

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

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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 (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:  $103 \pm 22$  d) 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:  $134 \pm 10$  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 fish 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

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## INTRODUCTION

Mobile links are organisms able to move between habitats and ecosystems, supporting 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

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are key organisms, as is the case with 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 organisation 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, 2 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 on different coastal habitats, by e.g. consuming a great proportion of seagrass annual primary production (Prado et al. 2007), drastically reducing seagrass canopy structure that can foster predation on seagrass-dwelling organisms (Pagès et al. 2012), or influencing the vertical distribution of canopy-forming algae (Vergés et al. 2009), as well as in other ways (e.g. Sala &

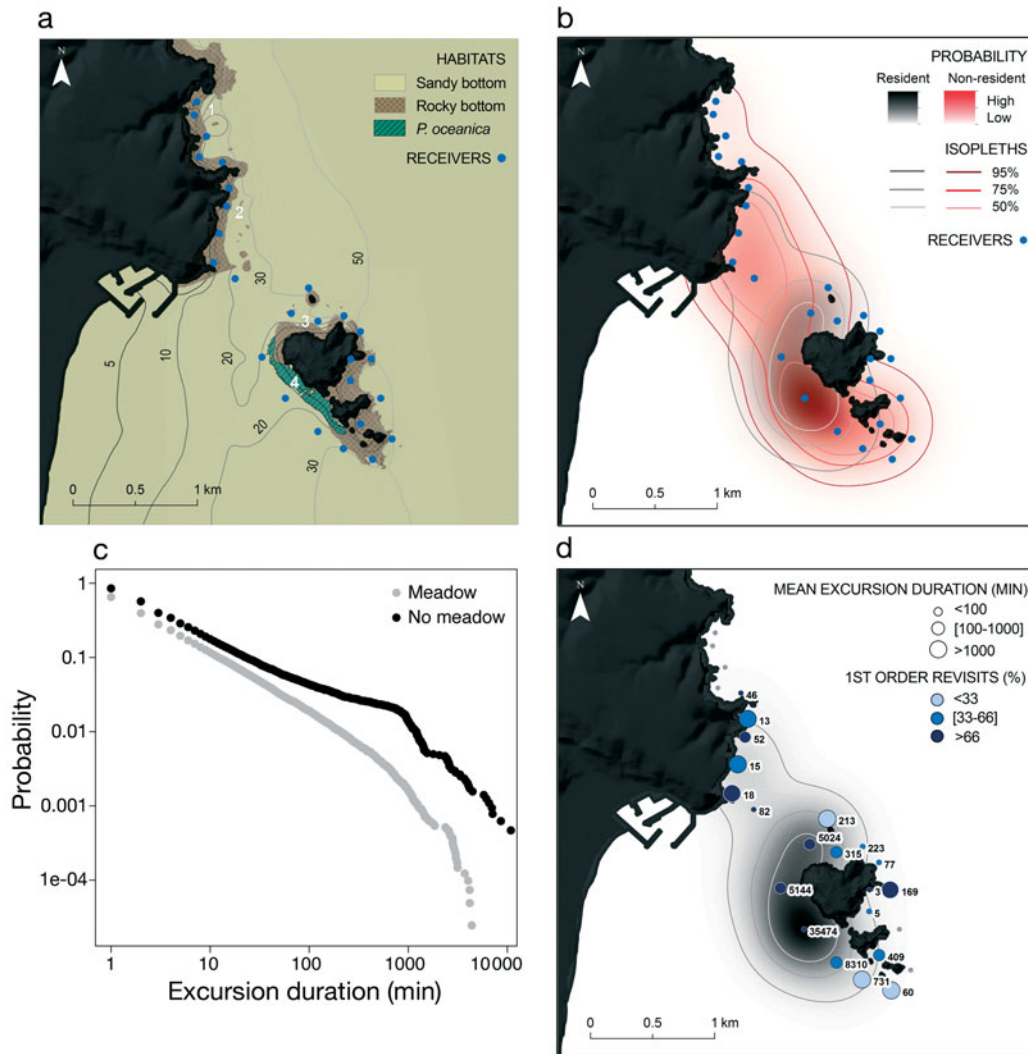
Boudouresque 1997). *S. salpa* are diurnal browsers and generalist herbivores, allocating most of their daytime to foraging (ca. 65% of their time) in both seagrass (Ferrari 2006, Jadot et al. 2006, Abecasis et al. 2012) and rocky habitats (Tomas et al. 2011). Nevertheless, it remains unclear whether 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 *Sarpa salpa* commutes between different habitats in a seascape mosaic, and to 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* does use different habitats and commutes between them, and if these patterns are sustained over time, we would be able to discuss the potential of this species to be considered an active mobile link.

## MATERIALS AND METHODS

### Study area and receiver setup

This work was conducted between October 2008 and October 2009 in the Medes Islands Marine Protected Area and the adjacent unprotected stretch of coast, located in the NW Mediterranean. The study area is a mosaic of habitats composed of sandy bottoms, *Posidonia oceanica* seagrass meadows, and macroalgal communities in rocky habitats (our Fig. 1a; Hereu et al. 2010, 2011). Rocky areas (with macroalgal communities) occupy a larger area compared to seagrass communities (for each part of seagrass habitats, there are 9 parts of rocky habitats; Fig. 1a). A fixed array of 26 single-channel omnidirectional hydrophones (VR2 receivers, VEMCO)



**Fig. 1.** Spatial patterns. (a) Study site's map of habitats with isobaths (in m). Numbers 1 to 4 represent the fishing-releasing sites (see 'Materials and methods'). *P. oceanica* = *Posidonia oceanica*. (b) Brownian bridge movement model (BBMM) space-use estimation for resident and non-resident populations. Note a higher intensity of use in the area with seagrass (especially for residents). (c) Log-log plot of the probability of making excursions of a given duration 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. Shaded area corresponds to the result of the space use estimation through BBMM for residents (same legend as panel [b])

was deployed around the Medes Islands archipelago and along the coast. The receivers' detection range was established by mooring tags at different distances from 4 receivers for a 24 h period each. The receivers tested (#3, #4, #5, and #6; see Fig. S1a in the Supplement at [www.int-res.com/articles/suppl/m000pYYY\\_supp.pdf](http://www.int-res.com/articles/suppl/m000pYYY_supp.pdf)) were among the most used by *Sarpa salpa* (see 'Results' and Fig. S2 in the Supplement) 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 (>75%; Fig. S1b in the Supplement) up to 100 m distance

from the receivers, and between 100 to 250 m, the average percentage of detection remained at 25 to 35%. Tags placed at distances beyond 250 m were generally not detected (Fig. S1b in the Supplement). 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 was ca.  $25 \pm 2\%$ ) in order to prevent the existence of undetectable areas. Receivers were retrieved, data downloaded, receivers cleaned of bio-fouling, and redeployed 5 times during the study (in November 2008 and January, May, August, and October 2009).

### Acoustic tagging procedure

*Sarpa salpa* individuals were fished on 16 and 17 October 2008. Twenty fish were captured at 4 different sites (see Fig. 1a; 5 fish per site) during daytime using a seine fishing net by circling schools of *S. salpa* fish. Since there is no evidence of sexual dimorphism in 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 d. 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 4 of the most frequently detected 5 fish (called residents, see next section) were captured in the meadow zone (see Fig. 1a; Table S1 in the Supplement).

### 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). Fish with an RI > 0.6 (i.e. fish that were detected within the array of receivers for >60 % of days during their TP, and tracked >5 d) were considered 'resident' as opposed to the 'non-resident' ones (RI < 0.6). Utilisation distributions (UDs) and home ranges were assessed for both resident and non-resident fish. For non-residents, these estimations should be viewed as minimum areas of utilisation, since the estimates may be biased due to the 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 BBMM approach (Horne et al. 2007, Kranstauber et al. 2012) to estimate individual fish UD. UD estimation provides an objective way to define an animal's normal activities (Powell 2000). UD 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 UD for those individuals with >50 data points (locations) and >5 d detected (see Table S1 in the Supplement; 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 the 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 us to take location error into account (see Calenge 2011 for a thorough comparison between the KUD and BBMM methods) (biotelemetry error, i.e. 250 m in our case; see text section 'Brownian bridge movement model (BBMM) implementation' in the supplement for a complete explanation of BBMM implementation for our data set; see an example of a data set in Table S2 in the Supplement). BBMM calculations were performed in R (R Development Core Team 2012) using the package BBMM (Nelson et al. 2011).

### Home ranges

Individual fish UD obtained from the BBMM were used to calculate individual home range areas. The smallest area accounting for 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 ArcGIS 10® (ESRI) and GME (Beyer 2011).

### Space use

On the other hand, the individual UD obtained from the BBMM were also used to assess population-level space use. We summed the cell values for all resident fish UD (n = 5) and the cell values of non-residents UD (n = 5) respectively, and then re-scaled their cumulative cell values to sum to 1 (since UD 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 fish, 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 *Posidonia 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 2 consecutive locations on the same receiver. We represented the excursion times in each habitat on a log-log scale. This is an adequate way to visualise fat tail distributions, i.e. 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 fish, 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 US Naval Observatory (Astronomical Applications Department, accessed 1 June 2011 at <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, 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 the 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, R Development Core Team 2012).

The temporal patterns of hourly detections were examined by visually inspecting the chronograms for each resident fish. A time-frequency analysis (the CWT) was then used with the pooled data set of all residents, in order to identify periodic patterns in *Sarpa 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 localised 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 normalised data (i.e. log-transformation) (Grinsted et al. 2004).

## RESULTS

### Spatial patterns

Five resident fish accounted for 96% of detections, while non-resident fish accounted for the remaining



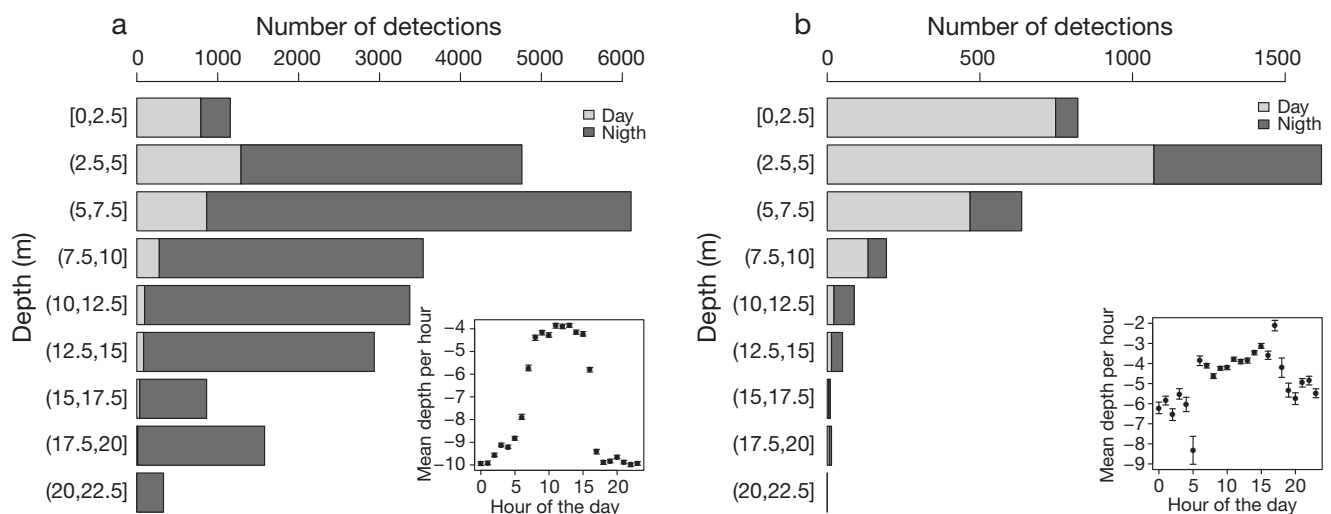
4% (Fig. S2, Table S1 in the Supplement). Home range areas for individual *Sarpa salpa* varied from 87.88 to 187.44 ha (Table S1, Fig. S3 in the Supplement). The mean home-range area for residents was  $143 \pm 18$  ha, and  $124 \pm 11$  ha for non-residents (averaging the individual home range areas 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 UD) evidenced that the seagrass meadow was intensively used, as shown by their core area that was centred on the meadow (Fig. 1). 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 UD) covered nearly all coastal zones of the study area (Fig. 1b). The non-resident population showed different cores of activity (50% isopleth), on the coast and on the islands, partially located on the seagrass habitat. Both resident and non-resident populations overlapped their core areas on the *Posidonia oceanica* habitat, on the southwestern 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 min (ca. 17 h) was low, but it was around 2 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, especially 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

*Sarpa 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:  $5.2 \pm 0.2$  m), whereas at night, detections were significantly deeper (mean nocturnal



**Fig. 2.** Depth patterns. Number of diurnal and nocturnal detections classified by depth in (a) seagrass and (b) rocky systems. Insets show the mean depth along the 24 h of the day. Note that a 24 h depth cycle is evident in the seagrass (inset (a)) whereas this is not the case in rocky systems (inset [b])

Table 1. ANOVAs. \* $p \leq 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ 

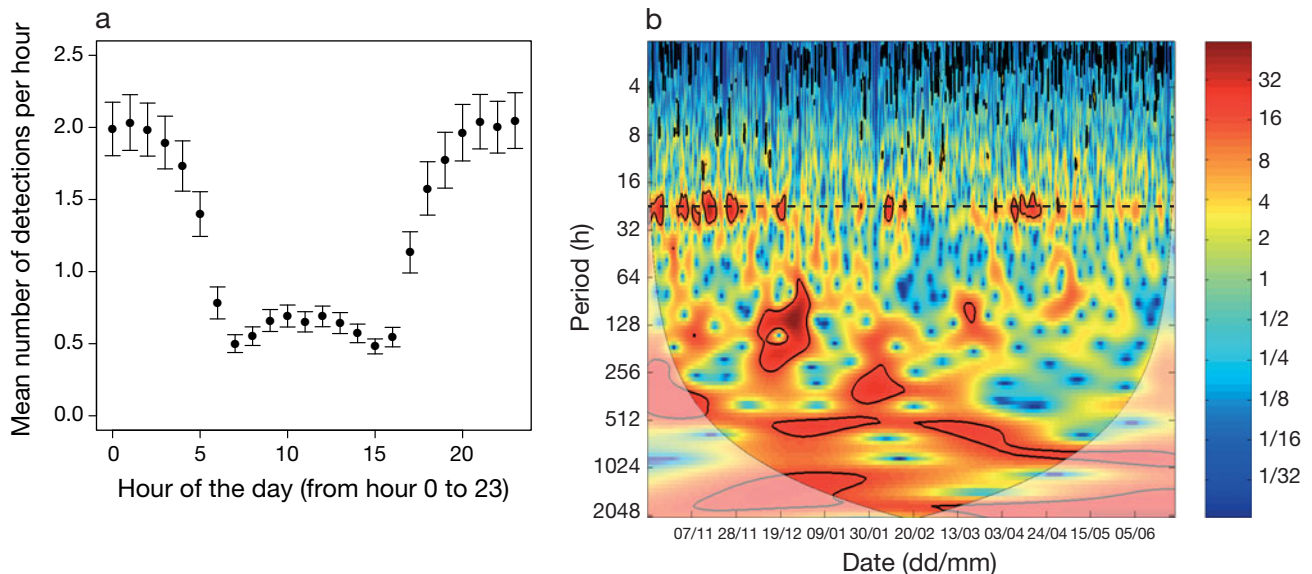
Effect	df	F	p
<b>Fish depth</b>			
Phase	1	12.6608	0.0026**
Habitat	1	5.0128	0.0397*
Phase $\times$ Habitat	1	2.0811	0.1684
Residuals	16		
<b>Frequency of detections</b>			
Habitat	1	96.87955	<0.0001***
Season	1	1.00469	0.3262
Phase	1	55.51481	<0.0001***
Habitat $\times$ Season	1	0.73442	0.3999
Habitat $\times$ Phase	1	112.90516	<0.0001***
Season $\times$ Phase	1	9.12524	0.0059**
Habitat $\times$ Season $\times$ Phase	1	2.35231	0.1382

depth:  $8.5 \pm 0.9$  m; inset Fig. 2a; Fig. S4 in the Supplement). In contrast, this cycle was not significant in rocky habitats, where fish remained most of the time at similar depths ( $p > 0.05$ ; inset Fig. 2b; Fig. S4 in the Supplement). It is worth noting 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 the Supplement). 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  $\times$  Season interaction in Table 1; see also Fig. S5b in the Supplement).

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



**Fig. 3.** Temporal patterns of the frequency of hourly detections pooling all residents. (a) 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 h (21 d). 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. Scale bar represents the intensity of the time-frequency space over time

## DISCUSSION

The large home ranges of *Sarpa 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 fish (i.e. those spending >60% of the 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 fish 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 to 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 has been applied to a marine data set. The application of BBMM to 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 in the Supplement). However, to correctly interpret the output of BBMM with passive acoustic telemetry data sets, one needs to be aware of 3 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 2 consecutive locations. This leads to a circular-shaped UD around that receiver. If the time lag between 2 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 of 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 *Sarpa salpa* and encompassing varying proportions of each habitat; see Fig. S1a in the Supplement), 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 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 in location error (see Fig. S10 in the Supplement, 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 from connecting 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 *Sarpa salpa* displayed large home range areas (overall mean of individual home ranges:  $134 \pm 10$  ha) that encompassed different kinds of habitats and ecosystems, with high variability among individuals. This was true for resident and for non-resident fish (Table S1 in the Supplement). Inter-individual vari-



ability in home range size has been generally found, both for *S. salpa* (Jadot et al. 2002), as well as for other species (e.g. Marshall et al. 2011). In addition, we found that *S. salpa* 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 in the supplement), 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 their large mobility, resident *Sarpa salpa* showed a clear and long-term (i.e. 1 yr) preference for the seagrass meadow evidenced by the high utilisation of this habitat, where they spent >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 TP 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 the low number of detections within the array.

### Temporal patterns

Temporal trends within each habitat were also observed. *Sarpa 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 in 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 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, 2012). In our case, the generating mecha-

nism 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 of the number of detections per hour was sustained for at least 6 mo, as shown by the CWT analysis, and no effects of seasonality were evident despite both seagrass and macroalgal biomass and production having a seasonal pattern in the study area (Alcoverro et al. 1995, Hereu et al. 2008). Diel cycles had already been identified for this species in the short term (i.e. 1 mo; Jadot et al. 2006), but it was unclear whether these were maintained for the whole year, since it has been suggested that *S. salpa* conduct 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 fish studied.

Additionally to the cycle of hourly detection rates, a diel cycle for 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 of Fig. 2a). These results match with the results discussed in the previous paragraph and with the higher herbivory rates generally observed in 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 about 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. 10 m in Fig. 1a). Thus, *Sarpa 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 of 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 *Sarpa 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 fish spent most of the time on seagrass habitat, the main transfer of energy would be between shallow and deep areas of the meadow on 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 fish 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 the 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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