Fisheries Research 253 (2022) 106362

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Mesoscale assessment of sedentary coastal fish density using vertical underwater cameras

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ARTICLE INFO

Keywords:
Absolute density
Unbaited cameras
Recreational fishing
Underwater cameras

ABSTRACT

Accurate and precise monitoring of the absolute density (i.e., number of fish per area or volume unit) of exploited fish stocks would be strongly advisable for deriving stock status and for designing proper management plans. Moreover, monitoring should be achieved at relevant (i.e., sufficiently large) temporal and spatial scales. This objective is particularly challenging for data-poor fisheries, as is often the case for recreational fisheries. Therefore, the feasibility of underwater video monitoring (vertical unbaited cameras) for estimating, as a proof of concept, the absolute density (and its ecological drivers) of a coastal sedentary fish species is demonstrated. The absolute density of a small serranid (*Serranus scriba*) targeted by recreational fishing was estimated along the southern coast of Mallorca Island (nearly 100 km). The median fish density ranged between 111 ind/km^2 (Es Molinar) and 14,110 ind/km^2 (Cabrera). Absolute density was correlated with fishing exposure, habitat, and depth. Site specific, seemingly long-term, effects of fishing exposure were negatively correlated with fish density, but short-term effects (assessed by the interaction between fishing exposure and before/after the season when recreational fishing occurred in the study area) were not detected. We suggest that the short-term effects of fishing may remain undetected because highly exploited sites could contain fish that are already not vulnerable to recreational fishing gear, irrespective of the short-term fishing pressure exerted. Such a process may explain some hyper-depletion patterns and should preclude the use of fisheries-dependent data for monitoring fish density. The results reported here indicate that monitoring fish abundance with vertical unbaited cameras at large spatial and temporal scales can be a reliable alternative for many species.

1. Introduction

Proper assessment of population dynamics is essential for ensuring sustainable management and effective conservation of species and habitats (Milner-Gulland and Rowcliffe, 2007). Specifically, supplying accurate and precise monitoring of the absolute density (i.e., number of fish per area or volume unit) of exploited fish stocks is strongly advisable for deriving stock status and for designing proper management plans (Giacomini et al., 2020; Pauly et al., 2013). Nevertheless, biological reference points of stock assessment are usually defined using fishery-dependent data, although it is well known that these data are prone to bias (Alós et al., 2015a, 2014; Alós and Arlinghaus, 2013; Saul et al., 2020); thus, they may lead to inappropriate management decisions (Simmonds, 2007). In addition, wildlife monitoring should be achieved at relevant (i.e., large enough) temporal and spatial scales for adopting management decisions (Pollock et al., 2002).

Monitoring problems are exacerbated in the case of recreational fishing (Post, 2013), whose impacts on resources are a matter of concern (Cooke and Cowx, 2004). Marine recreational fishing is one of the most extended leisure activities in coastal waters worldwide (Hyder et al., 2018; Post, 2013), and it is a particularly relevant activity along the Mediterranean coast, where it may represent approximately 10% of total

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https://doi.org/10.1016/j.fishres.2022.106362
Received 30 November 2021; Received in revised form 4 May 2022; Accepted 4 May 2022
Available online 21 May 2022
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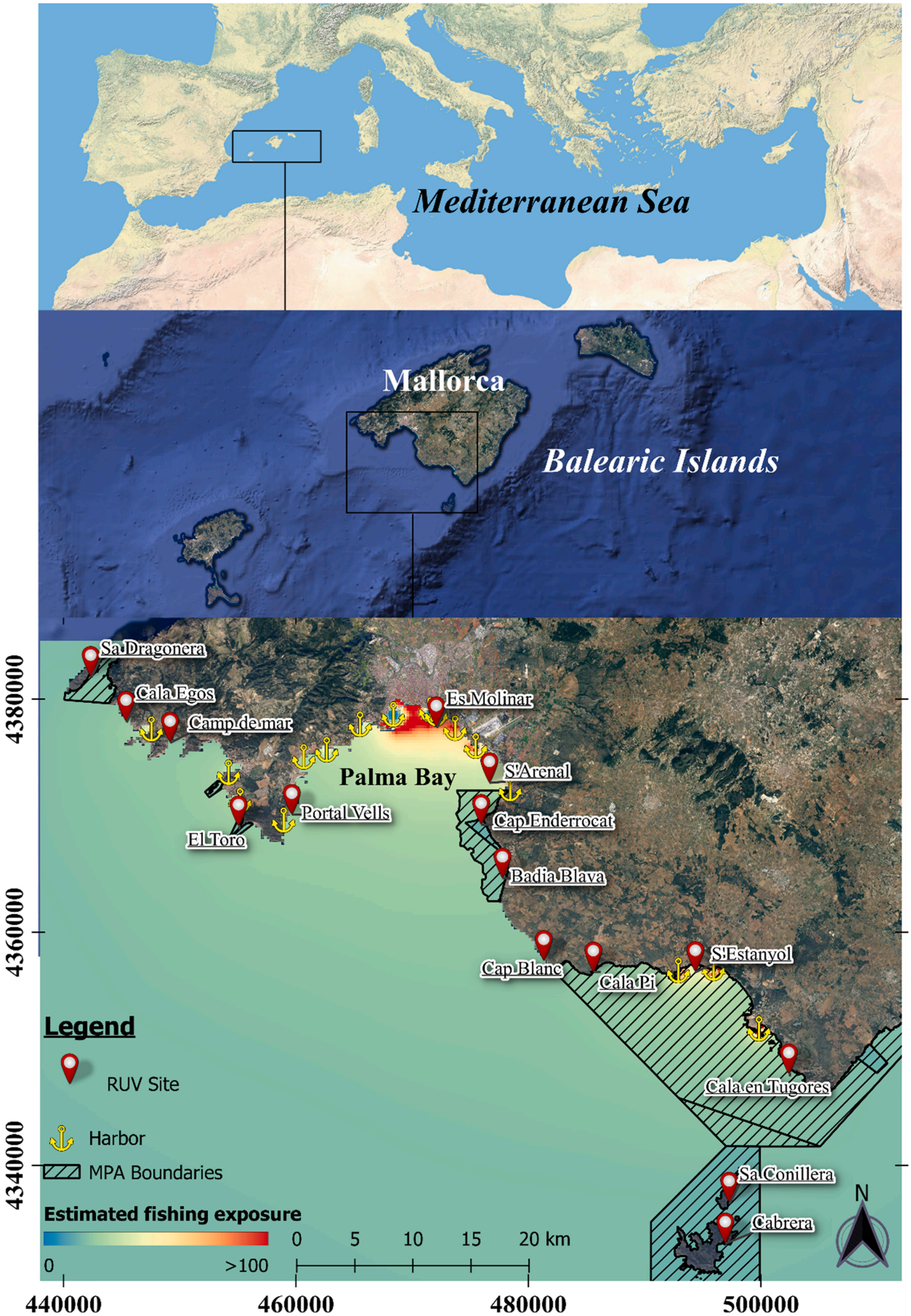

Fig. 1. Study area along the southern coast of Mallorca. The anchors (Harbor) represent the ports and marinas, the red buttons represent the sampling sites where remote underwater video cameras (RUV) were deployed, the polygons with lines represent the marine protect areas (MPAs), and the estimated fishing exposure (boat outings/km2/year) is denoted from blue (minimum fishing exposure) to red (maximum fishing exposure). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

catches and where it involves a large number of practitioners (Grau, 2008; Morales-Nin et al., 2015, 2005). However, monitoring recreational fishing exposure, catches and abundance is difficult; thus, predicting the effects of recreational fishing on the population dynamics of exploited species is a particularly elusive task (Arlinghaus and Cooke, 2005; Pita et al., 2020; Radford et al., 2018).

Given that underwater video techniques are increasingly used for monitoring reef fish, we aim to demonstrate, as a proof of concept, the feasibility of underwater video for estimating the absolute density of a coastal fish species heavily exploited by recreational fishing but commercially unexploited. Underwater cameras are already providing an unprecedented amount of fishery-independent data (Mallet and Pelletier, 2014; Przeslawski and Foster, 2018; Sheaves et al., 2020). Their use is currently so widespread that underwater cameras are reshaping the way the marine realm is observed (Mallet and Pelletier, 2014; Sheaves et al., 2020).

The relative abundance indices extracted from several camera settings have been extensively compared to each other and to underwater visual censuses (UVC) and other methods (Watson et al., 2005). Unfortunately, these empirical comparisons demonstrated that effective integration of relative abundance indices from different monitoring methods is problematic (Cheal et al., 2021).

In contrast to relative abundance indices (e.g., *N max* , or the maximum number of fish counted in any frame of a video), several methodological advances for estimating absolute density (i.e., number of fish per area or volume unit) have been recently proposed (Abolaffio et al., 2019; Campos-Candela et al., 2019, 2018; Follana-Berná et al., 2020, 2019). These contributions developed the theoretical framework, explored several statistical challenges via computer-simulated experiments (e.g., how to improve accuracy and precision), or addressed technical issues (e.g., accounting for fish detectability or improving device design). However, a real-world demonstration of the feasibility of estimating fish density under field conditions and at a scale large enough for supporting management decisions is still lacking. Such a real-world demonstration is essential because, despite the absolute density estimates obtained by these methodological advances seeming unbiased and accurate (Abolaffio et al., 2019; Campos-Candela et al., 2018), there is still some debate on whether the sampling effort needed for achieving a target precision is affordable (Abolaffio et al., 2019; Campos-Candela et al., 2019). Thus, our primary aim is to demonstrate the feasibility of underwater cameras for estimating the absolute density at the mesoscale (near 100 km along the southern coast of Mallorca Island) of a small serranid (*Serranus scriba*) exploited by recreational fishing (Dedeu et al., 2019).

Moreover, as a proof of concept, we evaluated the feasibility of the proposed framework for exploring the effects of different ecological drivers on fish abundance. Specifically, we evaluated the effects of three of the most typical drivers affecting coastal fish density: habitat type, depth, and fishing exposure (Stoner, 2004). Concerning fishing exposure, we attempted to discriminate the short-term effects from the site-specific effects by monitoring the same sites before and after summer, which is when most recreational fishing activity occurs in Mallorca (Cabanellas-Reboredo et al., 2014; March, 2014; March et al., 2014). The relevance of short-term effects was assessed by comparing the between-season differences in density along a gradient of fishing exposure (i.e., larger decreases in density after summer are expected at sites more exposed to fishing).

2. Materials and methods

2.1. Study area and sampling

The absolute density of *S. scriba* was estimated at 15 sites covering the southern coast of Mallorca Island (Fig. 1).

The selected sampling sites were distributed along nearly 100 km, and they displayed well-contrasted fishing exposure and management strategies (e.g., from heavily exploited sites to marine protected areas, MPAs) and cover the full environmental gradient range inhabited by *S. scriba*: from rocky bottoms to seagrass meadows of *Posidonia oceanica* and from the coastline to an approximately 30 m depth (March et al., 2010).

To assess the variability in fish density at a short spatial scale, at each sampling site, ten vertical underwater camera devices were randomly deployed per season (spring and summer) within an area between 0.5 and 1 km^2. All devices from a given site and season were deployed on the seabed in a single day and left from (approximately) 8:00–12:00, which ensured that each device recorded until the end of its battery life (approximately 3 h and 15 min). Cameras were deployed on suitable habitat for *S. scriba*, and distances between the cameras deployed in the same day were longer than 200 m to minimize between-camera spatial autocorrelation (Follana-Berná et al., 2020).

As stated above, two samplings were completed at each of the 15 sites to assess the short-term effects of the estimated fishing exposure on fish density: late spring and late summer. This sampling design should have provided 300 videos (15 sites, 10 cameras per site, and 2 seasons per site), but the actual number of videos finally analyzed was 257 because of diverse problems (cameras lost or theft, battery problems, camera malfunctions, landings on the seabed at the wrong angle, etc.). Sampling dates and the coordinates of all points where cameras were deployed are provided at repository https://doi.org/10.17632/8c5jwvkvsz.6.

The underwater camera device consisted of a vertical structure with two action cameras, Sony HDR AS50®, separated from each other by a distance of 20 cm and looking down at an angle of 45°. This design has already been successfully used for estimating the fish density of *S. scriba* (Follana-Berná et al., 2020). The device, built with PVC pipes, incorporated a counterweight at the base and a buoy at the top, which ensured its vertical position at any moment. The cameras were located 150 cm from the base of the device. The seabed area surveyed by a camera was 5.0 m^2 (Follana-Berná et al., 2020).

The videos were manually examined by an observer following a previously developed and tested protocol (Follana-Berná et al., 2020). Briefly, the first minute after the device made landfall on the seafloor was discarded to avoid any abnormal fish behavior. Then, the number of individuals in one single frame was counted every 120 s. The average number of frames counted per video was 90. Previous trials ensured that temporal autocorrelation between frames is not relevant at this counting frequency (Follana-Berná et al., 2020). In practice, the reading was made easier by using video viewing software that jumped from the actual target frame to a few seconds just before the next target frame. Fish movement largely facilitated fish detection during these few seconds, but only those fish that were strictly present at the target frame were counted.

2.2. Explanatory variables: estimated fishing exposure, habitat, and depth

The drivers of recreational fishing exposure tend to be complex, but they have been analyzed in depth in Palma Bay (March, 2014), which is well within the study area (Fig. 1). In Palma Bay, fishing exposure is modulated by weather (wave height), seasonality (temperature and day length), distance to coast, depth, sea bottom type, business/working day and fishing quality (yield, fish size and diversity), but the main driver is distance to ports (March, 2014). Provided that most of these variables are not available for some of the sampled sites outside Palma Bay, a new variable (*estimated_ fishing_exposure*) was estimated using distance to port only. Distance to port has also been used as a proxy of fishing exposure for explaining the spatial distribution of commercial fleets (Caddy and Carocci, 1999).

The relationship between fishing exposure and distance to port in Palma Bay is clearly nonlinear, reaching a maximum at intermediate distances and decreasing toward both greater and closer distances to port (March, 2014). Therefore, a unimodal model for *estimated_*

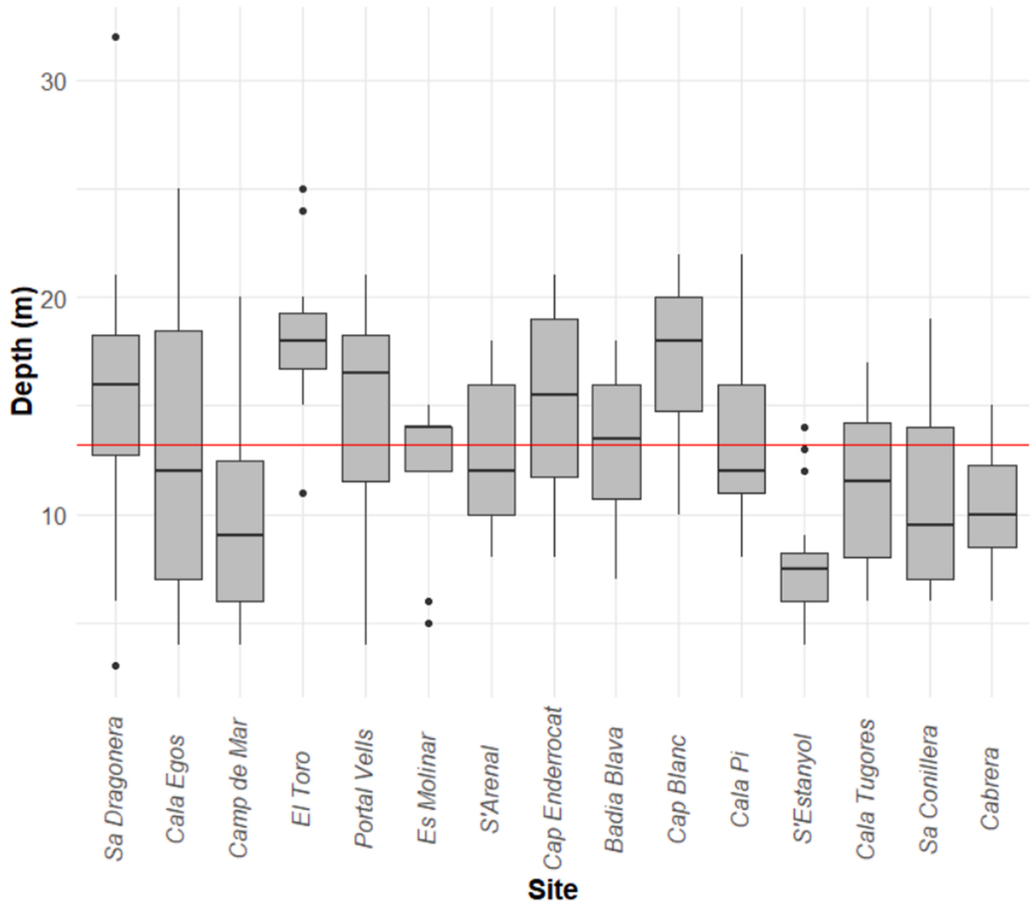

Fig. 2. Within-site and between-site variability for depth. Each boxplot corresponds to a site, and it shows the variability in depth between the exact positions where the 20 cameras from a site (10 cameras per season) were deployed. The line is the median, the upper and lower limits of the box represent the interquartile range, and whiskers represent 1.5 times the interquartile range of the box.

fishing_exposure was developed (Supplementary Material). The model was calibrated using the recreational fishing exposure (boat outings/km^2/year) provided by March (2014) for 143 sites in Palma Bay. Provided that the new variable (*estimated_ fishing_exposure*) was well correlated (r = 0.61) with fishing exposure in Palma Bay, we used the model for estimating *estimated_ fishing_exposure* at all sampled sites, but some caution should be exercised when translating *estimated_fishing_exposure* to fishing exposure.

As stated above, sea bottom type and depth are also expected to drive the density of most coastal fish. The *depth* of each exact point where a camera was deployed was extracted in situ using the boat's probe. The sea bottom type at the exact point where a camera device was deployed was quantified using the percentage cover of three discrete types of substrate (Follana-Berná et al., 2020): (1) percentage of patches with sand to gravel; (2) percentage of rocks or rocky patches with many crevices and sharp slope changes, with or without small-sized algae; and (3) percentage of seagrass. These cover percentages were transformed according to Aitchison (1983). Finally, a principal component analysis was completed on the transformed percentages, and the PCA scores on the two resulting axes (*habitat_1* and *habitat_2*) were used as explanatory variables summarizing the habitat characteristics.

2.3. Modeling fish density

One of the main challenges for translating fish count per frame into absolute density is to properly address environmental dependencies of detectability (*P_detection*, the probability of counting a fish that is actually within the surveyed area by the camera). Moreover, uncertainty in the detectability estimation must be properly propagated to the precision of fish density estimates. In the case of *S. scriba*, detectability was previously estimated to be 0.82, with a 95% Bayesian credibility interval between 0.52 and 0.99 (Follana-Berná et al., 2020). Moreover, *P_detection* has been demonstrated to be independent of sea bottom characteristics, at least within the environmental gradient considered (Follana-Berná et al., 2020).

According to the theoretical framework developed by Campos-Candela et al. (2018), $Counts_{i,j}$ (the number of fish counted by the ith camera device at the jth frame, where $i = 1$–257 videos and $j = 1$ to approximately 90 frames per video, or 24,299 frames) has been assumed to be Poisson distributed (Campos-Candela et al., 2018; Follana-Berná et al., 2020, 2019):

$$Counts_{i,j} \sim Poisson(\text{Area\_camera} \ * \ Density_i * \text{P\_detection}) \quad (1)$$

where $Density_i$ (fish/km^2) is the fish density around camera i and *Area_camera* is the area surveyed by the camera, which was estimated with negligible error (5.0 m^2). Fish density was modeled as a linear combination (at the log scale) of *estimated_ fishing_exposure*, the two quantitative variables describing habitat (*habitat_1* and *habitat_2*), and *depth*. The correlations between these four variables were small (the largest Pearsońs r^2 value was 0.06); thus, collinearity problems are not expected. A quadratic term was included for *habitat_1*, *habitat_2,* and *depth* to account for possible unimodal responses. Moreover, *season* was also included in the model, allowing for (1) different intercepts (between season differences) and (2) different slopes for the fishing exposure in late spring versus late summer (i.e., an interaction term). Finally, two random effects were considered. First, fish density at the point where a camera device was deployed (*camera*) was allowed to be

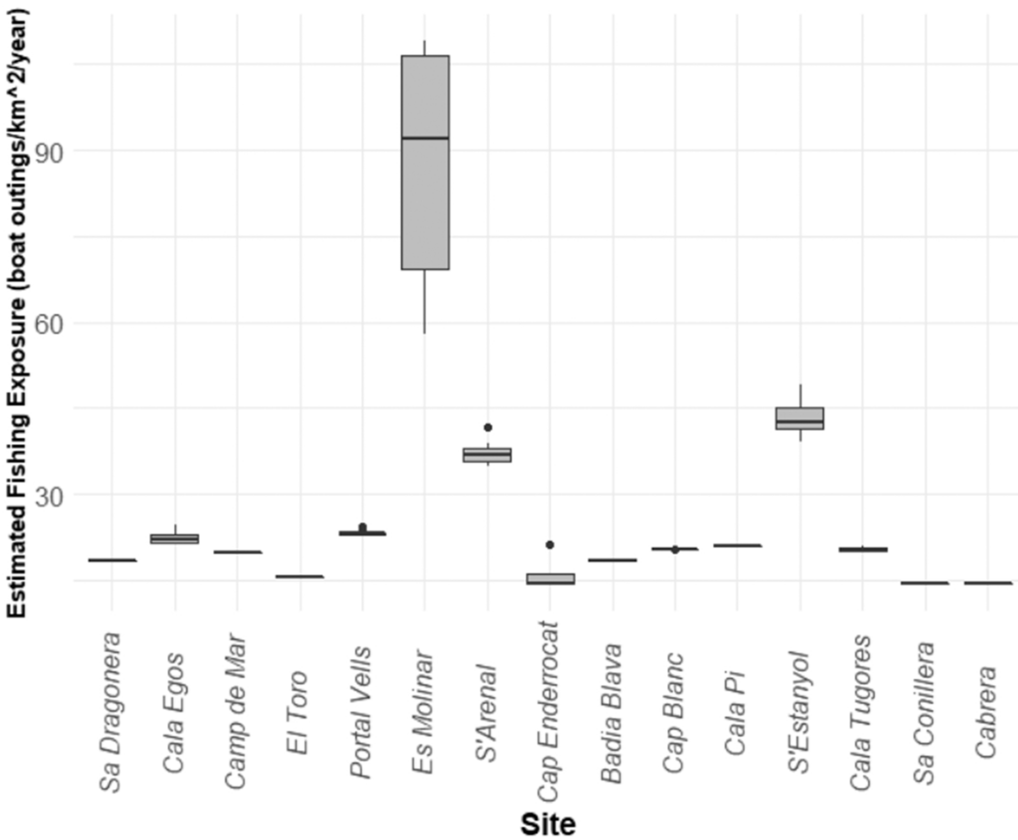

Fig. 3. Within-site and between-site variability for estimated_fishing_exposure (boat outings/km2/year). Each boxplot corresponds to a site, and it shows the variability in estimated_fishing_exposure between the exact positions where the 20 cameras from a site (10 cameras per season) were deployed.

normally distributed around the site mean, with a common standard deviation (σ_{camera}); thus, this random effect accounted for the between-camera variability at the site level that was not explained by the fixed factors. Second, the model intercept for a given site was allowed to be normally distributed (at the log scale) around a general intercept with a given standard deviation (σ_{site}); thus, the latter random effect accounted for the between-site variability that was not explained by the fixed factors:

$$\begin{aligned} log(density) = {} & habitat\_1 + habitat\_1^2 + habitat\_2 + habitat\_2^2 + depth \\ & + depth^2 + season + estimated\_\text{fishing\_exposure} + season \\ & * estimated\_\text{fishing\_exposure} + site + camera \end{aligned} \quad (2)$$

The explanatory variables were standardized (subtracting the mean and dividing by the standard deviation). The parameters of this model (Eq. 1 and 2) were fitted using a Bayesian approach. Samples from the joint posterior distribution of the parameters given the data (fish counts) were obtained using STAN and the *rstan* library (Stan Development Team, 2020) in the R package (R Core Team, 2021). Uncertainty in *P_detection* was injected into the model after adjusting the posterior distribution reported by Follana-Berná et al. (2020) to a beta distribution, which was performed using the *fitdistrplus* library (Delignette-Muller and Dutang, 2015) in the R package. The full code, the fish counts (response variable) and all explanatory variables are available at repository https://doi.org/10.17632/8c5jwvkvsz.6. Four chains were run. Chain convergence was assessed by visual inspection of the chains and was evaluated using the Gelman-Rubin statistic (Gelman et al., 2015). Posterior distributions of the model parameters were estimated by 4000 valid iterations after appropriate warm-up (the first 1000 iterations of each chain were discarded).

3. Results

The mean depth of all sampling sites was 13.3 ± 5.1 m. The depth range of the deployment points of the camera devices ranged from 2 m to 32 m (Fig. 2).

The variable *estimated_fishing_exposure* (boat outings/km^2/year) reached the highest values close to marinas (e.g., *Es Molinar, S'Arenal* and *S'Estanyol*; Fig. 3) and the lowest values in MPAs and at sites far from ports and marinas (i.e., *El Toro, Cap Enderrocat, Sa Conillera,* and*Cabrera*).

Regarding the habitat, the 257 exact points where cameras were deployed were classified according to seabed coverage (%), which after transformation and factorization (i.e., PCA) resulted in two axes (*habitat_1* and *habitat_2*) that explained 57% and 43% of the variability, respectively (Fig. 4).

Both axes were used as explanatory variables (Fig. 5). Axis 1 (*habitat_1*) was related to the gradient between sand and rock. Axis 2 (*habitat_2*) was related to the coverage of *P. oceanica*. Camera deployment points with large score displays covered close to 100%, while *P. oceanica* was almost absent at camera deployment points with small scores. Within-site variability was certainly noticeable.

The parameters of the statistical model are detailed above (Eq. 1 and 2) given that the counted number of fish per frame was successfully estimated (no divergences, E-BFMI indicated no pathological behavior, *Rhat* was always between 0.998 and 1.002, and the effective number of samples was always larger than 1000). A full table of the effect sizes of all variables included in the model and a full table of the estimates of fish density at each site are detailed in the Supplementary Material. Regarding the estimated densities of *S. scriba* (Fig. 6), the highest absolute densities were found at *Cabrera* (median: 14,110 ind/km^2; 95% Bayesian credibility interval, 95% BCI: 8245 to 27,836 fish/km^2), followed by *Cap Blanc* (5012 fish/km^2, 95% BCI: 3021 to 9327 fish/km^2)

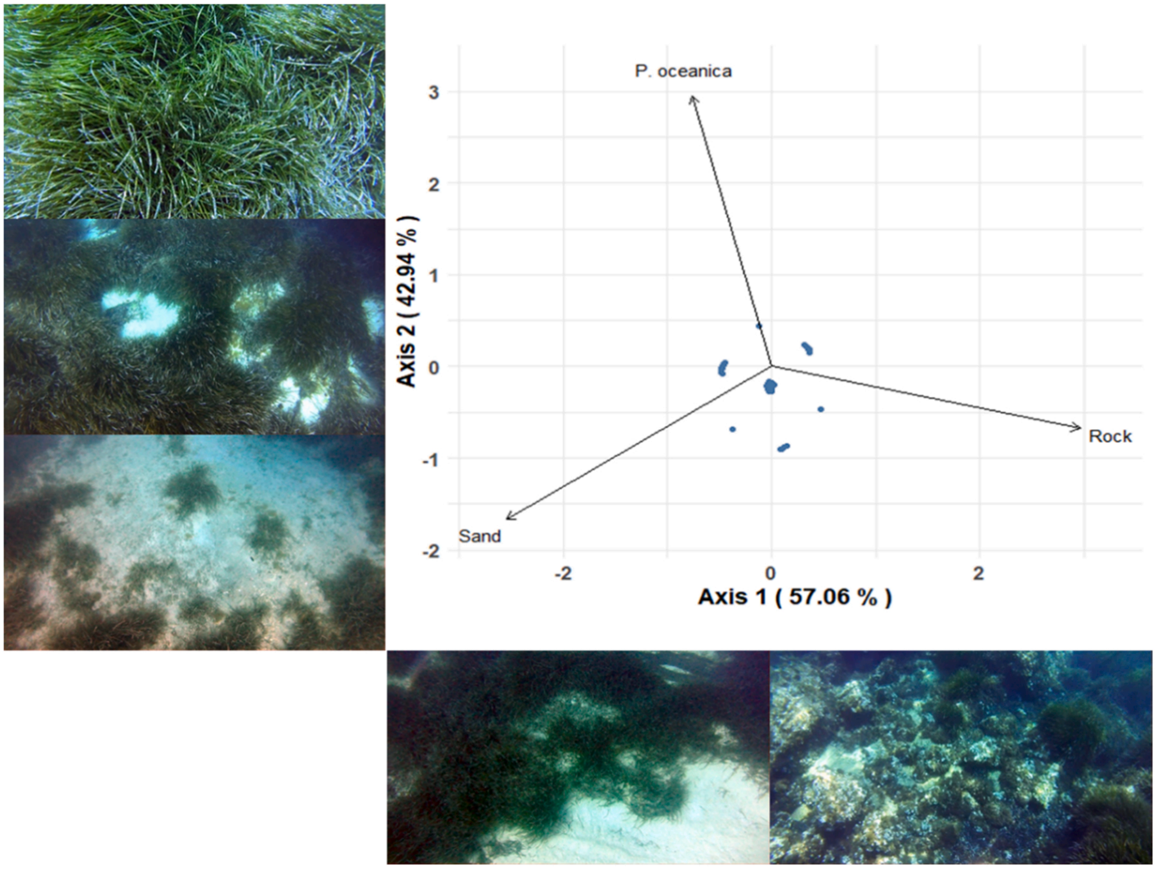

Fig. 4. PCA habitat scores. The images over Axis 1 (habitat_1) correspond to the camera deployment points displaying the largest and smallest scores, respectively. The images over Axis 2 (habitat_2) correspond to the camera deployment points displaying the largest, median, and smallest score.

and El Toro (4884 fish/km^2, 95% BCI: 2655 to 9739 fish/km^2). The lowest absolute densities were expected at *Es Molinar* (111 fish/km^2, 95% BCI: 6–1047 fish/km^2), followed by *Portals Vells* (685 fish/km^2, 95% BCI: 304–1492 fish/km^2) and *S'Arenal*(877 fish/km^2, 95% BCI: 279–2666 fish/km^2) (Fig. 6).

Concerning the variables included in the statistical model, the intercepts for late spring and late summer did not differ between each other (95% BCI included zero; note that *Season* in Fig. 7 is the quantity that should be summed to the late spring intercept for obtaining the late summer intercept), suggesting that the average density across sites remained the same between the two seasons of a given year.

However, relevant effects (95% BCI did not include zero) on fish density were detected for the slope of the habitat scores at the first dimension of the habitat descriptors and for its quadratic term (i.e., the response of fish density to the habitat gradient seemed to be a unimodal pattern). The slopes of the habitat scores in the second dimension were not relevant. According to these results, the worst habitat score for *S. scriba* along the habitat gradient sampled (Fig. 4 and Fig. 5) was − 0.37 (95% BCI: −0.94 to 0.11), which corresponded to uniform *Posidonia* meadows (Fig. 4). Fish density was expected to increase toward *Posidonia* meadows mixed with either rocks or sand (i.e., toward more heterogeneous habitats). The expected patterns when one explanatory variable by turn was allowed to change along the actual gradient while all other variables were kept constant at its average value are provided in Fig. 8A.

Similarly, the effect of *estimated_fishing_exposure* on fish density was relevant (Fig. 7). In both seasons, the larger the *estimated_fishing_exposure* was, the smaller the fish density was expected to be, which suggests that fishing was correlated with a reduction in the site-specific (i.e., averaged across seasons) fish density (Fig. 8B). Interestingly, 95% BCI of the difference (not shown in Fig. 7) between these two slopes did include zero (95% CI interval: −0.53 to 0.62), which strongly suggests that the interaction between *season* and *exposure_to_fishing* was not relevant and, thus, no short-term (between seasons) effects of fishing were detected.

Finally, relevant effects (95% BCI did not include zero) on fish density were also detected regarding *depth*. In that case, provided that the effect of the quadratic term was not relevant, the existence of an optimal depth within the sampled depth gradient (Fig. 2) was not supported; thus, the deeper a site was, the smaller the fish density was expected to be (Fig. 6 and Fig. 8C).

4. Discussion

The feasibility of underwater video monitoring for estimating the absolute density (fish/km^2) of coastal fish species was demonstrated. The absolute density of a small serranid (*S. scriba*) was estimated along the southern coast of Mallorca Island (nearly 100 km) with an affordable sampling effort (approximately 30 fieldwork days, or one day per site/season). Therefore, the proposed framework (i.e., (1) using vertical unbaited cameras, (2) counting fish per frame (one frame per period), and (3) analyzing the counts using the proposed statistical analysis, which includes (4) an independent estimate of fish detectability) represents a realistic approach for long-term monitoring of coastal fish at temporal and spatial scales that are relevant for adopting management decisions (i.e., at the mesoscale). In addition, the capability of the proposed framework for exploring the ecological drivers that explain fish density was also demonstrated. Certainly, the effects of habitat, fishing, and depth on coastal fish density are well known (Geraldi et al., 2019). Thus, the relevance here is that this framework seems fully capable of generating the data needed for testing other ecologically sound hypotheses with enlarged statistical power and at an affordable cost.

The proposed framework implies monitoring with vertical unbaited

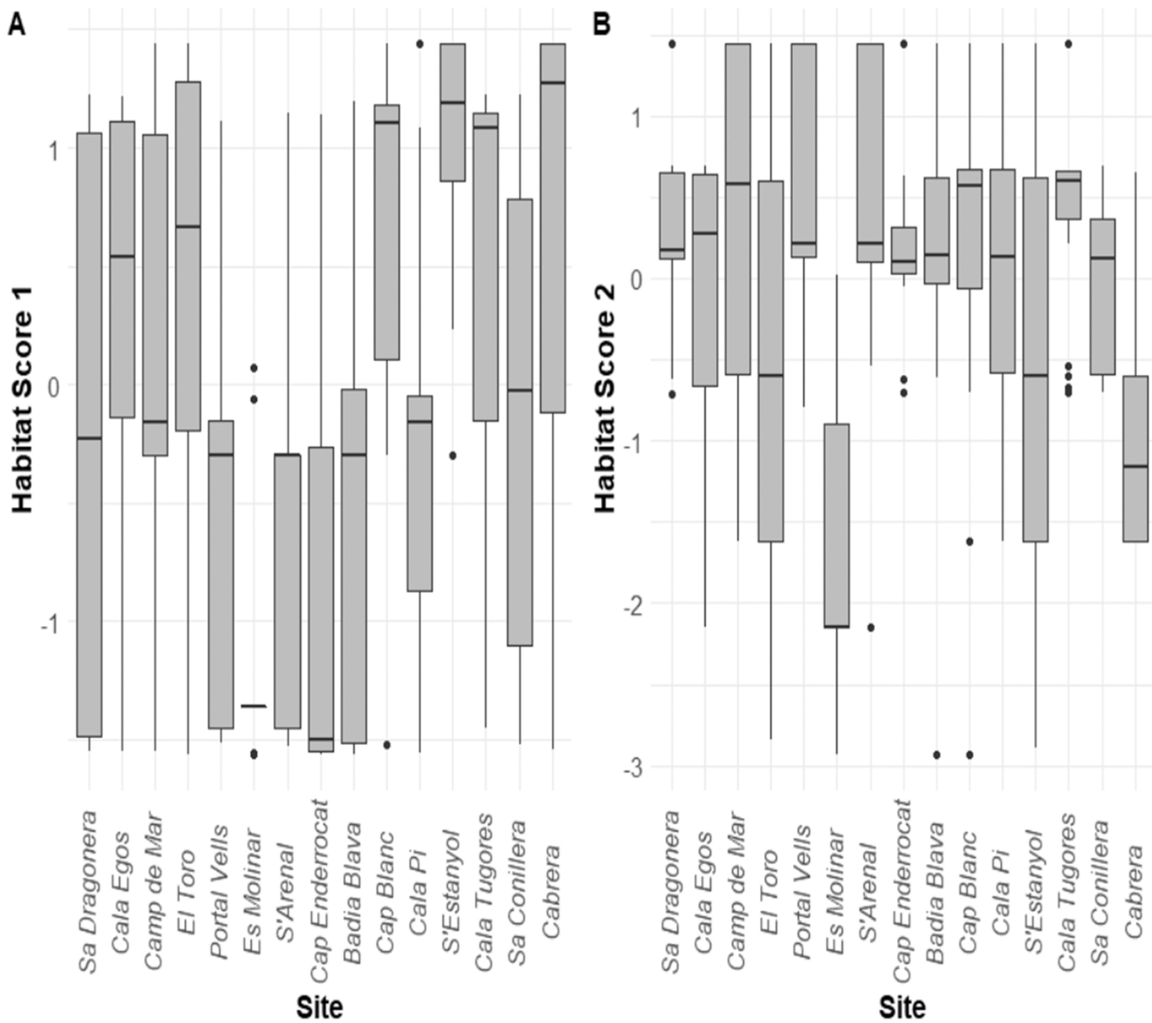

Fig. 5. Within-site and between-site variability for habitat_1 and habitat_2. Each boxplot corresponds to a site, and they show the variability in habitat_1 and habitat_2 between the exact positions where the 20 cameras from a site (10 cameras per season) were deployed.

cameras, which seems to be robust against the biases affecting other fishery-dependent sampling methods and other camera settings (e.g., horizontal cameras and baited cameras). The advantages and limitations of the vertical unbaited cameras are compared against the two fishery-independent methods most commonly used for monitoring coastal fish at similar temporal and spatial scales (baited cameras and UVC; Table 1). Cameras with horizontal field views are not explicitly included in Table 1 because irrespective of using bait or not, they suffer from a problem in which measuring the area surveyed is difficult or impossible (Sheaves et al., 2020). Although the area surveyed by a vertical camera can experience slight variations depending on substrate roughness and the precision when identifying area limits in a belt census depends on diver training, these uncertainties are negligible when compared with those from horizontal cameras. Apart from this, the advantages and limitations of horizontal cameras are those linked with the use of bait or not (Table 1).

Some generic advantages of cameras over visual censuses are the reduced risks for the staff (divers) and the wider gradient of extreme habitats that can be safely sampled (Mallet and Pelletier, 2014). Cameras also allow rechecking the interpretation of the videos (fish counts and species identification). Cost is certainly more difficult to compare, but overall, the initial investment of diver equipment and its maintenance seems larger when compared with action cameras, which are quickly becoming more affordable and with better quality. Thus, the number of cameras, the deployment time, or the area surveyed by a camera will not be an economically limiting factor in the near future (Aguzzi et al., 2020b, 2020a, 2015; Campos-Candela et al., 2019; Matabos et al., 2015, 2014; Struthers et al., 2015). The training cost of the divers and the staff cost per sample (fieldwork) are larger than those of the cameras.

Both visual censuses and vertical unbaited cameras can produce unbiased estimates of absolute fish density after species-specific fish detectability has been estimated. Detectability should preferably be estimated in an independent field survey (Follana-Berná et al., 2020, 2019; MacNeil et al., 2008; Pollock et al., 2002), but concurrent sampling with visual censuses and cameras offers a unique opportunity for intercalibration (Follana-Berná et al., 2019). Detectability estimation is species-specific and may need ad hoc solutions (Follana-Berná et al., 2020), but it is feasible to model environmental dependencies (Follana-Berná et al., 2020, 2019) and, thus, properly account for potentially confounding effects such as those related to water turbidity (Figueroa-Pico et al., 2020). Similarly, the area surveyed by visual censuses and vertical unbaited cameras can be measured with no or small error, thus allowing us to link fish counts to an area unit. As stated above, this is a major handicap of any camera setting with a horizontal field view.

Both visual censuses and vertical unbaited cameras can theoretically reach any target precision, but the number of samples needed may be unaffordable (Abolaffio et al., 2019). Nevertheless, this problem is exacerbated in the case of visual censuses because the cost per sample is

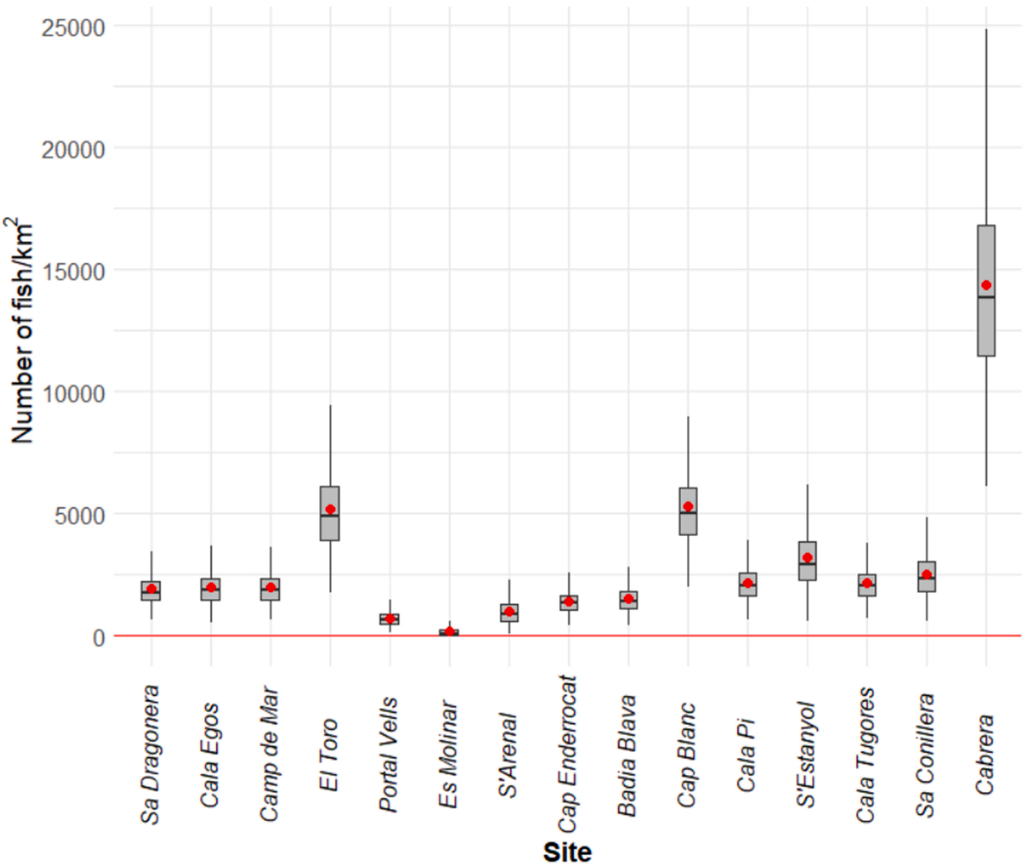

Fig. 6. Fish density (ind/km2). The red dots indicate the mean of the Bayesian posterior distribution; the black line indicates the median. Precision is denoted by the width of the box (interquartile range of the Bayesian posterior distribution) and the whiskers (1.5 times the interquartile range). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

larger. It should be noted here that the number of fish per frame follows an ergodic process concerning time and space, provided that fish density is constant at the surveyed temporal scale and that swimming speed ensures that fish counts can be performed at a frequency that ensures temporal independence between two consecutively counted frames (Campos-Candela et al., 2018). These assumptions seem to meet at the one-day temporal scale of sampling used here and for most coastal fish displaying a home-range pattern of space occupation, which is orders of magnitude larger than the area surveyed by the camera (Alós et al., 2016; Arechavala-lopez et al., 2019; Follana-Berná et al., 2020; Jadot et al., 2006; Jones, 2005; March et al., 2010; Palmer et al., 2011). Therefore, in terms of the accuracy and precision of fish density estimates, time and space can be interchanged, provided that the consecutive samples of the same surface remain temporally uncorrelated. In the case of *S. scriba*, no temporal autocorrelation was detected when counting fish every 120 s. Therefore, the effective area sampled by belt visual censuses (typically, in a range of 1000 m^2/day, assuming 4 censuses per day that are 50 m long and 5 m wide) may be even smaller than the effective area surveyed by the camera settings used here (4500 m^2/day: 90 frames per camera, 10 cameras, and 5.0 m^2). Computer simulation experiments suggest that the later sampling setting ensures a target accuracy of approximately 90% for *S. scriba* and for other coastal benthic fish displaying similar movement patterns (Campos-Candela et al., 2018; Follana-Berná et al., 2020, 2019). Nevertheless, some adjustment in the sampling setting will be needed for fish with a very narrow home range and/or very slow swimming speed. In those cases, temporal independence of consecutive counted frames can be achieved by reducing the number of counted frames per video and enlarging the number of cameras. On the other hand, pelagic fish usually do not meet the assumption of steady fish density at the space-time scale of sampling; thus, the proposed framework would be useless in those cases. However, with some species-specific exceptions, the use of vertical unbaited cameras and the proposed framework emerges as a plausible method for monitoring fish abundance at large spatial (as reported here) or temporal scales (e.g., permanent underwater observatories; Aguzzi et al., 2020a; Matabos et al., 2014).

The use of baited cameras is certainly widespread, but it is also well known that the fish counts provided by this method are biased (Cheal et al., 2021). To see more fish does not mean that the counted fish reflects the actual density. Bait interferes with fish behavior, and the attraction strength may depend on the bait characteristics (Ghazilou et al., 2016), hydrography of the area, dynamics of the odor plume (Taylor et al., 2013), species specificities (e.g., species-specific olfactory capability; carnivores versus herbivores, etc.) or even individual specificities (competitive interactions at either within- and between-species, satiety, or many other processes) (Bassett and Montgomery, 2011; Stoner, 2004). Certainly, some interesting attempts to model attraction dynamics have been made (Dunlop et al., 2015; Vabø et al., 2004), but the multiple processes involved and their complexity make it difficult to generalize a method for linking fish density with the fish counts recorded by a baited camera. Unbaited cameras and UVCs can also trigger some species- or individual-specific abnormal behavior (e.g., diver presence may trigger flight or hiding behavior; Pierucci and Cózar, 2015; Willis et al., 2000), but the responses would not be comparable with those of the baited cameras. An extreme case of potential bias could be permanent underwater observatories (e.g., https://imedea.uib-csic.es/sites/sub-eye/home_es/) that may act as artificial reefs (Aguzzi et al., 2015, 2020a,b). These potential drawbacks should be further and carefully analyzed, but they are expected to be minimized with, for example, the sampling settings adopted here (discarding the few

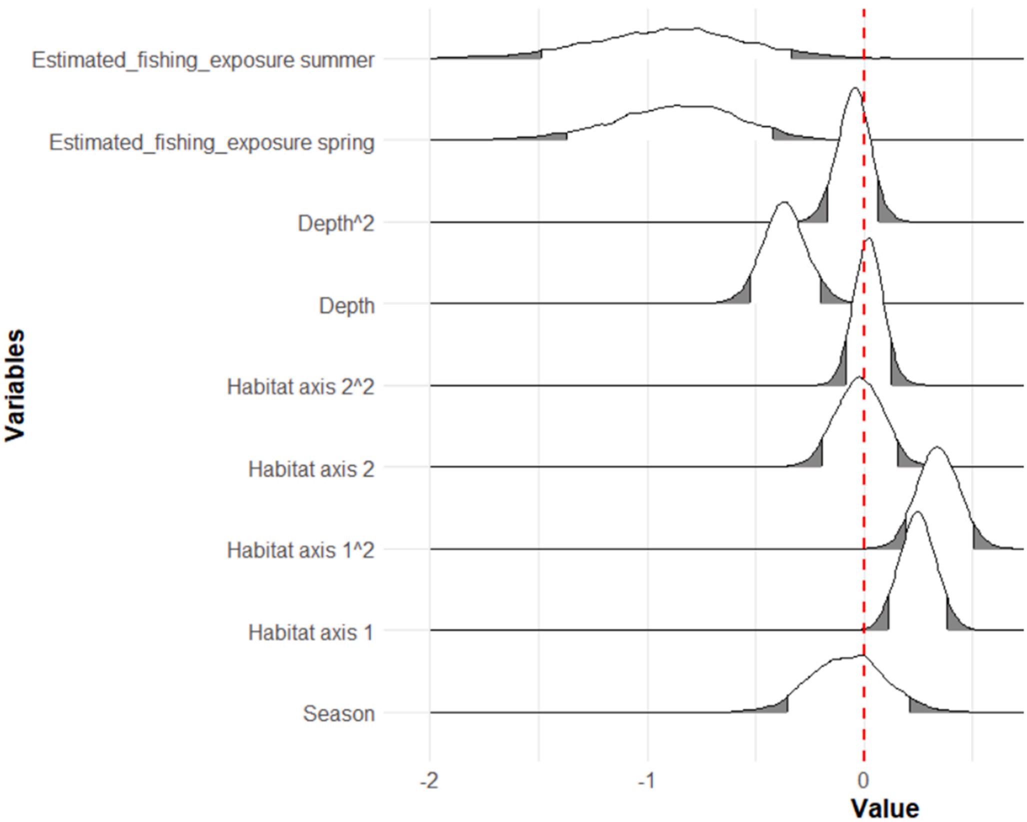

Fig. 7. Estimates of the size effects on fish density for all fixed variables included in the model. The gray areas denote the area of the distribution outside the 95% of the Bayesian posterior distributions. Estimated_fishing_exposure-spring and estimated_fishing_exposure-summer denote the season-specific slopes for estimated_fishing_exposure, and they relate to the interaction between estimated_fishing_exposure and season. Moreover, season denotes the size effect to be summed to the spring intercept to obtain the summer intercept. The vertical red line indicates no effect. The relevant effects were habitat_1, habitat_12, depth, and estimated_fishing_exposure. However, for the last variable, there were no relevant differences between spring and summer. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

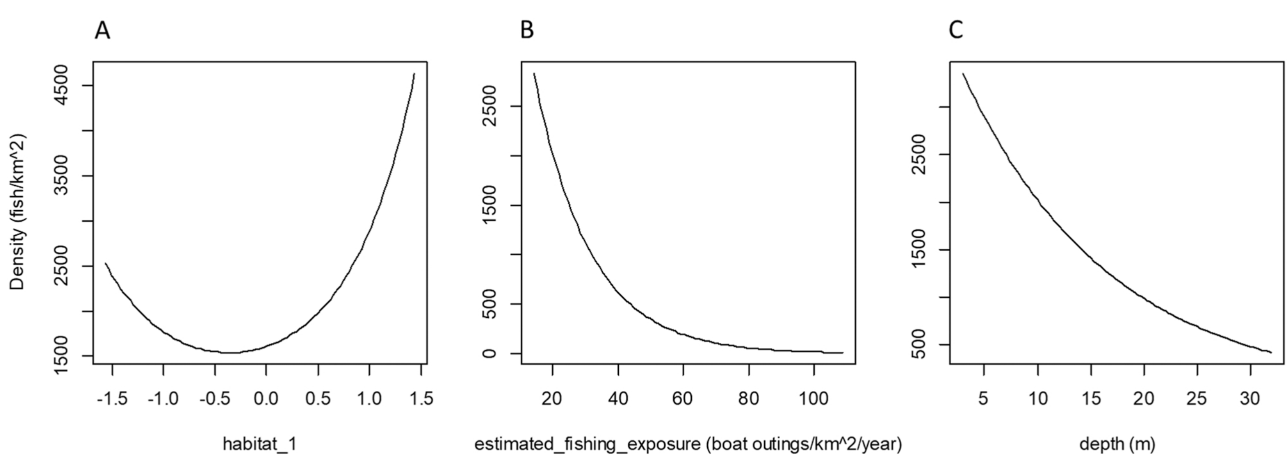

Fig. 8. Description of expected effects on fish density of A) habitat_1, B) estimated_fishing_exposure and C) depth.

minutes of video after the device lands on the seafloor and sampling during only a few hours).

Video postprocessing has been adduced as one of the major disadvantages of cameras in regard to censuses (Mallet and Pelletier, 2014). However, deep learning algorithms (Connolly et al., 2021; Ditria, 2020; Salman et al., 2019; Tabak et al., 2019) for automatically extracting information from fish images and videos are currently exploding in use (Álvarez-Ellacuría et al., 2019; Connolly et al., 2021; Martorell-Barceló et al., 2021; Moen et al., 2018; Palmer et al., 2022). Some operational (i.e., real-time) applications for counting fish may even be plausible soon (Meng et al., 2018), which may circumvent the memory bottleneck for video storage. Thus, it is expected that postprocessing time and effort may drop in the near future. Relatedly, it could be adduced that species identity may be easier to determine using cameras with a horizontal view. We recognize that this may be a drawback for some species. However, at least in our case, species identity can be determined from the top without doubt after some training of the observer; thus, it is expected that deep learning algorithms will be able to manage species identification even for challenging cases.

As stated above, absolute density, in addition to the obvious advantages when modeling population dynamics for informing management decisions, allows proper comparison between studies (Cheal et al., 2021). However, if fish detectability is not estimated, such a comparison should be done with some caution. Nevertheless, the figures provided by underwater censuses in the same region (Balearic Islands) seem comparable with the figures reported here, which suggests a high fish detectability of underwater censuses for *S. scriba*. For example, the densities of *S. scriba* on the northern coast of Mallorca Island (5000

Table 1
Subjective comparison between underwater visual censuses and cameras (baited and unbaited).

	Visual censuses	Baited cameras	Unbaited cameras
Risk to the observer	Medium-High	No	No
Suitable in extreme habitats	No	Yes	Yes
Disturbances to fauna/habitat	Soft	Soft	Negligible
Disturbances to fish behavior	Yes, due to diver presence	Yes, due to bait	Soft
Absolute density	Yes, after estimating detectability	No	Yes, after estimating detectability
Accuracy	Acceptable. Some species can be underestimated (fear) or overestimated (attraction)	Biased	Acceptable. Possible bias for cryptic and/or static species
Precision	Acceptable but at a larger cost	Unknown	Acceptable
Review/check is possible	No	Yes	Yes
Appropriate at a long temporal scale	Yes, but at a larger cost	Yes	Yes
Appropriate at a long spatial scale	Yes, but at a larger cost	Yes	Yes
Cost: Initial investment	High	Medium and falling	Medium and falling
Cost: Equipment maintenance	High	Medium	Medium
Cost: Training	Very high	Medium	Medium
Staff cost per sample	High	Medium	Medium
Cost: Postprocessing	Low	High, but expected to drop with deep learning algorithms	High, but expected to drop with deep learning algorithms

ind/km^2; Ordines et al., 2005), on the southwestern coast of Mallorca (11,300–18,500 ind/km^2; Deudero et al., 2008) or Cabrera (south of Mallorca; from 6400 to 22,400 ind/km^2; Reñones et al., 1997) fall within the densities estimated here. Similarly, the environmental preferences deduced from these studies fully agree with those reported here (e.g., *S. scriba* seems more abundant in shallow, heterogeneous *Posidonia* meadows), except in the case of Deudero et al. (2008), who suggested that the abundance of *S. scriba* was larger at deeper sites. The presence of rocks per se seems insufficient for enhancing density because *S. scriba* inhabits artificial reefs on seagrass meadows but is absent from the artificial reefs located in nearby sandy areas (Coll et al., 1998).

Similarly, the abundance and environmental preferences of *S. scriba* estimated from visual censuses in other Mediterranean regions are similar to those reported here: in the western Mediterranean (Serra Gelada: between 2000 and 14,500 ind/km^2; Arechavala-lopez et al., 2008; and Cabo de Palos: 10,200 ind/km^2; García-Charton and Pérez-Ruzafa, 2001); in the Adriatic Sea (between 4000 and 27,000 ind/km^2 on shallow rocky algal reefs, whereas lower density was reported in uniform *P. oceanica* meadows; Bonaca and Lipej, 2005); on the southeastern coasts of Italy (27,500 ind/km^2 in *P. oceanica* meadows and 17,500 ind/km^2 on rocky-algal reefs; Guidetti, 2000), or in the central Aegean Sea, where *S. scriba* displays habitat preferences similar to those reported here (Giakoumi and Kokkoris, 2013). Interestingly, also in agreement with the results reported here, *S. scriba* densities in marine protected areas seem larger than those in nonprotected areas (Guidetti et al., 2005).

The between-site variation reported here is well explained by three of the explanatory variables considered (fishing exposure, depth, and habitat characteristics). Certainly, recreational fishing exposure is difficult to estimate and, as mentioned above, can be affected by many factors. However, in our case, distance to port seems to be the main driver; thus, we estimated recreational fishing exposure from distance to port only. Although the model for estimating fishing exposure was calibrated with data based on observations in the same area (March, 2014) and the resulting variable (*estimated_ fishing_exposure*) was well correlated with fishing exposure, the results reported should be interpreted with some caution. Moreover, the correlational nature of this study precludes explicitly suggesting a cause-and-effect relationship between fish density and fishing exposure, but our results indicate that sites with smaller *estimated_ fishing_exposure* hold larger *S. scriba* densities. The same pattern has been described in the same area and for the same species (Alós and Arlinghaus, 2013; March et al., 2014).

Thus, assuming that *estimated_ fishing_exposure* is a proper surrogate of fishing exposure, the sites with the highest density of *S. scriba* densities (i.e., *Cabrera*, *El Toro,* and *Cap Blanc*) display large patches of suitable habitats and experience no or very low fishing exposure (Fig. 3, Fig. 4, Fig. 5). Recreational fishing is banned at *Cabrera* and is limited at *El Toro* (partial MPA but far from any port) and *Cap Blanc* (open site to fishing but far from any port). Sites with intermediate density display either low *estimated_fishing_exposure* values or large patches of suitable habitat for *S. scriba*. In the case of the MPA at *Cap Enderrocat*, the large number of harbors and marinas in Palma Bay may counteract the soft fishing limitations (fishing is allowed 4 days per week in most protected areas). The relatively low density estimated at *Sa Dragonera* deserves special attention because it is environmentally suitable for *S. scriba,* but it is subject to a relatively important recreational fishing exposure. However, this area has been recently declared a MPA (in 2019), just before the fieldwork reported here was completed. Therefore, this site offers a unique opportunity for monitoring fish density in the coming years and testing the effects of the establishment of the new fishing limitations. Finally, the smallest densities were found at sites displaying both a smaller proportion of optimally suitable habitat and larger values of *estimated_fishing_exposure* (*Es Molinar* and *S'Arenal*).

The sampling plan was specifically designed for discriminating short-term effects (i.e., between seasons in the same year) from site-specific effects (i.e., long-term effects) by monitoring the same sites before and after summer, which is when most recreational fishing activity occurs in Mallorca (Cabanellas-Reboredo et al., 2014; March, 2014; March et al., 2014). Therefore, short-term effects can be assessed by comparing the between-season differences in density along a gradient of fishing exposure (i.e., larger decreases in density are expected at sites more exposed to fishing). As stated above, the hypothesis of site specific, long-term effects of fishing seems supported by the results, but no short-term effect was detected. A plausible explanation for this may be that the few remaining *S. scriba* at heavily exploited sites were almost invulnerable to the recreational fishing gear; thus, the number of fish at those sites would remain constant after the increase in fishing exposure during summer. The existence of a spatial pattern in vulnerability (fish are less vulnerable to fishing gear along a gradient of fishing) has already been described for the same species and area (Alós et al., 2015b) and should be a note of caution against the use of catch-per-unit-effort (i.e., fishery-dependent data) as a surrogate of fish abundance (Alós et al., 2019; Monk et al., 2021) because hyper-depletion processes may give the wrong impression that fish abundance is smaller than it actually is (Ahrens and Walters, 2005; Hilborn and Walters, 2013).

The model for explaining the fish density of *S. scriba* presented here could also be used to map fish density along the southern coast of Mallorca. Moreover, the Bayesian approach developed is particularly suitable for producing maps of the credibility interval (precision) of fish density. These maps would be of primary interest for deriving stock status and for designing proper management plans. However, reliable maps for two out of the three environmental variables in the model are difficult to obtain. As mentioned above, accurately estimating recreational fishing exposure is challenging. Estimating sea bottom characteristics is a priori more easily affordable, but the maps available for the study area are partial (e.g., marine reserves) or the spatial detail is too coarse.

In summary, despite several difficulties, the results reported here suggest that monitoring absolute fish density with vertical unbaited cameras at large spatial and temporal scales can be a reliable alternative in the near future. The proposed monitoring framework may strongly benefit from the complementary role of diver censuses, and a combination of underwater cameras and artificial intelligence may represent a unique opportunity for a qualitative jump in the way marine wildlife is observed.

CRediT authorship contribution statement

Guillermo Follana-Berná, Miquel Palmer, and Pablo Arechavala-Lopez: Conceptualization and Methodology. **Guillermo Follana-Berná:** Investigation. **Guillermo Follana-Berná and Miquel Palmer:** Formal analysis. **Miquel Palmer, and Pablo Arechavala-Lopez:** Supervision. **Guillermo Follana-Berná:** Writing – original draft. **Guillermo Follana-Berná, Pablo Arechavala-Lopez, Miquel Palmer, Amalia Grau and Eduardo Ramirez-Romero:** Writing – review & editing. **Guillermo Follana-Berná, Eduardo Ramirez-Romero and Elka Koleva:** Data/evidence collection. **Guillermo Follana-Berná:** Data curation.

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.

Acknowledgments

This work was funded by the PHENOFISH R&D project (ref. CTM2015–69126-C2–1-R; MINECO) and CLOCKS R&D project (Grant num. PID2019–104940GA-I00; MICINN). This work is a contribution of the Joint Associated Unit IMEDEA-LIMIA. GFB was supported by a Spanish Ph.D. fellowship (ref. FPI-INIA 2015-0013 CPD2015- 0084) from the National Institute for Agricultural and Food Research and Technology (INIA). PAL was supported by a postdoctoral grant (Juan de la Cierva Incorporación; IJCI- 2015–25595) from the Spanish Ministry of Economy, Industry, and Competitiveness. We thank Joint Associated Unit IMEDEA-LIMIA staff members for helping with fieldwork. Fieldwork permits were provided by Cabrera Archipelago National Park and Direcció General de Pesca i Medi Marí (Govern de les Illes Balears).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106362.

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