Fisheries Research 278 (2024) 107115

Contents lists available at ScienceDirect

Fisheries Research

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

Full length article

The potential fish provisioning services of vegetated and unvegetated habitat in a lagoon nursery

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ARTICLE INFO

Keywords:
Fish provisioning services
Economic valuation
Maximum yield
$F_{0.1}$
Ria Formosa lagoon
Portugal

ABSTRACT

The potential fish provisioning services of the Ria Formosa lagoon (Portugal) were calculated for single cohorts of 7 commercially fished species, based on densities of juveniles sampled with beach seines on a monthly basis over a 17-month period at 41 locations. The potential maximum yield per recruit ($F_{0.1}$ criteria) was calculated for vegetated (V) and unvegetated (UV) habitat for low and high natural mortality values. Vegetated habitat enhanced yield (g m^{-2}) of 5 of the 7 species, with the greatest enhancement for the herbivore *Sarpa salpa* (137 and 150 fold for low and high M). At $F_{0.1}$, the calculated total potential yield of the 7 cohorts was 463 tons (low M) and 333 tons (high M), worth EUR 5,649,084 and 3,651,881, respectively. Mean annual landings of the 7 species from 1997 to 2017 ranged from 407 to 577 tons, with a mean of 495 tons (s.e. = 11.1), highlighting the importance of the lagoon nursery as a major source of recruits for local small-scale coastal fisheries. The methodology used here is the first to calculate the potential maximum yield and the corresponding fishing mortality ($F_{0.1}$) for single cohorts and for different habitats within an important fish nursery. It provides more realistic values of potential fish provisioning services and economic contribution to local fisheries than studies that do not consider fishing mortality.

1. Introduction

A number of studies have estimated the fish provisioning services or value of seagrass and other coastal habitats such as oyster beds and mangroves to fisheries by modelling adult fish biomass from juvenile abundance and life history parameters, combined with market or auction values (Peterson et al., 2003; Blandon et al., 2014a,b; zu Ermgassen et al., 2016; Jänes et al., 2020; Lai et al., 2020, zu Ermgassen et al., 2021, Erzini et al., 2022). Based on evidence of high site fidelity from mark-recapture (tagging) of juveniles in the Ria Formosa lagoon, Erzini et al. (2022) estimated juvenile densities in vegetated (V) and unvegetated (UV) habitats in the Ria Formosa lagoon and calculated the fish provisioning services of each habitat as the cohort lifetime or total biomass (*TB*), in the absence of fishing mortality. The economic value of a cohort was obtained by multiplying the lifetime biomass (kg) by the average first sale at auction price (€ kg^{-1}). Vegetated habitat enhancement of fish provisioning services in biomass and economic value were calculated by dividing the total lifetime biomass and value per unit area of V habitat by the total lifetime biomass and value per unit area of UV habitat for each cohort (Erzini et al., 2022).

However, none of the studies took into consideration fishing mortality (F), modelling of numbers-at-age (N_t) as a function only of natural mortality (M). By not including the instantaneous fishing mortality (F) and calculating fish provisioning services as cumulative lifetime biomass multiplied by the monetary value per kilo, very high economic values associated with seagrass enhancement were estimated (Blandon and zu Ermgassen, 2014a,b; zu Ermgassen et al., 2016; Jänes et al., 2020; Erzini et al., 2022). For example, Blandon and zu Ermgassen (2014b) estimated an average value of AUD 31,276 $ha^{-1}y^{-1}$ (approximately 19,840 EUR $ha^{-1}y^{-1}$) for 12 commercial fish species from seagrass habitat in southern Australia, while Jänes et al. (2020) reported an Australia-wide average of AUD 21,276 $ha^{-1}y^{-1}$, with considerable variability (AUD 150–60,500 $ha^{-1}y^{-1}$). For the Ria Formosa lagoon in Portugal, the estimated lifetime value of seagrass habitat for single cohorts of 12

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https://doi.org/10.1016/j.fishres.2024.107115
Received 29 July 2023; Received in revised form 28 June 2024; Accepted 8 July 2024

commercial species using the lagoon as a nursery ranged from EUR 22,028 ha^{-1} for low natural mortality values to EUR 10,700 ha^{-1} for high natural mortality values (Erzini et al., 2022). Vegetated habitat enhanced density (n m^{-2}) and biomass (g m^{-2}) of 7 of the 12 species, with enhancement ratios (V/UV) greater than 1 ranging from 1.7 to 130.3 for density and 1.6–173.5 for biomass (Erzini et al., 2022).

In this study, we used a whole lagoon approach to calculate the contribution of vegetated (V) and unvegetated (UV) sub-tidal habitat of the Ria Formosa lagoon, Portugal, to the coastal commercial and recreational fisheries of southern Portugal of 7 important commercial species using the lagoon as a nursery. Unlike previous studies (Peterson et al., 2003; Blandon and zu Ermgassen, 2014a,b; zu Ermgassen et al., 2016; Jänes et al., 2020; zu Ermgassen et al., 2021; Erzini et al., 2022) where numbers-at-age and biomass were modeled based only on natural mortality, we used yield-per-recruit (YPR) analysis (Thompson and Bell, 1934) to calculate numbers-at-age (N_t), biomass, yield (Y), and V enhancement of yield (Y_V/Y_{UV}) for single cohorts of the 7 species over a full range of plausible fishing mortality (F) values and low and high natural mortality (M) values for V and UV habitats of the Ria Formosa lagoon. We estimated the yield and the corresponding monetary value of the single cohorts if exploited at $F_{0.1}$, the fishing mortality where marginal yield-per-recruit is 10 % of its level for an un-exploited population, which is a proxy for F_{max}, the (fully recruited) instantaneous fishing mortality rate that maximizes yield per recruit (Gabriel and Mace, 1999; Zhou et al., 2012). The yield corresponding to $F_{0.1}$ is the biomass of fish that can be harvested from a fishery without depleting the stock. It is calculated based on the biomass of the individual cohorts and the instantaneous total mortality rate (Z), which is the sum of the instantaneous natural (M) and fishing (F) mortality rates ($Z = M + F$). The calculated yields (kg) and values corresponding to $F_{0.1}$ were compared with official landings statistics and with the lifetime cumulative biomass values obtained in the previous study that was based only on natural mortality (Erzini et al., 2022).

This study was carried out in the Ria Formosa lagoon in Portugal, one of the largest in Europe (Kjerfve, 1994; Razinkovas et al., 2008). It is the most important coastal ecosystem on the south and south-west coast of Portugal, supporting a variety of economic activities in the region, namely aquaculture (about 80 % of the national bivalve production), salt production (about 50 % of the national salt production), fishing, and eco-tourism (Rodrigues et al., 2021). Ecologically, it is an important nursery area for numerous fish species, including many commercial species among the more than 120 fish species that have been recorded in the lagoon (Monteiro, 1989; Andrade, 1990; Erzini et al., 2002, 2022; Ribeiro et al., 2006, 2008, 2012; Baptista et al., 2020). It is also a Natural Park recognized as a Ramsar site for its international importance for migratory birds and is part of the Natura 2000 Network (Newton et al., 2003; Baptista et al., 2020).

The Ria Formosa lagoon has the largest area of seagrass meadows in Portugal (Cunha et al., 2013), that together with saltmarshes encourage sediment stabilization, and improve water quality by reducing sediment re-suspension and nutrients in the water column (Verweij et al., 2008; Basset et al., 2013; Potouroglou et al., 2017; Newton et al., 2018). Seagrass habitats are widely recognized to be important nursery grounds for fish, with juveniles usually found at higher densities in seagrass beds than in adjacent unvegetated areas, resulting in enhanced production, recruitment to fisheries and yield (Heck et al., 2003; zu Ermgassen et al., 2021; Erzini et al., 2022). This arises from the high structural complexity offering protection from predators and abundance of trophic resources provided by seagrasses, resulting in higher survival and growth of juveniles and greater fish production (Tuya et al., 2014; Jänes et al., 2020; Erzini et al., 2022).

The importance of the Ria Formosa as a nursery for commercial species and as a source of recruitment to the coastal fisheries of the south of Portugal has long been recognized (Monteiro, 1989; Erzini et al., 2002). Indeed, the main reason for the implementation on the soft bottom nearby coastal areas of the largest artificial reef area in Europe was to provide habitat for juveniles migrating from the highly productive lagoon nurseries, thereby enhancing coastal fisheries (Monteiro and Santos, 2000; Santos and Monteiro, 2007).

In this study we calculated the potential fish provisioning services of vegetated and unvegetated sub-tidal habitats of the Ria Formosa lagoon for seven of the most important commercial species using the lagoon as a nursery. Unlike previous studies, we took into account fishing mortality by calculating yield per recruit, and yield and economic value corresponding to $F_{0.1}$ for single cohorts. This is an original and more realistic approach for calculating potential fish provisioning services, and the results have important implications for conservation and management of essential fish habitats such as the Ria Formosa lagoon and for informing sustainable fisheries management, and economic valuation and policies in coastal regions.

2. Methods

2.1. Study area

The Ria Formosa lagoon, in the south of Portugal, extends for 55 km along the coast with a maximal width of 6 km and an average depth of less than 3 m (Müller and Erzini, 2017). It covers an area of approximately 163 km^2 of salt marsh, mud flats, sand banks, main channels, secondary channels and tidal creeks (Monteiro, 1989; Monteiro et al., 1990; Ribeiro et al., 2006, 2008, 2012). The sub-tidal area is dominated by 15.9 km^2 of UV bottom, while the V habitat covers 3.1 km^2 (Erzini et al., 2022).

2.2. Sampling

Sampling was carried out in the Ria Formosa lagoon, on a monthly basis from September 2000 to January 2002 with the aim of studying the fish assemblages and the population dynamics of the most abundant species, using 25 m beach seines at 14 V and 23 UV and 50 m beach seines at 3 V and 1 UV sites, resulting in a total of 17,872 m^2 of V habitat and 25,886 m^2 of UV habitat sampled each month (Fig. 1). Both nets were 3.5 m high and sampling took place during a period 2 hours before to 2 hours after low tide, in days when the amplitude of the tide was less than 2 m, ensuring all the whole water column was fished. The 50 m beach seines were used in 4 sampling locations for comparison with a previous study on the fish assemblages of the Ria Formosa (Ribeiro et al., 2008). All the fish caught were identified, measured, and weighed, resulting in monthly length frequency distributions for V, UV and the combined (U + UV) sub-tidal habitats. Cohorts were identified by visual inspection of the time series of length frequency distributions, with unimodal distributions and modal progression used to identify cohorts. Age class 0 fish (juveniles) dominated the catches, with few individuals of older age classes and in most cases little or no overlap in size frequency distributions. An example of monthly length frequency distributions of a single cohort of the two-banded seabream, *Diplodus vulgaris*, showing clear modal progression and no evidence of more than one age class, is given in Appendix A. More detailed information on the sampling is given in Erzini et al. (2022).

2.3. Species

Given that the objective of this study was to evaluate the potential contribution of the Ria Formosa lagoon to the commercial fisheries of the coastal zone of southern Portugal, and to compare the results with those of Erzini et al. (2022) where fishing mortality was not taken into consideration in the calculation of fish provisioning services, the analysis focused on single cohorts of 7 of the same commercially important fish species that use the lagoon as a nursery (Table 1, Appendix B). To model cohort biomass and calculate yield von Bertalanffy growth parameters (K, L_∞, t_0), weight-length relationship parameters (a, b), maximum age ($t$max) were obtained from the literature. The key

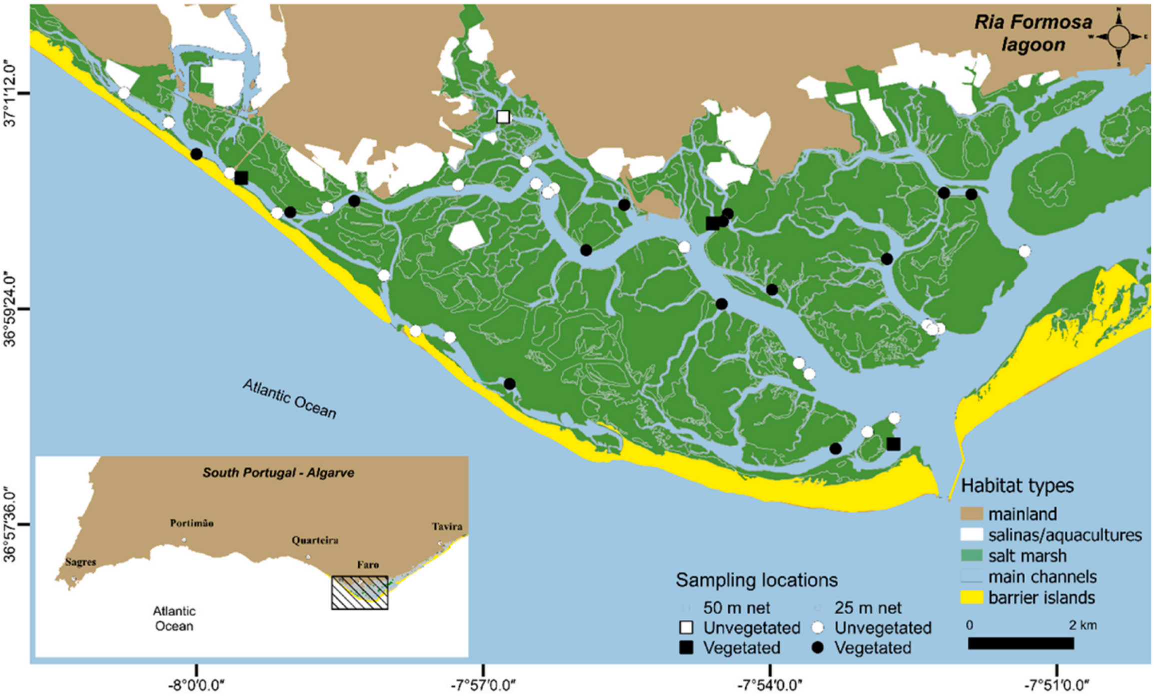

Fig. 1. Map of the western part of the Ria Formosa with the beach seine sampling locations: 24 unvegetated (open circles and squares), 17 vegetated (filled circles and squares). Modified from Erzini et al. (2022).

Table 1
List of species and parameters used in the calculations. *MLS* = Minimum Landing Size (cm), von Bertalanffy growth parameters (K, L_∞, t_0), maximum age (t_{max}), weight-length relationship parameters (a, b), low and high natural mortality (M) values, and numbers of recruits from vegetated ($N_{0.5\ V}$) and unvegetated habitat ($N_{0.5UV}$). More detailed information on the sources of the parameters are given in Appendices B and C.

Species	MLS	K	L_∞	t_0	t_{max}	a	b	Low M	High M	$N_{0.5\ V}$	$N_{0.5UV}$
Dicentrarchus labrax	36	0.14	99.3	-0.46	30	0.011	2.980	0.22	0.27	92,795	709,991
Diplodus puntazzo	15	0.18	54.1	-2.53	18	0.018	2.960	0.28	0.38	17,121	7,389
Diplodus sargus	15	0.18	40.9	-1.28	18	0.013	3.130	0.29	0.41	56,841	209,364
Diplodus vulgaris	15	0.18	34.5	-1.27	14	0.015	2.989	0.29	0.44	196,204	454,443
Sarpa salpa	18	0.14	45.1	-1.43	14	0.011	3.087	0.25	0.44	115,223	4,310
Sparus aurata	19	0.13	84.6	-1.59	22	0.013	3.040	0.22	0.29	8,047	105,298
Spondyliosoma cantharus	23	0.21	34.5	-1.22	13	0.010	3.109	0.32	0.48	141,075	295,573
Total										627,306	1,786,369

parameters used in the calculations are given in Table 1. The von Bertalanffy growth parameters (K, L_∞ and t_0) and the weight-length relationship parameters (a, b) of the 7 selected fish species were compiled mainly from studies from the south of Portugal (Appendix B). For species lacking fisheries biology parameters from Portugal (*Dicentrarchus labrax*, *Diplodus puntazzo*, *Sparus aurata*) we used age and growth studies from nearby areas, namely the Gulf of Cadiz for *D. labrax* and *S. aurata*, and the Canary Islands for *D. puntazzo* (Erzini et al., 2022, Appendix 2). Natural mortality (M) was calculated from empirical models (Pauly, 1980; Djabali et al., 1994; Then et al., 2015), and minimum legal landing sizes (MLS) from the Directorate General of Fisheries (www.dgrm.mm.gov.pt/pesca_cpt_especies) (Table 1, Appendix B).

Five of the 12 species from Erzini et al. (2022) were not included in this study because of their life history characteristics, namely high natural mortality (M) and growth (von Bertalanffy K) rates, and M/K ratios, making them unsuitable for yield-per-recruit analysis (Froese et al., 2016). The five species (*Boops boops*, *Diplodus bellottii*, *Mullus surmuletus*, *Sardina pilchardus*, and *Scorpaena porcus*) accounted for less than 2 % of the total value of the fish provisioning services of the 12 species calculated by Erzini et al. (2022).

2.4. Calculation of yield per recruit

For the single cohort of each of the 7 species, the total number of juveniles per month was calculated from the monthly length-frequency distributions for sub-tidal V and UV habitat. The observed maximum number of individuals per month was used as an index of recruitment and was divided by the area sampled with the beach seines to estimate the density (n m^{-2}) per habitat. Following zu Ermgassen et al. (2016), Jänes et al. (2020) and Erzini et al. (2022), the juveniles of the month with the maximum number of individuals were assumed to be 6 months old ($t_{0.5}$). The total number of age $t_{0.5}$ juveniles of each species ($N_{0.5}$) in each habitat was then calculated by multiplying the density by the total area of the sub-tidal habitat in the Ria Formosa lagoon (V: 3,060,000 m^2; UV: 15,940,000 m^2) (Erzini et al., 2022).

In contrast to the previous studies that assessed the monetary value in the absence of fishing mortality (zu Ermgassen et al., 2016; Jänes et al., 2020; Lai et al., 2020; Erzini et al., 2022), the instantaneous fishing mortality (F) was included in the analysis and the yield calculated based on the Thompson and Bell (1934) procedure. The number of surviving fish (per m^2), at each age class, for each species, was calculated using:

$$N_{t+1} = N_t e^{-(M+F)} \tag{1}$$

starting from $N_{0.5}$, the abundance at 6 months of age ($t = 0.5$) to the maximum age ($tmax + 0.5$). M and F are respectively the instantaneous natural and fishing mortality rates, and Z is the instantaneous total mortality rate:

$$Z = M + F \tag{2}$$

The annual number of deaths (D_t) was calculated by subtracting N_t from N_{t-1} ($D_t = N_{t-1} - N_t$). The catch in numbers (C_t) for each year was then calculated by multiplying the number of deaths (D_t) by the fraction of total mortality (Z) corresponding to fishing mortality (F):

$$C_t = D_t\left(\frac{F}{Z}\right) \tag{3}$$

The total yield (Kg) was calculated as the sum of the product of numbers caught at each age by the mean weight-at-age:

$$Yield = \sum\nolimits_{t=r}^{t=tmax} C_t W_t \tag{4}$$

where r is the age corresponding to the minimum legal size (MLS) and $t$max is the maximum age. EXCEL was used for all the analyses and calculations (spreadsheets are available from the corresponding author).

The total yield was estimated for a range of plausible values of F to calculate the potential contribution of a single cohort of each species to the local fisheries. $F_{0.1}$, defined as the point at which the slope of the yield curve is 1/10th the slope at the origin, was used instead of F_{max}, the fishing mortality at which yield is maximized, which was not possible to determine in most cases because the yield curves of the majority of the species were not dome shaped. Examples of yield curves, with F_{max} and $F_{0.1}$ from V and UV habitats for the European seabass (*Dicentrarchus labrax)* are given in Appendix C.

It was assumed that there was no fishing mortality ($F = 0$) for fish smaller than the minimum landing size (MLS). Therefore, there are two phases during the lifetime: the first for sizes up to MLS where there is only natural mortality ($Z = M$), and the second after the fish have reached the MLS and have been fully recruited to the fishery ($Z = M + F$).

Following Erzini et al. (2022), M values were estimated separately for age classes corresponding to sizes $<$ MLS and $\geq$ MLS. For each species, the lowest and highest values of M estimated using the Pauly (1980), Djabali et al., (1994)) and the two Then et al. (2015) empirical models were used in the YPR calculations (Table 1, Appendix D). These M values were attributed to all ages corresponding to sizes greater than or equal to MLS. For fish smaller than the MLS, size-dependent natural mortality was estimated using the Lorenzen (2000) equation:

$$M_t = M(L_m / L_t) \tag{5}$$

where M is the constant natural mortality rate (low and high) for exploited age classes calculated using the empirical models (Table 1, Appendix D), L_m = MLS, and L_t is the length at age t.

For each species, the expected lengths-at-age for fish from age $t = 0.5$ to their maximum age ($t_{\max} + 0.5$) were calculated using the von Bertalanffy growth model:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) \tag{6}$$

where K is the von Bertalanffy growth parameter, L_∞ is the asymptotic maximum size and t_0 is age corresponding to $L_t = 0$. Then, the average weight-at-age (W_t) was calculated from the length-at-age (L_t) using species-specific weight-length relationships:

$$W_t = aL_t^b \tag{7}$$

where a is the intercept and b is the slope.

The results of the approach based on potential yield per recruit, calculated as biomass corresponding to $F_{0.1}$, and those of the previous study that calculated fish provisioning services as the lifetime cumulative biomass (Erzini et al., 2022) were compared. The yields were also compared with the mean landings of each species from 1997 to 2017 in order to validate the approach based on yield for quantifying fish provisioning services.

2.5. Sensitivity analysis

For the most important species, the European sea bass, a sensitivity analysis was carried out. Sensitivity analysis in population dynamics and fisheries studies is carried out to evaluate the potential effects of parameter uncertainty on the output of the model or analysis (e.g. $F_{0.1}$ and corresponding yield in this case), by changing one parameter at a time, in a proportional manner (Annala and Breen, 1989; Lin et al., 2015). Maximum yield and $F_{0.1}$ were calculated by changing baseline values one parameter at a time (-20 %, +20 %). The sensitivity analysis was done for M, K, L_∞, t_0, $t$max, and the number of recruits ($N_{0.5}$). The choice of +/- 20 % was based on the range of M values obtained from the empirical models and the range of published values of the demographic parameters K, L_∞, t_0, and $tmax$.

2.6. Vegetated habitat enhancement of yield

The maximum yield per unit area (g m^{-2}) for V and UV habitat was determined for each species according to the $F_{0.1}$ criteria. The V enhancement of yield at $F_{0.1}$ was calculated by dividing the V habitat yield by the UV habitat yield (Y_V/Y_{UV}). Fish yield was determined to be enhanced by V habitat when $Y_V/Y_{UV} > 1.0$.

2.7. Economic valuation at maximum yield ($F_{0.1}$ criteria)

Official statistics for all species sold at auction in Algarve ports from 1997 to 2017 were obtained from the Directorate General for Natural Resources, Safety and Maritime Services (DGRM) and average first sale prices of the 7 species calculated. In Portugal, all commercial landings have to be sold at public auctions where sales are registered by species and vessel. The range, mean and s.e. of the landings and the first sale prices per kg were calculated from the official data set provided by the national agency (DGRM). The average first sale prices were used to calculate the total value and the value per hectare of each cohort for V, UV and total sub-tidal habitats of the Ria Formosa for $F_{0.1}$. Finally, the economic enhancement per hectare at $F_{0.1}$ by vegetated habitat was calculated by dividing the V (€ ha^{-1}) by the UV (€ ha^{-1}) values for each species.

3. Results

3.1. Maximum yields

Estimates of the yields (g m^{-2} $year^{-1}$ and total yield in kg) for $F_{0.1}$ for the whole Ria Formosa lagoon based on the total vegetated and unvegetated sub-tidal areas are presented in Tables 2 and 3 for the low and high M scenarios respectively. For the low M scenario (Table 2), vegetated habitat accounted for a total yield of 73,369 kg (16 % of the total yield), while the yield for UV habitat was 390,066 kg, corresponding to 236.7 kg ha^{-1} and 255.5 kg ha^{-1}, respectively. The total yield for the sub-tidal habitat was 463,435 kg (243.9 kg ha^{-1}). *D. labrax* was by far the most important species in both V and UV habitat, with 35,741 kg and 273,464 kg, corresponding to 48.7 % and 70.1 % of the total yield for all 7 species of the V and UV habitat respectively. The second most important species was *S. aurata*, followed by *D. sargus*, *S. cantharus*, *D. vulgaris*, *D. puntazzo* and *S. salpa*. The maximum yields (g m^{-2}) for V and UV habitats for the 7 species are shown in Appendices E.1 and E.2. Higher values of $F_{0.1}$ and lower yields (kg) were calculated for the high M scenario (Table 3). Total yields (kg) for V, V and V+UV habitat were 70.0 %, 72.3 % and 71.9 % respectively of those for the corresponding low M calculations (Table 2).

Table 2
Maximum yield (g m^{-2}) for $F_{0.1}$ criteria, vegetated habitat enhancement of yield (Y_V/Y_{UV}), average first sale price at auction (€ Kg^{-1}), value (€) and value per hectare (€ ha^{-1}) for V, UV and total (U + UV) habitat, for the low natural mortality (M) scenario.

			Yield (g m^{-2})		Y_V / Y_{UV}	Total yield (Kg) Value (€) Value (€ ha^{-1})									
Species	M	$F_{0.1}$	Y_V	Y_{UV}		V	UV	U + UV	€ Kg^{-1}	V	UV	U + UV	V	UV	U + UV
D. labrax	0.22	0.26	11.53	17.20	0.7	35,741	273,464	309,205	12.4	443,188	3,834,142	4,277,330	1,429.6	2411.4	3,841.1
D. puntazzo	0.28	0.40	2.20	0.18	12.2	9,792	2,952	12,744	5.8	56,794	73,915	130,709	183.2	46.5	229.7
D. sargus	0.29	0.32	2.30	1.59	1.4	6,369	23,451	29,820	8.1	51,589	241,542	293,131	166.4	151.9	318.3
D. vulgaris	0.29	0.57	1.90	0.84	2.3	5,739	13,291	19,030	3.8	21,808	72,314	94,122	70.3	45.5	115.8
S. salpa	0.25	0.25	3.00	0.02	150.0	5,659	325	5,984	0.6	3,395	3,590	6,986	11.0	2.3	13.2
S. aurata	0.22	0.21	1.50	3.86	0.4	5,049	66,066	71,115	10.4	52,510	739,596	7,92,106	169.4	465.2	634.5
S. cantharus	0.32	0.64	2.00	0.82	2.4	5,020	10,517	15,537	2.9	14,558	37,027	54,700	57.0	23.3	80.3
Total			**24.4**	**24.5**	**1.00**	**73,369**	**390,066**	**463,435**		**643,842**	**5,002,127**	**5,649,084**	**2087**	**3,146**	**5233**

Table 3
Maximum yield (g m^{-2}) for $F_{0.1}$ criteria, vegetated habitat enhancement of yield (Y_V/Y_{UV}), average first sale price at auction (€ Kg^{-1}), value (€) and value per hectare (€ ha^{-1}) for V, UV and total (U + UV) habitat, for the high natural mortality (M) scenario.

			Yield (g m^{-2})		Y_V / Y_{UV}	Total yield (Kg) Value (€) Value (€ ha^{-1})									
Species	M	$F_{0.1}$	Y_V	Y_{UV}		V	UV	U + UV	€ Kg^{-1}	V	UV	U + UV	V	UV	U + UV
D. labrax	0.27	0.34	8.30	12.39	0.7	25,742	196,959	222,701	12.4	319,201	2,442,292	2,761,492	1,029.7	1,536.0	2,565.7
D. puntazzo	0.38	0.51	1.93	0.16	11.9	5,991	2,586	8,577	5.8	34,748	14,999	49,747	112.1	9.4	121.5
D. sargus	0.41	0.50	1.67	1.20	1.4	5,175	19,064	24,239	8.1	41,918	154,418	196,336	135.2	97.1	232.3
D. vulgaris	0.44	0.70	0.86	0.39	2.2	2,675	6,196	8,871	3.8	10,165	23,545	33,710	32.8	14.8	47.6
S. salpa	0.44	0.55	1.85	0.01	136.8	5,734	215	5,949	0.6	3,440	129	3,569	11.1	0.1	11.2
S. aurata	0.29	0.28	1.30	3.31	0.4	4,018	52,574	56,592	10.4	41,787	546,770	588,557	134.8	343.9	478.7
S. cantharus	0.48	1.00	0.66	0.27	2.4	2,058	4,311	6369	2.9	5,968	12,502	18,470	19.3	7.9	27.1
Total			**16.6**	**17.7**	**0.94**	**51,393**	**281,905**	**333,298**		**457,227**	**3,194,654**	**3,651,881**	**1475**	**2009**	**3484**

3.2. *Sensitivity analysis*

The results of the sensitivity analysis for *D. labrax* are summarised in Table 4. Changes in four of the parameters (L_∞, t_0, *tmax* and $N_{0.5}$) had no effect on $F_{0.1}$. However, M was the parameter that had the greatest influence on $F_{0.1}$, with a decrease and increase of 20 % resulting in a 19.2 % decrease and 26.9 % increase in $F_{0.1}$, respectively. Similar but smaller changes in $F_{0.1}$ were associated with the von Bertalanffy growth parameter *K*. Changes in all parameters influenced yield, with the following decreasing order of importance: L_∞, *K, M*, $N_{0.5}$, *tmax* and t_0.

3.3. *Enhancement of yield by vegetated habitats*

Overall, there was no V habitat enhancement of yield ($Y_V/Y_{UV} = 1.0$ and 0.94 for low and high M). However, the maximum yields (g m^{-2}) of 5 of the 7 commercially important fish species were enhanced by V habitat with the greatest enhancement of yield by V habitat for *S. salpa* ($Y_V/Y_{UV} = 150.0$), followed by *D. puntazzo*, *S. cantharus*, *D. vulgaris* and *D. sargus*, with enhancement ratios of 12.2, 2.4, 2.3 and 1.4, respectively, for the low M scenario (Fig. 2). For *D. labrax* and *S. aurata*, the species with higher yields in UV habitat, the values of Y_V/Y_{UV} were 0.4 and 0.7, respectively. Similar values were obtained for the high M scenario (Table 4).

3.4. *Economic valuation at maximum yield ($F_{0.1}$ criteria)*

For the low M calculations the value of the total yield of the single cohorts of the 7 species at the maximum exploitation rate of $F_{0.1}$ for the whole lagoon is 5,649,084 € (5,233 € ha^{-1}), with V habitat accounting for 11.4 % of the total, with 643,842 € and 2,087 € ha^{-1}, while the total value of the yield of the UV habitat was 5,002,127 €, corresponding to 3,146 € ha^{-1} (Table 3). The most valuable species was the *D. labrax*, worth 4,277,330 €, accounting for 75.7 % of the total value, followed by the *S. aurata*, with 792,106€ (14.0 % of the total value). The values of yield at $F_{0.1}$ were lower for the high M calculations (Table 4). Total value (3,651,881 €), and value per hectare (3,484 € ha^{-1}) were respectively 64.6 % and 66.6 % of the low M values.

3.5. *Comparison of fish provisioning services based on lifetime biomass and maximum yield*

The maximum yields of the single cohorts of the 7 species are compared with the lifetime biomass estimates (Erzini et al., 2022), and the average landings sold at auction in the Algarve from 1997 to 2017 in Table 5. Overall, the total yield corresponding to $F_{0.1}$ for the 7 species is 94 % of the mean total landings for the 21-year period. Only two species, the European sea bass (*D. labrax*) and the gilthead seabream (*S. aurata*) have potential yields that exceed the average landings for the 21-year period.

Maximum yield at $F_{0.1}$ and lifetime biomass (Erzini et al., 2022) are highly correlated (*Maximum yield* $= 0.0863$ *xBiomass* $+ 4.975$, $R^2 = 0.990$; Appendix F). The general trend was for low yield-to-biomass ratios for the long-lived, slow-growing species and high yield-to-biomass ratios for the short-lived, fast-growing species. Potential yield to biomass ratios ranged from 0.07 for *S. salpa* and *S. aurata* to 0.36 for *S. cantharus* (Table 5).

Vegetated habitat enhancement of biomass and potential yield are also highly correlated: *Yield* $= 0.7945$ *xBiomass* $+1.533$ ($R^2 = 0.997$). The V yield enhancement ratio was greater than V biomass enhancement for 3 of the 7 species (*D. vulgaris*, *S. cantharus*, and *D. puntazzo*). Neither the yield nor the biomass were V enhanced for 2 species: *D. labrax* and *S. auratus* (Fig. 3).

4. Discussion

Coastal lagoons are important ecosystems that represent about 13 % of the world's coastal area (Barnes, 1980). Along with wetlands and coral reefs, these ecosystems are among the habitats with the highest value derived from the services they provide (Velasco et al., 2018). These include food provisioning (mainly fish and shellfish), freshwater storage, hydrological balance, climate regulation, flood protection, water purification, oxygen production, recreation, and ecotourism (Barbier et al., 2011; El Mahrad et al., 2020; Lopes and Videira, 2013; Solidoro et al., 2010). They support a wide range of economically important human activities, including fishing, aquaculture, harvesting of bait, as well as leisure and tourism (Newton et al., 2018).

Coastal nursery habitats provide various provisioning services, including the production of biomass that can sustain fisheries and support local livelihoods. Seagrass meadows play a particularly important role in supporting fisheries production and food security (Unsworth et al., 2019). A number of studies have calculated the lifetime biomass and corresponding value per hectare of fish and invertebrates from different habitats based on biomass modeling, using data on juvenile density, life history parameters, and commercial value (Peterson et al., 2003; Blandon et al., 2014a,b; zu Ermgassen et al., 2016; Jänes et al., 2020; Lai et al., 2020, Erzini et al., 2022). However, none of these studies took into consideration fishing mortality and therefore did not calculate the fish provisioning services in terms of potential yield per recruit.

This study is the first to calculate the maximum yield ($F_{0.1}$ criteria) for single cohorts of the most important commercial species using vegetated and unvegetated sub-tidal habitats of an important lagoon nursery, the Ria Formosa. In this case, the calculated maximum yield is the potential contribution in catches and value to the local commercial and recreational coastal fisheries of juveniles that used the vegetated and unvegetated sub-tidal habitats of the Ria Formosa as a nursery, if exploited at the fishing mortality rate of $F_{0.1}$.

Vegetated habitat enhanced the maximum yield of 5 of the 7 species, as was the case for lifetime biomass (Erzini et al., 2022). Although lifetime biomass and maximum yield are generally highly correlated, the yield to lifetime biomass ratios were smaller for the long-lived, slow-growing, high-value species such as the European seabass (*D. labrax*) and the gilthead seabream (*S. aurata*). These findings highlight the importance of taking fishing mortality into consideration when evaluating fish provisioning services. Fisheries yield is a function of life history parameters; small, fast growing, high natural mortality and relatively short-lived species are more productive and therefore have higher yield per unit biomass. On the other hand, the age structure of an

Table 4

Results of the sensitivity analysis for *D. labrax*. Baseline values correspond to the low M scenario. % diff. is the % difference from the baseline value.

Parameter	Baseline	-20 %	$F_{0.1}$	% diff.	Yield (kg)	% diff.	+20 %	$F_{0.1}$	% diff.	Yield (kg)	% diff.
M	0.22	0.176	0.21	-19.2	245,533	-10.2	0.264	0.33	26.9	204,615	-25.2
K	0.14	0.11	0.23	-11.5	178,196	-34.8	0.17	0.29	11.5	378,992	38.6
L_∞	99.3	79.4	0.26	0.0	147,410	-46.1	119.2	0.26	0	494,727	80.9
t_0	-0.46	-0.37	0.26	0.0	266,384	-2.6	-0.55	0.26	0	280,606	2.6
tmax	30	24	0.26	0.0	287,015	5.0	36	0.26	0	287,062	5.0
$N_{0.5}$	709,991	567,993	0.26	0.0	218,772	-20.0	744,122	0.26	0	328,157	20.0
$F_{0.1}$	0.26										
Yield (kg)	273,464										

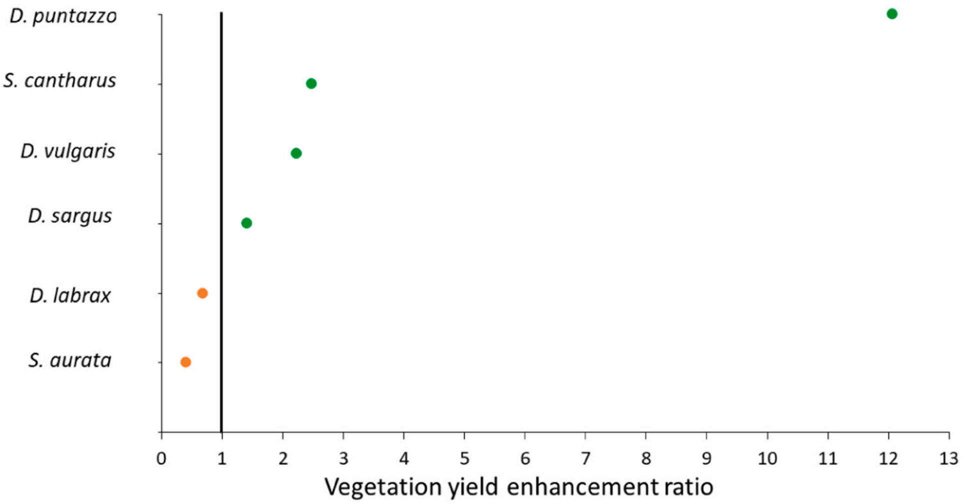

Fig. 2. Vegetation enhancement ratios (Y_V/Y_{UV}) of yield (g m^{-2}) at $F_{0.1}$ for the low M scenario. The vertical line (Y_V/Y_{UV} ratio = 1.0) corresponds to no difference in yield between V and UV habitats. Ratios > 1.0 mean that the yield of V habitat is greater than that of UV habitat. *S. salpa* (Y_V/Y_{UV} = 150.0) is not shown.

Table 5
Comparison of calculated yield ($F_{0.1}$), cumulative lifetime biomass (Erzini et al., 2022), for single cohorts for the whole Ria Formosa lagoon (V + UV habitat), and average annual Algarve commercial landings (s.e.) sold at auction (1997–2017) for the 7 species, for the low M scenario.

Species	Mean landings (t)	Yield (t)	Biomass (t)	Yield/ Biomass	Yield/ Landings
D. labrax	21.4 (1.6)	309.2	3,701.6	0.08	14.5
D. puntazzo	12.6 (0.8)	12.7	71.6	0.18	1.00
D. sargus	38.5 (8.3)	29.8	253.9	0.12	0.77
D. vulgaris	182.9 (12.4)	19.0	86.9	0.22	0.10
S. salpa	83.9 (5.8)	6.0	80.2	0.07	0.07
S. aurata	56.5 (4.1)	71.1	993.4	0.07	1.26
S. cantharus	53.7 (2.6)	15.5	43.6	0.36	0.28
Total	**494.8 (11.1)**	**463.3**	**5,231.2**	**0.09**	**0.94**

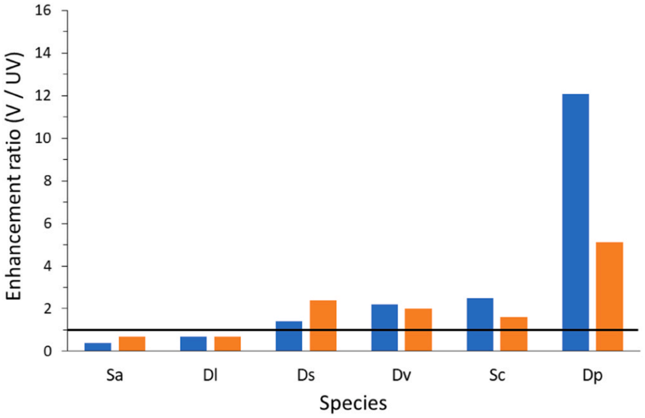

Fig. 3. Vegetation enhancement ratios for lifetime biomass (blue) where Z = M and potential yield (orange), calculated with fishing mortality (Z = M + F), for the low M scenario. Values greater than 1.0 represent V-enhancement. *S. salpa* is not included because of very high values (V_B/UV_B = 169.1, V_Y/UV_Y = 150.0). SA = *Sparus aurata*, Dl = *Dicentrarchus labrax*, Ds = *Diplodus sargus*, Dv = *Diplodus vulgaris*,Sc = *Spondyliosoma cantharus*, Dp = *Diplodus puntazzo*.

exploited stock of a long-lived, slow-growing species such as the European seabass is very different from that of an unexploited stock, with fewer age classes and smaller numbers of larger, older fish. This explains the low yield-to-lifetime biomass ratios found in this study and why very high lifetime biomass estimates were obtained for European seabass and gilthead seabream when fishing mortality was not considered (Erzini et al., 2022). Thus, our results provide a more realistic view of the contribution of vegetated habitat to commercially important fish stocks since not including fishing mortality in the calculation of fish provisioning services results in over-estimation of the real contribution of both vegetated and unvegetated habitats to coastal commercial and recreational fisheries.

Unlike the approach based only on natural mortality, where V habitat, covering 16.3 % of the sub-tidal habitat accounted for 27.1 % of the total fish production (Erzini et al., 2022), in this study the total yields (kg) for both V and UV habitat were proportional to the areas. The far greater total yield and value of UV sub-tidal habitat, which accounts for 84 % of the total sub-tidal area, is largely due to the overwhelming contribution of the high-value, long-lived European seabass (*D. labrax*) that is not V-enhanced, and to a lesser extent to two other high-value species, the gilthead seabream (*S. aurata*), also not V-enhanced, and the white seabream (*D. sargus*) that is V-enhanced. The European seabass (*D. labrax*) dominates in yield (kg) and in value in both habitats and for the whole lagoon. Based on the annual monitoring of juveniles since 2001 (unpublished data), this was an exceptionally strong year-class of *D. labrax*, as reflected in the landings of age classes 3–9 from 2004 to 2010 (Erzini et. al., 2022). If fished at $F_{0.1}$, under the high and low natural mortality scenarios, this single cohort would have yielded between EUR 2.8 million (high M) and EUR 4.3 million (low M) based on average first sale at auction values.

A limitation of this approach is that it is dependent on accurate estimates of life history parameters, namely von Bertalanffy growth parameters, weight-length relationship parameters, maximum age, and most importantly natural mortality. Ideally, these should be jointly estimated for the population or stock that is being studied. In this study, parameters from studies from other, nearby areas had to be used for some of the species and natural mortality was estimated using empirical models that give very different results (Mannini et al., 2020). Furthermore, to compare the contribution of vegetated and unvegetated habitat, habitat-specific life history parameters, namely young-of-the-year natural mortality and growth should ideally be used. However, as reported in Erzini et al. (2022), it was not possible to calculate mortality and growth parameters for both habitats for all the species and therefor we had to use the same parameter values for both types of habitat.

A second limitation of this approach is that YPR analysis results in overestimation of the maximum yield for species with high M and M/K values (Froese et al., 2016). For this reason, we focused our analysis on 7 of the 12 species analysed in Erzini et al. (2022), excluding 5 relatively short-lived, fast-growing species with high natural mortality rates. We believe that the estimates of $F_{0.1}$ for the seven species, especially the more long-lived, slow-growing European seabass and gilthead seabream are realistic.

The approach also does not take into account variability in recruitment and uncertainty in life history parameters. As expected, and shown by the sensitivity analysis, yield is dependent on recruitment, which can easily be monitored annually with a well-designed sampling program to obtain information on variability. However, yield is more sensitive to variability in M, which is difficult to estimate, and to von Bertalanffy growth parameters. Uncertainty in life history parameters could be addressed by fitting a population dynamics model to the observed data, using priors. This would allow parameters to be estimated and the calculation of the most likely values of $F_{0.1}$ and associated yield and confidence intervals.

In this study, we opted to focus on uncertainty in M, as maximum yield and biological reference points such as $F_{0.1}$ are highly sensitive to the instantaneous natural mortality rate, with lower M resulting in higher estimates of yield (King, 1995; Deriso, 2011; Punt et al., 2021; Hamel et al., 2023). As M is one of the most difficult parameters to estimate, we used four empirical models (Pauly, 1980; Djabali et al., 1994; Then et al., 2015) to estimate M and used the lowest and highest values for each species to calculate yield and maximum yield ($F_{0.1}$ criterion) for each species. However, we recognize that even the lowest values may be too high for some species given what is known about the fish assemblages and species caught in the coastal waters of southern Portugal, with few natural predators of commercial sizes of the 7 species studied (Stergiou et al., 2006, 2007; Leitão et al., 2014).

It is important to note that for long-lived, relatively slow growing and high value species such as *D. labrax* and *S. aurata*, the $F_{0.1}$ values are much lower than those of the other species, especially the very short-lived, high M and fast-growing species. Species such as *D. labrax* and *S. aurata* are highly sought after both by commercial and recreational fishers (Veiga et al., 2010) and it is very likely that the current fishing mortality rates are much higher than the estimates of $F_{0.1}$. This implies that the economic benefits to the fisheries of recruits originating from the lagoon could be much greater if fishing mortality rates were lower than they currently are.

The findings of this study on fish provisioning services based on the maximum yield of single cohorts of 7 species from nursery habitats of the Ria Formosa lagoon, are consistent with the results of other studies focusing on the lifetime biomass (Peterson et al., 2003; Blandon et al., 2014a,b; zu Ermgassen et al., 2016; Jänes et al., 2020; Lai et al., 2020, Erzini et al., 2022). However, by incorporating fishing mortality in order to estimate yield, the values obtained are an order of magnitude lower than those where only natural mortality was considered. Likewise, the commercial value of lifetime biomass far exceeds that of the maximum yield calculated in this study.

Overall, the calculated potential yields of 463 and 333 tons for low and high M scenarios of the single cohorts of 7 species of the Ria Formosa lagoon at $F_{0.1}$ are comparable to total landings the commercial fisheries in the south of Portugal of these species for the 21-year period from 1997 to 2017 (mean of 495 tons, s.d. = 51 tons). Had it been possible to calculate F_{max}, the corresponding maximum yields would have been even greater, since $F_{0.1}$ is a precautionary reference point that is smaller than F_{max} (Gabriel and Mace, 1999). Given that more than 120 species of fish are found in the Ria Formosa lagoon, with the majority using it as a nursery (Monteiro et al., 1987, 1990; Monteiro, 1989; Erzini et al., 2002, 2022), these findings highlight the importance of the Ria Formosa as a nursery for commercially important species and in terms of fish provisioning services and economic contribution to coastal fisheries.

5. Conclusion

This study is the first to quantify the fish provisioning services and economic contribution to local fisheries of individual cohorts of fish species using a coastal lagoon as a nursery in terms of maximum yield per recruit ($F_{0.1}$ criterion). Our results based on both natural and fishing mortality are more realistic than those of studies that estimated lifetime biomass per unit area, based only on natural mortality (Peterson et al., 2003; Blandon et al., 2014a,b; zu Ermgassen et al., 2016; Jänes et al., 2020; Lai et al., 2020, Erzini et al., 2022). The results highlight the critical importance and value of the Ria Formosa lagoon as a source of recruits, and the importance of conservation of critically important nursery habitats, especially sub-tidal seagrass habitat. The quantitative assessment of lagoon fisheries provisioning services and economic contribution to local coastal fisheries and estimates of $F_{0.1}$ for different natural mortality scenarios can be used to provide insight on the level of exploitation and the status of the stocks, inform management and conservation and to provide guidelines for monitoring programs and restoration of these threatened coastal ecosystems (zu Ermgassen et al., 2016; Lai et al., 2020). The approach applied in this study is applicable to any nursery habitat where it is possible to estimate recruitment (young-of-the-year abundance) for species with reliable estimates of life history parameters.

CRediT authorship contribution statement

Jorge Manuel dos Santos Gonçalves: Writing – review & editing, Project administration, Investigation. **Pedro Monteiro:** Writing – review & editing, Visualization, Investigation. **Pedro Gil Lino:** Writing – review & editing, Investigation. **Joaquim Ribeiro:** Investigation. **Frederico Oliveira:** Writing – review & editing, Visualization, Investigation. **Zineb Sadat:** Writing – original draft, Investigation, Formal analysis. **Karim Erzini:** Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Rui Pedro Coelho:** Writing – review & editing, Investigation. **Luís Bentes:** Writing – review & editing, Investigation, Data curation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Karim Erzini reports financial support was provided by Fundação de Ciência e Tecnologia, Portugal.

Data Availability

Data will be made available on request.

Acknowledgements

This work was funded by the ICTIORIA (Recruitment of sea breams (Sparidae) and other commercially important species in the Algarve (southern Portugal) project, Commission of the European Communities, DG XIV C1/99/061, and Portuguese national funds from FCT - Foundation for Science and Technology through projects UIDB/04326/2020, UIDP/04326/2020 and LA/P/0101/2020 to CCMAR. We are grateful to the Direcção-Geral de Recursos Naturais, Segurança e Serviços Marítimos – Directorate General for Natural Resources, Safety and Maritime Services (DGRM) for providing landings and economic data. We would like to thank our master fisher, Isidoro Costa, and all the students and volunteers who participated in the fieldwork and laboratory processing of the samples. We would also like to thank all the reviewers whose comments contributed greatly to improving the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107115.

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