Received: 9 June 2024 | Revised: 21 August 2024 | Accepted: 24 August 2024

DOI: 10.1111/faf.12859

ORIGINAL ARTICLE

FISH and FISHERIES WILEY

Fully protected marine areas linked to reduced home ranges of fishes

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Abstract

Home range size is a fundamental trait that can affect the probability of fish being harvested and, at the same time, may be affected by fishing. The relationship between home range size and fishing will impact the effectiveness of fully protected areas (FPAs), as it will influence the number of fish moving into fished areas, affecting both spillover and edge effects. One hypothesis is that individuals within FPAs will present reduced home range size relative to individuals in fished areas. This pattern can be driven by demographic selection (e.g. fishing of individuals with large home ranges leaving the FPAs), improved habitat requiring less foraging movements, or behavioural changes associated with reduced fishing threats. To test the relationship between home range size and protection, we compiled 1143 individual-level home range sizes based on acoustic tracking, covering 17 species from 11 FPAs in 7 countries, with information on distance from FPA borders. A dichotomic analysis (in/out of FPAs) did not support a significant change in the home range size between FPAs and fished areas. However, continuous analysis across the FPA borders demonstrated reduced home range size within the FPAs. We did not find an effect of FPA age or size on this pattern. While we cannot pinpoint the underlying mechanism for the pattern revealed, we suggest behavioural changes as the main driver for reduced home range within FPAs. This mechanism will lead to more resident populations within FPAs, reducing fishing mortality within FPAs yet limiting spillover benefits to adjacent fisheries.

KEYWORDS
acoustic telemetry, edge effects, fish movement, fully protected areas, home range, spillover

For affiliations refer to page 9.

1 | INTRODUCTION

Harvesting of fish species shapes their abundance, distribution, life history, behaviour, population structure, and genetics (Gandra et al., 2021; Steneck & Pauly, 2019). Fishing directly and indirectly affects fish, acting at the individual, population, and community levels (Conrad et al., 2011; Heino et al., 2015). Behavioural responses associated with fishing include increased fear of humans (Alós et al., 2015; Januchowski-Hartley et al., 2013), reduced schooling behaviour (Guerra et al., 2020a; Sbragaglia et al., 2021), and changing levels of boldness and exploration (Diaz Pauli & Sih, 2017). Fishing also acts as a strong and rapid selection force, potentially driving changes at the evolutionary level. For example, fishery-induced evolution is expected to favour faster life histories, expressed through early maturation, increased reproductive investment, and reduced post-maturation growth (Heino et al., 2015; Sharpe & Hendry, 2009). The behavioural and evolutionary changes associated with fishing are expected to be relaxed within fully protected areas (FPAs), a spatial management tool that effectively protects marine species and ecosystems from all fishing activities (Costello & Ballantine, 2015; Grorud-Colvert et al., 2021; Horta e Costa et al., 2016; Sala & Giakoumi, 2017). Nonetheless, even within FPAs, the degree of protection is a function of the fish centre of activity relative to the FPA border (Abecasis et al., 2014; Moffitt et al., 2009; Villegas-Ríos et al., 2021), with the highest protection provided within the FPA core and the lowest close to the border, where the probability to get caught increases (Di Franco et al., 2018; Ohayon et al., 2021).

Home range size, a measure of the space an animal uses regularly to satisfy its needs, is an important trait at the species and individual levels. From a conservation perspective, there is a consensus that FPAs have to be large enough to protect the home range of the target species (Di Lorenzo et al., 2014; Green et al., 2015; Kramer & Chapman, 1999) and that species with small home range, low mobility, and strong site fidelity relative to FPAs size will benefit more from FPAs protection (Abecasis et al., 2015; Di Franco et al., 2018; Grüss et al., 2011; La Mesa et al., 2012). From a fisheries perspective, FPA size relative to the target species' home range should be optimized to represent a trade-off between the conservation of fish populations and the contribution to fishing yields via spillover (Green et al., 2014; Takashina, 2019). However, while fish species can be characterized by a certain average home range size, individuals within a population can present large variability (Alós et al., 2012; Currey et al., 2014). Given an FPA of sufficient size, the home range size of an individual and its position relative to the border will define the probability of remaining safe within its boundaries or crossing them and exposing it to fishing mortality risk (Kramer & Chapman, 1999; Thorbjørnsen et al., 2021; Villegas-Ríos et al., 2021).

Besides direct mortality, fishing also has the potential to change fish behaviour as a function of their location relative to the FPA border. For example, fish individuals have been shown to have larger flight initiation distance (the distance at which a prey starts to flee at the approach of a potential predator) close to the border compared to individuals further inside the FPA (Januchowski-Hartley et al., 2013). In another study, individuals of the fishery-target species *Serranus scriba* presented increased vulnerability to angling within and near the boundary of an FPA compared with individuals in fished areas while it remained constant for the non-target species *Chromis chromis* (Alós et al., 2015). These examples demonstrate the effect of fishing on an individual's small-scale movements, yet they do not examine the potential effects of fishing and protection on the home range size. Several modelling studies have suggested that individuals of target fish species should present a decreased home range inside FPAs compared to individuals in fished areas (Jiao et al., 2018; Langebrake et al., 2012; Mee et al., 2017). A few field studies support this hypothesis, showing that for individuals whose centre of activity was within the protected area, larger home ranges were associated with decreased survival rate (Alós et al., 2015, 2016; Villegas-Ríos et al., 2017, 2021). However, the generality of smaller home ranges within FPAs and the conditions under which they appear have thus far not been assessed.

A potential mechanism that may lead to smaller home range size within FPAs may be the direct removal of individuals with large home ranges from the population after crossing the FPA boundaries and being exposed to fishing mortality (Alós et al., 2016). These individuals are expected to experience a high mortality rate as they are naïve to fishing risks (Alós et al., 2015; Januchowski-Hartley et al., 2013). Additional mechanisms for reduced home range sizes may be behavioural responses to improved environmental conditions within FPAs. For example, the absence of fishing threats lowers stress levels and avoidance behaviour, which may reduce the overall movement of individuals within FPAs (Januchowski-Hartley et al., 2013). The increase in population density within FPAs can potentially reduce home range size due to density-dependent effects (Trewhella et al., 1988). In addition, FPAs often offer fish higher-quality habitats, providing more food and shelter, which might require a smaller home range size to satisfy their biological needs (Langebrake et al., 2012; Lorenzo et al., 2016; Lowe et al., 2003). Reduced movement patterns of individuals living within the FPA can add to their survival. Hence, it may be a heritable trait, reinforcing the pattern of smaller home ranges in populations living within the FPA through the evolutionary pathway (Mee et al., 2017; Villegas-Ríos et al., 2017). Behavioural adaptations leading to smaller home ranges within FPAs are expected to increase the survival rates of individuals and strengthen the overall positive effect of FPAs on fish biomass. However, at the same time, such a pattern may also reduce the long-term spillover benefits of FPAs to fishers (Mee et al., 2017; Villegas-Ríos et al., 2017).

Alternatively, other mechanisms may drive increased home range size within FPAs relative to fished areas. For example, individuals in fished areas may spend more time hiding compared to individuals within the FPAs, leading to smaller home ranges. The need to escape from predatory fish, which are more abundant within FPAs, may also increase the home range size of individuals of some species in FPAs. Some fishing methods may target individuals with bold personalities, a behavioural trait that may be correlated with large home ranges, thus selecting individuals with smaller home ranges outside FPAs (Diaz Pauli & Sih, 2017). In addition, FPAs are commonly associated with an increase in the average body size of individuals, which may lead to a subsequent increase in their home range size (Campos-Candela et al. 2019).

Taken together, the effect of FPAs on the home range size of fish targeted by fishing is not clear and, importantly, has never been tested empirically across species. Moreover, an effect on the home range size of individuals is expected to occur only where fishing risk has been removed or significantly reduced, such as in highly enforced FPAs. Other key characteristics, such as the FPA age and size may also affect fish home range size, as a change may occur only in FPAs that are large or old enough to form populations that are free from fishing effects. Testing this requires data from multiple FPAs, representing a wide range of characteristics. In this study, we compiled multiple datasets containing individual-level home range sizes from acoustic telemetry studies performed in and around FPAs and characterized their location relative to FPA borders. We then tested the effect of protection on individual fish home range size, considering FPA characteristics such as age, size, and enforcement level. Understanding how fishing and protection affect the home range size of individual fish can enhance our understanding of processes taking place across FPA borders such as edge effects and spillover.

2 | METHODS

2.1 | Data collection

As we required detailed data not usually present in publications, we could not conduct a formal meta-analysis based on published work. Instead, we reached out directly to researchers in the acoustic telemetry community. To be included in the analysis, the data had to contain individual-level home ranges of fish from either inside and outside an FPA or from multiple locations within an FPA. We contacted 31 researchers in a request for information and received 12 positive responses to share information. The response variables in our study are the core range and home range sizes of individual fish, calculated as the 50% and 95% of a Kernel Utilization Distribution (KUD, in km^2), respectively. KUD is an estimate for an animal space use area, based on its positions which are calculated from the raw detection data. Each study used a slightly different method to calculate fish positions, to fit the specific data structure of the study. We highlight that these differences will not influence our results, as we do not directly compare between datasets but focus on comparing home range sizes among individuals within each dataset. We tested both the core and home range in our models and decided to use the home range metric as it is more relevant to our study question given our interest in the effects of fishing at the edges of the range. For each individual, home range values were calculated for a period of up to a year of tracking, hence some individuals who were tracked for extended periods had more than one home range value in the dataset. When possible, detection data from the breeding season was excluded from the home range calculations. The main predictor in our study is the location of the home range centroid relative to the FPA boundaries, which was tested in both a categorical and continuous manner. For the categorical analysis, the centroid location was classified either within the fully protected, partially protected, or unprotected area. For the continuous analysis, the linear distance (km) between the centroid and the FPA border was calculated. For these calculations, the FPA border was noted as zero (0), centroids located inside the FPA received negative values (−), and centroids located in the partially protected or unprotected area received positive values (+). Overall, we compiled 19 acoustic tracking datasets containing a total of 1143 individual-level home range sizes of fish with their location relative to FPA borders. Of the 1143 home range sizes, we included only one home range for each individual in the analysis, calculated from the first year of data ($n = 946$). We removed data from individuals who were translocated ($n = 10$) and restricted the data to −2 to 2 km relative to the border since more distant home ranges were few ($n = 14$), and since this is the range in which we expect biological responses to FPAs (Ohayon et al., 2021). The final dataset for analysis contained 19 datasets and 922 home range sizes, representing 17 fish species (Table S1).

2.2 | Complementary data on fish and FPAs

The dataset was complemented with FPA characteristics to serve as potential predictors for the home range size: (1) FPA age at the time of the study (years), (2) FPA size (in km^2; log_{10} transformed), (3) Enforcement level (low, medium or high), and (4) Habitat continuity across borders (continuous or non-continuous). The variables were completed based on the researchers' estimates and information on the study area. Summary information with FPA characteristics is presented in Table S2. Fish characteristics such as trophic guild, mobility, commercial value, and longevity were also compiled, but not further used in the analysis since they were relatively homogeneous across the datasets (i.e. representing commercial fish species with medium levels of mobility), and hence we could not test their effect.

2.3 | Statistical analysis

Our analysis focused on comparing home range sizes of individual fish of the same species and population (i.e. within each dataset).

2.3.1 | Dichotomic analysis

We first compared the home range sizes in a dichotomic manner using a meta-analytical approach using the "metafor" package in R (v2.4–0; Viechtbauer, 2010). Our first analysis compared home ranges located in FPAs to home ranges located in fished areas (either in partially protected or unprotected areas). In 11 datasets, the home ranges were located only in one zone, hence only 8 datasets were suited for this analysis (including 806 individual home ranges). We performed a second analysis, comparing home ranges within the fully protected "Core" area to the "Border" area, using −400 m as a cutoff (including 9 datasets and 544 individual home ranges). This distance was selected as it resulted in a relatively balanced number of samples in each category. We tested smaller and larger values (e.g. −200 and −600 m) to validate that results did not depend on the exact cutoff. For each study, we calculated the effect size using the Response Ratio method (Hedges et al., 1999):

$$\log(\mathrm{RR}) = \log\left(X_T / X_C\right), \quad (1)$$

where X_T and X_C are the mean values of home ranges (KUD 95%) within the treatment (e.g. protected area) and control areas (e.g. fished area), respectively. The log(RR) and the variance around this value were calculated using the "escalc" function. For studies extending over several years, a separate effect size was calculated for each FPA age. A random effect meta-analysis model was fitted to the data using the "rma.mv" function, to account for the expected variation between species and locations. Since datasets of several species originated from the same FPA, we used a nested random effect in the model (fish species nested within FPA). We added the "knha" adjustment to account for small sample size. The heterogeneity in the data was calculated using the restricted maximum likelihood estimator (method='REML'). We then performed a meta-regression, testing the potential effect of FPA age, size, and enforcement level (each tested independently, as some interaction between factors could be expected) by incorporating them as moderators in the model.

2.3.2 | Continuous models

The above models do not allow testing for complex non-linear effects of distance from the FPA border, which may be prevalent. Hence, we further analysed the data continuously, using General Additive Models (GAMs) from the "mgcv" R package (Wood, 2017). Our main predictor in the model was the distance of the home range centroid from the FPA border (km) and the response variable was the home range size (KUD 95%). We standardized home range within each study, by subtracting from each value the mean home range of the dataset and dividing it by the standard deviation. We considered the standardized fish length (cm, for each individual) as a predictor in the models, to control for the potential effect of fish size on the home range. To find the best model formulation, we fitted a set of hierarchical GAMs (Pedersen et al., 2019) which included: (1) Only a random effect – the unique identification of each dataset. (2) A single global smoother for the main predictor (i.e. distance from the FPA border) + random effect. (3) A single global smoother for distance + fish length + random effect. (4) A group-level smoother for distance within each dataset + fish length + random effect. (5) A global smoother for distance + group-level smoother for distance + fish length + random effect. In all the models, we used a Thin Plate Spline (TPS, bs = "tp") with $k = 5$ as the basis function for smoothing the main predictor (distance from the border), and maximum likelihood to estimate the model performance (method='ML'). Models were evaluated by comparing their Akaike information criterion (AIC) and deviance explained (DE). We performed a cross-boundary analysis, applying the model to the complete dataset containing home ranges from within the FPA and fished areas (19 datasets, $n = 922$ home ranges), as well as a restricted analysis on a reduced dataset containing home range sizes only from withing the FPAs (19 datasets, $n = 809$ home ranges).

We constructed additional GAMs to test the potential effects of the FPA size, age, and enforcement level. We first tested FPA age and size as continuous predictors, testing their interaction with distance from the FPA border using a tensor product. For easy visualization, we also converted these variables into categorical predictors, using their median values in the dataset as cutoff (FPA size: ≤3 km^2 ~ small, $n = 724$; >3 km^2 ~ large, $n = 198$; FPA age: ≤7 ~ young, $n = 475$; >7 ~ old, $n = 447$). Data from FPAs with "medium" enforcement levels was limited ($n = 98$), hence it was merged with the "low" enforcement level, to create a more balanced comparison with highly enforced FPAs (high: $n = 482$; low: $n = 440$). We then tested the effect of these categorical predictors on the home range size as a function of their distance from the FPA border using the "by" argument.

Two of the datasets were significantly larger than all the others; *Gadus morhua* dataset contained 521 home ranges (from 397 individuals) and *Xyrichtys novacula* dataset contained 291 home ranges (from 291 individuals). The number of home ranges in all the other datasets ranged from 6 to 39. We thus applied the above-mentioned GAM models also to a balanced dataset containing 30 random samples from each of the large datasets ($n = 294$). We repeated the balanced data analyses 10 times over different random sampling iterations.

3 | RESULTS

We compiled 19 acoustic tracking datasets of individual-level fish home ranges, representing 17 species from 11 FPAs, located in 7 countries: Italy, France, Spain, Portugal, Norway, Australia, and New Zealand. Summary information of the fish species and FPAs included in the datasets are presented in Tables S1 and S2.

In a dichotomic comparison of home ranges from FPA to fished areas (either partially protected or unprotected) 6 out of 8 effect sizes were negative, yet we did not find a significant effect of protection on the home range size (Figure 1a, $t=-1.74$, $p=.12$). When we compared home ranges from the FPA core areas to the border areas, using −400 m as a cutoff value, the overall effect was centred around zero and again non-significant (Figure 1b, $t=-0.07$, $p=.93$). Using smaller or larger values as cutoffs between the core and border areas (−200 m or −600 m respectively) did not change this result (Figure S1). We did not find a significant effect of FPA age, size, or enforcement level on home range effect sizes in both analyses (Figure 2).

Examining the patterns of home range continuously using GAMs, we found that the best-supported model included both the global effect and the group-level effect of distance from the FPA border (Table 1, Δ AIC = 11.75 compared to the next best-supported model). The global effect presents an overall increase in home range size from within the FPA towards fished areas (partially protected or unprotected), supporting a reduction in the home range size within FPAs (Figure 3a). At the same time, the group-level smoother reveals large variations in patterns among studies and species (Figure 3b; Figure S2). Much of the variation was found around the FPA border area which can partially explain why the dichotomic meta-analysis did not detect a significant difference. The results remained significant also when we

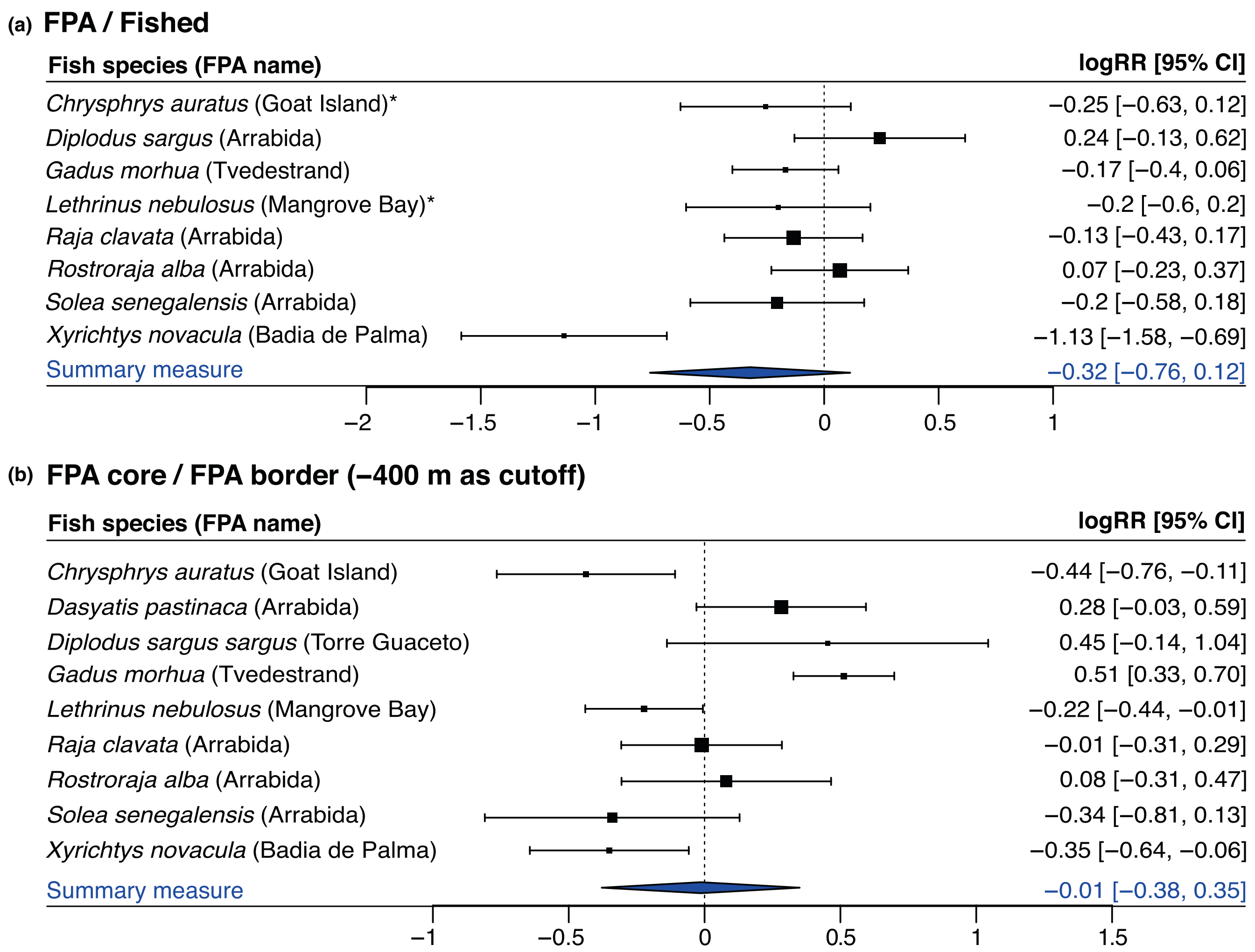

FIGURE 1 Forest plot results for the meta-analyses comparing individual-level home range effect sizes under a dichotomic approach. A positive effect size means that the average home range is smaller outside the FPA, and a negative effect size means that the average home range is smaller inside the FPA. (a) Comparison of home range sizes from FPAs versus fished areas (partially protected or unprotected) (heterogeneity: $Q=25.26$, $df=7$, $p=.0007$; $I^2=77.75\%$; overall effect: $T=-1.74$, $p=.12$). (b) Comparison of home range sizes from FPA core (distance from border <−400 m) versus border (distance from the border ≥−400 m and ≤0) (heterogeneity: $Q=52.4$, $df=8$, $p<.0001$; $I^2=81.36\%$; overall effect: $T=-0.07$, $p=.93$). In Figure (a), species marked by the star are from FPAs surrounded by unprotected areas, and all others are from FPAs surrounded by partially protected areas.

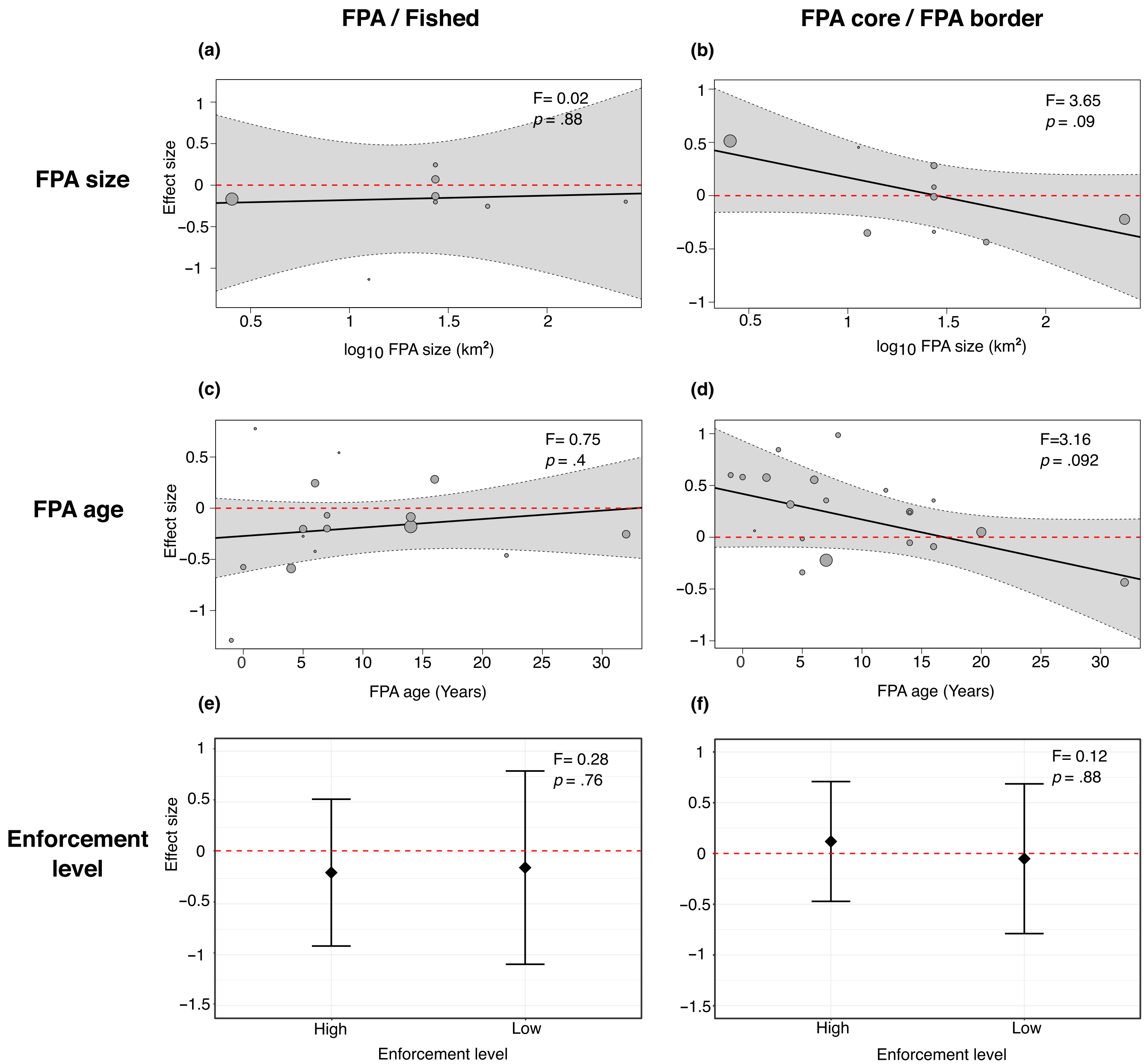

FIGURE 2 A meta-regression for the effect of FPA size (a,b), FPA age (c,d), and enforcement level (e,f) on home range effect sizes (log RR). A positive effect size means the average home range is smaller outside the FPA and a negative effect size means the average home range is smaller inside the FPA. In the left panels, the effect sizes (y-axes) are from the comparison of home ranges between the FPAs to fished areas (partially protected or unprotected). In the right panels, the effect sizes are from the comparison of home ranges between the FPA core and the border (using −400 m as a cutoff). In figures a–d, the size of the circles is proportional to the weight that each study received in the analysis, calculated as the inverse of the within-study variance (i.e. studies with low variance received higher weight in the analysis and represented by larger circles). The shaded areas around the model curves in a–d and error bars in e–f denote 95% confidence intervals.

used a balanced data design (a reduced dataset including 30 random samples from each of the two large datasets, Figure S3a,b) or when we applied the model to data only from within the FPA (Figure S3c). These patterns further hold whether we controlled or not for fish size, which, as expected, strongly affects home range size (Figure S4).

Incorporating FPA age, size, and enforcement level as interaction terms with distance from the FPA border did not improve the models' performance (Table 2, Δ AIC <2). Similarly, testing FPA characteristics as categorical predictors on a balanced dataset did not improve the model results. Nonetheless, the general pattern of decreased home range size within the FPA was still apparent (Figure S5).

4 | DISCUSSION

We found evidence for smaller home ranges of fishes inside FPAs using continuous analyses. Patterns of smaller home ranges of

TABLE 1 Model comparison results for the GAMs with varying formulations for individual-level home range size as a function of distance from the FPA border.

GAM formula	AIC	Δ AIC	DE (%)
HR ~ Distance + Distance (by = unique ID) + Fish length + Unique ID (random effect)	2384.322	0	20.3%
HR ~ Distance (by = unique ID) + Fish length + Unique ID (random effect)	2398.24	13.91	20.2%
HR ~ Distance + Fish length + Unique ID (random effect)	2476.576	92.25	8.9%
HR ~ Distance + Unique ID (random effect)	2553.008	168.68	1%
HR ~ Unique ID (random effect)	2554.686	170.36	0.0002%

Abbreviations: Distance, the distance (km) of the home range centroid from the FPA border; Fish length, standardized fish length; HR, standardized home range size; Unique ID, identifier code for each dataset.

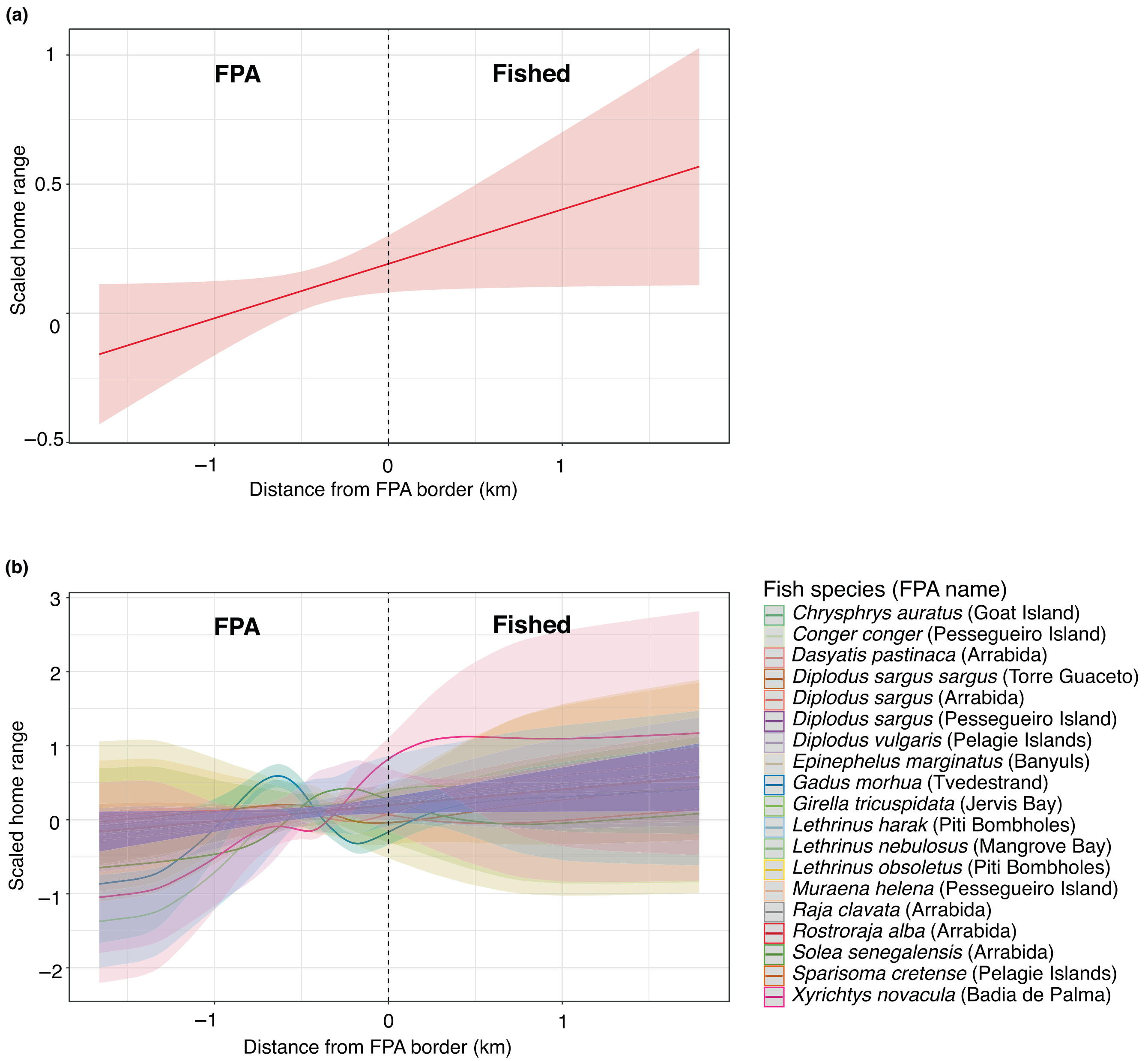

FIGURE 3 The spatial patterns of individual-level home range sizes as a function of distance from the FPAs border. (a) The global effect of distance from the FPA border (*x*-axes, in km) on home range size (*y*-axes, home range is standardized). (b) The species-level effect of distance from the FPA border on home range size (each colour represents a different dataset). Both (a) and (b) present the marginal effects of the best-supported GAM model (Table 1). We note that it is difficult to discern the exact shape of the curve for specific species, thus we show the species-level patterns in Figure S2. The dashed vertical lines represent the FPA border. The shaded areas around the model curves denote 95% confidence intervals.

TABLE 2 Model comparison results for GAMs incorporating FPA age (years), size (km^2; log_{10} transformed), and enforcement level (high or low) as interaction terms with distance from the FPA border.

GAM formula	AIC	Δ AIC	DE (%)
HR ~ Distance + Distance (by = unique ID) + Fish length + Unique ID (random effect)	2384.32	0	20.3%
HR ~ Distance (by = Enforcement level) + Distance (by = unique ID) + Fish length + Unique ID (random effect)	2385.18	0.86	20.4%
HR ~ Distance × FPA age (tensor product) + Distance (by = unique ID) + Fish length + Unique ID (random effect)	2386.01	1.69	20.3%
HR ~ Distance × FPA size (tensor product) + Distance (by = unique ID) + Fish length + Unique ID (random effect)	2386.17	1.85	20.3%

individuals within FPAs may result from demographic selection in the population, i.e., removal of individuals with large home ranges, as well as from behavioural plasticity of individuals reducing or increasing their home range in response to differences between FPAs versus fished areas. These differences include fishing threats and potentially also environmental differences in habitat quality. The implication of our finding of smaller home ranges inside FPAs for their effectiveness and benefits to surrounding fisheries will depend on the exact mechanisms driving this pattern.

One process that can drive smaller home ranges within FPAs is demographic selection in the population, driven by the mortality of individuals with large home ranges fished after crossing the FPA boundaries (Alós et al., 2016; Villegas-Ríos et al., 2021). In this scenario, fish mortality will remain high even in old FPAs, as large home-range individuals will continue to cross the FPA boundaries and get caught. This mechanism will imply spillover benefits for fishers, but at the same time, a reduction in population size within the FPA, especially in the periphery, producing edge effects (Ohayon et al., 2021; Takashina, 2019). Nonetheless, under this scenario, we would expect smaller home ranges only for individuals at the FPA periphery, while at the FPA core, where fishing mortality is eliminated, home ranges should be larger. We did not find such a pattern, as the home range sizes were the smallest in the FPA core (Figure 3), suggesting that other mechanisms are more likely to be at play, or that fishing in the examined FPAs impacts the FPA core as well (e.g. due to their small size).

Fishery-induced behaviours may also affect individual home range size (Diaz Pauli & Sih, 2017). Avoidance from fishers, fishing gear, or fishing vessels may drive fish to higher rates of movement, translated into larger home ranges outside FPAs compared with individuals within the FPAs who are released from this threat (De Robertis & Handegard, 2013; Guerra et al., 2020b; Hemmings, 1973; Tran et al., 2016). In support, naïve fish exported from FPA can change their behaviour even after short exposure to fishing (Lovén Wallerius et al., 2019) and increase their home range. Thus, if exposure to fishing increases individuals' home range size, then its absence within FPAs can lead to reduced home range size, providing individuals and populations an added survival benefit (Thorbjørnsen et al., 2021). Reduced home range size within the FPAs driven by behavioural changes is likely to decrease edge-effect distance, as fishers along the FPA perimeter will catch fewer fish compared to situations in which fish have large home ranges. At the same time, it may also reduce the spillover effect and hence the benefits of FPAs to surrounding fisheries (Villegas-Ríos et al., 2017).

It is important to note that the behavioural changes associated with fishing will likely depend on the type of fishing practised outside the FPA (Conrad et al., 2011; Diaz Pauli & Sih, 2017). Passive fishing techniques (angling, pots, traps, gillnets, etc.) have higher catch success for mobile individuals, which may be translated into smaller home ranges in populations exposed to fishing and therefore mask the pattern of smaller home ranges within the FPA (Alós et al., 2012). Active fishing techniques (trawls, seines) may differentially catch relatively sedentary individuals, therefore selecting individuals with larger home ranges and reinforcing the pattern of smaller home ranges within FPAs.

In some fish species, there is an allometric relationship between body size and home range size (Dhellemmes et al., 2023; Kramer & Chapman, 1999). Therefore, if the average size of individuals is larger within FPAs due to protection, we expect also the average home range size to be larger within FPAs compared to the average home range in fished areas. In our dataset, we found the expected strong positive relationship between fish size and home range size (Figure S4a) and a non-significant trend for larger individuals within the FPAs (Figure S4b). However, the pattern we found, of smaller home range sizes within FPAs, holds despite the counteracting effect of body size (Figure 3 and Table 1), indicating that body size is unlikely the driver for the change in home range size across FPA borders.

As an additional alternative mechanism to the pattern of smaller home range within FPAs, we note that FPAs often present high-quality habitats containing more food and shelter, either because they are placed in favourable locations (Edgar et al., 2004) or as a result of the protection to the habitat from physical destruction (Turner et al., 1999). In this case, individuals living within high-quality habitats may require smaller home ranges to satisfy their biological needs compared to individuals residing in poorer habitats outside the FPA (Jiao et al., 2018). In addition, home range may be limited by habitat discontinuities coinciding with FPA boundaries (Kramer &

Chapman, 1999). Thus, we cannot rule out the possibility that patterns observed here are driven or reinforced by the improved habitats associated with FPAs, and not by fishing per se.

In addition, one of the most important effects of FPAs on marine species is the increase in population density. In terrestrial systems, it is well known that an increase in density may lead to a decrease in the territory size of individuals (Trewhella et al., 1988), which is a core component of home range size. In non-protected areas, the territories of these species may be larger due to the lack of encounters with conspecifics, forming a negative relationship between space use and density (Šálek et al., 2015). For example, in this study, the pearly razorfish *Xyrichtys novacula* showed one of the strongest decreases in home range size within FPAs compared to fished areas (Table 1). In FPAs, the abundance of this species is 5–6 times higher compared to fished areas (Alós et al., 2016), which results in a denser packing of territories and a decrease in the home range size compared to fished areas (Aspillaga et al., 2021). While higher density may be associated with smaller home ranges, if intraspecific competition in FPAs is strong enough, even small home-range individuals may relocate to regions of lower competition (e.g. fished areas), enhancing spillover.

Small home range size is a trait that can give an added survival benefit to individuals residing within FPAs, hence it may be reinforced through genetic selection. Evolutionary processes are expected to be more pronounced in larger and older FPAs, which have a higher chance of retaining self-sustained populations and sufficient time for evolutionary processes to take place. In our study, smaller home range sizes of fish inside FPAs were not associated with FPA age, size, or enforcement level. A possible reason for this may be large-scale mixing of fish eggs and larvae exported from the FPA to adjacent fishing grounds, meaning that the scale of most FPAs tested here is too small to produce consistent evolutionary changes in home-range size (Di Franco et al., 2012, 2015; Kough et al., 2019; Le Port et al., 2017). Nonetheless, we do not rule out the contribution of evolutionary selection to the pattern we found and note that our sample size is restrictive, and hence, our ability to detect complex interactions, such as FPA age or size with distance from FPA borders, is limited.

The pattern of smaller home range size of fishes inside FPAs was evident in the continuous analysis using GAMs, however, when we compared home range sizes in a dichotomic manner in the meta-analysis (i.e. comparing FPAs to fished areas, or FPA core to the border) no significant differences were found. Nonetheless, we note that in the dichotomic comparison of home ranges in FPAs to fished areas, effect sizes were mostly negative, leaving the possibility that smaller home ranges inside the FPAs were not detected due to low statistical power. The ambiguous results found for the dichotomous analysis can be explained by the large variability in home range patterns across the FPA borders (Figure 3b). This variability means that for each species the estimated home range response ratio will depend on the exact distance from the FPA border used as a cutoff to calculate the average home range, causing patterns to largely disappear when averaging across many species.

This study compiled the largest dataset testing the effect of protection on individual-level home range sizes. We acknowledge the limitation of the data, both in terms of the number of individuals within each dataset and the number of independent studies (several datasets originated from the same FPA). However, we note that the large datasets presented clearer patterns, with some species displaying small home ranges within FPAs, strengthening our confidence in the results, and other species presenting a more variable pattern (Figure S6). Additional datasets with larger sample sizes, taxa, and spatial cover are required to increase the certainty of our findings. In acoustic tracking studies focused on marine protected areas, it is typical to provide better coverage of the acoustic receivers array within the protected area boundaries, and less coverage outside the protected area (Aspillaga et al., 2016; Harasti et al., 2015; Mason & Lowe, 2010). This could potentially bias some of the results. However, we still found patterns of increased home range towards the FPA border when we restricted our analyses to data from within the FPAs (Figure S3c). Nevertheless, we cannot dismiss the possibility that sampling design, including acoustic receiver location or fish capture and tagging locations, affected the results.

5 | CONCLUSIONS

Here we describe a pattern of smaller home ranges within fully protected areas compared to unprotected fished areas, for which we propose a set of possible mechanisms. However, due to the nature of the datasets, we cannot unequivocally identify which mechanisms are responsible for the highlighted pattern. Behavioural changes leading to smaller home range sizes within FPAs will contribute to the formation of a more resident population within the FPA and thus increase the survival of individual fish. This mechanism will increase the positive effect of FPAs on fish biomass, but, at the same time, may limit the net biomass spillover into adjacent fisheries. In the context of FPAs, acoustic telemetry studies have aimed to characterize fish home range size to find the optimal FPA size that will maximize protection benefits for fishery-targeted species. In this study, we highlight the need to take a complementary view and explore the dynamic effect of fishing and protection on target fish home range size and the mechanisms driving these effects.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The dataset compiled in this study will be available upon request.

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How to cite this article: Ohayon, S., Abecasis, D., Almeida, P. R., Alós, J., Aspillaga, E., Belo, A. F., Costa, J. L., Di Franco, A., Di Lorenzo, M., Ferguson, A., Guidetti, P., Kraft, S., La Mesa, G., Olsen, E. M., Parsons, D., Pickholtz, R., Quintella, B. R., Silva, A. F., Taylor, B. M., … Belmaker, J. (2024). Fully protected marine areas linked to reduced home ranges of fishes. *Fish and Fisheries*, *00*, 1–12. https://doi.org/10.1111/faf.12859