Evaluating a key herbivorous fish as a mobile link: a Brownian bridge approach

Running headline: Herbivorous fish movements link seascape mosaics

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Abstract

By moving between habitats, mobile link organisms serve as vectors of material and energy transport between ecosystems. Additionally, if these mobile species are key organisms, their movement patterns can have profound consequences on the functioning of the ecosystems they link. The Mediterranean herbivorous fish, *Sarpa salpa*, has been defined as a key organism in seagrass and rocky macroalgal habitats. Our objective in this study was to evaluate the potential of this species to be considered a mobile link by (1) assessing its capacity to connect different habitats, the strength of these connections, and the habitat use; and by (2) determining whether the patterns observed were consistent on a diel basis and over an annual period. We used the recently developed Brownian bridge movement models (BBMM) framework to analyse the movement patterns of 18 fish tracked with passive acoustic telemetry (mean tracking duration 103 ± 22 days) and a time-frequency analysis to assess their temporal patterns. Our results showed that *S. salpa* performed trips between different and distant habitats (on the order of km) with large home ranges (overall mean 134 ± 10 ha). Despite its high mobility, *S. salpa* used seagrass more intensively rather than rocky habitats. In addition, our results confirm the existence of diel patterns for this species, mostly observed in the seagrass habitat, with fishes moving from shallow areas during the day to deeper areas at night. These patterns were visible for most of the year. Taken together, these results suggest that *S. salpa* may act as a mobile link by connecting shallow and deep areas of the meadow on a daily basis and linking different and distant habitats over longer temporal scales.

Key words: Brownian bridge movement models; BBMM; seascape; spatial patterns; *Sarpa salpa*; temporal patterns.

Introduction

Mobile links are organisms able to move between habitats and ecosystems that support essential functions by connecting areas and contributing to ecosystem resilience (Gilbert 1980, Nyström & Folke 2001). Connections may be achieved by organisms passively drifting from one habitat to another (e.g. larvae in seawater, anemochorous seeds) or by their active movement. Active mobile links are animals that provide a multitude of different functions such as pollination, seed dispersal and translocation of nutrients (Ogden & Ehrlich 1977, Meyer et al. 1983, García et al. 2013), which can have substantial effects on ecosystem functioning and structure (Lundberg & Moberg 2003). Additionally, if these mobile species are key organisms, as is the case of some herbivores, their movement patterns can have profound consequences on the functioning of the ecosystems they link. Indeed, herbivores play a central role in the organization of communities and ecosystems (Burkepile & Hay 2006, Gruner et al. 2008) and often they do not distribute their impacts uniformly among the habitats they travel across (e.g. McCook 1997, Knapp et al. 1999). Foraging theory predicts habitat selection on the basis of resource quality and abundance (Charnov 1976), but other factors such as predation risk (Brown & Kotler 2004, Hoey & Bellwood 2011), animal state (Schuck-Paim et al. 2004) or landscape spatial configuration (Haynes & Cronin 2003, Fortin et al. 2005, Hoey & Bellwood 2011) also influence animal foraging decisions and movement patterns. Therefore, to fully assess whether an organism can effectively function as an active mobile link between habitats or ecosystems, two key issues should be addressed: the spatial arrangement of habitats and the movement patterns of the animal.

Marine landscapes (i.e. seascapes, Pittman et al. 2011) are assumed to have a higher level of connectivity than terrestrial ones (Tanner 2006), which reinforces the possibility of generalist mobile fish herbivores to serve as mobile links. In seascapes, where GPS positioning is not possible, acoustic telemetry has become increasingly used to track animals in space and time. Descriptive analyses (frequency distribution of detections) and or space utilisation methods (minimum convex polygons and kernel utilisation distributions) have been widely applied, providing key information on animal space use. However, the temporal component between successive locations, which is crucial to assess the connection between habitats, is often overlooked (Jacoby et al. 2012). Brownian bridge movement models (BBMM, Horne et al. 2007, Kranstauber et al. 2012) consider both the spatial and the temporal component of movement. BBMMs explicitly address the problem of connections (i.e. bridges) between successive locations, and thus, are useful to determine whether or not highly mobile species act as links between habitats.

In the Western Mediterranean the herbivorous fish *Sarpa salpa* (L.) exerts a profound impact in different coastal habitats that include the consumption of a great proportion of seagrass annual primary production (Prado et al. 2007), drastic reductions on seagrass canopy structure that can foster predation on seagrass-dwelling organisms (Pagès et al. 2012), or its influence on the vertical distribution of canopy-forming algae (Vergés et al. 2009), among others (e.g. Sala & Boudouresque 1997). *S. salpa* are diurnal browsers and generalist herbivores, allocating most of their daytime to foraging (ca. 65% of their time) in both seagrass (Ferrari 2006, Jadot et al. 2006, Abecasis et al. 2012) and rocky habitats (Tomas et al. 2011). Nevertheless, it remains unclear whether individuals are systematically capable of connecting different habitats or if, on the contrary, individuals found in rocky habitats belong to different populations from those in seagrass beds (as seen by Fox & Bellwood 2011 with rabbitfishes in coral reefs). Given that seagrass beds and rocky habitats are usually found forming a mosaic, it seems reasonable to assume individual commuting among habitats. If these trips were frequent and enough time was spent in each habitat to imply a translocation of materials and energy, the ecological implications would be sound.

Our study aims were (1) to determine whether the herbivorous fish *S. salpa* commutes between different habitats in a seascape mosaic, characterise the strength and variability of these connections and the habitat use in each of these systems; and (2) to determine if the patterns observed are consistent on a diel basis and over an annual period. To address objective (1) we analysed the movement data recorded by passive acoustic telemetry with the BBMM framework, and we used a time-frequency analysis (Continuous Wavelet Transform, CWT) to evaluate the temporal patterns for this species along the tracking period (objective 2). If *S. salpa* uses and commutes between different habitats, and these patterns are sustained on time, we will be able to discuss the potentiality of this species to be considered an active mobile link.

Materials and Methods

Study area and receiver set up

This work was conducted between October 2008 and October 2009 in Medes Islands Marine Protected Area and the adjacent unprotected stretch of coast, located on the north-western Mediterranean. The study area is a mosaic of habitats composed of sandy bottoms, *Posidonia oceanica* seagrass meadows and macroalgal communities in rocky habitats (Fig. 1a; Hereu et al. 2010, Hereu et al. 2011). Rocky areas (with macroalgal communities) occupy a larger area compared to seagrass communities (for each part of seagrass habitats there are nine parts of rocky habitats, see Fig. 1a). A fixed array of 26 single-channel omni-directional hydrophones (VR2 receivers, VEMCO, Nova Scotia, Canada) was deployed around the Medes Islands archipelago and along the coast. Receivers' detection range was established by mooring tags at different distances from 4 receivers for a 24-hour period each. The receivers tested (#3, #4, #5, #6, see Fig. S1a), were among the most used by *S. salpa* (see results, Fig. S2) and were located on the southwestern side of the islands. Their ranges encompassed varying proportions of each habitat (see Fig. 1a). The average percentage of tag detections was very high (above 75%, Fig. S1b) until 100 m away of receivers, and between 100 to 250 m average percentage of detection remained at 35-25%. Tags placed at distances beyond 250 m were generally not detected (Fig. S1b). This distance threshold (250 m) was thus considered the receivers' detection range. The average spacing between receivers was 210 m (detection probability at this distance ca. 25 ± 2 %) in order to prevent the existence of undetectable areas. Receivers were retrieved, data downloaded, cleaned of biofouling, and redeployed 5 times during the study (in November 2008, January 2009, May 2009, August 2009 and October 2009).

Acoustic tagging procedure

S. salpa individuals were fished on the 16th and 17th October 2008. Twenty fishes were captured at four different sites (see Fig. 1a, five fishes per site) during daytime using seine fishing net by circling schools of *S. salpa* fish. Since there is no evidence of sexual dimorphism on this species, individuals were not assigned a sex. Each fish was measured to the nearest 0.5 cm (Total Length) and tagged following the protocol in Jadot et al. (2006). After recovery, they were returned to their respective sites. We used VEMCO acoustic transmitters (V9P-2L, 9 mm diameter × 47 mm length) with 120 s average repeat rate, a depth accuracy of ± 2.5 m and an estimated battery life of 522 days. Previous studies have shown that surgical tag implantation has a very limited impact on the behaviour and physical status of this species (Jadot 2003). It should be noted that four of the most frequently detected five fishes (called residents, see below) were captured in the meadow zone (see Fig. 1a, Table S1).

Spatial patterns

For each fish, we calculated the total period between its releasing date and its last day of detection (total period of detection or tracking period, TP), as well as the number of days detected (DD), following March et al. (2010). These descriptors were used to calculate the Residence Index (RI) per fish, defined as the quotient between DD and TP for that individual (March et al. 2010). Fishes with a RI > 0.6 (i.e. fishes that were detected within the array of receivers for more than the 60 % of days during their tracking period, and tracked more than 5 days) were considered 'resident' as opposed to the 'non-resident' ones (RI < 0.6). Utilisation distributions and home ranges were assessed for both resident and non-resident fishes. For non-residents, these estimations should be viewed as minimum areas of utilisation, since their estimates may be biased due to their low number of detections within the array. Further analyses were run only for residents, which accounted for the vast majority of detections (see Results).

We used the recently developed Brownian bridge movement model (BBMM) approach (Horne et al. 2007, Kranstauber et al. 2012) to estimate individual fish utilisation distributions (UD). Utilisation distribution estimation provides an objective way to define an animal's normal activities (Powell 2000). UDs are probability density functions that provide the animal's probability of use for each cell (i.e. pixel) of a given grid (raster map). We only calculated UDs for those individuals with more than 50 data points (locations) and more than 5 days detected (see Table S1, i.e. 5 resident and 5 non-resident fishes). UD estimation through BBMM has several advantages over the classical location-based kernel density estimator (KUD). While KUD method only assesses the spatial arrangement of locations, BBMM considers the time dependence between them. This makes BBMM a particularly useful method to assess the capability of an animal to behave as a mobile link, given that it is especially successful at detecting the connectivity between highly used areas. Moreover, it assumes the animal is moving following a conditional random walk movement model between pairs of locations (i.e. a random walk conditioned by a known starting and ending location); and finally, it allows to take location error into account (see Calenge 2011 for a thorough comparison between KUD and BBMM methods) (biotelemetry error, i.e. 250 m in our case; see supplementary for a complete explanation of BBMM implementation to our data set; see an example of a data set in Table S2). BBMM calculations were performed in R (RDevelopmentCoreTeam 2012) using the package BBMM (Nelson et al. 2011).

Home ranges: Individual fish UDs obtained from the BBMM were used to calculate individual home range areas. The smallest area accounting for the 95 % of the total probability of use is usually defined as the animal home range (Powell 2000). Thus, for each individual UD we calculated the home range area as the 95% volume isopleth of the UD and the core areas of usage were also calculated as the 50% volume isopleth of the UD. These calculations were performed in ARCGIS10® (ESRI, Redlands, CA, USA) and GME (Beyer 2011).

Space use: On the other hand, the individual UDs obtained from the BBMM were also used to assess population-level space use. We summed the cell values for all resident fish UDs (n = 5) and the cell values of non-residents UDs (n = 5) respectively and then re-scaled their cumulative cell values to sum to 1 (since UDs are probability density functions, Powell 2000). In this way we obtained the population-level UD for residents and non-residents respectively. This is equivalent to projecting each individual UD onto a grid, and allows for the spatial assessment of the overall most used areas of that population (see e.g. Horne et al. 2007, Sawyer et al. 2009).

Occasional excursions from each habitat: For resident fishes, we assessed the importance of occasional movements by calculating the probabilities of a fish making an excursion of a given duration departing from a given habitat (meadow or no-meadow areas). First, receivers were grouped according to the presence or absence of *P. oceanica* in their range of detection. We labelled the receivers in the seagrass habitat as 'meadow' (the 4 receivers with seagrass within their detection range, see Fig. 1a) and 'no-meadow' (the rest of the receivers). We define excursion time as any time interval between two consecutive locations on the same receiver. We represented the excursion times in each habitat in a log-log scale. This is an adequate way to visualize fat tail distributions, that is, distributions where extreme values show non-negligible probabilities (Pueyo 2006, Sims et al. 2007).

Receiver-based descriptors: In order to determine whether receivers are located in travelling zones or in intensively used areas within the habitat, we computed, for the resident fishes, the percentage of consecutive revisits to the same receiver as the ratio between consecutive revisits and the sum of consecutive with non-consecutive revisits. Non-consecutive revisits are those that reach a particular receiver after having been detected previously in another receiver. Low ratios of consecutive visits suggest the receivers are located in a travelling zone, whereas high ratios suggest the receivers are in intensively used areas. We complemented this information with the mean excursion duration from each receiver (time interval between consecutive detections on that receiver) and the number of detections in each receiver (see results).

Temporal patterns

To study fish behaviour on the depth axis, we assessed day and night depth distribution for resident fish in meadow and no-meadow habitats. Data were split into periods of day and night, according to the sunset-sunrise time calendar obtained from the U.S. Naval Observatory (Astronomical Applications Department, accessed 1st June 2011 http://aa.usno.navy.mil). We calculated the mean depth per day and night for the whole data set for each fish. Then, the dependent variable fish mean depth was analysed with a 2-way ANOVA to test the effects of the fixed factors habitat (2 levels: meadow, no-meadow) and phase of the day (2 levels: day, night). Normality and homoscedasticity were tested and fulfilled.

We also tested whether there were differences in the frequency of detections according to the fixed factors phase of the day (2 levels: day and night), habitat (2 levels: meadow, no-meadow) and season (just 2 levels: autumn, winter, because we did not have enough fish individuals [replicates] for the rest of seasons). Detection frequencies were fit to a linear model and the variance structure of heteroscedastic variables (season and habitat) was included as weights within the linear model. The best weighted model was selected using Akaike's Information Criterion (AIC) (Zuur et al. 2009). Normality was tested and fulfilled. Data were analysed with the package nlme in the statistical software R (Bates et al. 2011, Pinheiro et al. 2011, RDevelopmentCoreTeam 2012).

The temporal patterns of hourly detections were examined by visually inspecting the chronograms for each resident fish. A time-frequency analysis (the Continuous Wavelet Transform – CWT) was then used with the pooled data set of all residents, in order to identify periodic patterns in *S. salpa* hourly detections (as used in e.g. March et al. 2010, Alós et al. 2012). Time-frequency methods are more powerful than frequency ones because they allow us to track periodicity across time (Subbey et al. 2008). Most traditional mathematical methods examine periodicities in the frequency domain, and therefore implicitly assume that the underlying processes are stationary in time. In contrast, wavelet transforms expand time series into time frequency space and can therefore find localized intermittent periodicities (Grinsted et al. 2004). We computed (Matlab) a 2-dimensional wavelet spectrum (i.e. Morlet wavelet) and a point-wise test (95% significance level) on previously normalized data (i.e. log-transformation) (Grinsted et al. 2004).

Results

Spatial patterns

Five resident fish accounted for the 96% of detections, while non-resident fishes accounted for the remaining 4% (Fig. S2, Table S1). Home range areas for individual *S. salpa* varied from 87.88 ha to 187.44 ha (Table S1, Fig. S3). The mean home-range area for residents was 143 ± 18 ha, and 124 ± 11 ha for non-residents (averaging the individual home range areas of the 5 residents, and the 5 non-residents respectively). Residents' space use (i.e. the spatial projection of the sum of all resident individual UDs) evidenced that the seagrass meadow was intensively used, as shown by their core area that was centred on the meadow. Residents also used rocky habitats from the islands and even from the coast 1.5 km apart from their core area, an evidence of large scale commuting (Fig. 1b,d). Non-residents population space use (i.e. the projection of non-residents' individual UDs) covered nearly all coastal zones of the study area (Fig. 1b). Non-resident population showed different cores of activity (50 % isopleth), on the coast and on the islands, partially located on the seagrass habitat. Both residents and non-residents populations overlapped their core areas on the *P. oceanica* habitat, in the south-western coast of the islands (Fig. 1a,b).

The probability distribution of a resident fish to perform an excursion of a particular duration showed a fat-tailed decay, in particular with a power law like scaling (i.e. a straight-lined decay in Fig. 1c). This held for meadow and no-meadow receivers, showing that regardless of the habitat the vast majority of excursions departing from a receiver were very short in duration, but from time to time very long excursions also occurred. The probability of performing very long excursions was not negligible and depended on the habitat the receiver was located in, excursions departing from no-meadow receivers being larger than those departing from meadow receivers. For example, the probability of making excursions of 1000 minutes (ca. 17 hours) was low, but it was around two orders of magnitude higher in the no-meadow receivers compared to those in the meadow (Fig. 1c). These results suggest a larger site fidelity to meadow compared to no-meadow areas. More generally, meadow receivers showed a higher number of detections, high consecutive revisits ratio (Fig. 1d), and low mean excursion duration. This should not come as a surprise given that the set of receivers located in the meadow showed the highest space use probability (Fig. 1d). The set of receivers located in no-meadow areas, specially those at the edges of the receiver's array, showed a lower consecutive revisits ratio, a high variability on excursion durations, and a much lower probability of space use (Fig. 1d).

Temporal patterns

S. salpa depth preference differed significantly between habitats and phase of the day (Fig. 2, Table 1). In seagrass habitat, the majority of detections during daytime were in shallow depths (mean diurnal depth = 5.2 ± 0.2 m), whereas, at night, detections were significantly deeper (mean nocturnal depth = 8.5 ± 0.9 m, inset Fig. 2a, Fig. S4). In contrast, this cycle was not significant in rocky habitats, where fish remained most of the time at similar depths (p-value > 0.05, inset Fig. 2b, Fig. S4). It is worthy to note that *S. salpa* depth use in the area of the meadow (Fig. 2a) matches seagrass habitat depth distribution (Fig. 1a).

We found a significant effect of habitat type and day phase on the frequency of detections (p-values < 0.05, Table 1), but no direct effects of seasonality (Table 1). Receivers in meadow areas presented a higher amount of detections than receivers in no-meadow areas. In the former most detections were nocturnal, whereas in the latter most detections were received during the day (see Fig. S5a). In autumn there was a significantly higher frequency of detections at night compared to daytime, but these differences were not significant in winter (see the significant Phase × Season interaction in Table 1; see also Fig. S5b).

Inspecting the chronograms from individual resident fishes (Fig. S6), a diel pattern became evident when considering hourly detection rates. The similarities observed at the individual level (Fig. S7, with some variability), allowed us to aggregate the data for all residents. The diel cycle persisted, with the highest rate of detections per hour at night, while at sunrise and late afternoon there was the minimum number of detections and, during daytime, the detection rate remained low (Fig. 3a, see also individual level data in Fig S7). Wavelet spectrograms of the time series evidenced the existence of a diel cycle on the residents' hourly detection rate (period = 24 hours, see dashed lines in Fig. 3b; see individual-level wavelet spectrograms, Fig. S8). This pattern was significant (with some non-significant patches) for most of the time series until most fishes stopped transmitting. For periods around 128-256 hours (5-10 days) and especially around 512 hours (21 days) there were also significant patches (Fig 3b).

Discussion

The large home ranges of *S. salpa,* the connection observed between areas with the BBMM models, the trips observed between distant habitats and the consistency of these patterns in time suggest that *S. salpa* might act as a mobile link. Despite its high mobility, *S. salpa* used seagrass more intensively rather than rocky habitats, especially resident fishes (i.e. those spending more than 60% of time within the area of detection of the receivers network). In addition, our results confirm the existence of diel patterns for this species, mostly observed in the seagrass habitat, with fishes moving from shallow areas during the day to deeper areas at night. These patterns were visible for most of the year and also highlight the potential link between shallow and deep areas of seagrass meadows.

Applying BBMM on passive acoustic telemetry data sets

Despite the acknowledged suitability of BBMM to provide insight into the movements of terrestrial tracked animals using GPS data (Horne et al. 2007, Sawyer et al. 2009), this is the first time the method is applied to a marine data set. The application of BBMM on passive acoustic telemetry data has allowed us to detect which of the highly frequented areas are more likely to be connected. This would not have been possible with the classical KUD approach, which does not account for the actual path the animal has travelled (compare the UD obtained with the BBMM in Fig. 1d with the UDs obtained with the KUD in Fig. S9). However, to correctly interpret the output of BBMM with passive acoustic telemetry data sets one needs to be aware of three specific issues. Firstly, when individuals consecutively revisit the same receiver, the model assumes the existence of a pure diffusive movement (not bridged) around that receiver, which is proportional to the time spent between the two consecutive locations. This leads to a circular-shaped utilisation distribution around that receiver. If the time lag between two consecutive locations at the same receiver is very large, then the local UD (around the receiver) could be overestimated because it might well be the case that the animal departed the area out of the network receivers and returned to the same area later on. Thus, the BBMM method is very suitable for species that move throughout the receivers' network area, while it is less appropriate for species that display permanent site-fidelity with low mobility, or that display movements much broader than the receivers network area of detection. Secondly, the presence of acoustic shadows, i.e. areas within the receiver detection range where the transmitter cannot be located (e.g. in crevices, holes, behind big boulders, etc.) may result in non-realistic bridges. As an example, if an animal went from receiver A to receiver C, without being detected at the intermediate receiver B, then a non-realistic bridge would be modelled. Thus, it is important to check that no gaps without transmitter detection exist between receivers. Thirdly, the amount of uncertainty of utility distribution and home range area estimation through BBMM is dependent on the amount of location error. In acoustic telemetry, location errors are dependent on receivers' detection ranges. In our case, we used a single location error to calculate BBMM (the average of the 4 receivers most used by *S. salpa* and encompassing varying proportions of each habitat, see Fig S1a), but according to Horne et al. (2007), if researchers have reasons to believe that each location (i.e. in acoustic telemetry, each receiver) has a unique error, this can be incorporated into the BBMM. For example, if receivers within different habitat types consistently displayed differential detection ranges, as it has been observed in coral reefs (Welsh et al. 2012), one could perform the BBMM with a location error for each habitat. Nevertheless, the method is resilient to small differences on location error (see

Fig S10, which shows the output of BBMM with our data set using different location errors).

Spatial patterns

Demersal fishes have been generally found to display restricted home ranges and high site fidelity (e.g. Chapman & Kramer 2000, Topping et al. 2005, March et al. 2010, Alós et al. 2012). These small home range sizes do not prevent fishes to connect habitats that are close enough one to each other. For example, habitat connection has been thoroughly demonstrated for Haemulidae fishes in back-reef habitats (Meyer et al. 1983, Verweij & Nagelkerken 2007). However, we found that *S. salpa* displayed large home range areas (overall mean of individual home ranges = 134 ± 10 ha) that encompassed different kinds of habitats and ecosystems, with high variability among individuals. This was true for resident and for non-resident fishes (Table S1). Inter-individual variability in home range size has been generally found, both for *S. salpa* (Jadot et al. 2002), as well as for other species (e.g. Marshell et al. 2011). In addition, we found that *S. salpa* fishes conducted long trips (on the order of some km) between distant habitats. Indeed, they even often crossed the sand channel that separates Medes Islands from the coast (see the bridge between the islands and the coast in Fig. 1b,d, see also Table S1), although several studies have shown that species usually avoid crossing habitat edges, especially among those that are highly contrasting (known as hard edges), such as seagrass-sand edges (Chapman & Kramer 2000, Haynes & Cronin 2003, 2006).

Despite its large mobility, resident *S. salpa* fishes showed a clear and long-term (i.e. one year) preference for the seagrass meadow evidenced by the high utilisation of this habitat, where they spent more than 88% of time on average. They allocated a low proportion of time to rocky compared to seagrass systems, but the connection between both types of habitats was non-negligible. In contrast, non-resident fish (75% of the tracked individuals) were characterised by frequent excursions out of the receiver array and by a very short tracking period that resulted in a much lower number of detections. Hence, it is difficult to fully assert whether this group could have a major role in connecting the habitats within the network of receivers to other distant habitats or whether they were simply residents in seagrass habitats out of the network of receivers only sporadically visiting the area of study. Because of that, non-resident estimates of space use and home ranges should be viewed as minimum areas of utilisation, since these could be biased due to their low number of detections within the array.

Temporal patterns

Temporal trends within each habitat were also observed. *S. salpa* was more often detected in the seagrass at night than during the day; this cycle was consistent despite the fact that *S. salpa* is a diurnal feeder that increases its activity during daytime (Verlaque 1990, Ferrari 2006). There is some controversy on how cycles on the rate of detections may arise. It has been suggested that detection frequency and movement rate may be negatively correlated (Topping et al. 2005), or even that cycles may arise as a result of the environmental noise (Payne et al. 2010), but a growing number of studies have related changes in habitat use with diel cycles (March et al. 2010, Alós et al. 2011, Alós et al. 2012). In our case, the generating mechanism is very likely to be related to the loss of acoustic transmission inside the canopy of seagrass meadows, already described by other authors (which can decrease the number of detections by up to 80%, March et al. 2010). The aforesaid technical restriction could, in fact, be used as a proxy for *S. salpa* activity in the meadow. For this species it is well established that diurnal time is allocated to foraging in the seagrass (Verlaque 1990, Ferrari 2006), thus, the low detection rates observed during the day may mean the animal is feeding in the meadow, in close contact with the canopy, which is known to produce high acoustic losses. Conversely, at night the higher number of detections might suggest the animal is outside the canopy. This day-night cycle on the number of detections per hour was sustained for at least 6 months, as shown by the CWT analysis, and no effects of seasonality were evident despite both seagrass and macroalgal biomass and production have a seasonal pattern in the study area (Alcoverro et al. 1995, Hereu et al. 2008). Diel cycles had already been identified for this species on the short-term (i.e. one month, Jadot et al. 2006), but it was unclear whether these were maintained for the whole year, since it had been suggested that *S. salpa* fishes conducted a migration from shallow waters to deeper ones (i.e. below 30 m) in autumn-winter in order to spawn (Verlaque 1990). Our results challenge this migration hypothesis, in spite of the low number of fishes studied.

Additionally to the cycle on hourly detection rates, a diel cycle on depth use was also observed in the seagrass habitat, with mean depths moving from 4-5 m at daytime to 9-10 m at night (see inset Fig. 2a). These results match with the results discussed in the previous paragraph and with the higher herbivory rates generally observed on shallow areas compared to deeper ones (Vergés et al. 2012). Indeed, in the studied seagrass meadow it may be optimal to restrict feeding activity to the shallow waters, where seagrass is 2.7 times denser and with 3 times more cover compared to the deeper part of the meadow (Romero et al. 2012). High detection rate in deeper grounds at night give us a clue on the behaviour of this species that has been described to rest at night at the seagrass-sand edge (Ferrari 2006, Jadot et al. 2006) (see that the seagrass-sand edge is at ca. 10m in Fig. 1a). Thus, *S. salpa* fishes could be exporting organic matter from their feeding grounds (shallower parts of the meadow) to their resting sites (seagrass-sand edge), as has been observed for other mobile fishes (Meyer et al. 1983, Verweij & Nagelkerken 2007). Conversely these diel patterns on depth preference were not observed in rocky habitats.

Conclusions

The integration of the spatial and temporal habitat use with both fish mobility and the proportion of area occupied by each habitat in the seascape mosaic identifies the fish *S. salpa* as a potential mobile link. While previous studies pointed out that *S. salpa* acted as a key herbivore in seagrass and rocky macroalgal habitats independently (e.g. Prado et al. 2007, Vergés et al. 2009), our study connects the use of both habitats by the same individuals. On the one hand, mobile links can potentially transfer energy, matter and other functions (Nyström & Folke 2001, Lundberg & Moberg 2003). Energy and matter transfer might be provided by *S. salpa*, since fishes foraging in seagrasses have been observed to defecate pellets with algal traces from nearby rocky reefs and vice versa (Tomas et al. 2010). The long gut transit times (ca. 5 gut lengths per body length; Havelange et al. 1997) observed in *S. salpa* could facilitate this transfer. However, since the studied fishes spent most of the time on seagrass habitat, the main transfer of energy would be between shallow and deep areas of the meadow at a daily basis (see previous paragraph). On the other hand, *S. salpa* is also a voracious herbivore, substantially shaping seagrass and macroalgal habitats. Even though the proportion of seagrass habitats in the studied area was clearly lower than macroalgal-dominated rocky areas (Fig. 1a), the fishes spent more time on seagrass habitat, and thus, seagrasses would be more susceptible to grazing by *S. salpa* than macroalgal communities from rocky areas. In this work we did not directly assess the relationship between *S. salpa* movement patterns and their functional consequences in the ecosystem. However, works in the same geographic area suggest that the movement patterns we have found resonate with grazing intensity spatial patterns. In Medes Islands area, *S. salpa* has been observed to intensively defoliate seagrass plants in summer (Tomas et al. 2005, Prado et al. 2007) compared to a more limited fish grazing effect in macroalgal communities (Hereu et al. 2008). Thus to understand the seascape-dependent distribution of fish herbivory impacts it becomes important not merely to know the consumption rates, diets and preferences of these species within the system, but also herbivore movements across time and space, along with the spatial configuration of the seascape mosaic.

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Table 1. Analyses of variance performed. d.f. degrees of freedom. Significance codes: P-value < 0.001***, < 0.01**, ≤ 0.05*

Response variable	**Effect**	**Df**	**F-value**	**P-value**
Fish depth	Phase	1	12.6608	0.0026 **
	Habitat	1	5.0128	0.0397 *
	Phase × Habitat	1	2.0811	0.1684
	Residuals	16		
Frequency of detections	Habitat	1	96.87955	<.0001 ***
	Season	1	1.00469	0.3262
	Phase	1	55.51481	<.0001 ***
	Habitat × Season	1	0.73442	0.3999
	Habitat × Phase	1	112.90516	<.0001 ***
	Season × Phase	1	9.12524	0.0059 **
	Habitat × Season × Phase	1	2.35231	0.1382

Fig. 1. Spatial patterns. (a) Study site's map of habitats with isobaths. Numbers (1-4) represent the fishing-releasing sites (see methods). (b) BBMM space use estimation for resident and non-resident populations. Note a higher intensity of use on the area with seagrass (specially for residents). (c) Log–log plot of the probability of making excursions of time 'x' in 'Meadow' and 'No-meadow' habitats. Note the higher probability of conducting very long excursions in 'No-meadow' habitats compared to 'Meadow' ones. (d) Residents' mean excursion duration and percentage of consecutive revisits for each receiver. The shaded area corresponds to the result of the space use estimation through BBMM for residents (same legend as Fig. 1b).

Fig. 2. Depth patterns. Number of diurnal and nocturnal detections classified by depth in (a) seagrass and (b) rocky systems. The insets show the mean depth along the 24 hours of the day. Note that a 24-hour depth cycle is evident in the seagrass (inset (a)) whereas this is not the case in rocky systems (inset (b)).

Fig. 3. Temporal patterns of the frequency of hourly detections pooling all residents. (a) The mean number of detections per hour (pooling all residents) evidences a diel cycle, with higher detection rate at night compared to daytime. (b) Wavelet spectrum for the number of hourly detections of resident fishes pooled together. Significant cycles were detected for a 24 h period (horizontal dashed line) and for periods around 512 hours (21 days). The thick contour designates the 95% confidence level. The cone of influence where edge effects might distort the picture is shown as a lighter shade. The scale bar represents the intensity of the time-frequency space over time.

Fig. 1

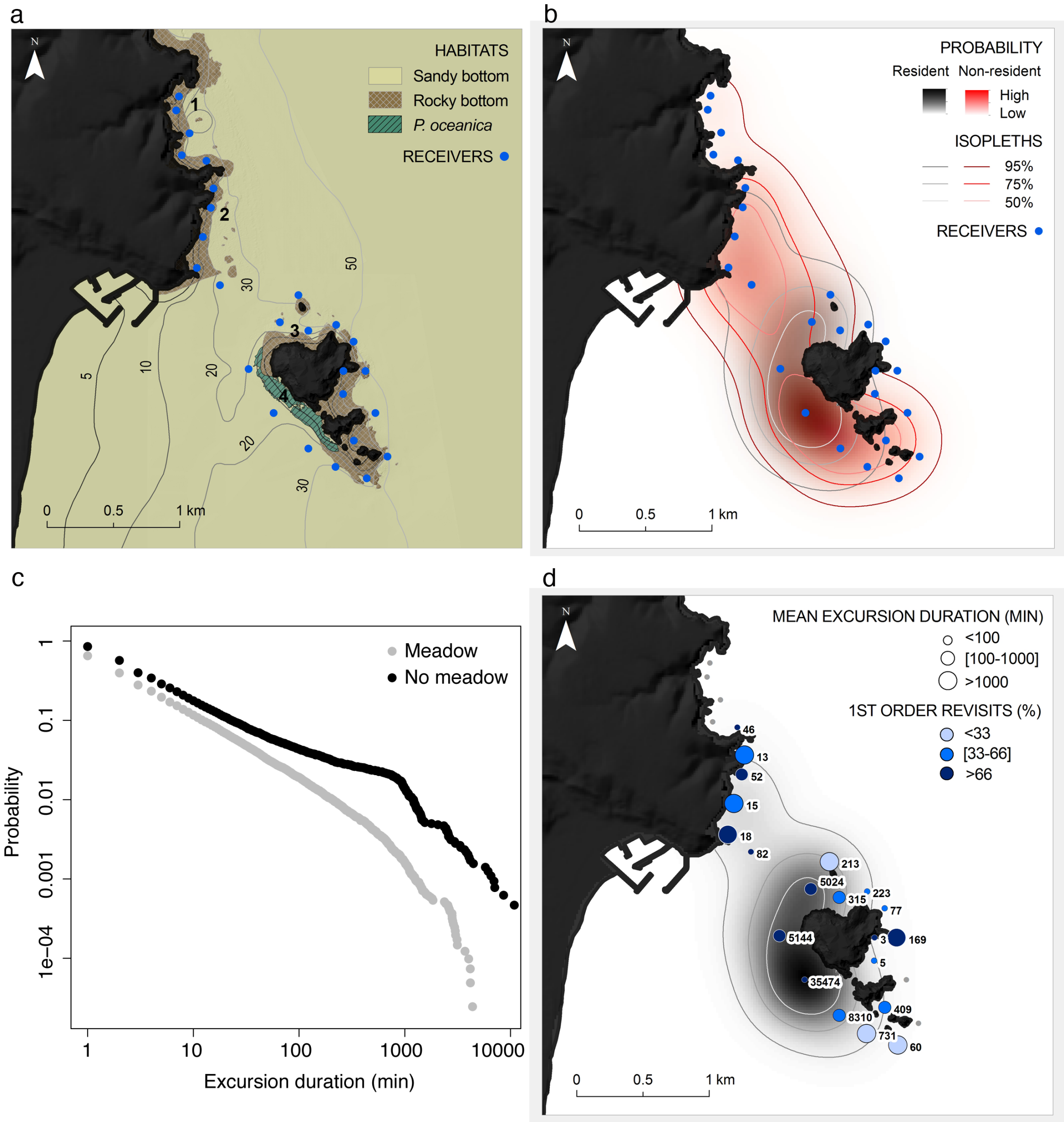

a
HABITATS
Sandy bottom
Rocky bottom
P. oceanica
RECEIVERS
1
2
3
4
5
10
20
30
50
0
0.5
1 km
b
PROBABILITY
Resident
Non-resident
High
Low
ISOPLETHS
95%
75%
50%
RECEIVERS
0
0.5
1 km
c
Meadow
No meadow
Probability
1
0.1
0.01
0.001
1e−04
1
10
100
1000
10000
Excursion duration (min)
d
MEAN EXCURSION DURATION (MIN)
<100
[100-1000]
>1000
1ST ORDER REVISITS (%)
<33
[33-66]
>66
46
13
52
15
18
82
213
5024
315
223
77
5144
169
3
5
35474
409
8310
731
60
0
0.5
1 km

Fig. 2

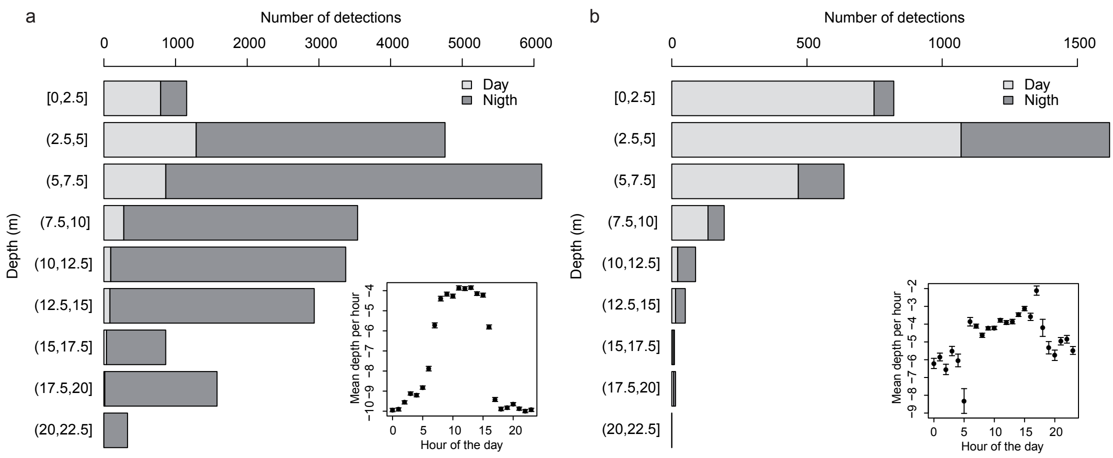
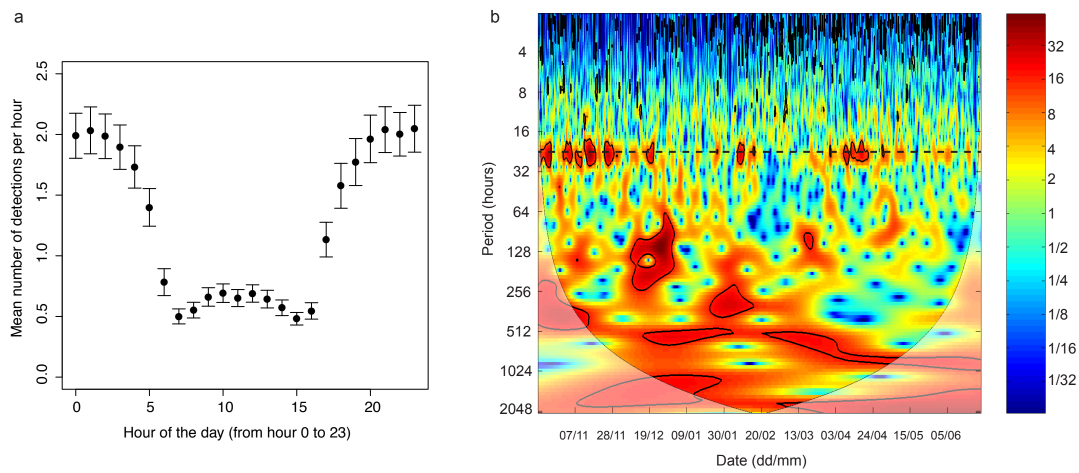

a
Number of detections
0
1000
2000
3000
4000
5000
6000
Day
Nigth
Depth (m)
[0,2.5]
(2.5,5]
(5,7.5]
(7.5,10]
(10,12.5]
(12.5,15]
(15,17.5]
(17.5,20]
(20,22.5]
Mean depth per hour
−10 −9 −8 −7 −6 −5 −4
0 5 10 15 20
Hour of the day
b
Number of detections
0
500
1000
1500
Day
Nigth
Depth (m)
[0,2.5]
(2.5,5]
(5,7.5]
(7.5,10]
(10,12.5]
(12.5,15]
(15,17.5]
(17.5,20]
(20,22.5]
Mean depth per hour
−9 −8 −7 −6 −5 −4 −3 −2
0 5 10 15 20
Hour of the day

Fig. 3.


a
Mean number of detections per hour
0.0
0.5
1.0
1.5
2.0
2.5
0
5
10
15
20
Hour of the day (from hour 0 to 23)
b
Period (hours)
4
8
16
32
64
128
256
512
1024
2048
07/11
28/11
19/12
09/01
30/01
20/02
13/03
03/04
24/04
15/05
05/06
Date (dd/mm)
32
16
8
4
2
1
1/2
1/4
1/8
1/16
1/32

Supplementary Materials

Evaluating a key herbivorous fish as a mobile link: a Brownian bridge approach

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BBMM implementation

To implement BBMM, the data set of each animal should contain a column of coordinate locations and a column with the time each location was reached. In passive acoustic telemetry, location coordinates are those of the receiver that is detecting a given transmitter. However, since the BBMM allows for uncertainty around the starting and ending locations (i.e. location error), the real location is not a constant position, but a Gaussian probability density function around that point (with a mean, i.e. the receiver coordinates; and a variance around that mean, i.e. receiver's detection range, in our case 250 m) (Horne et al. 2007). The column with the time stamps is used to produce a vector of time lags between locations. Since this is a vector of increments of time, its length is thus a row less than the column of time and coordinates. Care should be taken to remove from the data set simultaneous receptions from the same fish (i.e. leading to time lags equal to zero; e.g. if the fish was detected by two or more overlapping receivers at the same time, or for any other reason). See the first rows of SS91 data set (Table S2) prepared for BBMM estimation of the UD.

Calculations were performed in R (RDevelopmentCoreTeam 2012) using the package BBMM (Nelson et al. 2011), which computed the UDs for each fish by assigning a probability to each cell of a grid (in our case the grid = 226 x 226 cells, cell size = 20 m). To avoid assigning a space use probability to land cells, we subtracted all land probabilities ad hoc and renormalized the UD cell matrix sum to 1, given that utilisation distributions are probability density functions (Powell 2000).

Table S1. Summary of the monitoring data for the 18 successfully tracked fish. ID = fish code; TL = total length; DD = number of days detected; TP = tracking period (total period of detection); TD = total number of detections; RI = residence index; NR = number of receivers that detected each fish; AR = area of release; Rel. Date = date the fish was released (yyyy/mm/dd); HR size = home range size; Connect.I-C = did the fish moved between the islands and the coast?

ID	TL (cm)	DD (days)	TP (days)	TD	RI	NR	AR	Rel. Date	HR size (ha)	Connect.I-C
SS70	28	22	28	308	0.79 (resident)	3	4	2008/10/16	87.88	no
SS77	25	96	98	15473	0.98 (resident)	10	3	2008/10/16	140.08	yes
SS78	27.5	12	184	182	0.07 (non-resident)	9	3	2008/10/16	138.2	yes
SS79	27	18	206	250	0.09 (non-resident)	6	3	2008/10/16	124	no
SS80	27	20	93	248	0.22	7	1	2008/10/16	-	no
SS81	26	26	51	607	0.51 (non-resident)	16	1	2008/10/16	118.64	yes
SS82	22.5	3	3	237	1	9	3	2008/10/16	-	no
SS83	27	4	216	48	0.02	3	1	2008/10/16	-	no
SS84	24	7	95	42	0.07	4	1	2008/10/16	-	no
SS85	25	2	5	57	0.40	11	1	2008/10/16	-	yes
SS86	23	14	27	86	0.52 (non-resident)	4	2	2008/10/17	88.08	no
SS87	23.5	4	84	279	0.05	2	2	2008/10/17	-	no
SS88	23	1	1	45	1	1	2	2008/10/17	-	yes
SS89	22.5	3	179	227	0.02 (non-resident)	4	2	2008/10/17	153.12	yes
SS90	25	8	35	23	0.23	2	3	2008/10/16	-	yes
SS91	28	346	372	24330	0.93 (resident)	15	4	2008/10/16	123.92	yes
SS92	32	79	112	10764	0.71 (resident)	12	4	2008/10/16	175.64	yes
SS93	34	62	71	5557	0.87 (resident)	17	4	2008/10/16	187.44	yes

Table S2. First rows of SS91 data set prepared for BBMM estimation of the UD. The first column corresponds to the time the fish reached each location (in Julian minutes in this case), the second column are the UTM coordinates on the x-axis and the third column the UTM coordinates on y-axis. The time lags between locations are the difference between the time the next location will be reached and present time.

Julian	**x**	**y**
20403030	518238.2	4654958
20403040	518238.2	4654958
20403043	518238.2	4654958
20403059	518238.2	4654958
20403074	518499.5	4654690
20403077	518238.2	4654958
20403082	518238.2	4654958
20403088	518238.2	4654958
20403093	518238.2	4654958
20403097	518238.2	4654958
20403102	518238.2	4654958
20403107	518238.2	4654958
20403121	518238.2	4654958
20403127	518238.2	4654958
20403136	518238.2	4654958
20403142	518238.2	4654958
20403146	518238.2	4654958
20403150	518238.2	4654958
20403154	518238.2	4654958
20403159	518238.2	4654958

Fig. S1. (a) Map showing the 4 receivers for which range tests were conducted. (b) Barplot showing the probability of tag detection at increasing distances from acoustic receivers. Note the sharp drop in tag detection for distances beyond 100 m and the undetectability of tags beyond 250 m.

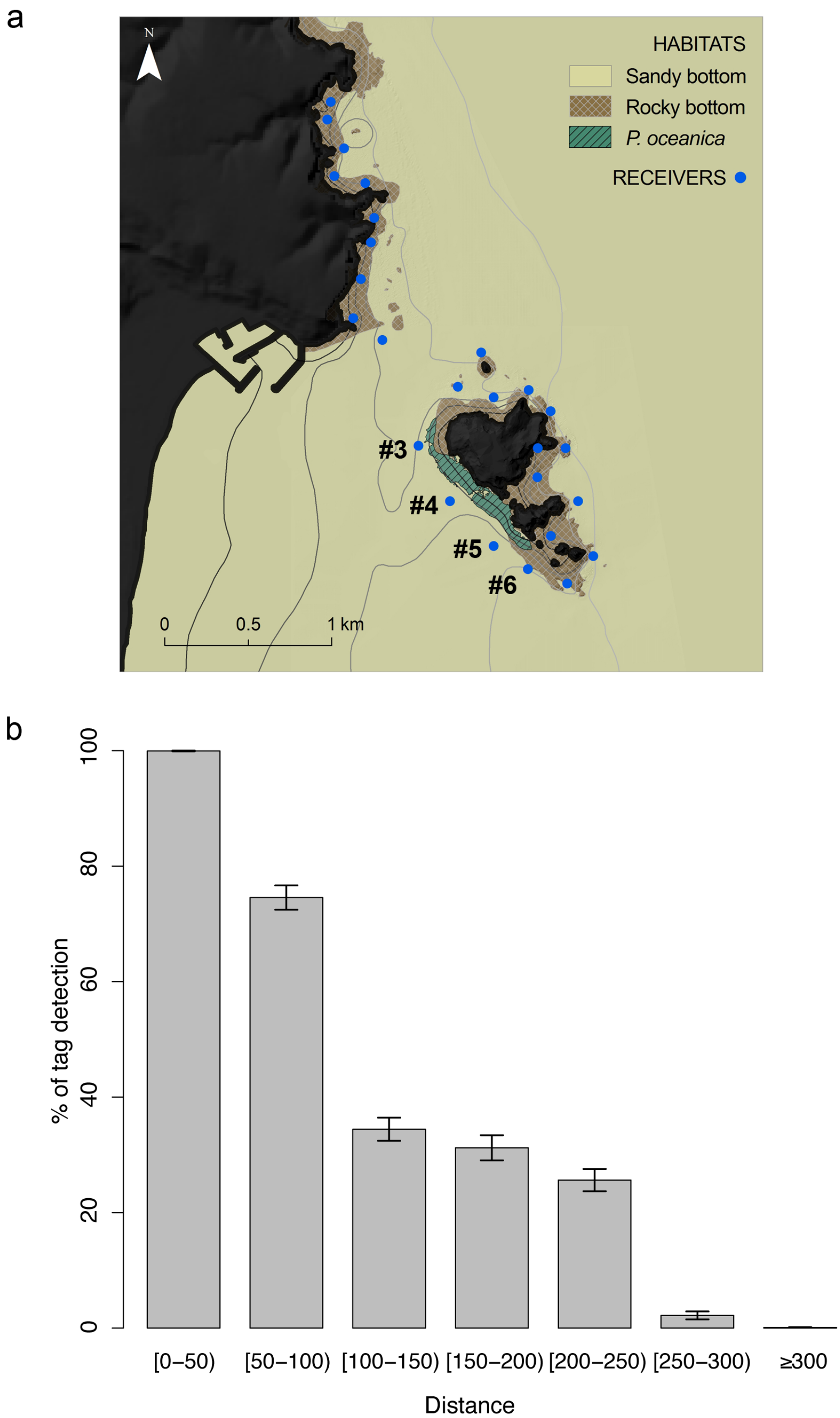


Fig. S2. Raw data distribution. Bar width on the X-axis relates to the number of total detections per fish. Bar length on the Y-axis relates to the number of detections per receiver for that fish. Note that the vast majority of detections (95.5 %) come from only four fishes (SS77, SS91, SS92, SS93). These fishes plus SS70 were considered resident to our receiver network, since they spent within the array more than the 60 % of days of their tracking period (see Table S1). Note also that receivers #3, #4 and #5 accumulate most of detections. These receivers presented seagrass habitat ('meadow') within their range.

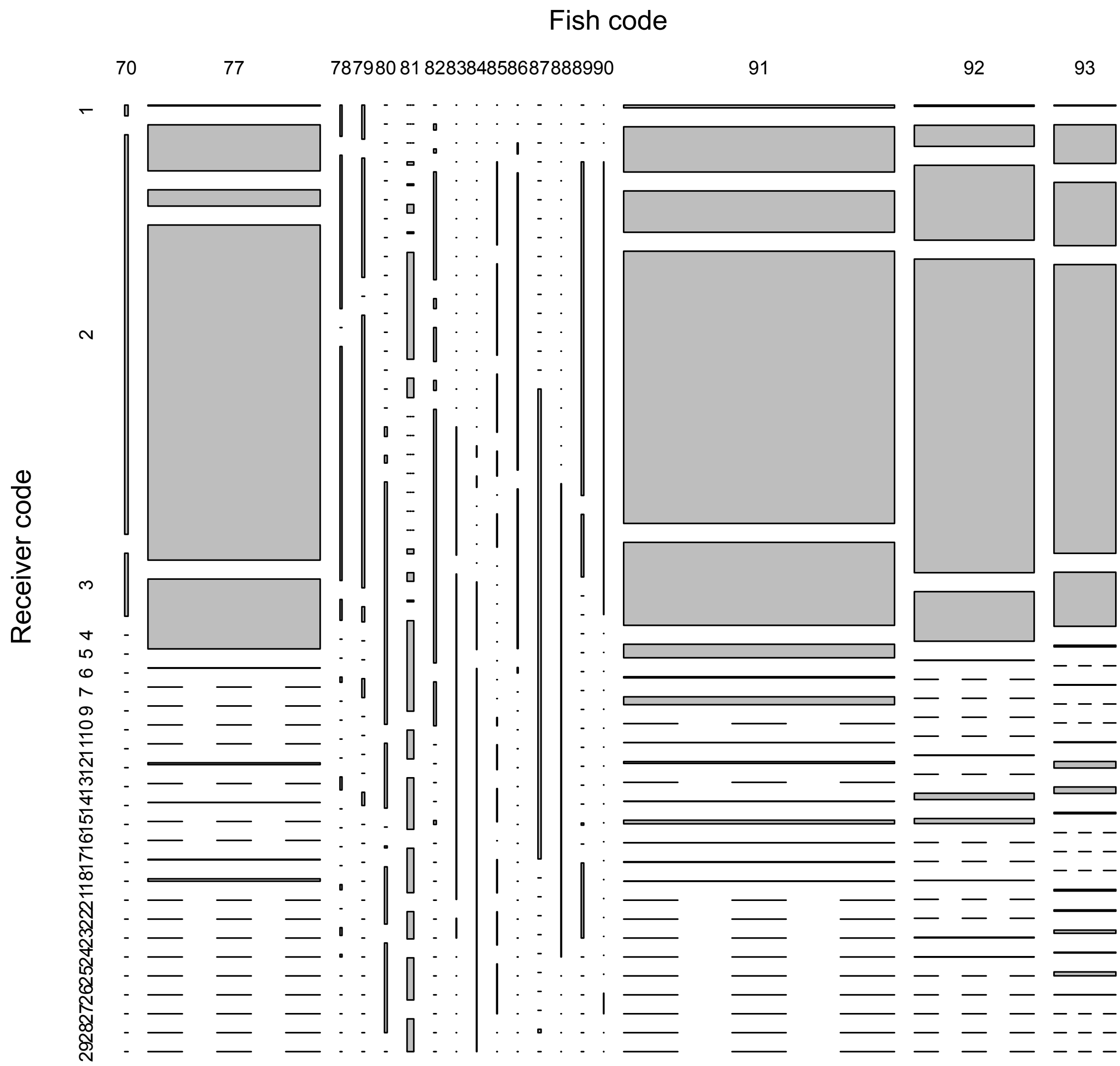
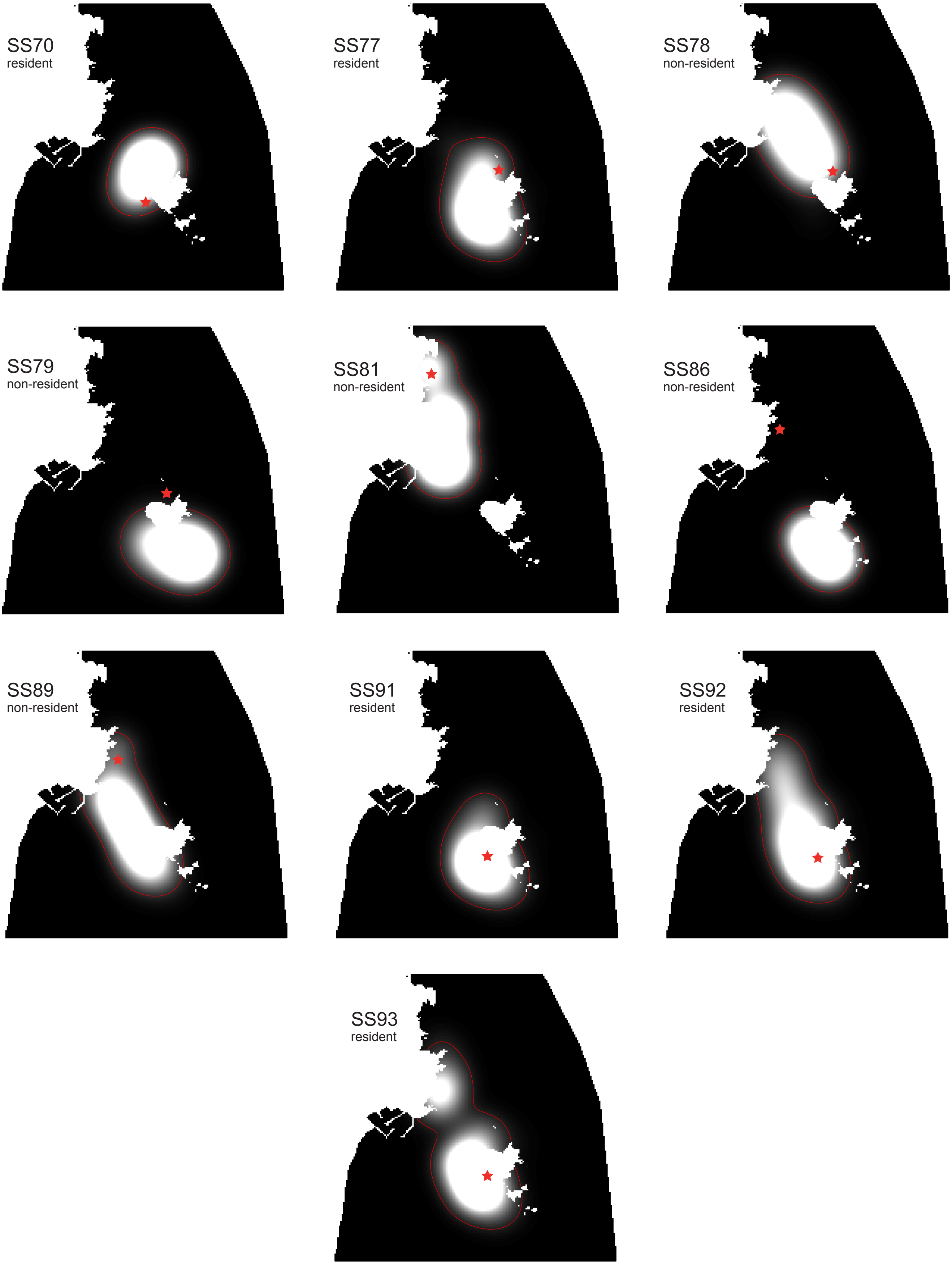


Fig. S3. Individual BBMM utility distributions of all fishes. Black colours indicate low probability and colours from grey to white indicate increasing probabilities of finding an individual. The red line encompasses the 95 % probability of use for a given individual. Stars correspond to the respective sites of capture and release. Note that resident fishes used with a high intensity the areas corresponding to seagrass habitat in Fig. 1a (from the main manuscript). In addition, 3 out of 5 non-resident fishes did also use these meadow areas. Note also, that while fish SS78 very frequently connected the islands with the coast, other fishes (e.g. SS89, SS92, SS93) connected both areas regularly (both areas enclosed by the 95 % isopleth [red line]).



SS70
resident
SS77
resident
SS78
non-resident
SS79
non-resident
SS81
non-resident
SS86
non-resident
SS89
non-resident
SS91
resident
SS92
resident
SS93
resident

113

Fig. S4. Day and night mean depths for the resident population in meadow and no-meadow habitats. Different lower case letters indicate significant statistical differences. There were significant differences in fish mean depth according to the phase of the day in meadow habitat, but not in no-meadow habitat.

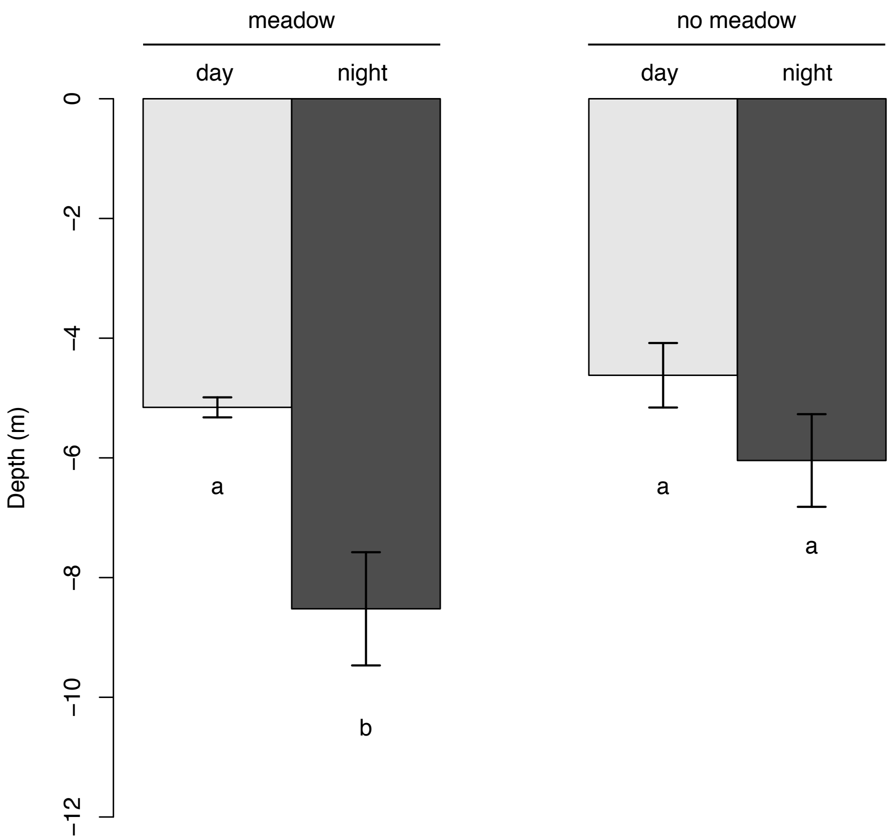


Fig. S5. Day (light grey) and night (dark grey) mean % of detections for the resident population (a) in meadow and no-meadow habitats and (b) in different seasons. Different lower case letters indicate statistical significant differences.

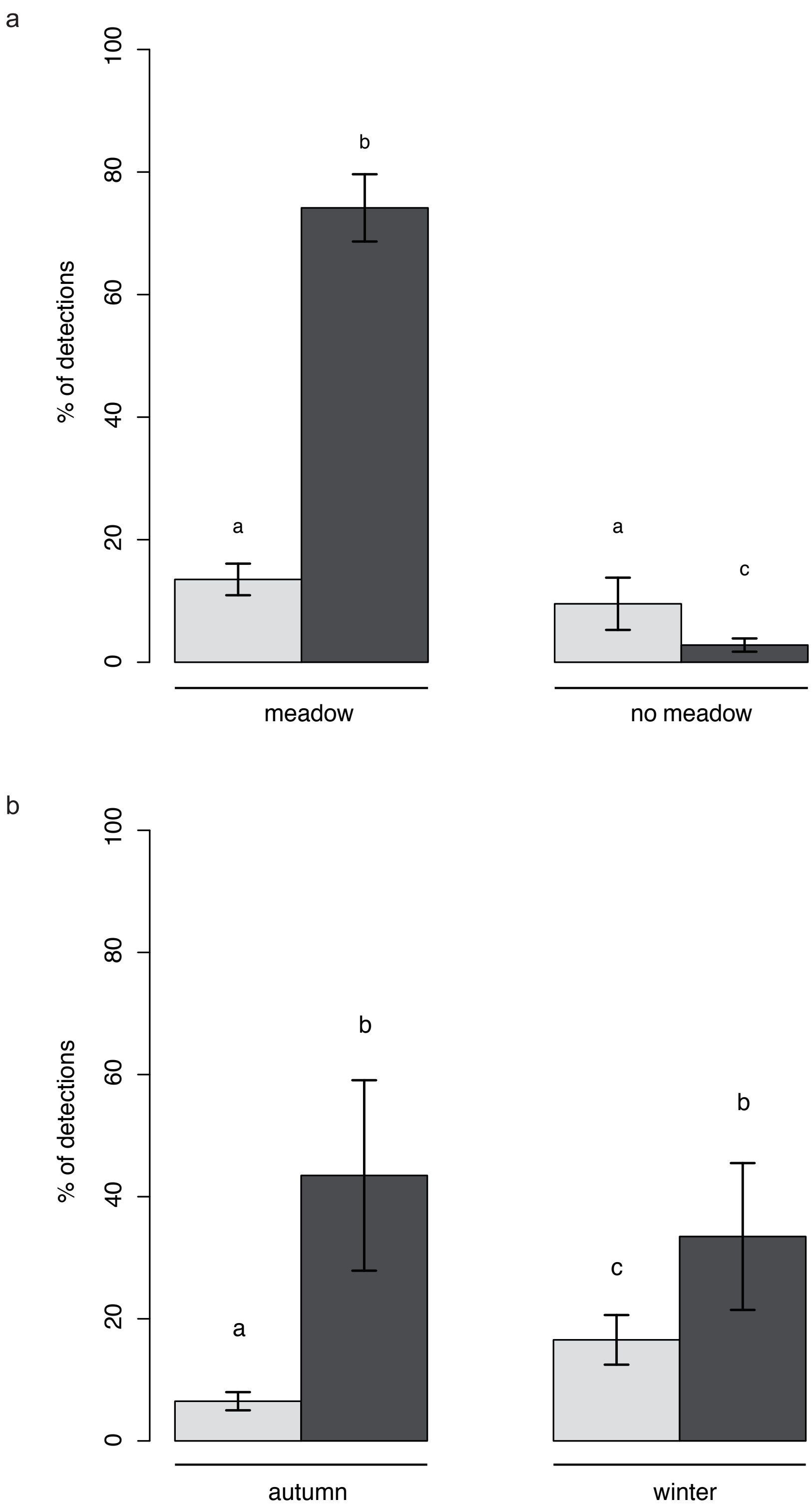


Fig. S6. Resident fishes' number of hourly detections for a subset of the time series. Vertical stripes indicate day (white) and night (grey) related to the local sunrise and sunset time. Note the higher number of nocturnal detections for fishes SS77, SS91, SS92 and SS93 and a reversed cycle (i.e. higher number of diurnal detections) for fish SS70.

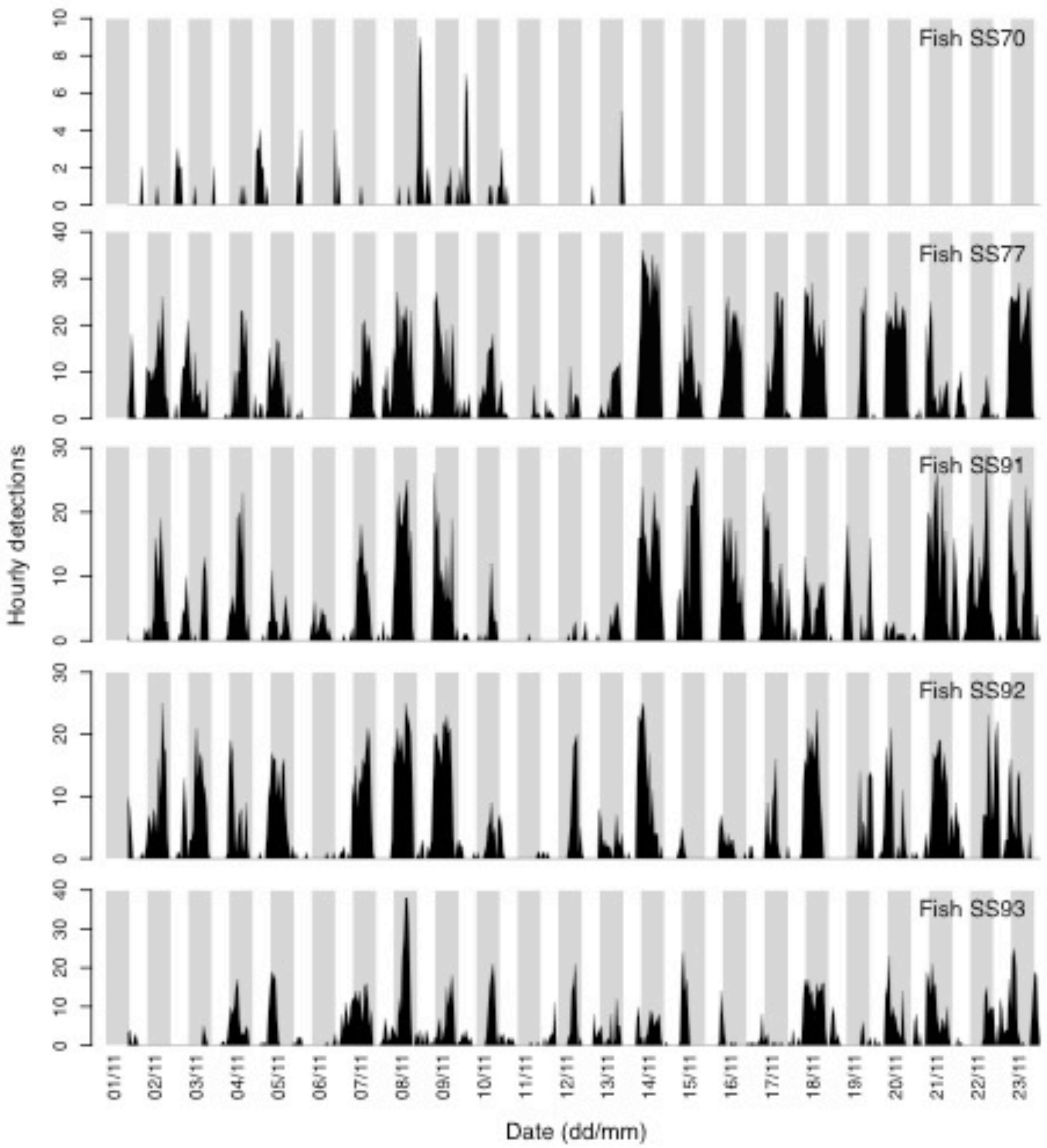


Fig. S7. Individual temporal patterns of the mean number of hourly detections for resident fishes along a 24h cycle. Note the different scales on the y-axis. We observe that 4 out of 5 resident fishes behaved very similarly, with only fish SS70 with a reversed cycle, but with a lower contribution to the whole dataset compared to the rest of fishes (see Table S1 and Fig S2). Note this temporal pattern (24 h cycle) remains visible even after taking the average of these 5 resident fishes (see Fig. 3a from the main manuscript).

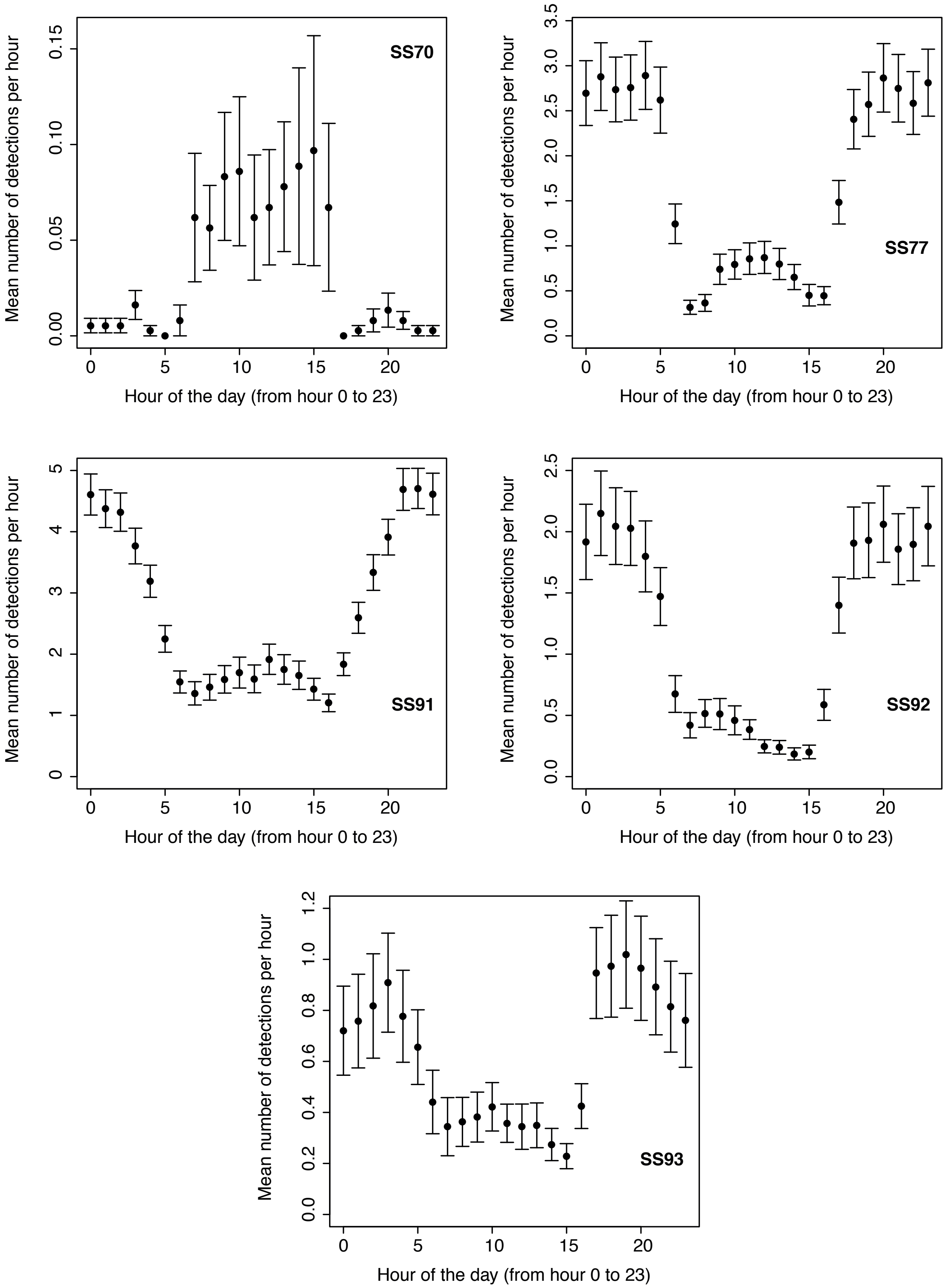


Fig. S8. Wavelet spectrum for the number of hourly detections of each resident fish individually. Significant patches on the 24 h period were detected for all residents (horizontal dashed line). The pattern was significant (with some non-significant patches) for most of the time series for fish SS77, SS91 and SS92. It was less evident for fish SS93. Fish SS70 had also a significant 24 h cycle but, with a reversal in the phase (see Fig. S6, S7). Since all resident fishes displayed similarities also on these analyses, the wavelet spectrum for the pooled population of resident fishes gave very similar results (see Fig. 3b main manuscript). The thick contour designates the 95% confidence level. The cone of influence where edge effects might distort the picture is shown as a lighter shade. Light rectangles correspond to holes in the time-series without fish detections where assessing periodicity makes no sense. The scale bar represents the intensity of the time-frequency space over time.

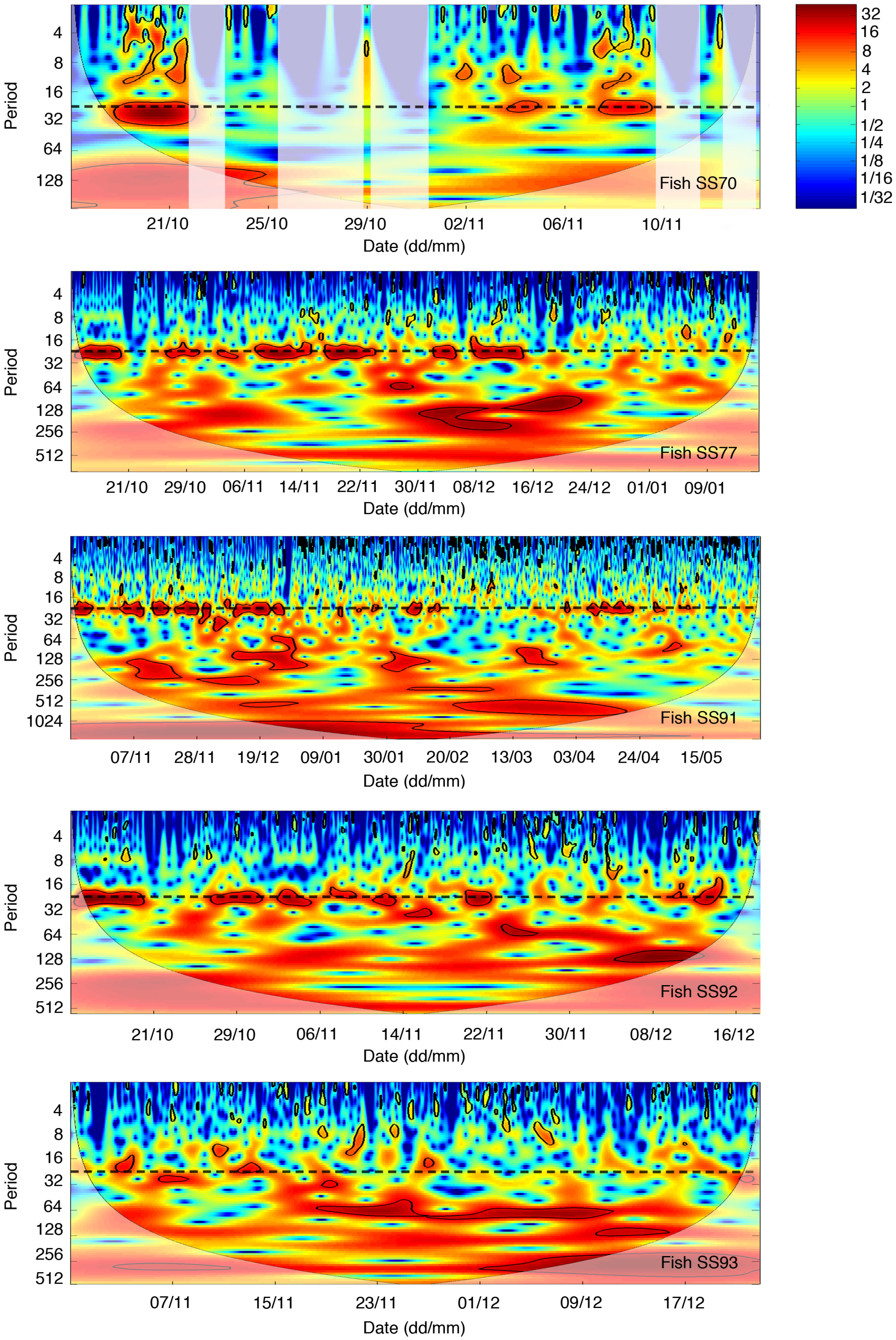

Period
4
8
16
32
64
128
21/10
25/10
29/10
02/11
06/11
10/11
Date (dd/mm)
Fish SS70
32
16
8
4
2
1
1/2
1/4
1/8
1/16
1/32
Period
4
8
16
32
64
128
256
512
21/10
29/10
06/11
14/11
22/11
30/11
08/12
16/12
24/12
01/01
09/01
Date (dd/mm)
Fish SS77
Period
4
8
16
32
64
128
256
512
1024
07/11
28/11
19/12
09/01
30/01
20/02
13/03
03/04
24/04
15/05
Date (dd/mm)
Fish SS91
Period
4
8
16
32
64
128
256
512
21/10
29/10
06/11
14/11
22/11
30/11
08/12
16/12
Date (dd/mm)
Fish SS92
Period
4
8
16
32
64
128
256
512
07/11
15/11
23/11
01/12
09/12
17/12
Date (dd/mm)
Fish SS93

Fig. S9. Utility distributions of resident fishes obtained with the kernel density estimator (KUD). Differences between panels arise as a result of different smoothing parameters: (a) h = 50, (b) h = 100, (c) h = 250. Solid lines correspond to the 50% and 95% isopleths, and cooler colours indicate higher intensity of use. While the BBMM successfully identified connections between the islands and the coast (see Fig 1b,d in the main manuscript), KUD did not. In addition, the BBMM identified specific connections (bridges) between receivers with a higher intensity of use than others. This is not possible with the KUD, since it only takes location distribution into account. In contrast, the BBMM considers not only the locations but also the time dependence between them (the actual path the animal has followed), assumes the animal has moved following a conditional random walk between pairs of locations and allows for accounting for a location error (in our case we specified a telemetry error of 250 m).

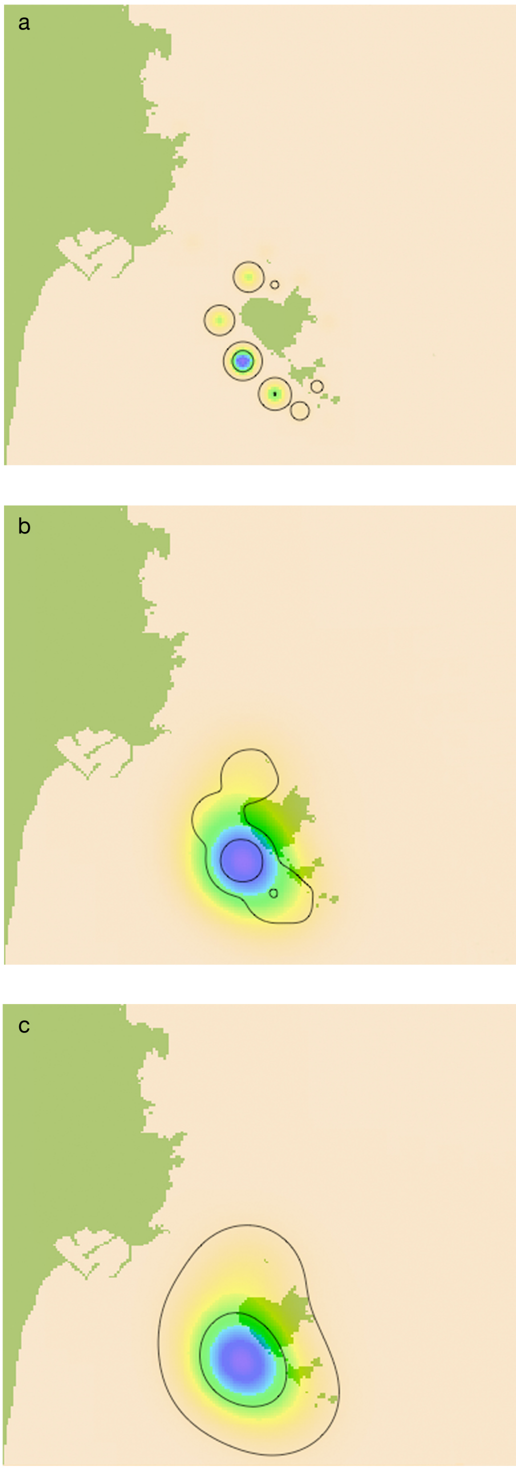
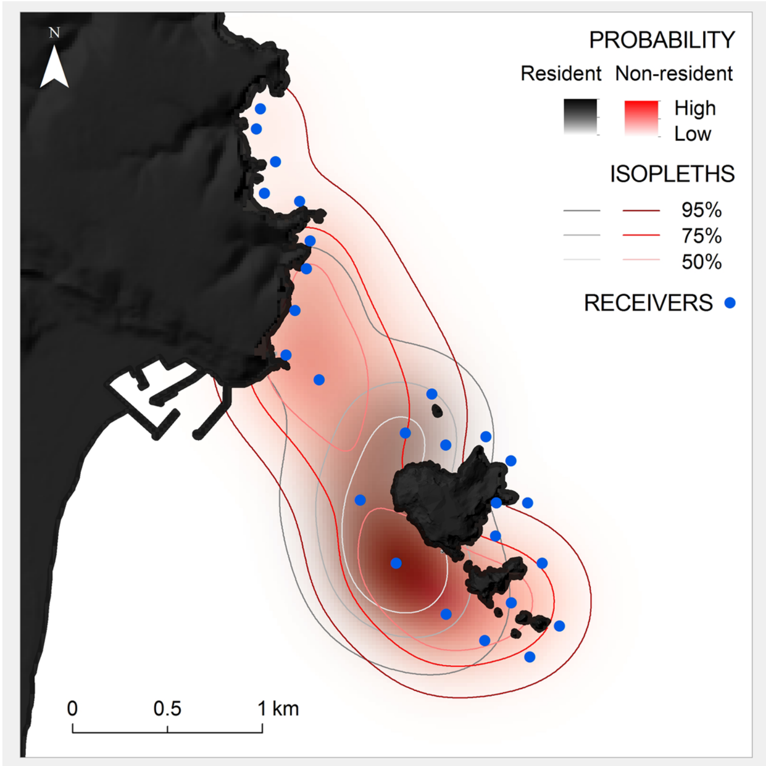
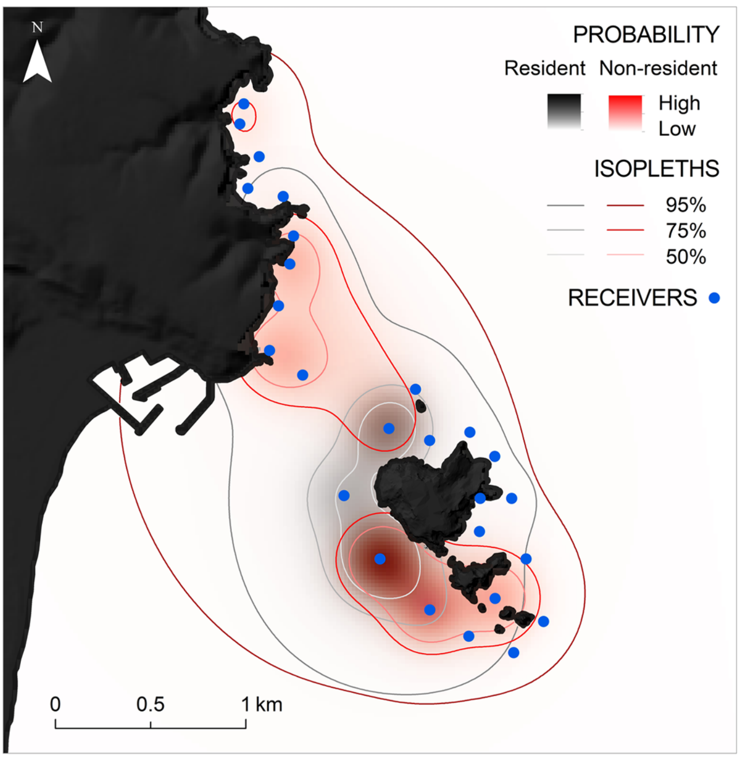

a
b
c

Fig. S10. Comparison of the BBMM output using a location error of 250 m (a) and a location error of 150 m (b). Note the BBMM with greater location error (a) concentrates the probability of use on a wider area around each receiver, and that this implies a smaller utility distribution, since the total probability sum must still be equal to 1 (remember a UD is a probability density function).

a



b



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