

Among-individual variation in white seabream (*Diplodus sargus*) spatial behaviour and protection in a coastal no-take area

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Marine protected areas (MPAs), and specially no-take areas (NTAs), play an important role in protecting target populations from fisheries. When developing spatial conservation and management tools, the design has mainly focused on population-level measures of fish home ranges, spawning and feeding areas, and migration routes. Intraspecific differences in fish behaviour, however, are often not accounted for, even though they could influence the level of realized protection. In this study, we investigated the intraspecific variation in spatial behaviour of a harvested fish, *Diplodus sargus*, and how it impacts the degree of protection granted by a NTA in the south of Portugal. We identified four behavioural types according to their spatial behaviour: residents, commuters, seasonal visitors, and single users. Time at risk (i.e. outside the NTA) greatly varied among the four groups, but also over the year for the seasonal and the single users. Our study shows how acoustic telemetry can assist spatial conservation and fisheries management and provides novel insight regarding the role of individual variation in behaviour to understand protection granted by MPAs to harvested species. It also suggests that incorporating such information into all stages of MPA design and implementation can result in increased resilience of the protected populations.

Keywords: acoustic telemetry; conservation; *Diplodus sargus*; fisheries management; marine protected areas; no-take area; spatial behaviour.

Introduction

Marine protected areas (MPAs), where human activities are restricted, and especially no-take areas, where no extractive activity is permitted, play an important role in protecting target populations from fisheries (Sala and Giakoumi, 2018; Zupan *et al.*, 2018). MPAs have been shown to preserve biodiversity within and beyond their boundaries, with positive effects on abundance, biomass, and species richness (Edgar *et al.*, 2014; Abecasis *et al.*, 2015b; Di Franco *et al.*, 2018). However, MPA effectiveness largely depends on its spatial configuration and the ability to encompass the range of movements and habitats used by the target species during the different phases of the life cycle (e.g. spawning and feeding) (Apostolaki *et al.*, 2002; Chateau and Wantiez, 2009; Bryars *et al.*, 2012).

Yet, inference about MPA effectiveness is typically based on overall populations' behaviour. In contrast, recent studies highlighted the relevance of intraspecific variation in spatial behaviour to understand the degree of protection granted by MPAs to the individuals and ultimately their fitness (Parsons *et al.*, 2010; Mee *et al.*, 2017; Thorbjørnsen *et al.*, 2021; Villegas-Ríos *et al.*, 2021). There is a general perception that sedentary and site attached species obtain greater benefit from MPAs than migratory species, due to reduced exposure to the fishery operating outside the MPAs (Breen *et al.*, 2015). Yet, movement polymorphisms among individuals of the same resident

fish population relevant for evaluating MPAs have been described (Meyer and Holland, 2005; Secor *et al.*, 2009; Maggs *et al.*, 2019). In particular, for relatively mobile species (such as *Diplodus sargus*) fish were described as residents and commuters (Dingle, 1996; Meyer and Holland, 2005; Kerwath *et al.*, 2009). Residents have been described as individuals whose activities and movements remain in a specific core area, with size varying depending on the level of species territorialism (Grüss *et al.*, 2011). Commuters' behaviour has been related to individuals that show wider movements among different habitats, related to foraging, sheltering, or resting activities, while maintaining a specific core area (Larson, 1980; Parrish, 1989; Meyer and Holland, 2005). Thus, these two behaviours are defined based on the use of a given area and do not take into consideration long excursions away such area (Kokko *et al.*, 2006; Burgess *et al.*, 2016).

In this study, we investigated the intraspecific variation in spatial behaviour of a high value commercial fish species, the white seabream, *D. sargus*, and how it impacts the degree of protection granted by a coastal no-take area. We also explored the temporal variation in time spent under protection. We hypothesised that (1) within a population of *D. sargus*, different behavioural types could be defined based on the site attachment to a no-take area, and (2) time spent inside the no-take area would vary on a diel and seasonal basis. We selected *D. sargus* for our study because this species has been shown to

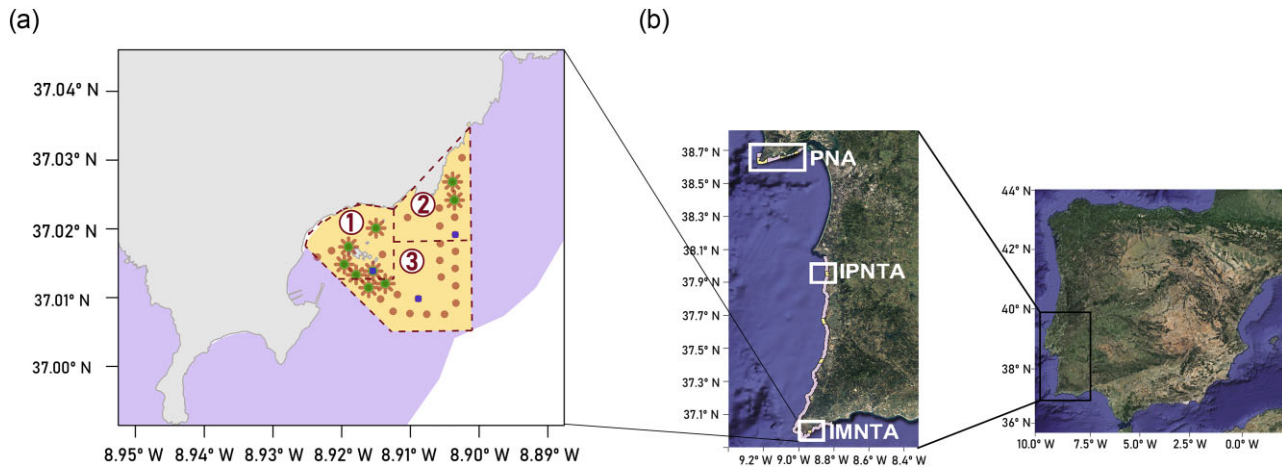


Figure 1. Map of the study area. a) Study area showing the no-take area limits (yellow area), the limits of the “Parque Natural do Sudoeste Alentejano e Costa Vicentina” – PNSACV (purple area), and the different sections (surrounded by the red dotted line): 1. Islands section, 2. Nearshore section, 3. Offshore section. The red dots represent the stations (receivers) of the detection array; those with star represent the release points. The green points represent the capture locations. The blue points represent the location of the sentinel tags where some of the individuals were detected by other acoustic telemetry arrays (PNA: “Parque Natural da Arrábida”, IPNTA: “Ilha do Pessegueiro” – PNSACV; IMNTA: “Ilhotes do Martinhal” – PNSACV).

benefit from no-take areas due to its high site fidelity ($\sim 75\%$ average residency index) and small home ranges (max. value reported $\sim 3.9 \text{ km}^2$), in the Mediterranean and the Portuguese Atlantic coast, where it is commercially targeted (D’Anna *et al.*, 2011; Abecasis *et al.*, 2013; Di Lorenzo *et al.*, 2014; Abecasis *et al.*, 2015b; Giacalone *et al.*, 2018, Giacalone *et al.*, 2022). However, there is also evidence of long-distance movements in this species (D’Anna *et al.*, 2004; Abecasis *et al.*, 2009; Di Franco *et al.*, 2012; Belo *et al.*, 2016), as well as variations in home range associated with habitat, seasons, time of the day, and spawning season, which generally lasts from November to July with a peak between March and April (Mouine *et al.*, 2007; Abecasis *et al.*, 2013, 2015a; Aspillaga *et al.*, 2016; Di Lorenzo *et al.*, 2016; Giacalone *et al.*, 2022). The white seabream therefore makes an interesting case for the study of intraspecific variation in behaviour and its relevance for impact on conservation management.

Materials and methods

Study area

This study was conducted in the natural park “Parque Natural do Sudoeste Alentejano e Costa Vicentina” (PNSACV). Established in 2011, this is the largest coastal MPA in mainland Portugal, extending up to 2 km offshore and covering around 130 km of the coastline ($\sim 290 \text{ km}^2$). The PNSACV includes four no-take areas. For our study, we selected a small no-take area of 4.2 km^2 known as *Ilhotes do Martinhal* (IMNTA, the southernmost in the PNSACV), which potentially covers the maximum home range registered for the study species ($\sim 3.9 \text{ km}^2$). To assess individual habitat use, we considered three distinct zones within the no-take area (1) the islands area, a rocky zone made up of nine islets, with depths between 0 and 23 m, (2) the nearshore area conformed by rocky reefs with depths between 0 and 25 m, located in the eastern part of the study area and forming a continuous habitat connected with the adjacent outside area, and (3) the offshore area, a deeper sandy zone with depths between 20 and 40 m (Figure 1).

Fish tagging and acoustic monitoring system

Fish were caught using hook and line complying with the requirements established by the ICNF (National Institute for the Conservation of Nature and Forests) license no. 12205881, to catch, and tag *D. sargus* in the PNSACV. Fish were tagged with acoustic transmitters following the procedure described by Abecasis and Erzini (2008). The depth of the catches varied between ~ 10 and 15 m and no signs of barotrauma were detected. Within about ~ 15 min of releasing the fish, their behaviour followed the pattern observed later on in the study. The transmitters implanted were Innovasea V9-2X (3.6 g air/2 g water), V9P-2x (4.9 g air/2.8 g water) with a delay of 20–60 s and pressure sensor. Expected lifetime was 404 d for all transmitters except one that did not carry the pressure sensor (651 d). Tag weight (in water) corresponds to 1.3% of the weight of the smallest tagged fish. The incision was closed with absorbable sutures and using cyanoacrylate tissue adhesive. No anaesthesia was used, reducing the recovery time, and avoiding behavioural modifications or delayed mortality (Davis, 2010). The overall procedure took ~ 3 min per individual. Each fish was kept in a small onboard tank until normal ventilation and swimming behaviour were observed, and then released at the capture location.

Our acoustic array included 32 Innovasea VR2W receivers (Figure 1). Twenty-eight receivers were deployed in a double line surrounding the borders of the no-take area, whilst the other four were deployed inside the no-take area. According to the three distinct zones within the no-take area described above, sixteen receivers were placed in the islands section ($n = 8$; between ~ 5 and 23 m deep) and the nearshore section ($n = 8$; between ~ 18 and 25 m deep), whilst 16 in the offshore section (between ~ 22 and 38 m deep). All receivers were attached in cement moorings about 20 cm above the seabed, with the hydrophone pointing upwards. Three sentinel tags were at three different receiver locations (Figure 1), attached to the mooring lines 1 m above the receiver. Receiver spacing was kept at ~ 250 m to ensure good overlap in detection ranges. Range tests were conducted at different depths, habitats, and weather conditions. These tests showed that, in our

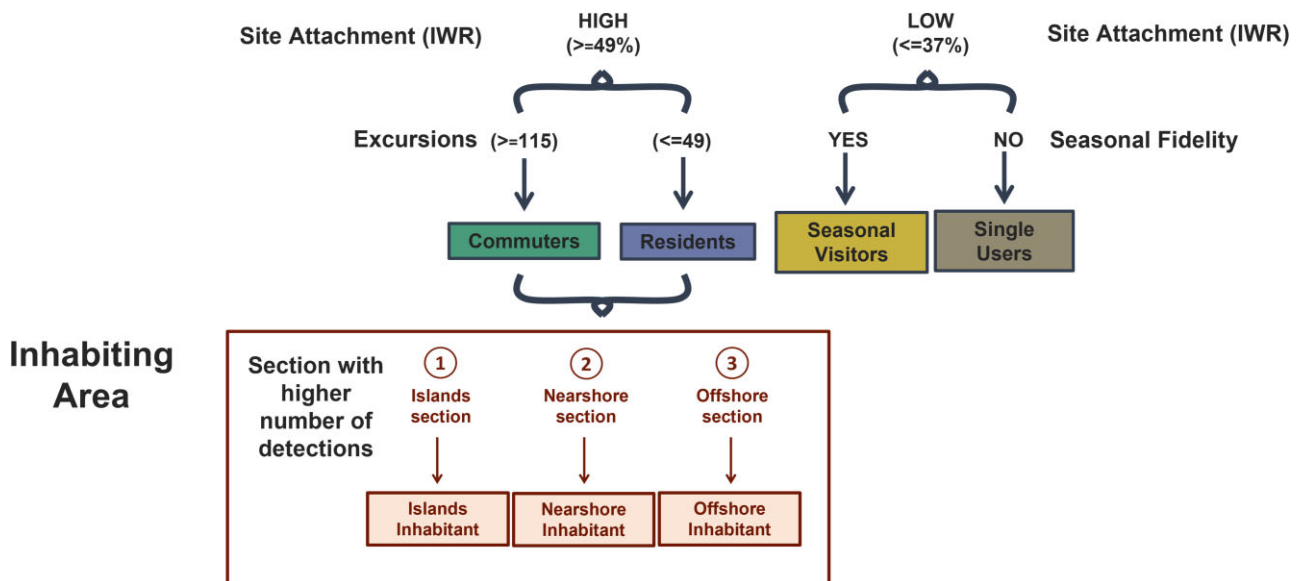


Figure 2. Behavioural type-based classification system. IWR: weighted residence index; Excursions: number of excursions over 12 h; and Inhabiting Area: specific step for Ilhotes do Martinhal no-take area to determine the preferred area used by those individuals with high site attachment.

study, an average of 50% of transmissions are detected when the receiver spacing is 250 m. Several trials were conducted with fixed acoustic receivers at similar depths and with 50 m spacing until 500 m distance. Additionally, active tracking trials were conducted with a hand-held receiver and communication box (VR100).

At the end of the study period, detections were downloaded from 25 of the 32 receivers. The remaining seven receivers were either not found ($n = 4$) or damaged ($n = 3$) and detections could thus not be downloaded. We note that the loss of these receivers, although unfortunate, does not severely impact the analyses since the receiver array was purposely designed to ensure overlap (i.e. transmissions being detected by more than one receiver). Additionally, some detections were registered by other acoustic receiver arrays outside our study area: Ilha do Pessegueiro (IPNTA), in the same MPA ~104 km north of the northernmost in the MPA, and in another no-take area in the Parque Natural da Arrábida (PNA) ~169 km north (see Figure 1 and Supplementary Appendix B—Figures 1 and 2).

Data analysis

Identification of behavioural types

To investigate the use of the no-take area by *D. sargus*, a weighted residence index (IWR), as proposed by Lino (2012), was calculated for each tagged individual as

$$\text{IWR} = \left(\frac{D_d}{D_t} \right) \times \left(\frac{D_i}{D_t} \right)$$

with D_d being days with at least one detection, D_t the number of days between tagging date and end of battery life for each individual, and D_i the days between the first and last detections of each fish. We selected this metric to be able to account for the time spent outside without being sure of the fate of the individuals.

A K-means cluster analysis was performed to identify subgroups based on the IWR, to assess differences in site attach-

ment to the no-take area among individuals of the studied population. Specifically, the Elbow Method and the Average Silhouette Method (Syakur *et al.*, 2018; Shi *et al.*, 2021) were applied to determine the optimal number of clusters minimizing the intra-cluster variation and measuring the quality of the clustering ($k = 1:10$, $n = 33$). Both methods identified two clusters as optimal for this dataset, through the use of the “fviz_cluster” function from the “factoextra” package in R (Kassambara and Mundt, 2020): high site-attached individuals, with $\text{IWR} = >49\%$, and low site-attached individuals with $\text{IWR} = <37\%$. The clustering analyses and classification into behavioural types were motivated by recent studies suggesting that average behaviour (across all individuals) is an insufficient indicator of movement behaviour in a fish population, and that protective measures such as MPAs require knowledge about the level of among-individual variation in behaviour to fulfil conservation goals (Parsons *et al.*, 2010; Mee *et al.*, 2017; Thorbjørnsen *et al.*, 2021; Villegas-Rios *et al.*, 2021).

For those with high site attachment, a proxy of fish boldness was estimated: the number of excursions along the whole study period, as proposed by Knip *et al.*, (2012), to acknowledge differences on the use of the no-take area. Acoustic signal transmission and detection can be influenced by factors that may vary along the study period (i.e. tag orientation, water properties, water movement or meteorological conditions, and noise, among others; Gjelland and Hedger, 2013; Mathies *et al.*, 2014; Huveneers *et al.*, 2016; Ammann, 2020). Thus, the maximum time without detections was assessed to establish a threshold over which the individuals would be considered to be outside the no-take area (and not undetected). For that, we compared the real detections from the sentinel tags (Figure 1a) and the “theoretical” ones based on the acoustic transmitters delay times. We found a maximum of 12.37 h without detections on April 12 of 2019, with an average time without detections of $2.13 \text{ min} \pm 0.002 \text{ SE}$. Thus, a conservative 12 h threshold was chosen to avoid confounding movements towards outside with absence of detections. Only exits

and entries detected by receivers located at the boundary of the no-take area and separated by >12 h were considered as excursions. The mean time of the excursions (MTE) for each individual was also estimated. Then, to better understand movement patterns within and beyond the no-take area among the high-site-attachment fish, a cluster analysis with the number of excursions was performed again for this group of fish ($k = 1:5$, $n = 22$). The optimal number of clusters was two: residents, with <49 excursions over the study period and commuters with >115 excursions. No significant influence of the MTE was observed in the clustering process.

Individuals with low site attachment were also divided into two groups based on a qualitative assessment, as suggested by Goodson *et al.*, (2003). Single users were defined as those individuals that left the no-take area within the first three months and never came back, and seasonal visitors were defined as fish that left the study area during the first three months but returned to the no-take area several months later. Those staying >3 months were considered as high site attachment by the cluster analysis detailed above.

To assess the differences on the preferred areas used within the no-take area for the high site-attached fish, the number of detections registered by each receiver was summed for each individual. Considering the location of each of the receivers (islands, offshore, and nearshore sections), the section with most detections was assigned as the preferred area (Figure 2). Only the commuters were found to be inhabiting both in the islands and the nearshore. No individuals preferred the offshore section.

Estimation of time at risk

Time at risk (TAR) was defined as the percent of time spent outside the no-take area out of the total study period for each individual (i.e. the number of days between tagging and end of battery life), defined as

$$\text{TAR (\%)} = \frac{\text{Time spent outside (d)}}{\text{Total study period (d)}} \times 100.$$

The time (in days, d) spent outside the no-take area was calculated as the sum of the days without detections (after departure, as defined above for excursions) and the total duration (days) of the excursions, as follows:

$$\begin{aligned} \text{Time spent outside (d)} &= \text{Days without detections (d)} \\ &+ \text{Time of the excursions (d)}. \end{aligned}$$

Time spent in other no-take areas was also included in the computation of TAR.

The TAR, the number of excursions, and the mean time of the excursions were estimated for the total duration of the study, as well as for the different seasons (winter: 22nd December–19th March, spring: 20th March–20th June, summer: 21st June–21st September, Fall: 22nd September–21st December) and diel periods (considering the time of sunrise and sunset for each specific day), separately for each individual and behavioural type.

Variation in time at risk

The potential relationship between time at risk (TAR) and behavioural types, inhabiting areas, and diel times was assessed by means of three separate one-way ANOVA (one per explanatory variable) using a normal distribution. Differences in TAR among seasons were assessed with Kruskal–Wallis non-

parametric tests due to non-normality of residuals, for the residents, and with one-way ANOVA for the commuters. For the individuals with low site attachment, the variation of the TAR among diel times was only assessed for the periods of time that they remained inside the no-take area.

To assess if the exit and entry times varied throughout the year, circular plots showing the hour at which these movements (over 12 h) occurred were plotted for both the residents and the commuters.

The potential effect of body size in TAR was assessed through a one-way ANOVA. The influence of sex could not be determined by external assessment, and, thus, no differences on the TAR were assessed.

All analysis and figures were performed using R studio version 4.2.0 (R Core Team, 2022).

Results

A total of 35 white seabreams (22.7–37.0 cm total length \pm 0.68 cm SE) were caught and tagged between January and March 2019, in three different campaigns. Of these, two individuals were discarded from the study as they were detected for <2 weeks. The remaining 33 individuals generated 1,719,227 detections between January 2019 and April 2020. Individual #9072, however, was transmitting detections until October 2020 (without the depth sensor). Also, 0.1% ($n = 1668$) of the detections were recorded by three fish at acoustic arrays in other two marine no-take areas (inside the same MPA, in *Ilha do Pessegueiro*, and in another MPA, *Parque Natural da Arrábida*) (see Supplementary Appendix B—Figures 1 and 2). These dispersals were characterized by a maximum distance of 169 km towards *Parque Natural da Arrábida* during an average period of 15.5 d. Two of the fish (#4750 and #4752) did an average intermediate stop of \sim 0.96 d in *Ilha do Pessegueiro* (104 km northwards) 12 d after leaving Ilhotes de Martinhal (see Supplementary Appendix B, Table 2 and Figure 1). A total of 79% of the tagged fish survived and remained in the studied area throughout the whole study period, whilst 21% dispersed (left the no-take area permanently before the end of the battery).

Behavioural classification

Four distinct behavioural types were found among the 33 tagged individuals analysed in this study: 10 residents, 12 commuters, 5 seasonal visitors, and 6 single users. Additionally, among the individuals with high site attachment, 16 individuals were identified as inhabiting the islands (10 residents and 6 commuters), and 6 inhabiting the nearshore section (all commuters) (Figure 2).

Time at risk

Behavioural types and time at risk

We estimated that, on average, the individuals spent 45.9% (\pm 5.8% SE) of the study period outside the no-take area. The individuals with low site attachment, seasonal visitors ($74.0 \pm 8.5\%$ SE), and single users ($88.8 \pm 2.3\%$ SE) spent 2.96 times more TAR than individuals with high site attachment [residents and commuters; Figure 4 (ANOVA test: F -value = 47.03, $P < 0.05$)]. Likewise, the commuters ($43.6 \pm 5.9\%$ SE) showed TAR values five times higher than those of the residents ($8.7 \pm 3.1\%$ SE, Figure 3) (ANOVA test: F -value = 24.4, $P < 0.05$). Three seasonal visitors (#4750, #4752, and #4754)

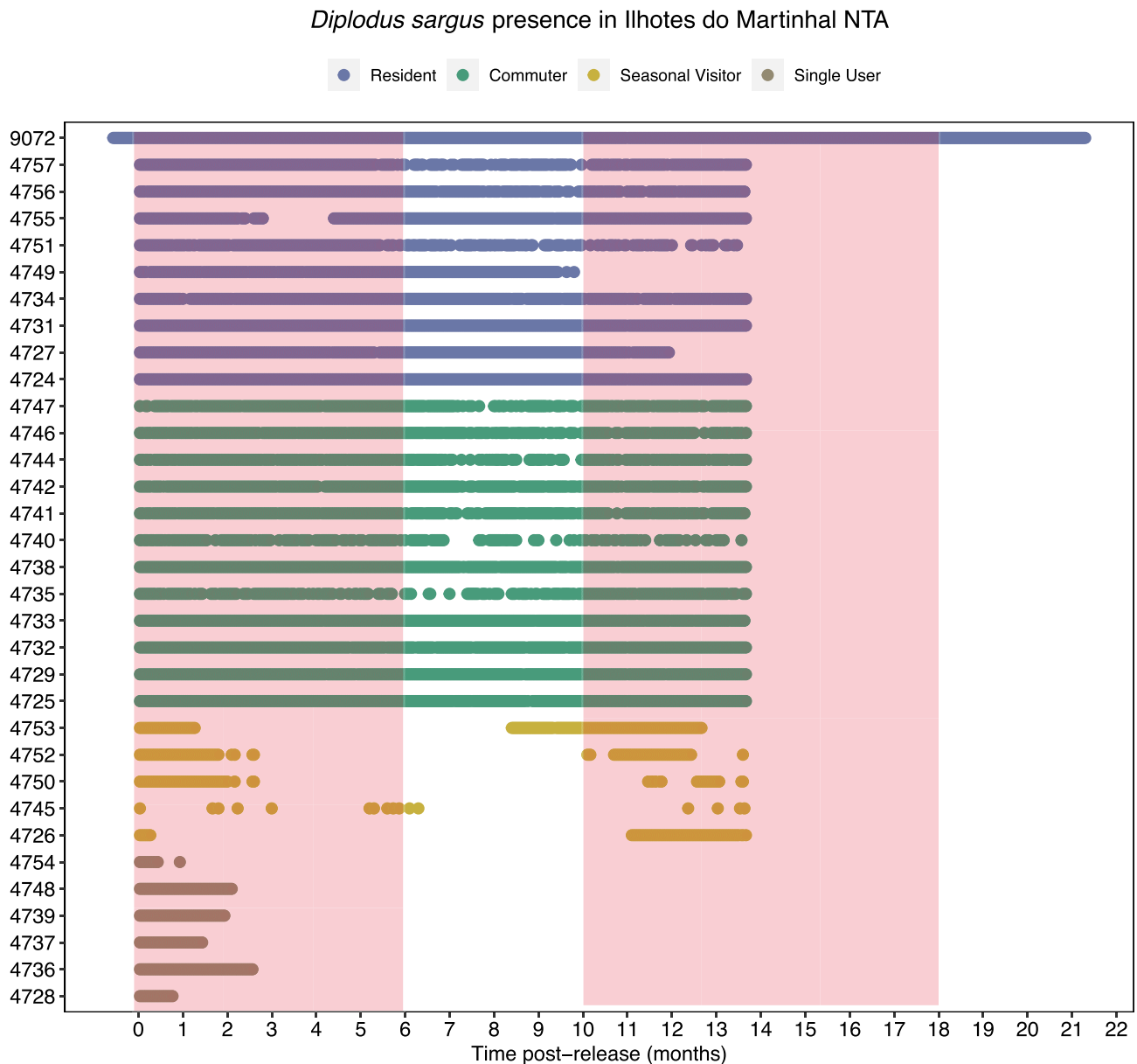


Figure 3. Individual's presence in Ilhotes do Martinhal no-take area, grouped by behavioural types. Spawning seasons represented in pink (Mouine *et al.*, 2007; Giacalone *et al.*, 2022).

(see Supplementary Appendix B, Figures 1 and 2) spent 3.44% of the study period in other no-take areas, evidencing long-distance migrations.

Both the seasonal visitors and the single users, when inside the no-take area, showed a similar behaviour to the residents with high site attachment and a low number of excursions (Figure 3). No significant differences on the mean time of excursions (MTE) (Kruskal–Wallis rank sum test: $\chi^2 = 0.2$, $P = 0.7$) were observed between residents and commuters.

Additionally, the seasonal visitors proved to be significantly larger than the rest of the behavioural types (ANOVA test: F -value = 2.89, $P = 0.05$). Specifically, seasonal visitors were 11% times larger than residents and 17% larger than commuters and single users.

Seasonal variation of time at risk

No statistical differences were observed in the TAR between seasons for those individuals with high site attachment

(Kruskal–Wallis rank sum test: $\chi^2 = 1.7$, $P = 0.6$), neither for the residents (Kruskal–Wallis rank sum test: $\chi^2 = 0.96$, $P = 0.81$) nor for the commuters (ANOVA test: F -value = 3.05, $P = 0.38$).

Nevertheless, commuters undertook more excursions out of the no-take area during Winter than during the rest of the year (ANOVA test: F -value = 3.23, $P < 0.05$): 24% more than in spring, 33% more than in summer, and 27% more than in Fall (Figure 4). However, no significant differences were observed on the mean time of the excursions (Kruskal–Wallis rank sum test: $\chi^2 = 1.86$, $P = 0.60$) (Figure 5).

Residents did not show any significant difference on the number of excursions or their MTE among seasons (Kruskal–Wallis rank sum test: $\chi^2 = 0.96$, $P = 0.81$).

For the seasonal visitors, significant differences in the TAR between seasons were observed (ANOVA test: F -value = 2.732, $P < 0.1$). This, however, can be related to the fact that these individuals left the area before summer and did not re-

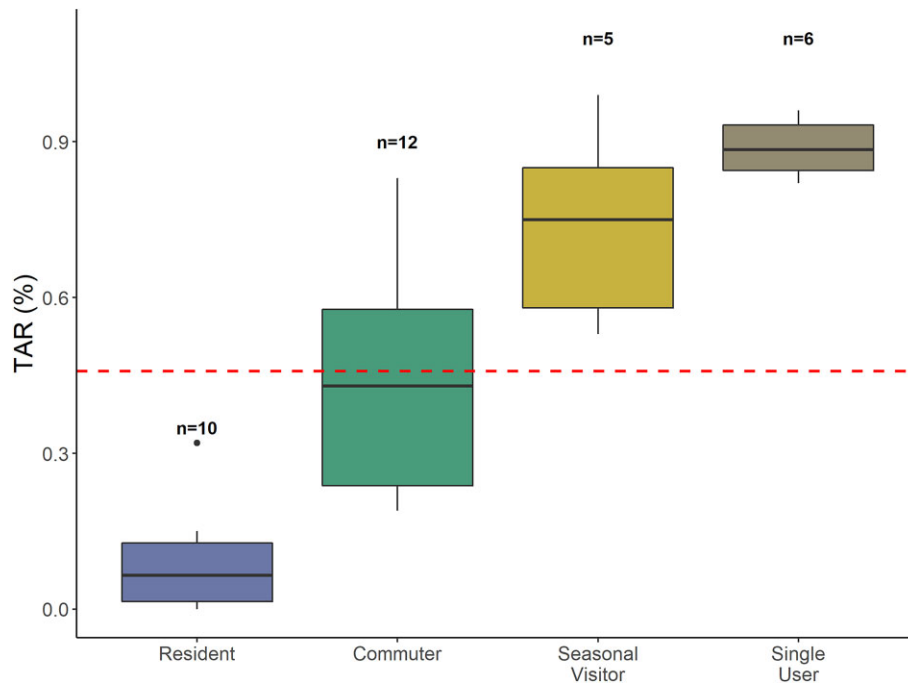


Figure 4. Time at risk (%) for the different behavioural groups towards the mean TAR value for all the individuals (dashed red line).

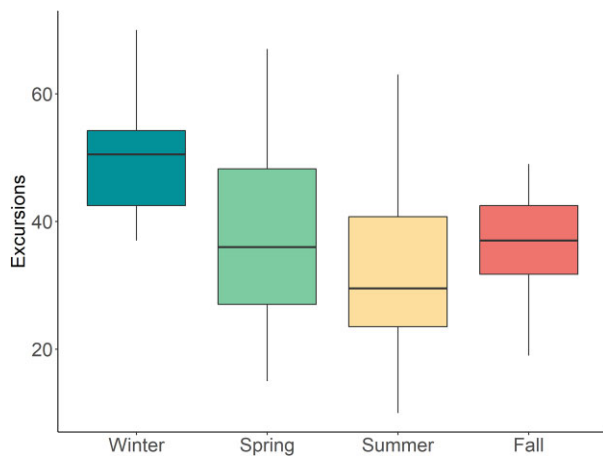


Figure 5. Number of excursions of the commuters along the different seasons during the study period. An excursion is defined as exits and entries detected by receivers located at the boundary of the no-take area that are separated by more than 12 h.

turn until the following winter, with the exception of individual #4745, which spent 2.2 d inside the no-take area during summer, and individual #4753, which spent 29.6 d inside the no-take area during Fall (Figure 3, and Supplementary Appendix B, Table 2). No seasonal analysis on the TAR of the single users was run as they left the area before Summer and never returned (Figure 3).

Diel variation in time at risk.

No significant differences were found in the amount of time spent outside the no-take area during the day and during the night, neither for the high-site-attachment (day TAR: $28.6 \pm 5.3\%$ SE; night TAR: $29.4 \pm 5.3\%$ SE) nor for the low-site-attachment fish (day TAR: $86.5 \pm 3.14\%$ SE; night TAR: $82.5 \pm 3.7\%$ SE).

The residents tended to exit and enter to the no-take area on dusk and dawn, respectively. In contrast, commuters showed differences on the exiting and entering movements (from and to the no-take area) between those inhabiting in the islands and those inhabiting the nearshore. Although these differences did not prove to be statistically significant, commuters inhabiting in the islands tended to exit the NTA during the dawn and enter during the dusk. On the contrary, commuters inhabiting in the nearshore exit mostly during dusk and enter to the area throughout the day, although with slightly higher frequencies during dawn (Figure 6).

The residents did not show different diel patterns among months, but for commuters, movements towards outside the no-take area matched the sunrise times during the period between February and June (Supplementary Appendix C).

Inhabiting areas and time at risk

Significant differences were observed on the time at risk (TAR) between the commuters living in the islands ($30.8 \pm 6.2\%$ SE), and the nearshore ($56.3 \pm 7.1\%$ SE) (ANOVA test: F -value = 7.43, $P < 0.05$). Commuters were the only group considered for the analysis for being the only one inhabiting in both areas. Nearshore individuals spent almost two times more TAR than the individuals inhabiting in the islands. In the same way, significant differences were observed on the duration of the excursions between the commuters inhabiting the nearshore (1.31 ± 0.14 SE) and the ones inhabiting in the islands (0.92 ± 0.18 SE). No significant differences were observed among commuters on the TAR between seasons or in a daily basis.

Discussion

In this study, we have shown how acoustic telemetry can be used to inform spatial conservation and fisheries management tools by linking individual behavioural information to MPA performance. By detailed analyses of fish movement, we esti-



Figure 6. Circular plots showing the hourly distribution of the excursions, exit (left panel) and entry (right panel), for those individuals with high site attachment (SA), per behavioural class (Residents - top - and Commuters - bottom).

mate that the population of white seabream, *D. sargus*, inhabiting the *Ilhotes do Martinhal* no-take area spent, on average, almost half of the study period in unprotected areas, at risk of being fished. Importantly, the level of risk was not homogeneous across individuals, nor throughout the duration of the study. Our study revealed that the effectiveness of this no-take zone, as with other no-take areas, likely depends on fish move-

ment patterns that are influenced by variability in individual behaviour, a phenomenon that has received little attention in MPA science.

White seabream differed in terms of individual site fidelity, with 22 individuals being highly attached to the no-take area (i.e. residents and commuters), five individuals displaying seasonal fidelity (seasonal visitors), and six individuals display-

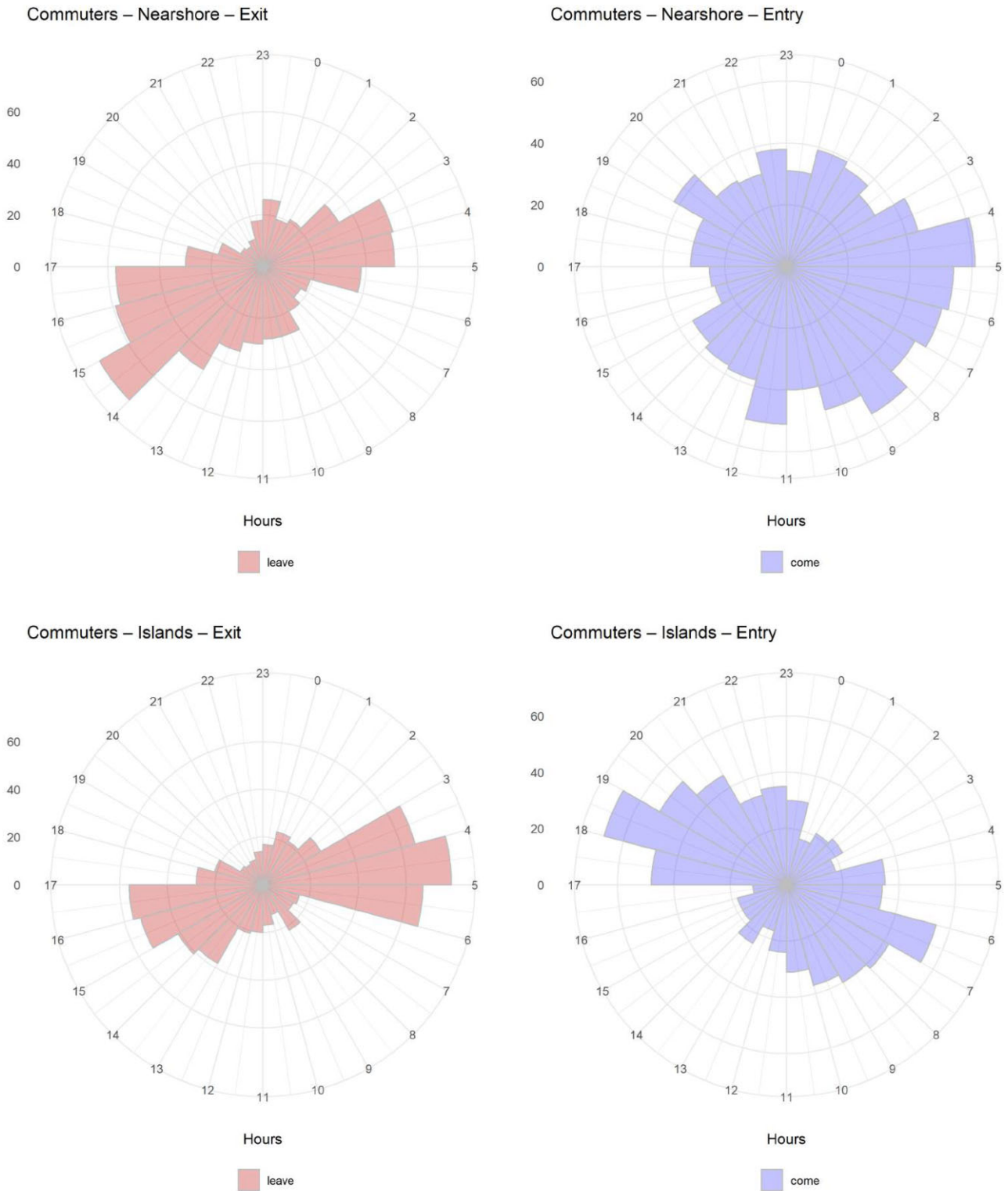


Figure 6 – (continue) Circular plots showing the hourly distribution of the excursions, exit (left panel) and entry (right panel), for the Commuters showing the difference between the inhabiting areas (Nearshore - top - and Islands - bottom).

ing no site fidelity (single users). Our results support previous studies that described *D. sargus* as a species with high site fidelity and small home ranges (D’Anna *et al.*, 2011; Abecasis *et al.*, 2015b), something we can infer for the residents and commuters that barely left this small study area (4.2 km²). We also observed some long-distance movements to other MPAs,

supporting the idea that this species can undertake longer migrations (D’Anna *et al.*, 2004; Abecasis *et al.*, 2009; Di Franco *et al.*, 2012; Belo *et al.*, 2016). Although some previous studies have explored the consequences of species movements outside no-take areas, these studies have focused mainly on dispersal movements or home ranges (Di Lorenzo *et al.*, 2014;

Edgar *et al.*, 2014; Aspillaga *et al.*, 2016; Pereira *et al.*, 2017). In our case, different levels of risk among individuals related to different behavioural polymorphisms were observed. These differences among individuals of the same population, and specifically for those ones with low site attachment that spent almost three times more time at risk than the ones with high site attachment, suggest that an important part of the population of *D. sargus* is not fully protected by this small no-take area. These contradict previous studies that have primarily focused on high-site-attachment species where home-ranges could be reliably estimated (Abecasis *et al.*, 2014; Abecasis *et al.*, 2015b; Belo *et al.*, 2016).

While the majority of the individuals were highly attached to the no-take area, the significant variation in behaviour among fish within high-site-attachment individuals has consequences for their level of protection. Residents remained protected for most of the study period, while in comparison, commuters spent five times more time outside the boundaries of the no-take area than the residents. This resulted in more than one-third of the study period at risk. Further, residents inhabited the Islands while commuters showed preference both for the Islands and the Nearshore area, the later spending two times more time at risk than the former. The nearshore is formed by continuous rocky reefs that spread eastwards outside the no-take area, which is the direction followed by all the nearshore individuals when exiting and entering the no-take area. On the contrary, the islands rocky reefs are surrounded by sandy bottoms, which may act as barriers to frequent movements (Coll *et al.*, 1998, Chapman and Kramer 2000). Further, the number of excursions of the commuters (both inhabiting the islands and the nearshore) was significantly higher in winter. Earlier, Abecasis *et al.*, (2015a) observed a similar increase in the frequency of forays and distance covered during the reproductive season.

Although there were no significant differences in the level of protection over the hours of the day, high-site-attachment individuals performed excursions out of the no-take area at predictable times. This information can be used to inform management measures and priority timings of enforcement (e.g. patrolling the limits of the NTA during the predictable times).

Our receiver array did not include an acoustic receiver station outside the no-take area, which prevented us from locating fish in unprotected areas with precision. However, both the array design and the way of estimating movements outwards allowed us to be relatively confident when an individual was outside the study area (as opposed to undetected but inside the no-take area). In the case of the single users, TAR may be overestimated as we do not know precisely what happened during the time they spent outside the area. However, in previous situations, fishers harvesting tagged fish returned the tag. Accounting for harvest mortality would, in fact, reduce the overestimation of TAR.

In the case of individuals with low attachment to the no-take area, we observed two different behaviours: seasonal visitors and single users. Seasonal visitors showed spatial displacements from the no-take area and migratory trends, spending long periods outside the no-take area but showing seasonal fidelity towards this area in winter and spring. This seasonal fidelity seems to be highly related to the spawning season, which generally lasts from November to July with a peak between March and April (Mouine *et al.*, 2007; Giacalone *et al.*, 2022). All the seasonal visitors were detected within the limits of the no-take area during the expected

peak spawning period. Therefore, the migratory movements of the seasonal visitors suggest that the region where *Ilhotes do Martinhal* no-take area is located might represent a spawning ground for these individuals. This is reinforced by a large increase on local land-based fisheries in the surroundings, targeting this species during the reproduction season (Veiga *et al.*, 2010). In addition, the fact that, within the study population, seasonal visitors, those showing a greater dispersive tendency, are the individuals with larger body size supports the theory that body size and dispersal movements may be interlinked (Hillebrand, 2004). In recent years, interest in the connectivity between no-take areas has increased, particularly in achieving maximum effectiveness in the protection of migratory species (e.g. elasmobranchs or tunas) through the establishment of marine migratory corridors (Pendoley *et al.*, 2014, Shaver *et al.*, 2016, Harris *et al.*, 2018). However, the large distances covered by some of these species, including the high seas, and different exclusive economic zones (EEZs), have been considered difficult to address in MPA planning. In our study three of the individuals' performed movements towards other no-take areas up to 104 km north, in the same MPA, and 169 km north, in another MPA. As previously mentioned, these returning movements seem to be related to the spawning season, a crucial moment for the survival of any species (Taylor *et al.*, 2019). Thus, we acknowledge the need of a deeper study of the migratory movements of this species, not only related to the spawning season but also related to identify the movement corridors, so protection strategies can be developed.

Our study provides compelling evidence that protection will depend on intraspecific behavioural differences. This finding goes beyond most previous studies, where the design of MPAs has focused on population home ranges and movements without considering behavioural polymorphisms (Kramer and Chapman, 1999; Abesamis and Russ, 2005; Abecasis *et al.*, 2015b; Di Franco *et al.*, 2018). In the same way, this study provides empirical support to models that show how the protection generated by MPAs is reduced when species frequently move to adjacent unprotected areas (Gerber *et al.*, 2005). These movements, in populations with behavioural polymorphisms, expose part of the population to fisheries, potentially eroding the portfolio effect (Schindler *et al.*, 2010). Ecosystems resiliency is usually related to diversity of species. In the same way, resiliency of a population can be related to behavioural polymorphisms, facilitating the adaptability of the species to changes that may occur in the environment (Schindler *et al.*, 2010). Therefore, ignoring behavioural strategies when designing MPAs may reduce population variability, fostering resident individuals, and thus decreasing population resilience (Petitgas *et al.*, 2010; Tillotson and Quinn, 2018; Maggs *et al.*, 2019).

We hope that the results of this study will contribute to raising awareness of how the different behavioural types within a fish population can give rise to differences in the use of MPAs. Our study suggests that considering populations as homogeneous units when planning MPAs may be an oversimplification of reality, leaving an important part of the population out and therefore not benefiting from these management tools (Villegas-Ríos *et al.*, 2021).

Supplementary Data

Supplementary material is available at the ICESJMS online.

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Author contributions

BHC, LB, and IS conceived and planned the project and designed the model. CBA analysed the data and performed the calculations. CBA, BHC, LB, IS, MP, DVR, and EMO contributed to the interpretation of the results. CBA took the lead in writing the manuscript. All authors supported in the shape, message, and writing of the manuscript with critical feedback. All authors approved the manuscript.

Conflict of interest

Authors declare no conflict of interests.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request. Data will be available in the European Telemetry Network (ETN) platform.

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