2 & \text{cov}(y, x) \\ \text{cov}(y, x) & \sigma_y^2 \end{bmatrix} \right)$$

which defines its shape and size, and the means of the x and y that define its location. The eigenvalues (λ) and eigenvectors (v) of Σ then give the lengths of the semi-major axis $a = \lambda_1^{-1}$ and the semi-minor axis $b = \lambda_2^{-1}$, and the angle of the a with the x-axis $\theta = \sin^{-1}(v_{12})$. The SEA is then given by πab, and can be plotted as such.

To display the PCA results, the file produced by PrCoord was used as the species data file in the

CANOCO PCA method, with scaling of scores focussed on inter-sample distance, no post-transformation of species scores and centering by species only. The output with the values for PC axes 1 and 2 was subsequently used to carry out several tasks: plot TAs and SEAs for each species individually, calculate the overlap between the TAs of the species, calculate the overlap between the SEAs of the species and compare the differences in the percentage overlaps between the TAs and SEAs for each species. These tasks were all performed in R software (R Development Core Team 2015) using the package stable isotope analysis in R (SIAR) (Parnell et al. 2010).

2.3. Sample size dependency

The dependency of TA and SEA on sample size was tested. Despite saturation in the number of behaviours observed over time (Figs. S2 & S3), different sample sizes can change the distribution of time spent exhibiting each behaviour. To account for this, and thus investigate the possible change in the values of TA and SEA of each species depending on the number of individuals sampled, 1000 resamplings for each sample size ranging from 10–90 individuals were simulated by adding Poisson noise to the behavioural time series. For each empirical sampling, the average number of behaviours was calculated

and the probability of obtaining 1, 2, 3, 4, … k behaviours for each individual was estimated. Subsequently, the time spent in each behaviour was randomly distributed, accounting for the distribution of time in each behaviour observed in the empirical sampling. All simulations were performed in Octave software version 4.2.0 (Eaton et al. 2017).

3. RESULTS

3.1. Fish behaviour

Overall, 2651 behavioural observations were recorded for the 177 individuals sampled in the Indian Ocean, while 9815 behavioural observations were made for the 327 individuals sampled in the Mediterranean. Total sampling time was approximately 144 h; 6 h site^{-1} in the Seychelles and 12 h site^{-1} in Mallorca. The numbers of individuals sampled were evenly distributed in each location for all species studied (Table S2).

The observational data for all species sampled in the Seychelles demonstrated a preference for horizontal open space; 3 out of 4 species also spent a proportion of time associated with open vertical areas, which, in the case of *Chaetodon trifasciatus*, was the highest at 23% (Fig. 2). *Pomacentrus caruleus* spent the most time concealed (12%), but their behaviour
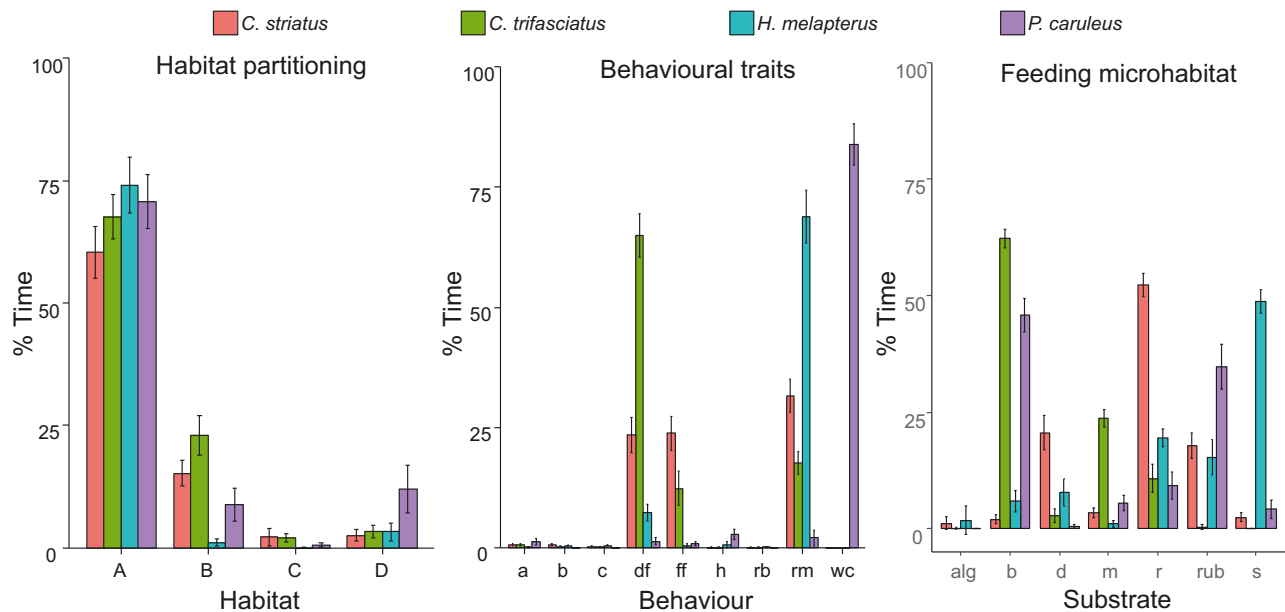

Fig. 2. Graphic representation of the time spent for each species in the Seychelles according to habitat partitioning patterns (A: open horizontal; B: open vertical; C: underside; D: concealed), behavioural traits (a: intraspecific aggression; b: interspecific aggression; c: cleaning; df: diffused feeding; ff: focussed feeding; h: hovering; rb: rubbing; rm: roaming; wc: water column feeding) and feeding habitat preferences (alg: algal; b: branching; d: dead; m: massive coral morphotypes; r: rock; rub: rubble; s: sand). Error bars: ±SE

was mainly concentrated feeding in the water column (83.9%). The behaviours of *Hemigymnus melapterus* mainly involved roaming (68.9%); and for *C. trifasciatus*, diffused feeding (65%). The latter species also demonstrated roaming and focussed feeding behaviours. *Ctenochaetus striatus* divided their time among roaming (31.7%) and focussed (23.8%) and diffused feeding (23.3%). For the feeding locations, *C. striatus* demonstrated a preference for rock, dead coral and rubble (52.3, 20.6 and 17.8%, respectively). *C. trifasciatus* fed mainly within branching (62.2%) and massive coral (23.6%), while *H. melapterus* spent most of the time feeding within the sand habitat (48.7%). The water-column feeding of *P. caruleus* occurred mainly over branching coral (45.8%) and rubble substrates (34.7%).

In Mallorca, the observational data across all species revealed a majority preference for horizontal open space, which, in the case of *Sarpa salpa*, was as high as 89.7% of the total observational time (Fig. 3). The remaining 3 species demonstrated a small preference for open vertical areas, spending on average 20% of their total time in this surface type. The dominant behaviour for all 4 species was roaming. *Diplodus vulgaris* demonstrated hovering (17.1%), a behavioural characteristic that was unique to this species, as well as searching (13.3%), which was also demonstrated by *Coris julis* (29.5%). With regards to the feeding modes, *S. salpa* was the only

species to spend more time focussed (23.2%) rather than diffused feeding (10.1%). For the feeding microhabitats, turf and erect tree-like algal morphotypes were the preferential morphotypes chosen by all species. *D. vulgaris* (21.2%) and to some extent *C. julis* (17%) also demonstrated feeding within the filamentous algae morphotype. While no other species spent any notable time feeding within *Posidonia* beds, *S. salpa* spent 31.4% of the total feeding time within this habitat. All species required two 5 min periods to express ≥80% of all the behaviour types, thus each individual's behaviour was recorded for 10 min (Figs. S1 & S2).

3.2. TA and SEA

Clear differences in the size of the RN surface areas were observed between TA and SEA for all species, both in the Seychelles and at Mallorca (Table S3). Subsequently, the degree of RN overlap between species also revealed great differences in the amount of overlap depending on whether it was considered for TA or SEA.

For the Seychelles species, the highest degree of RN overlap was observed between *H. melapterus* and *C. striatus* (Fig. 4, Table 1); these species also exhibited a very small TA RN overlap with *C. trifasciatus*, but neither overlapped with *P. caruleus*. Con-
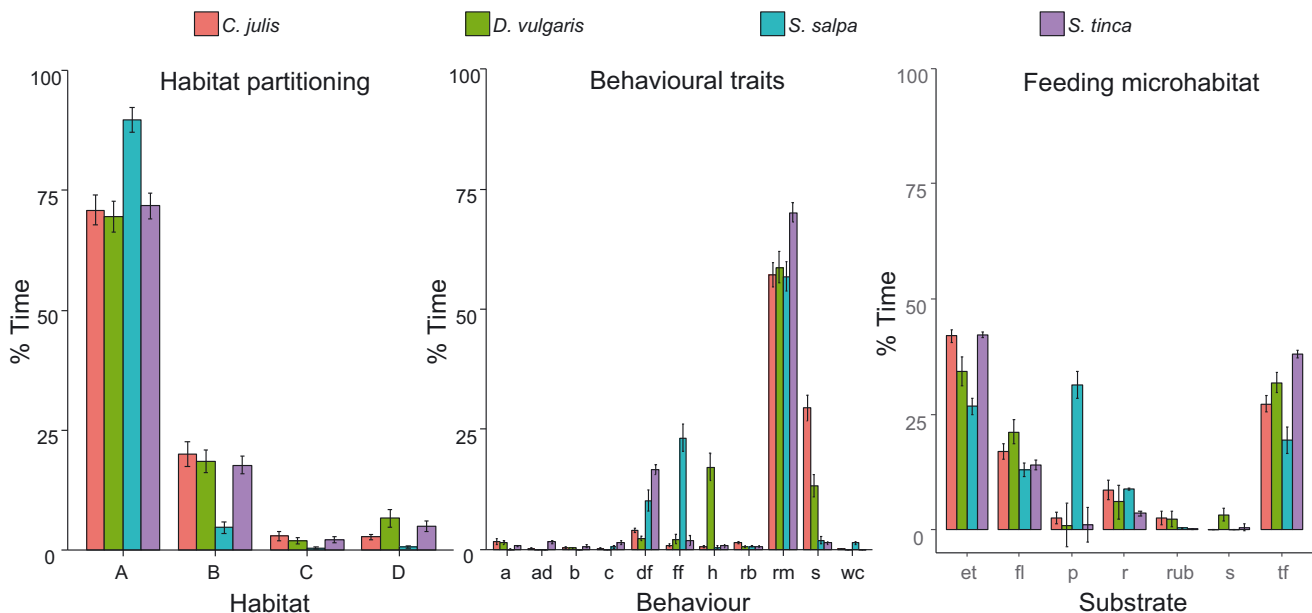

Fig. 3. Graphic representation of the time spent for each species in Mallorca according to habitat partitioning patterns (A: open horizontal; B: open vertical; C: underside; D: concealed), behavioural traits (a: intraspecific aggression; ad: advertising; b: interspecific aggression; c: cleaning; df: diffused feeding; ff: focussed feeding; h: hovering; rb: rubbing; rm: roaming; s: searching; wc: water column feeding) and feeding microhabitat preferences (et: erect treelike; fl: filamentous algal morphotypes; p: *Posidonia*; r: rock; rub: rubble; s: sand; tf: turf). Error bars: ±SE
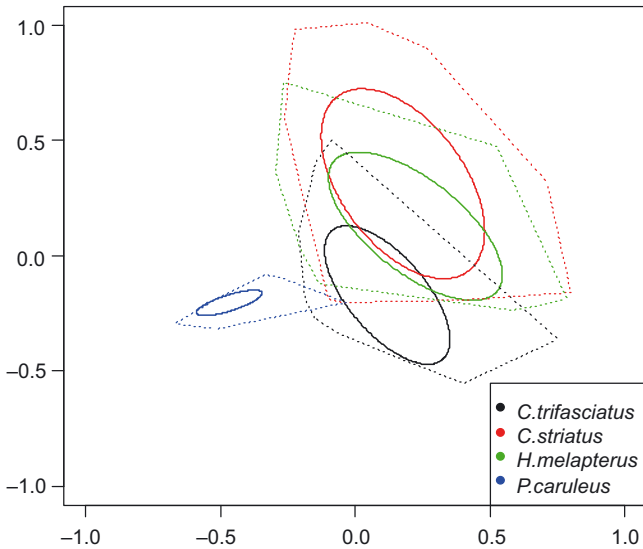
Fig. 4. Total area of the convex hull (dotted lines) and standard ellipse area (continuous lines) realised niche volumes of the 4 species sampled in the Seychelles

Table 1. Calculations of the realised niche overlap between species based on the total area of the convex hulls (TA) and standard ellipse areas (SEA) in the Seychelles, expressed in % of the total area of the 4 species analysed: *Ct*: *C. trifasciatus*; *Cs*: *C. striatus*; *Hm*: *H. melapterus*; *Pc*: *P.caruleus*

		TA				SEA		
	Ct	*Cs*	*Hm*	*Pc*	*Ct*	*Cs*	*Hm*	*Pc*
Ct		54.6	55.4	1.5		5.2	11.4	0
Cs	30.1		69	0	2.6		57.2	0
Hm	40.5	91.5		0	7.8	79.2		0
Pc	10.5	0.5	0		0	0	0	

versely, *P. caruleus* demonstrated a small TA RN overlap with *C. trifasciatus* and *C. striatus*, however no SEA RN overlap was evidenced for this species. A large difference in the degree of overlap between the TA and SEA RN was observed between *C. trifasciatus* and *C. striatus* and *C. striatus* and *C. trifasciatus*, as well as between the RNs of *C. trifasciatus* and *H. melapterus* and *H. melapterus* and *C. trifasciatus*.

The Mallorca species demonstrated a larger degree of RN overlap overall, both for TA and SEA, compared to those in the Seychelles, although the same pattern was observed: the RN overlap of the TA was greater between all species than that of the SEA (Fig. 5, Table 2). The highest degree of overlap was observed between the RNs of *C. julis* and *D. vulgaris*. A large degree of overlap was also seen between the RNs, for both SEA and TA, of *Symphodus tinca* with *C. julis* and *S. tinca* with *D. vulgaris*. On the other hand, the RN overlap *C. julis* and *D. vulgaris* with *S. tinca* expressed high TA overlap values, while the SEA

overlap values indicated a medium degree of RN overlap. Highly pronounced differences between the TA and SEA niche overlap were observed in most remaining combinations of overlaps. Finally, despite indicating a large–medium TA RN overlap, no SEA RN overlap was indicated between *S. tinca* and *S. salpa*, nor between *S. salpa* and *S. tinca*.

3.3. Sample size dependency

By simulating different sample sizes, changes in the values of TA and SEA — and thus their dependency on the sample size — were observed. The simulated values followed similar patterns for all species in the Seychelles and Mallorca (Figs. 6 & 7). The variability for both TA and SEA was reduced with increasing sample size. For the maximum number of samples simulated, however, the variation was always smaller for SEA than TA (in many cases the
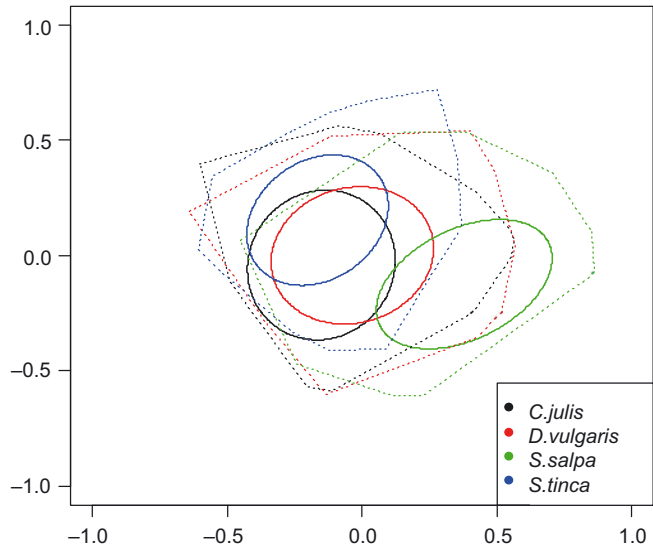

Fig. 5. Total area of the convex hull (dotted lines) and standard ellipse area (continuous lines) realised niche volumes of the 4 species sampled in Mallorca

Table 2. Calculations of the realised niche overlap between species based on the total area of the convex hulls (TA) and standard ellipse area (SEA) in Mallorca, expressed in % of the total area of the 4 species analysed: *Cj*: *Coris julis*; *Dv*: *Diplodus vulgaris*; *Ss*: *Salpa salpa*; *St*: *Symphodus tinca*

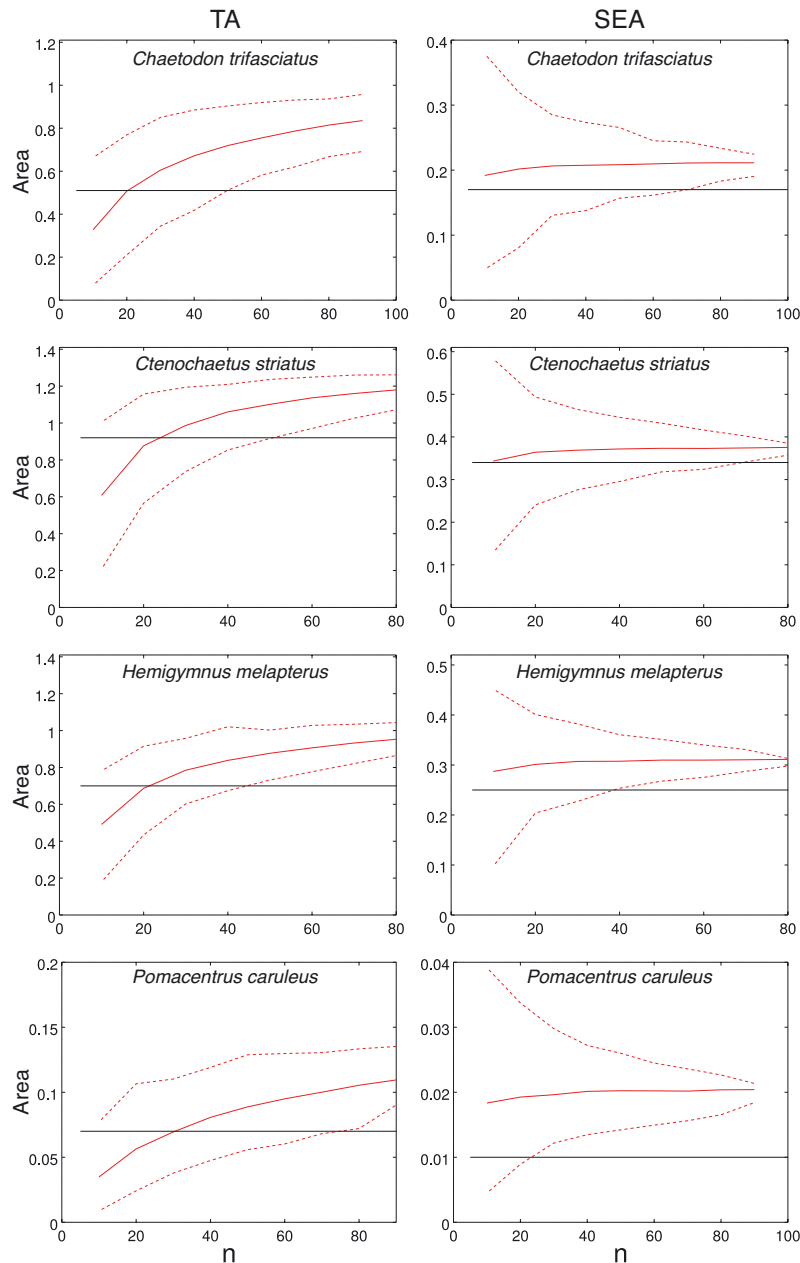|		TA				SEA		
	Cj	*Dv*	*Ss*	*St*	*Cj*	*Dv*	*Ss*	*St*
Cj		91.9	74.3	75.3		73.6	1.4	53.6
Dv	86.1		81.9	69.6	73.3		12.2	47.9
Ss	64.4	75.9		49.8	1.5	13.1		0
St	85.3	84.2	65		65.8	59	0	

Fig. 6. Realised niche width using increasing sample size for total area of the convex hull (TA; left column) and standard ellipse area (SEA; right column) for the Seychelles species. Solid black line: observed total niche area for each metric calculated from the observation data; solid red line: mean TA (left) and SEA (right) values calculated for 1000 random selections of individuals with increasing sample size (n + 5). Red dotted lines: lower and upper CI (0.05 and 99.95%) for the niche area estimates after each of the 1000 resamplings with increasing sample size

values estimated by the model were proximate to the empirical SEA values of the species. Finally, with increasing sample numbers the TA values increased, eventually tailing off, while the SA values generally remained unaffected after a very small number of samples for both Seychelles and Mallorca.

4. DISCUSSION

The vast majority of current literature using empirical data to quantify RNs and their overlap comes from stable isotope studies, where the feeding niche of the species is represented by data points corresponding to individual diets expressed as paired isotopic coordinates (Herzka 2005, Cherel et al. 2010, Bas et al. 2019). Stable isotope analysis is certainly useful for assessing the trophic position of individuals, and it offers information about major foraging habitats; however, different prey admixtures may result in similar stable isotope ratios, and hence some of the interspecific differences in RNs may go unnoticed in studies relying only on stable isotope analysis (Newsome et al. 2007). Furthermore, behaviour may differ between species with similar diets, resulting in lower functional redundancy than that suggested by isotopic niches. Sympatric *Coris julis* and *Symphodus tinca* in Mallorca offer a good example, as they have very similar C and N stable isotope ratios (Jennings et al. 1997), but when standard ellipses are considered (this study), it becomes clear that they overlap only partially in their behavioural patterns. On the contrary, sympatric *C. julis* and *Diplodus vulgaris* in Mallorca have very

variation for SEA was reduced to zero). For the Seychelles, the model predicted higher values for both TA and SEA compared to the observed values from the data; however, the overestimate in the case of SEA was much smaller in comparison. For Mallorca, the resamplings also predicted higher values of TA than those observed empirically; however, the SEA

similar behavioural patterns (this study) but differ greatly in their stable isotope ratios of C and N (Jennings et al. 1997). Using behavioural data to estimate niche overlap may also account for differences resulting from changes in predation risk while stable isotope analysis alone cannot (Skinner et al. 2019). Hence, behavioural data offer a complementary approach
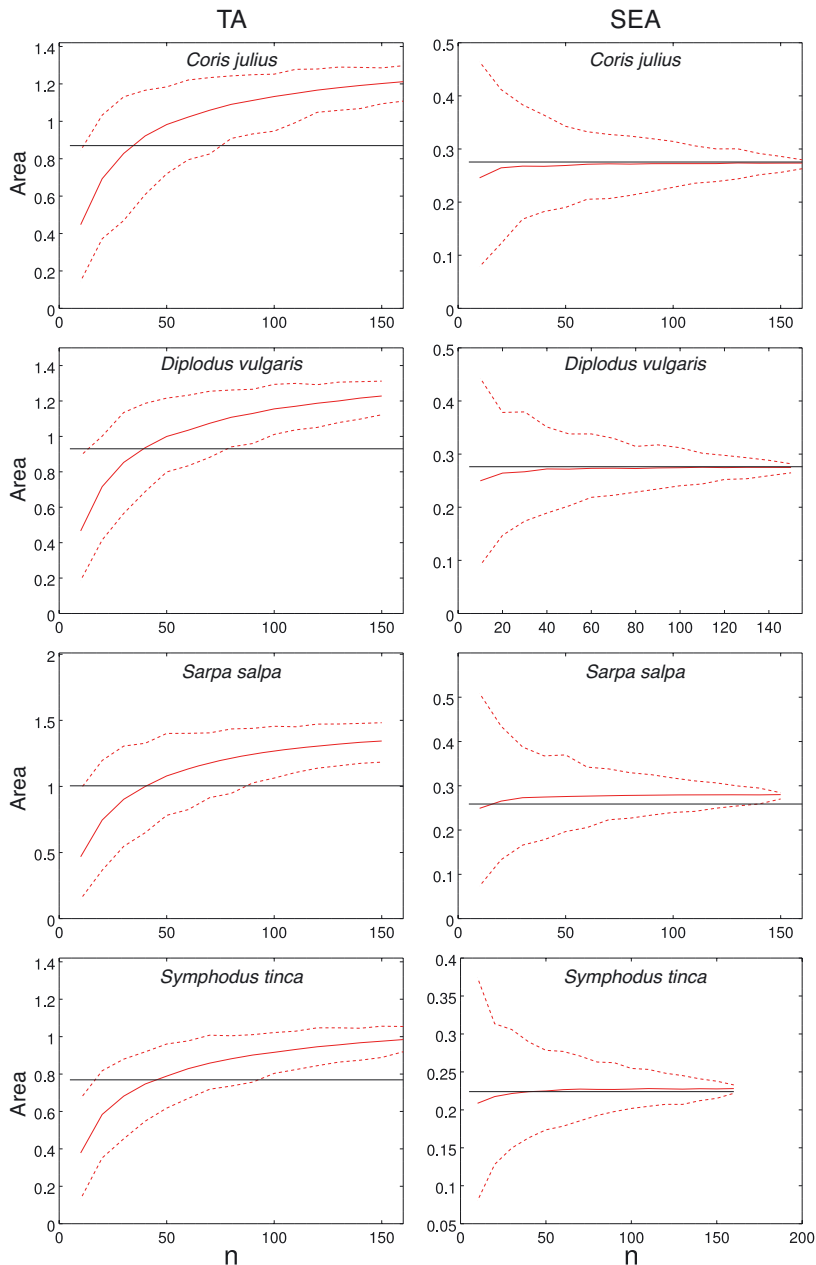
Fig. 7. Realised niche width using increasing sample size for total area of the convex hull (TA; left column) and standard ellipse area (SEA; right column) for Mallorca species. See Fig. 6 for data descriptions

not only due to exceptionally high species diversity in certain habitats, but also as a result of the logistical constraints associated with collection of behavioural data (e.g. requiring long observations). This means that the use of behavioural data to characterize RNs will always be limited to a set of species selected based on the research question. Here, we studied 4 species in each region and could have included others, but it was certainly impossible to include them all.

Our results also revealed major differences between TA and SEA as a result of TA being more sensitive to the number of observations than SEA (Figs. 6 & 7) (Worton 1995, Jackson et al. 2011). TA values are influenced by the most extreme individuals, and it is logical to think that the chance of discovering additional individuals lying outside the current niche would increase by increasing sampling effort. Thus, if the sample size is larger, the niche would likely be larger when using the TA method, even if only a few individuals exhibit unusual behaviours. In this case, while several individuals could be found outside and would subsequently increase the initial niche size, many would likely fall within a smaller niche area. Consequently, using the TA method for measuring niche sizes emphasises the importance of the few, while not equally considering that of the majority—which can be interpreted as not entirely representative of the largest part of population. Studying populations with less variation, in theory, give more precise niche size estimates using this method; however, it is difficult to know what the real ranges are at the population level if only a small number of individuals have been analysed (Syväranta et al. 2013). The TA method would thus give a more accurate measurement of niche size by sampling more individuals from the given population.

Comparing niche sizes from populations with unequal samples using the TA measurements can provide inaccurate results if the number of individuals sampled determines the niche size. However, despite its shortcomings, the TA method considers

to describe the RNs of the assemblage and trophic redundancy in natural communities, with the additional advantage of being compatible with stable isotope data, as demonstrated in this study.

Although it is desirable to include most species within the assemblage, and while both methods are capable of analysis of complementarity and redundancy among large numbers of species simultaneously, it might not always be logistically feasible to empirically sample the behaviour of entire communities. This is

information on intraspecific variation, which is important when describing the niche of a population (Bolnick et al. 2003).

Independent of the measurement metric used in our study, a high degree of RN overlap was observed only between *Hemigymnus melapterus* and *Ctenochaetus striatus* in the Seychelles and *C. julis* and *D. vulgaris* in Mallorca. The sizes of the RNs, as well as the overlap among species, were always larger when calculated using TA than SEA, with some extremely large differences observed for several species. Thus, by using the same data but calculating the niche sizes via different metrics, contradictory results were obtained, providing evidence for a high degree of redundancy (large niche overlap), while also suggesting extensive complementarity among species (small niche overlap) in both geographical areas studied. The results using the TA method in this case indicated that the species studied delivered their function over a wide range of microhabitats, with high variance among individuals and consequently large niche sizes, leading to a high degree of overlapping and extensive complementarity (except perhaps not to such an extent in the case of *Pomacentrus caruleus*). On the other hand, in the Seychelles the niche sizes calculated using the SEA method were at least half the size of those calculated using the TA method, while in Mallorca, they were over 3 times smaller for each species. These findings suggest a much more restricted microhabitat use pattern leading to less niche overlapping and more complementarity. It is, however, not surprising that only the planktivorous species experienced limited overlap with the remaining species (as they were all benthic feeders), suggesting that the overlap is likely species-dependent. Consequently, and since the RN of a species is a function of the species' ecology and its potential interactions with other members of the assemblage, in order to represent the entire assemblage, most of the species within the community should be considered in the future.

Despite the obvious statistical implications of using different measurement metrics, the ecological consequences of using one or the other are likely to be extremely important. Informed use of RN measurement metrics in ecology should be based on an appropriate research question, and not just the statistical significance of the results. For example, the priority of a conservation study may be to ensure the persistence of the genetic diversity, often captured by the behavioural variability of the population, while the aim of a rapid population assessment study might be only to identify the most frequent and dominant

behaviours characterising the population. In this case, the TA metric would be preferred in the former study, while the use of the SEA metric would be better for the latter. This is, of course, coupled with several trade-offs reflected in the logistical possibilities of the project and other limitations, which also need to be considered. Sufficient sample sizes required for each method (one of the limitations) has already been discussed in the context of isotopic niches (Jackson et al. 2011, Syväranta et al. 2013).

By simulating different sample sizes, this study demonstrated that the accuracy of each method for the measurement of the RN, based on the time contribution of behaviours to the microhabitats in the multidimensional space, is influenced by the number of samples considered. Sample size for TA appears to have a significant effect on the accuracy of the measurement, and thus strongly impacts the size estimates of the niche area. Increasing sample size for the SEA improves accuracy but does not result in notable changes in niche area sizes. Consequently, to know how reliable the TA metric is for a particular study, it is important to have an understanding of what proportion of the population is being sampled.

In this study, the TA model predicted higher values than those empirically observed in both the Seychelles and Mallorca, thus perhaps indicating an insufficient sample size in this study to accurately measure TA values. The model made a better prediction for SEA values, although it was not as accurate in the Seychelles as in Mallorca, where the predictions were almost identical to the observed values. Since the number of samples taken in the Seychelles was lower than that in Mallorca, these findings indicate that even though the SEA values were a good approximation, a larger sample size was required for the Seychelles to obtain entirely accurate SEA niche values. Regardless of the location or species sampled, the model-predicted TA and SEA values tailed off and the variability decreased for both metrics with increased sample size. This suggests that if a sufficient sample size is considered, both methods will accurately reflect the RN of a species, but SEA is always likely to provide a better estimate of the niche position of the bulk of the population while TA will give a more accurate estimate of niche area.

We demonstrated that both measurement metrics can be successfully adapted for analysis of different niche components. In view of this evidence, conducting studies on RN measurements and overlap based on just one and completely disregarding the other method is potentially problematic in terms of ecological validity, if the data (as in this case) can simulta-

neously be interpreted as indicating redundancy and complementarity of the same species. While the studies reviewing the use of the same methodologies in the isotopic niche calculations ultimately suggest the use of SEA over TA, recommendations from this study cannot be as straightforward. TA metrics have been successfully used for the calculation of RNs in the marine environment (Brandl & Bellwood 2014), whereas in this study we calculated RNs using SEA as well. Based on these findings, it is evident that both methods provide ecologically relevant information about the species and communities they represent, and as such should be considered in future studies of niche analysis in ecological communities, and not only in stable isotope studies. Contrary to the stable isotope studies, however, in an ideal scenario and for complete transparency of the findings, we recommend representing the RNs using both methods with sufficient sample sizes, followed by a study-specific argument giving one or the other method more importance based on the ecological questions the study aims to answer.

Finally, owing to the identical sampling techniques employed and the uniformly applicable niche size estimation methodologies used here, comparisons of the fish species' niches and their overlaps were possible across the different habitats studied. Specifically, ecologically similar species of comparable feeding strategies and guilds but from different locations—herbivorous *C. striatus* and *S. salpa* and macroinvertebrate feeders *H. melapterus* and *Symphodus tinca*—were found to have similar RN sizes in their respective tropical and temperate locations regardless of the niche measurement metric used. On the other hand, the remaining species at each location were ecologically different and were characterised by distinct feeding strategies, and their RN sizes also differed. It is possible that had additional species been compared, the same patterns of similarities and differences in niche sizes between locations could have been observed. Consequently, for example, if *Chromis chromis* from temperate reefs were sampled, due to the previously reported similarities in behaviour and microhabitat use of many pomacentrids regardless of the geographic location, as well as the personal experience of the observers in the study of the behaviour of the 2 species, a niche size comparable to that of the *P. caruleus* sampled in the tropics would likely have been observed (Medeiros et al. 2010). The empirical evidence provided here could serve as a base for exploring this theory further. Subsequent efforts are necessary to determine, empirically, whether the size of RNs of similar species are comparable across locations, regardless of the habitat and biological diversity characterising them— something that to date has only been theoretically hypothesised (Rosenfeld 2002, Hooper et al. 2005). Since the RNs of the common species and those representative of only 2 locations were measured in this study, future sample sizes can be improved upon. As a result, further studies are encouraged, incorporating individual behavioural observations of additional study species and different habitats.

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