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Short Communication

Site fidelity of fish on a rocky intertidal in the south of Portugal

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ABSTRACT

The short-term site fidelity of intertidal fish species was studied in a rocky intertidal zone in southern Portugal using visible implant elastomer tagging. Eleven fish species were caught, tagged and released, seven of which were recaptured. The larger tide pool with the highest complexity level and located at a lower position in the shore level did not have recaptures, while in others the individual fish species recaptured rate ranged from 11.1 to 38.9%, suggesting that the shore height is a dominant factor influencing site fidelity. Although the breeding season seems not to be the only explanation for the recapture rate, the higher mean recapture rates of *Parablennius sanguinolentus*, *Lipophrys pholis* and *Gobius cobitis* may be related to the parental behaviour of these species during that period. Site fidelity of juveniles of *Scorpaena porcus* in tidepools is reported for the first time, showing the importance of this habitat as a nursery ground.

1. Introduction

Intertidal fish species tend to move out of their home pools at high-tide feeding excursions (Gibson, 1999). Homing behaviour of intertidal fishes after these excursions allow them to return to earlier occupied safe tide pools, and thereby avoid or reduce adverse conditions and being predated upon (Griffiths, 2003a). The number of displaced fish returning to their point of capture varies widely within and between species (Gibson, 1999). The extent to which fish remain faithful to their pools is not static over time and will be related to the ability to learn during their lifetime (Martins et al., 2017; White and Brown, 2013). In this vein, homing behaviour and site fidelity should be positively influenced by knowledge accumulated with age (Griffiths, 2003a). Among other spatial learning and memory skills, tide-pool fish have the ability to remember locations according to visual, topographical (Dodd et al., 2000; Griffiths, 2003a) and olfactory cues (Khoo, 1974) or even a compass orientation related to sun's position (Berti et al., 1994). This learning will be especially important for permanent resident fish, since they remain within the intertidal zone for their entire lives, while secondary residents spend only part of their life history in this habitat, mostly as juveniles (Gibson and Yoshiyama, 1999; Griffiths, 2003b).

Habitat complexity (De Raedemaecker et al., 2010; Macpherson, 1994), rocky pool size (Bennet et al., 1984; Compaire et al., 2019) and its position with respect to tidal height (Cox et al., 2011; Malard et al., 2016) are commonly used to explain the differences in the abundance, diversity, fish assemblage structure and site fidelity in littoral communities. Because regular emersion periods strongly influence the stress to which intertidal organisms are subjected (Blanchette et al., 2016) and the extent of movement within the intertidal zone is closely tied to the physiological needs of the organism (Wuitchik et al., 2018), tidal cycles must also be taken into account studying site fidelity. Physical factors such as wave action, rainfall, runoff or extreme temperature and salinity fluctuations set the upper limits for most intertidal organisms. At the same time, at mid and lower shore levels, these boundaries are governed by biological interactions (Hill et al., 1998) such as the appearance of subtidal competitors and predators during high tide (Davis, 2001; Gibson and Yoshiyama, 1999). Consequently, the ability of fish to remain in home pools over successive tidal cycles may be affected by

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pool location according to shore height by emersion time.

In this study, we conducted a small-scale field experiment of mark-recapture to provide insight into the short-term site fidelity of permanent intertidal fishes caught from three pools located at different shore heights, and were therefore exposed to different levels of the aforementioned subtidal risks (Davis, 2000). We hypothesized that although both habitat complexity and pool size may influence community structure since they increase access to shelter (Gibson, 1999) and provide more stable habitat (Davis, 2000), permanent residents (species belonging to Blenniidae, Clinidae, Gobiesocidae and Gobiidae) would show higher site fidelity in pools with shorter periods of time immersed or in contact with surge and the subtidal system.

2. Materials and methods

Permanent resident fish were monitored biweekly from 11th March to 22nd April 2016 from three rocky pools across the tidal range at Praia do Manuel Lourenço (37° 04′ 35.9″N – 8° 18′ 37.3″W) (southern Portugal) (Fig. 1A) during the daytime low spring tide. This region has a semi-diurnal mesotidal regime with a mean spring tidal range of 2.8 m (Vousdoukas et al., 2011). To evaluate if pool's emersion time could affect the fishes' capacity to return to the original marking pool the beach-face slope was divided into three vertical levels: low, medium and high, and one pool was selected at each level. The heights of the pools were obtained from a Digital Terrain Model (DTM) of coastal areas from 2011 at 1 m resolution. Pools were categorized according to their heights above mean sea level as lowest ($L = 0.72$ m), medium ($M = 1.03$ m) and highest ($H = 1.38$ m) (Fig. 1B). The L pool is closest to low tide shore line and spends shorter periods of time isolated from water inflow and subtidal system than M and H pools. The approximate percentage of time that the pools were fully immersed or in contact with surge over the 6-week study period was calculated using data from the Albufeira tide gauge, the closest to the study area. The percentage of time was 25, 14 and 4% for L, M and H, respectively.

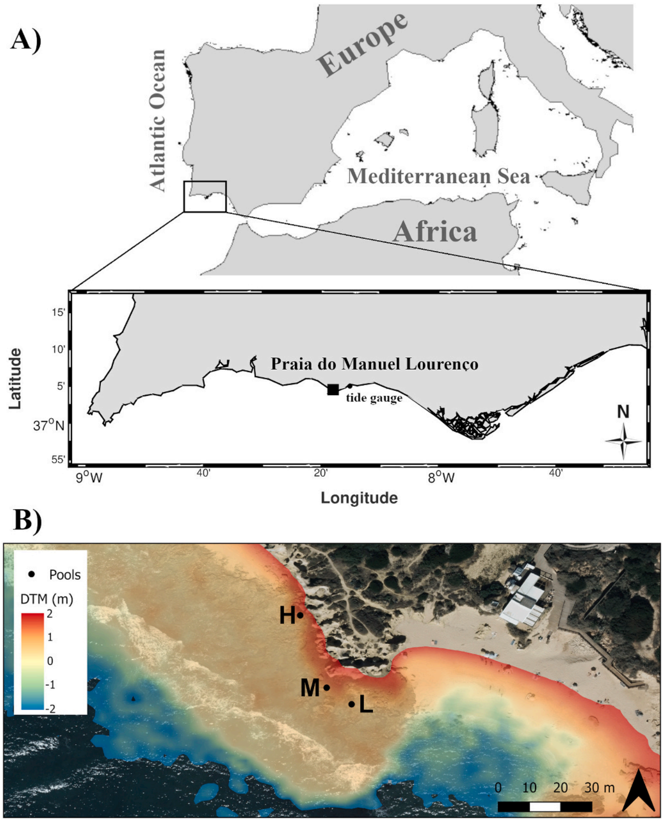

Fig. 1. A) Map of the Algarve (southwestern Europe) showing the study location. The square indicates the sampling site (Praia do Manuel Lourenço), and dot indicates tide gauge location. B) Aerial view (orthophotos) of the rocky intertidal shore. The colorbar indicates the elevations obtained from Digital Terrain Model. Dots indicate pools according to their positions regarding shore height: L (lowest), M (medium), and H (highest).

Distances between pools were obtained using orthophotos of coastal areas from 2014 at 0.1 m resolution. Linear distances between rocky-pool pairs were L - M = 10 m, M - H = 30 m, and L - H = 39 m (Fig. 1B). The DTM data and the orthophotos were obtained from the Direção-Geral do Território of Portugal, while data from the tide gauge, were obtained from the Instituto Português do Mar e da Atmosfera (IPMA) of Portugal.

Each pool was measured (surface area and depth) and the habitat complexity rugosity (SR) was estimated using the chain link method (Luckhurst and Luckhurst, 1978). This method calculates the ratio between two points contoured over the bottom and the linear distance between such points. Measurements were made in both dimensions (length and width) and averaged to obtain the final complexity value for each pool (Table 1).

Fish were caught using clove oil at a concentration of 40 mg l^{-1} as an anaesthetic (Griffiths, 2000) and hand nets. No mortalities were observed. Total length of each specimen was measured (0.1 cm), and Visible Implant Elastomer (VIE) tags were implanted beneath the skin on the cheek (Northwest Marine Technology, Inc.) with different colours used to mark fish according to pool of capture (i.e., L, M or H). VIE tags have been previously used successfully in tagging studies involving small cryptic fishes (Malone et al., 1999; Roma et al., 2018). Untagged individuals found during each sampling event were tagged, except those from the last census. To test if the intertidal fish caught returned to the pool of origin after tagging, they were allowed to recover from anaesthesia in buckets of fresh seawater. After that, they were returned to the closest pool at the same shore height (less two meters away from the 'home' pool in a straight line) to avoid being anaesthetized again and to reduce their probability of being predated upon. Despite different release distances for each 'home' pool, which undoubtedly could affect recapture rates, it has been demonstrated that homing success for permanent residents is not affected by displacement distance lesser than 30 m (White and Brown, 2013). The average short-term site fidelity of each species at each pool was calculated as the percentage of fish found in the same pool where they were previously tagged. Only original locations were searched for tagged fish.

Fisher's exact test was used to investigate association between recapture and pools. To evaluate if homing abilities can be affected by body size, a non-parametric Kruskal-Wallis test was used to test the total length differences between recaptured and all tagged individuals for those species with more than one recaptured fish (i.e., *Lipophrys pholis*, *Parablennius sanguinolentus*, *Gobius cobitis* and *Gobius paganellus*). Percent similarity of fish species composition for all individuals collected between each pair of rocky pools was measured with Jaccard's coefficient (J') (Jaccard, 1901). This analysis is widely used for measuring similarity of intertidal fish communities (Barreiros et al., 2004; Navarrete et al., 2014; Santos et al., 1989). Diversity was estimated using Shannon-Wiener index (H′). Pearson's correlation coefficient was used to examine the strength of the relationship between fish abundance and diversity with habitat complexity. A significance level of $p < 0.05$ was considered throughout the study.

Table 1
Surface, depth, and substrate rugosity (SR) (mean ± standard deviation) of each pool. Pools are named according to their positions regarding shore height as L (lowest), M (medium), and H (highest).

Pool	Surface (m^2)	Depth (m)	SR
L	8.32	0.35	1.56 ± 0.43
M	4.56	0.18	1.32 ± 0.16
H	2.48	0.15	1.10 ± 0.10

3. Results

A total of 121 fish were collected, of which 85 were tagged and 20 recaptured. The abundance of fish caught for the first time and previously tagged for each sampling event is shown in Table 2 (see Appendix I for detailed information on the total length of tagged and recaptured fish for each pool). The percentage of fish recaptured for individual species ranged from 11.1 to 38.9%. In general terms, the most abundant species were *G. cobitis*, *G. paganellus*, *P. sanguinolentus* and *L. pholis*, accounting for 74% of the total abundance and 85% of the total recaptured fish.

All recaptured fish were found in the same home pool where they were tagged, i.e., fish returned to the place formerly occupied instead of going to other pools. However, the distribution, abundance and recapture patterns were different depending on each pool. There were no fishes recapture in *L* pool, while the mean recapture level in other pools was 32.7% for pool *M* and 28.6% for pool *H*. There was a relationship between the recapture and pool (Fisher's exact test, $p = 0.019$). *L. pholis* and *G. cobitis* in *M* pool, and *P. sanguinolentus*, *Lepadogaster lepadogaster* and *Scorpaena porcus* in pool *H* had a recapture equal or greater than 50% (Table 3). In most species, the average length of recaptured fishes was slightly greater than that of tagged individuals, but these differences were not statistically significant (Kruskal-Wallis test, $p > 0.05$, Table 3).

The highest similarity value between pools was obtained for *M* and *H* (J' = 70%), followed by *H* and *L* (J' = 60%) and *M* and *L* (J' = 58.3%). The SR values ranged from 1.10 in the less topographically complex pool to 1.56 in the pool of greater surface area and depth (Table 1). The diversity in pool *M* ($H' = 2.80$) was slightly higher than that of pools *L* ($H' = 2.62$) and *H* ($H' = 2.52$). There was no relationship between abundance (total or for each species) or diversity and habitat complexity ($p > 0.05$).

4. Discussion

We examined the abundance and recapture of permanent resident fishes from three rocky pools of different shore levels to explore short-term site fidelity. Larger pools located at the lower intertidal levels have higher stability because fluctuations in physico-chemical parameters such as temperature, oxygen and salinity are dampened by more frequent water renewal (Huggett and Griffiths, 1986). Although fish may prefer those pools to avoid physiological stress during low-tide, in our study, the larger tide pool with the highest complexity level and located at lower position in the shore level did not have any fish recaptures, whereas seven of the 11 tagged species were recaptured between the other two pools. The present result suggests that the shore height is a dominant factor influencing site fidelity. This apparent contradiction could be due to intertidal fish tending to move to avoid predators (Gibson, 1999), especially in the more exposed intertidal areas (Yoshiyama et al., 1992), and the degree of wave exposure, which can affect an individual's ability to home (Green, 1971). Albeit blennies and gobies show behavioral and morphological adaptations to avoid being washed away by turbulent waves (Almada and Santos, 1995; Zander, 2011), sites more exposed to wave energy have previously been negatively correlated with intertidal fish abundance (Compaire et al., 2019; Setran and Behrens, 1993), being less desirable habitats than sheltered higher pools (Griffiths, 2003a). Prior short-time tagging experiments with relatively small fish sample sizes proved to be successful in studying site fidelity in shallow coastal areas in the southern Portugal (Abecasis and Erzini, 2008). Nevertheless, and due to the low number of analysed pools, further studies covering different pool sizes and habitats complexity at different shore heights are necessary to corroborate this relationship.

Table 2
Abundance of individuals captured for the first time and previously tagged for each sampling event.

Sampling event	First caught	Previously tagged
1	37	–
2	16	2
3	24	6
4	24	12

Strong homing abilities observed in permanent residents allow them to return to their original low-tide pools after being displaced more than 100 m (Martins et al., 2017). Therefore, although we relocated the tagged fish during low tide to another rockpool, and they had time to become familiar with the new rockpool before the tide came in (White and Brown, 2013), it is not surprising that all recaptured fish in our study were always found in the same home pool where they were tagged. Such behaviour seems to confirm that permanent residents are familiar with the landmarks of their territory and use this knowledge to return to specific rockpools (Gibson, 1999; White and Brown, 2013).

In contrast to the specificity of homing sometimes demonstrated by permanent resident fish, a large number of studies have shown that half of the tagged intertidal fish are never recaptured at their home rockpool, suggesting that they have moved elsewhere (Gibson, 1999). The failure of some fish to be recaptured in their original rockpool may be related to several factors. The large decline in fish abundance observed after the first census (Table 2) may be to a large extent due to stress caused by the capture and tagging at the initial census, causing them to perceive the pool as unsuitable temporarily (Wuitchik et al., 2018). Displaced fish can explore the new area to find out if the pool offers sufficient resources (Griffiths, 2003a), and provide adequate microhabitats to establish its new home pool. The fluorescent tags could also influence the rate of returning fish to their home pool, since marked fish may be more visible to predators (Griffiths, 2003a). However, VIE tags have been shown to not increase susceptibility to predation in reef gobies (Malone et al., 1999). Differences in the rate of recapture among species in the same habitat may reflect individual behavioral traits (Gibson, 1999). The absence of significant differences in fish length between recaptured and all tagged fish in most species agrees with several studies that reported there was no relationship between fish length and homing success for most species on rocky shores (Griffiths, 2003a; White and Brown, 2013; Yoshiyama et al., 1992).

The similarity values higher than 50% among pools are consistent with previous studies in fish communities on rocky shores (Barreiros et al., 2004; Santos et al., 1989). Species that showed a higher mean recapture were the permanent residents: *G. cobitis* (38.9%), *P. sanguinolentus* (36.4%), *L. pholis* (30%), and juveniles of *S. porcus* (33.3%). While on the other hand, the low abundances of *Coryphoblennius galerita, Salaria pavo*, *Clinitrachus argentatus* and *Gobius incognitus* did not allow the study of their site fidelity. The mean recapture rate of *P. sanguinolentus*, which breeds between March and May (Compaire et al., 2018a), was close to that reported for its congener *P. parvicornis* (Thyssen, 2010). The rate of recapture of *L. pholis* was close to that found in another study carried out during its breeding season (Martins et al., 2017). While there is no specific literature about *Lipophrys trigloides* site fidelity, this species has been described as abundant in the low intertidal (Faria and Almada, 2006), and its breeding season would occur during cold-water periods on the Atlantic coast (Ferreira et al., 2010). The greater number of recaptures of *G. cobitis* than *G. paganellus* in pool *M* may be due to their preference for different strata on rocky shores, upper and lower pools, respectively (Gibson, 1972). Also, the sampling took place during the breeding season of *G. cobitis* (February–May, Compaire et al., 2018a). The percentage of *G. paganellus* returning to its home rockpool was similar to that previously reported by Roma et al. (2018). The reproductive strategy of blennies and gobies consists of the laying of demersal eggs cared for by the male until hatching (Almada and Santos, 1995; Mazzoldi et al., 2011). Thus, parental behaviour could be the reason for the higher mean recapture rates of *P. sanguinolentus*, *L. pholis* and *G. cobitis*. To address this issue, in future studies fish should be sexed and rockpools searched for nests with eggs, in order to confirm the higher recaptures in sites with nest-

Table 3
Number of tagged and percentage of recaptured fish (average length ± standard deviation in cm) for each species and pool. Fishes were not recaptured in *L* pool. Kruskal-Wallis test results (KW) comparing total length for recaptured and all tagged individuals are shown*. Abbreviations of pool height as in Table 1.

		Tagged fish abundance (average length ± S.D.)			% of recaptured fish (average length ± S.D.)			
Family	*Species*	*L*	*M*	*H*	*L*	*M*	*H*	KW (df = 1)
Blenniidae	***Coryphoblennius galerita***	1 (3.7)	–	–	0	–	–	–
	Lipophrys pholis*	–	3 (10.1 ± 1.7)	7 (10.5 ± 1.4)	–	66.7 (11.0 ± 0.9)	14.3 (11.3)	H = 1.03, $p = 0.31$
	Lipophrys trigloides	1 (6.5)	3 (7.5 ± 1.0)	–	0	33.3 (8.2)	–	–
	Parablennius sanguinolentus*	2 (12.4 ± 3.5)	7 (12.2 ± 2.1)	2 (9.1 ± 1.6)	0	42.9 (13.3 ± 1.1)	50 (8.0)	H = 0.52, $p = 0.47$
	Salaria pavo	1 (4.0)	1 (6.5)	1 (7.1)	0	0	0	–
Clinidae	***Clinitrachus argentatus***	–	1 (4.0)	–	–	0	–	–
Gobiesocidae	***Lepadogaster lepadogaster***	2 (6.7 ± 1.0)	5 (6.0 ± 0.9)	2 (4.8 ± 0.6)	0	0	50 (4.3)	–
Gobiidae	***Gobius cobitis****	4 (14.0 ± 2.7)	13 (12.4 ± 4.2)	1 (10.2)	0	53.8 (12.9 ± 2.6)	0	H = 0.21, $p = 0.65$
	Gobius incognitus	1 (4.4)	–	–	0	–	–	–
	Gobius paganellus*	9 (6.4 ± 1.1)	15 (7.1 ± 1.7)	–	0	20.0 (7.0 ± 1.0)	–	H = 0.29, $p = 0.59$
Scorpaenidae	***Scorpaena porcus*****	1 (5.0)	1 (4.6)	1 (5.6)	0	0	100 (5.6)	–

*Only fish species with more than one recaptured individual were analysed, ** indicates the secondary resident species, only juveniles were caught.

guarding males. The low recapture of *L. lepadogaster*, a species that occurs almost exclusively under boulders whose breeding occurs during our sampling period (Henriques et al., 2002), might be due to the greater mobility of species living under stones (Gibson, 1999). Finally, the recapture of juveniles of *S. porcus* is described on rocky shores for the first time, and confirms that this habitat provides important nursery grounds for this species of commercial value in the Mediterranean (Morte et al., 2001) and Atlantic coasts (Compaire et al., 2018b). More field sampling maintained through time will be necessary to verify these findings.

CRediT authorship contribution statement

Jesus C. Compaire: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Juan Montes:** Software, Formal analysis, Writing – review & editing. **Jorge M.S. Gonçalves:** Resources, Writing – review & editing, Funding acquisition. **Milagrosa C. Soriguer:** Conceptualization, Resources, Writing – review & editing. **Karim Erzini:** Conceptualization, Methodology, Investigation, Resources, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2022.102202.

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