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Influence of seagrass meadows on nursery and fish provisioning ecosystem services delivered by Ria Formosa, a coastal lagoon in Portugal

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ABSTRACT

This study is the first to evaluate the fish provisioning services of a whole transitional landscape (Ria Formosa lagoon, Portugal), in parallel with the enhancement of growth, survival and production of single cohorts of the most important commercial fish species by vegetated and unvegetated sub-tidal habitats. Based on monthly beach seine samples, total density and biomass of 96 species of fishes were 1.89 and 3.03 times greater in vegetated habitats than unvegetated habitats, respectively. Vegetated habitat enhanced survival in six of eight commercial species for which survival could be estimated in both habitats. The total production of all 12 commercially important species within vegetated habitat was approximately double that of unvegetated habitat, with production enhancement in 7 of 12 species ranging from 1.8 to 169-fold for the vegetated habitats. Within the lagoon, vegetated sub-tidal habitat covers an area 5-fold smaller than unvegetated habitat, yet it accounts for 27.1 % of fish production. Estimated total lifetime economic values of the single cohorts of the 12 commercial species were between 30 million and 59 million EUR. An exceptionally strong year class of the European seabass (*Dicentrarchus labrax*), a species with higher density and biomass in unvegetated habitat, accounts for the higher overall values per hectare for unvegetated habitat (Low natural mortality (*M*): EUR 32,844 ha^{-1}; High *M*: EUR 16,751 ha^{-1}) than for vegetated habitat (Low *M*: EUR 22,028 ha^{-1}; High *M*: EUR 10,700 ha^{-1}). These results highlight the enormous importance of temperate coastal lagoons as a nursery and source of recruits for coastal fisheries. Our evaluation of fish provisioning services based on data for individual cohorts of fish for a whole transitional landscape is a stronger and more valid approach for estimating future biomass and value than previous studies based on mean densities and biomasses of fish that did not distinguish between cohorts.

1. Introduction

Transitional landscapes such as coastal lagoons and estuaries are widely recognized as important habitats for juvenile fish, with numerous studies on their role and importance as nursery areas for marine species that contribute to subsistence, commercial and recreational fisheries in adjacent coastal waters (Whitfield, 2017; Baker et al., 2020). The inclusion of habitat that is necessary to maintain a sustainable fishery (Essential Fish Habitat; EFH), in the law governing marine fisheries management in the U.S. (Magnuson-Stevens Act) and in the Common Fisheries Policy of the European Union (CFP, 2013) highlights the importance of specific areas for conservation and management.

Over time, the definition of nursery areas has shifted (Whitfield, 2017), with the mere presence of juveniles in particular habitats considered insufficient by Beck et al. (2001), who proposed the Nursery Role Habitat (NRH) criterion based on differences in density of juveniles between habitats. Dahlgren et al. (2006) introduced the concept of Effective Juvenile Habitat (EJH), differentiating the importance of juvenile habitats by their relative contributions to adult populations. Sheaves (2009) broadened the definition by advocating the importance

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of connectivity within the framework of a coastal ecosystem mosaic (CEM), with a focus on the ecology of key connections during different life history stages rather than on specific habitats. Within estuarine or lagoon systems, this implies studying landscape ecology, the use by juvenile fishes of a mosaic of fragmented habitats, the movements between habitats such as vegetated and unvegetated areas and of edge effects (Sheaves, 2009; Nagelkerken et al., 2015; Whitfield, 2017). Fodrie et al. (2009) stressed the implications of linking location-specific differences in demographic parameters such as growth and mortality rates with overall population fitness and contributions to adult stocks.

Nursery value of different coastal habitats has been measured and compared using density, growth, condition factor, feeding, survival and production per unit area of juveniles (age class 0 or 0-group fish) as proxies of habitat quality. Increased production and recruitment to adult populations is associated with greater density, survival, condition and growth in nurseries (Nelson, 1998; Franco et al., 2010; Janes et al., 2019).

Studies on fish provisioning ecosystem services in coastal and transitional landscapes have focused mainly on fisheries enhancement by particular habitats, especially seagrass, rather than on the whole landscape. The value of fisheries enhancement of seagrass habitat has been quantified using different approaches. Blandon and zu Ermgassen (2014a), Blandon and zu Ermgassen (2014b) carried out a meta-analysis based on 11 studies across southern Australia where juvenile fishes were sampled in vegetated and unvegetated areas with fine mesh gear, mainly beach seines. They estimated enhancement by seagrass as the difference in density (individuals m^{-2}) of 0.5-year-old fishes between seagrass and unvegetated habitats. Using species-specific natural mortality rates (M), age at first harvest, maximum age, von Bertalanffy growth parameters and weight-length relationship parameters for 12 commercial species, they calculated the total annual enhancement of each species (g m^{-2}) by summing the incremental increase in weight for an average fish of each species in each year class *i* multiplied by the density of fish in each age class:

$$N_i = N_{0.5} \times e^{(M \times (i-0.5))} \tag{1}$$

The estimated total annual seagrass enhancement was 980 g m^{-2}, corresponding to 9.8 t per hectare for the commercial fisheries. The value of seagrass nurseries was estimated at AUD 31,650 ha^{-1} y^{-1} (approximately EUR 19,840 ha^{-1} y^{-1}). Jänes et al. (2020) used the same approach to estimate the average enhancement in annual fish biomass production from seagrass, mangrove and tidal marsh habitats in Australia and found that compared to unvegetated areas, seagrass habitats were the most productive, with 55,000 more fish per hectare, while mangroves and tidal marshes provided 19,000 and 1,700 more fish, respectively. Jackson et al. (2015) used a seagrass residency index to calculate the contribution of seagrass habitat provisioning service to the Mediterranean commercial fisheries landings value (CFV) and recreational fisheries value (RFV), estimating that approximately 4 % of CFV and 6 % of RFV were directly linked to seagrass, corresponding to approximately EUR 77.7 million (CFV) and EUR 112.6 million (RFV). Based on fish abundance data, Tuya et al. (2014) estimated that seagrass value to inshore fisheries was EUR 606,239 y^{-1} for Gran Canaria Island (NE Atlantic).

While the value of ecosystem services provided by individual habitats has a rich history (Campagne et al., 2015; Tuya et al., 2014; United Nations Environment Programme, 2020), valuing the services from an entire coastal lagoon is infrequent (Lillebø et al, 2016; Newton et al., 2018). For the evaluation of fish provisioning services, a whole lagoon approach is important because during their nursery phase, juveniles may not generally experience single habitats but the entire landscape (Sheaves, 2009).

Coastal lagoons account for approximately 11 % of the global coastline (Kjerfve, 1994) and are important nurseries for many coastal commercial species, providing recruits and enhancing fish yields (Monteiro et al., 1990; Erzini et al., 2002; Tournois et al., 2017). The Ria Formosa is the largest coastal lagoon in Portugal, with the greatest area of vegetated sub-tidal habitat (Cunha et al., 2013) and high juvenile fish diversity and densities, especially of commercially important coastal species (Monteiro et al., 1990; Erzini et al., 2002; Ribeiro et al., 2012).

In this study, we use a multi-method approach to evaluate the nursery function and fish provisioning services of the whole Ria Formosa lagoon. Unlike previous, questionnaire-based studies (e.g. Sousa et al., 2013), or studies that did not evaluate the lifetime contribution of distinct cohorts (e.g. Tuya et al. 2014; Jänes et al., 2020), we used time series of length frequency distributions, density and biomass of single cohorts of 12 marine commercial species to estimate population dynamics parameters, and biomass modelling to estimate the fish provisioning services of the Ria Formosa lagoon. The main objectives of the study were: 1) to estimate the potential economic contribution of the whole lagoon to coastal fisheries, and 2) to compare density, biomass, survival, production and the economic value of sub-tidal vegetated and unvegetated habitat within the lagoon.

2. Methods

2.1. Ria Formosa lagoon

Ria Formosa is a mesotidal coastal lagoon located in southern Portugal with minor contributions of freshwater tributaries, which extends 56 km along the coast (Fig. 1). The semi-diurnal tide amplitude ranges from 1.3 to 3.5 m on neap and spring tides, respectively, exposing large intertidal areas where the seagrass *Zostera noltei* develops. The seagrasses species *Z. marina* and *Cymodocea nodosa* occupy the shallow subtidal areas.

2.2. Sampling of juveniles

Sampling of the ichthyofauna took place in the Ria Formosa lagoon over a 17-month period from September 2000 to January 2002 at 24 unvegetated (UV) and 17 vegetated (subtidal seagrass meadows, V) sites in the major and minor channels of the lagoon (Fig. 1) with beach seines. While we have carried out seasonal annual monitoring in a subset of our 41 sampling locations since 2001, we selected these data because sampling was monthly, allowing a cohort-based approach. There have been no significant changes in the relative importance of the 12 main species used in the analysis, and no substantial change in habitat type or cover at our sampling sites since 2001 (Ribeiro et al. 2006, Ribeiro et al., 2008, 2012, unpublished data).

Beach seines are the gear of choice for quantifying juvenile fish density as they are encircling gear that fish the whole water column and sample a relatively large area. Two types of beach seine were used: a 50 m, 14 mm stretched mesh size beach seine from January 2001 to January 2002 at 4 sites and a 25 m, 9 mm beach seine from September 2000 to October 2001 at 37 sites. Both nets were 3.5 m high in the middle and sampling always took place during a period 2 h before to 2 h after low tide, in days when the amplitude of the tide was<2 m. The two nets were deployed differently: following Monteiro (1990), one end of the 50 m net was held on shore and a boat was used to set the net in a circle, while the 25 m beach seine was towed parallel to the shore by the boat and researchers on the shore before being hauled to the shore. Based on GPS measurements the average sampled area with the 25 m beach seine was 1,087 m^2, while that of the 50 m beach seine was 295 m^2. However, three 50 m beach seine sets were made in succession at each location and the catches pooled, resulting in a total sampled area of 885 m^2. The catches were placed in labelled bags and transported to the laboratory for sorting, identification, measuring and weighing. Following Monteiro et al. (1990), species were classified as resident, occasional or migratory, with the latter consisting of young-of-the-year of species using the Ria Formosa as a nursery. The monthly beach seine samples in unvegetated and vegetated sites were used to obtain fish

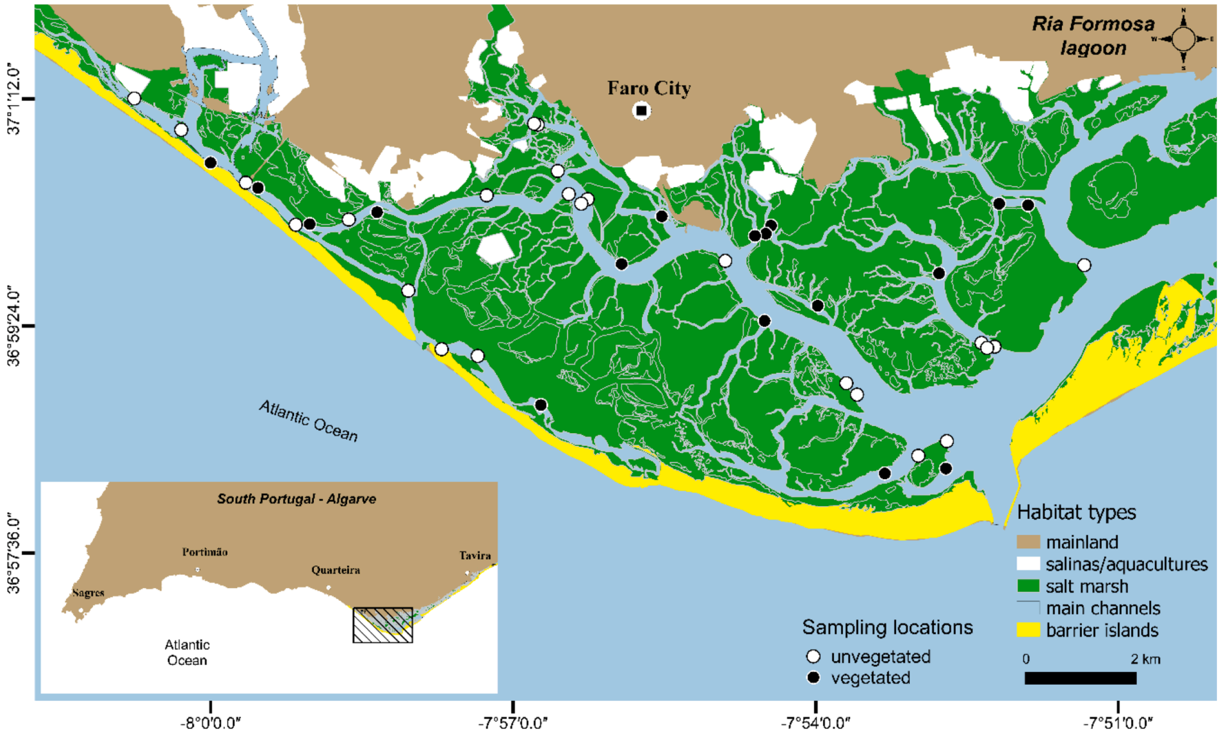

Fig. 1. Map of the western part of the Ria Formosa with the 41 beach seine sampling locations: 24 unvegetated (open circles), 17 vegetated (filled circles).

density and biomass per unit of sampled area and lengths and weights of juveniles of marine commercial species that use the lagoon as a nursery.

2.3. *Tagging (site fidelity)*

To compare habitats in terms of growth, mortality and production, it was necessary first to evaluate site fidelity and the association of individuals of the different species with each habitat. Tagging was used to study site fidelity and spatio-temporal dynamics. Tagging of fish occurred from September 2000 to January 2002 with a total of 73 beach seine sets over 19 fishing days at 26 locations devoted exclusively to tagging. Depending on the location, either the 25 m or the 50 m beach seine was used to catch fish for tagging. After capture, fish were placed in a floating cage besides the boat and teams of researchers measured, tagged (Floy T- tags) and recorded the data (date, location, species, total length, and tag number). Tag wounds were treated with a providone-iodine solution (Betadine) and the tagged fish were placed in the floating cage for a recovery period of approximately 30 min before being released back into the Ria at the location of capture.

2.4. *Population dynamics*

Monthly length frequency distributions for 2001 were used to estimate population dynamics parameters and production for 12 of the most abundant commercial species using the lagoon as a nursery, that had a single, main cohort of juveniles (i.e. age class 0) that could be clearly followed over time: *Boops boops* (bogue), *Diplodus bellottii* (Senegal seabream), *D. puntazzo* (sharpsnout seabream), *D. sargus* (white seabream), *D. vulgaris* (two-banded seabream), *Dicentrarchus labrax* (European seabass), *Mullus surmuletus* (striped red mullet), *Sardina pilchardus* (sardine), *Sarpa salpa* (salema), *Scorpaena porcus* (black scorpionfish), *Sparus aurata* (gilthead seabream) and *Spondyliosoma cantharus* (black seabream). These species recruit to the lagoon in the late winter or spring and leave by the end of the year.

Analysis of single cohorts, with large sample sizes simplifies the analysis of growth, mortality and production (Hayes et al., 2007; Rigler and Downing, 1984). Unlike other studies (Dolbeth et al., 2008; Franco et al. 2010; Verdiell-Cubedo et al., 2013), there was no need for the use of length frequency analysis to decompose length frequency distributions as there was a single clearly identifiable 0-group for all 12 species, as can be seen in the example of monthly length frequency distributions of a single cohort of *S. cantharus* from vegetated habitat, in Appendix A (Supplementary materials).

From the time series of length frequency distributions for vegetated (V), unvegetated (UV) and total (V + UV) habitats, the following were determined: month of birth ($t = 0$), month of recruitment (settlement), length-at-age (L_t), numbers at age (N_t), densities (n m^{-2}) and biomass (g m^{-2}). Month of birth was estimated by extrapolating L_t backwards and confirmed using data on month of capture with a 1 mm mesh codend Riley pushnet of the earliest post-larval juvenile stages (1–2 cm) found in the lagoon, under the assumption that post-larval juveniles of this size are at most 4 to 8 weeks old (Nelson, 1998, Erzini et al. 2002, Ribeiro et al. 2012). The Gompertz model:

$$L_t = L_0 \times e^{\left(G1\times\left(1-e^{(-g2\times t)}\right)\right)} \tag{1}$$

considered to be the most appropriate for describing age class 0 growth (Gamito 1998, Diouf et al. 2009) was fitted to the length-at-age data. L_t is the total length, t the age in months, L_0 is the hypothetical length at $t = 0$, $G1$ and $g2$ are growth parameters, $G1g2$ is the size-specific instantaneous rate of growth at $t = 0$ and $g2$ is the instantaneous rate of decrease of $G1g2$ (Saila et al., 1988). The Hotelling T^2 test was used to test the null hypothesis that there is no difference between the growth parameters of fish from vegetated and unvegetated habitats (Bernard, 1981; Srivastava and Carter, 1983). The SAS software was used to fit the Gompertz model (NLIN procedure) and to carry out the Hotelling T^2 test (SAS Institute Inc., 2013). The instantaneous monthly growth rate (G) was also estimated from.

$$ln(L_t) = ln(L_0) + G \times t \tag{2}$$

where t is age in months (Nelson, 1998).

Instantaneous total mortality (Z) was estimated by fitting a regression to the descending limb of the plot of the natural logarithm of numbers-at-age against age in months (Ricker, 1975):

$$ln(N_t) = (Z \times t) + c \tag{3}$$

Given that there is no significant fishing mortality during the lagoon juvenile phase, the estimates of total mortality (*Z*) can be considered equal to natural mortality, *M*. For all species, densities increased after initial recruitment to the lagoon at sizes of<2 cm, reaching maximum numbers between 5 and 7 months of age. Thus, the estimates of *Z*, based on the descending part of the catch curve, correspond to natural mortality of the older juveniles in the period before emigration from the lagoon to the adjacent coastal zone. Under the assumption of a steady-state condition and negative exponential mortality, *Z* equals the production to biomass ratio (*P/B*) (Allen, 1971). Catch curve analysis was carried out for each of the species separately for V and UV habitats as well as for the combined data (V + UV). Seagrass enhancement of survival (*S*) was calculated as S_V/S_{UV}, where.

$$S = e^{-Z} \tag{4}$$

and values of $S_V/S_{UV} > 1$ correspond to seagrass enhancement of survival.

2.5. Production

Production of a cohort is the generation of biomass per unit area per unit time, integrating biomass, recruitment, growth and mortality into a single dynamic measure that is the best indicator of quantitative performance of a fish population (Ricker 1975, Randall and Minns 2000, Hayes et al. 2007). Production was estimated from growth increments for single cohorts for vegetated and unvegetated habitats (Rigler and Downing, 1984; Hayes et al., 2007; Dolbeth et al., 2008):

$$P = \sum_{t=0}^{T-1} \left(\frac{N_t + N_{t+1}}{2}\right).(\overline{W}_{t+1} - \overline{W}_t) \tag{5}$$

where N_t is density (numbers per m^2) and $\overline{W}_t$ is mean weight of the cohort in month *t*. Densities were calculated by dividing the numbers caught in each month in each habitat by the total area sampled each month (25,886 m^2 for 24 unvegetated habitat locations and 17,873 m^2 for 17 vegetated habitat locations). Weight-length relationships:

$$W = a \times L^b \tag{6}$$

were fitted and used to calculate the mean weights-at-age of the cohort ($\overline{W}_t$) from the cohort length frequency distributions for each month from the time of recruitment to the lagoon until migration from the lagoon to the coastal waters. Total production per cohort for the whole lagoon was calculated using the estimated cohort production per m^2 and the total estimated subtidal areas of seagrass and unvegetated habitats (3,060,000 m^2 and 15,940,000 m^2, respectively; unpublished data).

2.6. Economic valuation

Calculation of the lifetime economic value of each cohort to coastal fisheries was based on the methodologies of Blandon and zu Ermgassen (2014a), Blandon and zu Ermgassen (2014b), zu Ermgassen et al. (2016) and Jänes et al. (2020). Von Bertalanffy growth parameters, maximum age, and weight-length relationship parameters were compiled for each species (Appendix E). For the majority of the species these were from our own studies in the Algarve or other regions from continental Portugal (Appendix E). For species lacking fisheries biology parameters from Portugal (*D. labrax, D. puntazzo, S. porcus, S. aurata*) we used age and growth studies from nearby areas, namely the Gulf of Cadiz for *D. labrax* and *S. aurata*, the Canary Islands for *D. puntazzo*, and Algeria for *S. porcus*. The instantaneous natural mortality rate (*M*) for fully fishery recruited age classes was estimated using four empirical models: Pauly (1980):

$$log_{10}(M) = -0.0066 - (0.279 \times log_{10}L_\infty) + (0.6543 \times log_{10}K) + (0.4634 \times log_{10}T) \tag{7}$$

Djabali et al. (1994):

$$log_{10}(M) = 0.0278 - (0.1172 \times log_{10}L_\infty) + (0.5092 \times log_{10}K) \tag{8}$$

Then et al. (2015):

$$M = 4.899 \times \left(tmax^{-0.916}\right) \tag{9}$$

$$M = 4.118 \times \left(K^{0.73}\right) \times \left(L_\infty{}^{-0.33}\right) \tag{10}$$

where *K* and L_∞ are von Bertalanffy growth parameters, *tmax* is maximum age and *T* is the mean annual water temperature in southern Portugal (16 °C). In addition, size-dependent natural mortality rates for pre-recruit ages were calculated using the Lorenzen (2000) model:

$$M_t = M \times (L_m/L_t) \tag{11}$$

where M is natural mortality calculated using the above-mentioned empirical models, L_t is length at age *t* and L_m is the minimum legal landing size (MLS; https://www.dgrm.mm.gov.pt/peixes). For *S. porcus* the size at first maturity was used for L_m as there is no minimum legal landing size.

The von Bertalanffy parameters were used to calculate lengths-at-age from $t = 0.5$ to $t = tmax + 0.5$ and the mean weights-at-age (W_t) calculated with the weight-length relationships. Natural mortality rates (M_t) for age classes with mean sizes below the MLS were calculated using the Lorenzen (2000) model, while a constant *M* calculated using the four empirical models was used for all the age classes of fish equal to or greater than the MLS.

The maximum monthly abundance for each species was obtained from the length frequency distributions for V and UV habitats (see for example Appendix A) and used as $N_{0.5}$ in the life table analysis to calculate numbers-at-age up to the maximum age. Given the age-specific survival rate $S_t = e^{-M_t}$, the evolution in numbers of the cohort was calculated by $N_t = N_{t-1} \times S_{t-1}$. The total biomass by age class was calculated by multiplying the numbers-at-age by the corresponding mean weights-at-age. The cohort lifetime or total biomass (*TB*), in the absence of fishing mortality, was obtained by summing the biomasses of all fully recruited age classes: $TB = \sum_{t=r}^{t=tmax} N_t \times W_t$, where *r* is the youngest age class with a mean length equal to or greater than the MLS.

In Portugal, commercial fishermen must sell their catches in official auctions where landings and first sale prices are recorded. Official data for all species sold at auction in Algarve ports from 1997 to 2017 was obtained and average first sale prices of the 12 species calculated. The average prices were used to calculate the total value and the value per hectare of each cohort for the whole lagoon and for each habitat separately. Finally, the vegetation economic enhancement per hectare of the vegetation habitat was calculated by dividing the value obtained for the vegetated area by the one of the unvegetated area.

3. Results

3.1. Site fidelity

A total of 4,315 fish were tagged and released, with 4 species accounting for 95.9 % of the total tagged fish, namely *Diplodus vulgaris* (60.4 %), *Dicentrarchus labrax* (13.3 %), *Diplodus sargus* (11.8 %) and *Spondyliosoma cantharus* (10.4 %) (Appendix B). During the monthly beach seine sampling at the 41 sites, a total of 305 (7.1 %) tagged fish were recaptured (Table 1). Some of these fish were recaptured several times (some up to 5 and 6 times) (Table 1), with a total of 225 (5.2 %) different fish recaptured at least once. Although recapture percentage is relatively high, most of these fishes were recaptured during the course of

Table 1
Total numbers of tagged and recaptured fish of each species, total number of recaptures per species and the number of times individual fish were recaptured.

Species	Total tagged	Number recaptured	Total recaptures	Number of times recaptured 1	2	3	4	5	6
Diplodus vulgaris	2606	189	261	143	31	8	4	2	1
Spondyliosoma cantharus	448	17	23	13	3		1		
Diplodus sargus	511	15	17	13	2				
Dicentrarchus labrax	575	3	3	3					
Sparus aurata	11	1	1	1					
Total	4151	225	305	173	36	8	5	2	1

the fishing trials for this project, and only 6 specimens were returned by commercial and sports fishermen.

Of 225 recaptured individuals, 35.7 % were recaptured within 100 m of the tag and release location and were considered to have high site fidelity, while 54.4 % of the recaptures occurred between 100 and 500 m of the tagging location (Table 2). Only 25 individuals (8.2 %) travelled from 500 m to 2 Km, 3 individuals (1.0 %) from 2 to 5 Km and 1 individual>5 Km. In terms of time spent between capture and recapture, the majority of the fish (98.4 %) were recaptured in the first 3 months after being tagged (Table 2).

3.2. Vegetated habitat enhancement of density and biomass

A total of 155,064 fish of 96 species were caught in the monthly sampling from September 2000 to January 2002 (Appendices C and D). Seventeen (8 migratory, 9 resident) and 21 species (10 migratory, 11 resident) accounted for 95 % of the total catch in numbers and biomass respectively.

Based on an estimated total sampled area of 609,086 m^2 (vegetated: 247,567 m^2; unvegetated: 361,519 m^2) density and biomass were 0.354 fish m^{-2} and 1.792 g m^{-2} in the vegetated habitat, and 0.187 fish m^{-2} and 0.881 g m^{-2} in the unvegetated habitat. Vegetated habitat enhanced density by 89.3 % (V/UV = 1.893) and biomass by 103.7 % (V/UV = 2.037) in the Ria Formosa for all species. Of the 96 species, 67.7 % (65 species) had a higher density in vegetated habitat, while 64.6 % (62 species) had a higher biomass in vegetated habitat. The fish density and biomass enhancement in vegetated habitats was more than twice for 63 % and 60 % of the species, respectively. At the individual species level there was considerable variation, with the herbivorous *Sarpa salpa* having density and biomass 130 and 174 times greater in vegetated than in unvegetated habitats. Species' densities and biomasses were higher at unvegetated than vegetated habitats ($V/UV < 1.0$) for several of the most abundant species. The lowest V/UV values were for the anchovy (*Engraulis encrasicolus*), with density and biomass 15 and 21 times greater in unvegetated than in vegetated habitats (Supplementary materials appendices C and D). Density and biomass enhancement results for the 12 selected species are given in Table 3. Vegetated habitat enhanced density and biomass for 8 of the 12 commercial species, most notably for *S. salpa*, *S. porcus*, *P. puntazzo* and *D. bellottii*, but not for *D. labrax*, *M. surmuletus*, *S. pilchardus* and *S. aurata* (Table 3).

Table 3
Density (n m^{-2}) and biomass (g m^{-2}) for vegetated (V) and unvegetated (UV) habitats, with enhancement ratios (V/UV). Enhancement due to vegetation ($V/UV > 1$) in bold.

Species	UV (n m^{-2})	V (n m^{-2})	V / UV (n m^{-2})	UV (g m^{-2})	V (g m^{-2})	V / UV (g m^{-2})
B. boops	0.0005	0.0009	**1.7**	0.0017	0.0027	**1.6**
D. labrax	0.0155	0.0052	0.3	0.1108	0.0809	0.7
D. bellottii	0.0006	0.0048	**8.1**	0.0009	0.0079	**9.2**
D. puntazzo	0.0001	0.0018	**15.7**	0.0012	0.0064	**5.1**
D. sargus	0.0019	0.0040	**2.1**	0.0088	0.0208	**2.4**
D. vulgaris	0.0070	0.0175	**2.5**	0.0738	0.1473	**2.0**
M. surmuletus	0.0011	0.0007	0.7	0.0117	0.0102	0.9
S. pilchardus	0.0213	0.0188	0.9	0.0455	0.0332	0.7
S. salpa	0.0001	0.0069	**130.3**	0.0001	0.0242	**173.5**
S. porcus	0.0003	0.0040	**13.9**	0.0080	0.1157	**14.5**
S. aurata	0.0010	0.0005	0.5	0.0251	0.0186	0.7
S. cantharus	0.0058	0.0157	**2.7**	0.0429	0.0685	**1.6**

3.3. Vegetated habitat enhancement of growth and survival

For the study of growth, mortality and production of the cohorts of the 12 selected species, the months of January 2001 to January 2002 were used as all the selected species recruited in late winter or spring and left the lagoon by November and December. The Gompertz model could be fitted to both V and UV data for 6 of the 12 species (Table 4). Significant differences in growth parameters between V and UV habitats were found for *D. sargus*, *D. vulgaris*, *S. cantharus* and *S. porcus* (Hotelling's T^2; $P > 0.05$). For *S. salpa*, the growth model could only be fit to data for V, while for *D. bellotii*, *D. labrax* and *D. puntazzo*, the parameters could only be estimated for UV. The model could not be fitted to U and UV age-length data for B. *boops* and M. *surmuletus*. The instantaneous growth rate per month (G) was greater for V for only 4 species (*D. sargus*, *D. vulgaris*, *S. aurata* and *S. pilchardus*). However, differences in G were small, with overlapping V and UV confidence intervals for G for all species (Fig. 2).

The estimated total mortality rates for individual cohorts were estimated for 10 of the 12 species in V and for 9 species in UV (Table 5). Vegetated habitat enhanced survival for 6 out of 8 species for which it was possible to calculate mortality and survival for both V and UV habitats, especially for *D. sargus* (72 %) and *S. aurata* (43 %) (Table 5).

Table 2
Number of recaptures by interval of time and distance (m) travelled between tagging and recapture locations, for all species.

Time between tagging and recapture	Distance <100 m	100–500 m	500–2000 m	2000–5000 m	>5000 m	Total
<1 week	34	39				73
1–2 weeks	20	31		1		52
2 weeks to 1 month	26	66	6			98
1–3 months	28	30	17	2		77
3–6 months	1		1			2
>6 months			1		1	2
Total	**109**	**166**	**25**	**3**	**1**	**304**

Table 4
Gompertz model parameters parameters (*L0*, *G1* and *g2*) for vegetated (V) and unvegetated (UV) habitat, with results of the Hotelling T^2 test. *: Gompertz model parameters could not be estimated. In bold, significant differences between V and UV.

		Gompertz (V)			Gompertz (UV)			Hotelling	
Species	Code	*L0*	*G1*	*g2*	*L0*	*G1*	*g2*	T^2	P
B. boops	*Bb*	*	*	*	*	*	*		
D. bellottii	*Db*	*	*	*	0.1522	4.163	0.212		
D. labrax	*Dl*	*	*	*	0.0004	10.285	0.518		
D. puntazzo	*Dp*	*	*	*	0.9420	3.508	0.187		
D. sargus	*Ds*	0.002	8.383	0.392	0.0640	5.084	0.303	0.263	**0.850**
D. vulgaris	*Dv*	1.726	6.180	0.035	1.1920	3.321	0.106	1.359	**0.302**
M. surmuletus	*Ms*	*	*	*	*	*	*		
S. aurata	*Sa*	0.033	6.619	0.314	0.0220	6.845	0.352	8.729	0.013
S. cantharus	*Sc*	0.035	5.423	0.259	0.0073	7.161	0.407	0.071	**0.974**
S. pilchardus	*Spil*	2.034	1.249	0.351	3.3940	0.883	0.165	3.819	0.032
S. porcus	*Spor*	3.336	3.212	0.055	2.8055	2.751	0.084	1.557	**0.244**
S. salpa	*SS*	2.008	2.734	0.131	*	*	*		

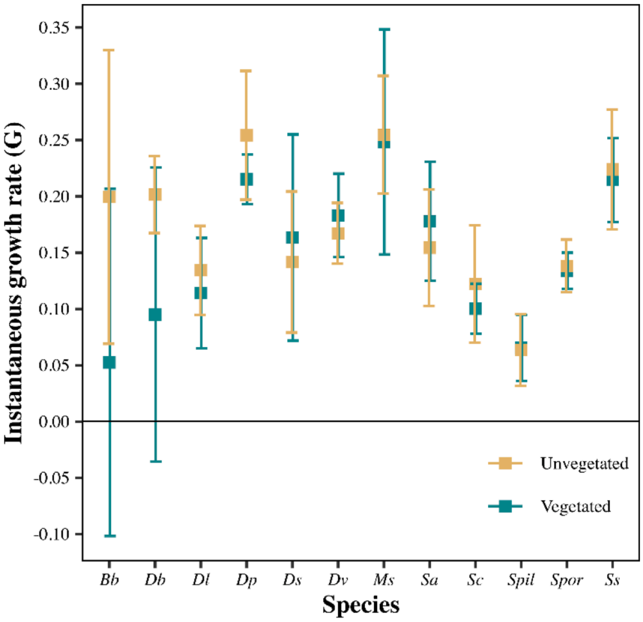

Fig. 2. Instantaneous growth rates (G) with 95% confidence intervals for vegetated and unvegetated habitats. Species codes are given in Table 4.

Table 5
Estimated total instantaneous mortality rates (Z_V, Z_{UV}), standard errors (s.e.) of Z, survival (S_V, S_{UV}) and vegetated habitat enhancement of survival (S_V/S_{UV}) with higher survival in vegetated habitat ($S_V/S_{UV} > 1$) in bold. *: Z and S could not be estimated.

Species	Z_V	s.e.	S_V	Z_{UV}	s.e.	S_{UV}	S_V/S_{UV}
B. boops	*	*	*	*	*	*	*
D. labrax	*	*	*	0.44	0.16	0.65	*
D. bellottii	1.14	0.44	0.32	*	*	*	*
D. puntazzo	0.61	0.07	0.55	*	*	*	*
D. sargus	0.50	0.08	0.60	1.05	0.20	0.35	**1.72**
D. vulgaris	0.56	0.09	0.57	0.70	0.08	0.49	**1.15**
M. surmuletus	0.34	0.04	0.71	0.38	0.05	0.69	**1.04**
S. pilchardus	0.57	0.15	0.57	0.76	0.20	0.47	**1.22**
S. salpa	0.94	0.23	0.39	0.39	0.35	0.68	0.58
S. porcus	0.06	0.04	0.94	0.08	0.09	0.93	**1.01**
S. aurata	0.37	0.15	0.69	0.73	0.04	0.48	**1.43**
S. cantharus	0.31	0.06	0.73	0.17	0.05	0.85	0.87

3.4. *Enhancement of production*

The production (g m^{-2} y^{-1}) of single cohorts in vegetated habitat was higher than for the unvegetated one for 7 out 12 species of the most important commercial species (Fig. 3). Particularly noteworthy in terms of seagrass enhancement of production is the herbivorous *S. salpa*, with vegetated habitat being 169.1 times more productive than unvegetated. Of the 8 Sparidae, only *B. boops* and *S. aurata* had lower productivity in vegetated habitat than in the unvegetetated one. The European seabass (*D. labrax*), sardine (*S. pilchardus*) and red mullet (*M. surmuletus*) were also more productive in unvegetated habitat. The vegetation enhancement ratio ($V_{production}$ / $UV_{production}$) was higher than 1 in 6 species (Fig. 4), ranging from 1.8 for the black seabream (*S. cantharus*) to 169.1 for *S. salpa* (not shown in the figure).

Total annual production estimated for the whole Ria Formosa lagoon based on total vegetated and unvegetated subtidal surface areas was 20,569.1 kg (Table 6) and ranged from 5,072 Kg for the most productive species (*D. vulgaris*) to 193 kg for *B. boops*. Overall, the seagrass habitat was almost twice as productive (1.824 g m^{-2} y^{-1}) as unvegetated habitat (0.940 g m^{-2} y^{-1}), but it only accounted for 27.1 % of the total annual production as its total area was 5-fold lower (19.2 %) than unvegetated habitat. The total annual production of the 12 cohorts of juveniles was worth 129,353 € (Table 6). This total value corresponds to 78.6 € ha^{-1} for vegetated habitat and 66.1 € ha^{-1} for unvegetated habitat.

3.5. *Cohort lifetime economic value*

The results of the economic evaluation are given in Table 7. Given the wide range of natural mortality (*M*) values obtained with the four empirical models, results are presented only for the lowest and the highest natural mortality (*M*) for each species. For low values of *M*, the total contribution of the single cohorts of the 12 species over their lifetime is almost EUR 59.2 million, with the seagrass habitat accounting for 11.4 %. For high *M*, the corresponding values are EUR 30.0 million and 10.9 %. The far greater importance of unvegetated habitats 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*) and red mullet (*M. surmuletus*) that are also not V-enhanced. Total value per hectare of V habitat ranged from EUR 10,700 (high M) to EUR 22,028 (low *M*), with corresponding values of EUR 16,751 and EUR 32,844 for UV habitat. Nine out of 12 species were V-enhanced (EUR ha^{-1}), with greatest enhancement (224.4) for the herbivorous *S. salpa*.

The importance of the strong cohort of European seabass is reflected in the Algarve official landings data (Fig. 5). Based on the length-at-age relationship and the minimum legal size of 36 cm total length, seabass

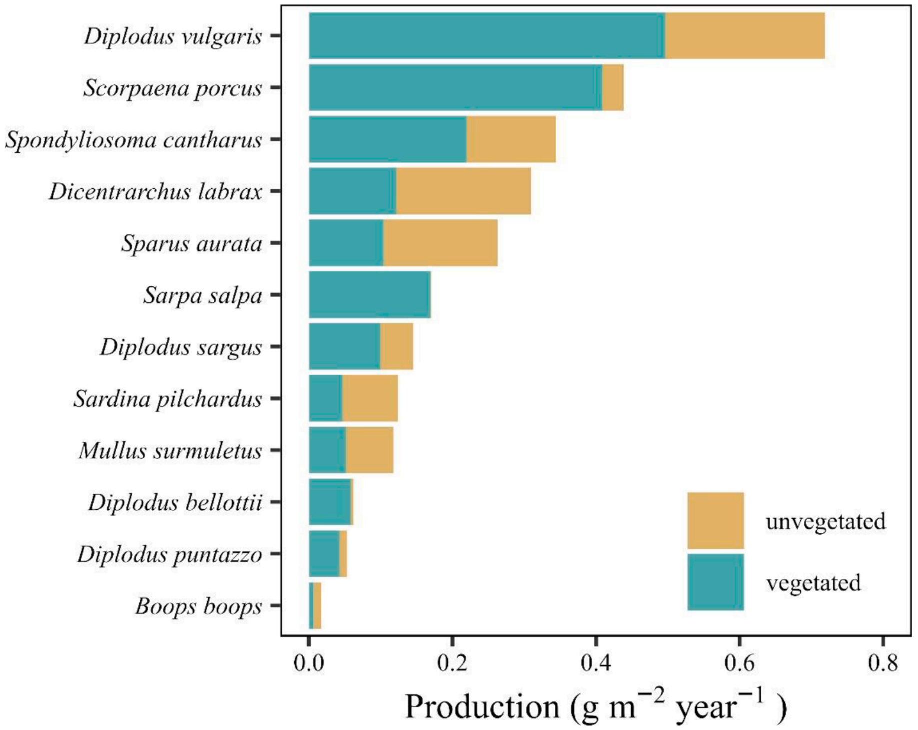

Fig. 3. Production (g m^{-2} y^{-1}) for unvegetated (brown) and unvegetated (green) habitats. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

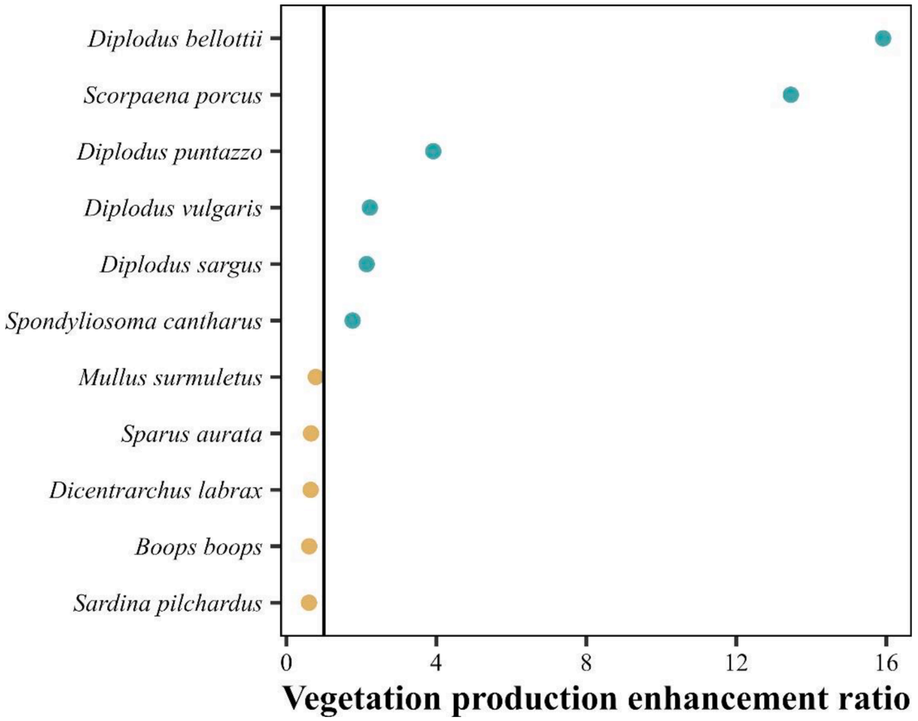

Fig. 4. Vegetation production enhancement ratios ($V_{production}/UV_{production}$). *Sarpa salpa*, with an enhancement ratio of 169.1 is not shown. The vertical line (V/UV ratio = 1) corresponds to no difference in production between V and UV habitats. Ratios > 1 mean that vegetated habitat is more productive than unvegetated habitat.

that were juveniles in 2001 would have recruited to the fishery in 2004–2005 and contributed significantly to the landings for the next 4 to 5 years, as can be seen in the increase in landings from 2004 to 2005 to 2009–2010.

4. Discussion

This study is the first to evaluate the fish provisioning services of a whole transitional landscape, the Ria Formosa lagoon, in parallel with the enhancement of growth, survival and production of single cohorts of

Table 6
Production estimates (g m^{-2} y^{-1}) and values (€) for vegetated (V), unvegetated (UV) habitats and for the whole Ria Formosa for single cohorts (age class 0) of each species.

	Vegetated habitat (V)		Unvegetated habitat (UV)							
Species	Production (g m^{-2} y^{-1})	Annual production (kg)	Production (g m^{-2} y^{-1})	Annual production (kg)	V/UV production	Total annual production (kg)	€ kg^{-1}	V (€)	UV(€)	Total value (€)
D. labrax	0.122	372.5	0.188	2994.2	0.648	3366.7	12.4	4619.0	37128.1	41747.1
S. aurata	0.104	319.0	0.159	2527.5	0.657	2846.5	10.41	3319.8	26303.2	29623.0
D. vulgaris	0.496	1518.5	0.223	3553.6	2.226	5072.0	3.8	5770.3	13503.7	19273.6
M. surmuletus	0.052	158.5	0.066	1051.8	0.785	1210.4	12.38	1962.7	13024.1	14988.0
D. sargus	0.099	303.3	0.046	738.1	2.141	1041.4	8.07	2448.8	5959.4	8408.2
S. cantharus	0.220	672.4	0.124	1983.2	1.766	2655.6	2.85	1916.3	5652.1	7568.5
S. porcus	0.408	1249.5	0.030	483.7	13.456	1733.2	2.00	2499.0	967.4	3466.4
D. puntazzo	0.042	129.7	0.011	172.4	3.917	302.1	5.8	753.6	1001.6	1755.2
S. pilchardus	0.047	142.8	0.077	1234.5	0.603	1377.3	1.01	144.9	1252.9	1397.9
B. boops	0.007	20.2	0.011	172.8	0.608	193.0	2.42	48.8	417.9	466.7
S. salpa	0.169	517.5	0.001	15.9	169.179	533.4	0.63	325.9	10.0	336.0
D. bellottii	0.058	179.0	0.004	58.6	15.917	237.5	1.36	243.2	79.6	322.7
TOTAL	**1.824**	**5582.7**	**0.940**	**14,986.4**		**20,569.1**		**24,052**	**105,300**	**129,353**

commercial fish species by vegetated and unvegetated sub-tidal habitats. The fish provisioning services of the Ria Formosa lagoon, estimated as the lifetime economic value (Dewsbury et al. 2016) of single cohorts of 12 commercial species for high and low natural mortality scenarios, ranged between 31.6 and 59.0 million EUR. The corresponding values per hectare of sub-tidal habitat were 16,615 and 31,102 EUR ha^{-1}. These findings highlight the importance of Ria Formosa as a nursery and major source of recruits to local coastal fisheries.

These estimates are similar to those of other studies that have estimated the fisheries economic value of coastal vegetated habitats such as seagrass meadows, mangrove forests and tidal marshes (Blandon and zu Ermgassen (2014a), Blandon and zu Ermgassen (2014b); Jänes et al., 2020). Jänes et al. (2020) reported that 99 % of the economic value of vegetated coastal habitats in Australia was associated with seagrass habitat, with an average value of 21,276 AUD ha^{-1} y^{-1} (approximately 13,337 EUR ha^{-1} y^{-1}). For southern Australia, the value of seagrass nurseries was estimated to be 31,650 AUD ha^{-1} y^{-1} (approximately 19,840 EUR ha^{-1} y^{-1}) by Blandon and zu Ermgassen (2014a), Blandon and zu Ermgassen (2014b).

The value of transitional landscapes in terms of fish provisioning services is supported by other studies that have provided evidence of the link between lagoon or estuarine nurseries and coastal commercial fisheries. Based on otolith microchemical analyses Tournois et al. (2017) found that >80 % of adult gilthead seabream (*S. aurata*) captured in the coastal zone in the Gulf of Lion (France) originated from 4 coastal lagoons, while Lett et al. (2019) reported that individual lagoons in the south of France contributed up to 18 % of the local coastal exploited stock of *S. aurata*. Otolith elemental fingerprinting was also used to assign nursery origin of coastal species in Portugal, including *D. labrax* and the *D. vulgaris* (Vasconcelos et al., 2008; Correia et al., 2011). However, neither study reported estuarine or lagoon origin for *D. vulgaris*, suggesting that rocky inshore areas along the coast of Portugal are also likely to be important nurseries for this species.

Even though the cohort lifetime economic value of 9 out of the 12 species studied was enhanced by seagrass meadows, the overall economic value of the unvegetated habitat was higher. This was due to the exceptionally high recruitment of the European seabass, a high value, long-lived species with higher density and biomass in unvegetated habitat, that accounted for 76 to 81 % of the total lifetime economic value per hectare. Our long-term, annual summer monitoring of juveniles (unpublished data) shows that in the year of the study, 2001, there was a very strong recruitment of this species, which is reflected in the high commercial landings from 2004 to 2010, with age classes 3 to 9 of the 2001 cohort dominating the landings.

The relatively greater economic importance of vegetated habitat is apparent when considering the cohort annual production, rather than the lifetime monetary value of the 12 species. The value of vegetated habitat production of the cohorts of those species was 78.6 € ha^{-1} y^{-1} while that of unvegetated habitat was 66.1 € ha^{-1} y^{-1}. These values are similar to those obtained by Tuya et al. (2014) for *Cymodocea nodosa* meadows off Gran Canaria Island, where the economic value of the production of juveniles of 8 commercial species was estimated to be 95.75 € ha^{-1} y^{-1}, with two species (*Sparisoma cretense* and *M. surmuletus*) accounting for 83 % of the economic value.

In this study, production of 7 of the 12 species was greater in vegetated habitats, with enhancement by an order of magnitude or more for *S. salpa*, *D. bellottii* and *S. porcus*. Greater fish production in vegetated habitat is expected due to the nursery role of structurally complex habitats such as seagrass meadows that enhance survival and growth by providing shelter from predators and rich feeding grounds (periphyton and invertebrates) for juveniles of many fish species (Gillanders, 2006; Wong and Dowd, 2016). In the case of the Ria Formosa, enhanced fish production seems to be mainly due to the higher densities, biomass and survival in vegetated habitat for most of the species, rather than to higher growth. Heck et al. (2003) reported that 3 out of 6 fish species had higher growth rates in vegetated habitat, while higher survival in vegetated or structured habitat was more common. In a more recent global meta-analysis, McDevitt-Irwin et al. (2016) found that seagrass enhancement of survival of juvenile fishes was more common than enhancement of growth.

The density and biomass of most of the commercially important fish species were higher in vegetated habitats (i.e. 8 of 12 species), though dependence on vegetated habitats varied with diet. The greatest difference was for the herbivorous *S. salpa*, which feeds on seagrasses and algae (Goldenberg and Erzini, 2014), followed by *S. porcus*. As an ambush predator feeding mainly on decapod crustacea and fish (Compaire et al. 2018), higher densities of *S. porcus* in vegetated habitat is to be expected. Juveniles of the 6 other species, all Sparidae, with higher densities and biomass in vegetated habitat, are omnivores, feeding mainly on invertebrates associated with seagrass and algae (Gonçalves and Erzini, 1998; Pita et al., 2002; Müller et al., 2020). Of the four species that had higher density and biomass in unvegetated habitat, *S. pilchardus* is a pelagic filter feeder, schooling in open water and thus not expected to have an affinity for seagrass, while *M. surmuletus* and *S. aurata* feed mainly on benthic invertebrates on unvegetated bottoms (Bentes, 1996; Mazzola et al., 1999; Pita et al., 2002). *D. labrax* density and biomass were also greater in unvegetated habitat, in contrast to what was observed in seagrass habitats of estuaries along the Portuguese coast (Vasconcelos et al., 2010) and of the Adriatic Sea (Bussotti and Guidetti, 2011). However, *D. labrax* juveniles in salt marshes of Mont Saint Michel Bay (France) did not depend exclusively on vegetated tidal flats, feeding mainly on mysids and amphipods in different habitats, including tidal creeks (Laffaille et al. 2001).

Higher densities in vegetated habitat are associated not only with

Table 7
Average first sale price at auction (EUR kg^{-1}), cohort biomass (t) for vegetated (V) and unvegetated (UV) habitat for lowest and highest M values for each species, total value of each cohort (EUR) and vegetation enhancement per hectare (EUR ha^{-1}). V (EUR ha^{-1})/UV EUR ha^{-1} ratios > 1.0 are in bold. Since official auction statistics group all the different scorpionfishes, the auction price for *S. porcus* was based on personal observation of fish market prices (average of 4 EUR kg^{-1}), with auction price assumed to be half the market price.

		Low M					High M					EUR ha^{-1}				
		Cohort biomass (t)		Value (EUR)			Cohort biomass (t)		Value (EUR)			Low M		High M		
Species	€/kg	V	UV	V	UV	U + UV	V	UV	V	UV	U + UV	V	UV	V	UV	V/UV
B. boops	2.42	9.7	8.3	23,440	20,110	43,550	3.2	2.7	7,696	6,603	14,298	77	13	25	4	**6.1**
D. labrax	12.40	427.9	3273.7	5,305,421	40,592,720	45,898,141	214.4	1,640.2	2,658,180	20,338,208	22,996,389	17,338	25,466	8,687	12,759	0.7
D. bellottii	1.36	13.2	7.1	17,967	9,698	27,666	2.3	1.2	3,102	1,674	4776	59	6	10	1	**9.7**
D. puntazzo	5.81	50.0	21.6	290,178	125,234	415,411	30.7	13.3	178,343	76,969	255,312	948	79	583	48	**12.1**
D. sargus	8.07	54.2	199.7	437,758	1,612,406	2,050,164	25.5	93.9	205,781	757,958	963,739	1,431	1,012	672	476	**1.4**
D. vulgaris	3.80	26.2	60.7	99,508	230,479	329,987	5.2	12.2	42,374	46,140	88,514	325	145	138	29	**2.2**
M. surmuletus	12.38	0.8	7.1	9.857	88,239	98,096	0.7	5.6	8,197	68,910	77,107	32	55	27	43	0.6
S. pilchardus	1.01	15.2	44.8	188,726	45,435	234,160	3.5	10.2	43,125	10,382	53,507	617	29	141	7	**21.6**
S. salpa	0.63	77.3	2.9	78,429	1,821	80,250	20.8	0.8	21,149	491	21,640	256	1	69	0.3	**224.4**
S. porcus	2.00	2.9	1.2	1,813	2,393	4,206	0.1	0.0	47	62	110	6	2	0.15	0.04	**3.9**
S. aurata	10.41	70.5	922.9	141,061	9,604,597	9,745,658	39.5	516.8	78,983	5,377,798	5,456,780	461	6,025	258	3,374	0.1
S. cantharus	2.85	14.1	29.5	146,287	83,935	230,222	2.6	5.5	27,325	15,678	43,003	478	53	89	10	**9.1**
Total		**762**	**4,580**	**6,740,444**	**52,417,068**	**59,157,512**	**348**	**2302**	**3,274,302**	**26,700,873**	**29,975,175**	**22,028**	**32,844**	**10,700**	**16,751**	

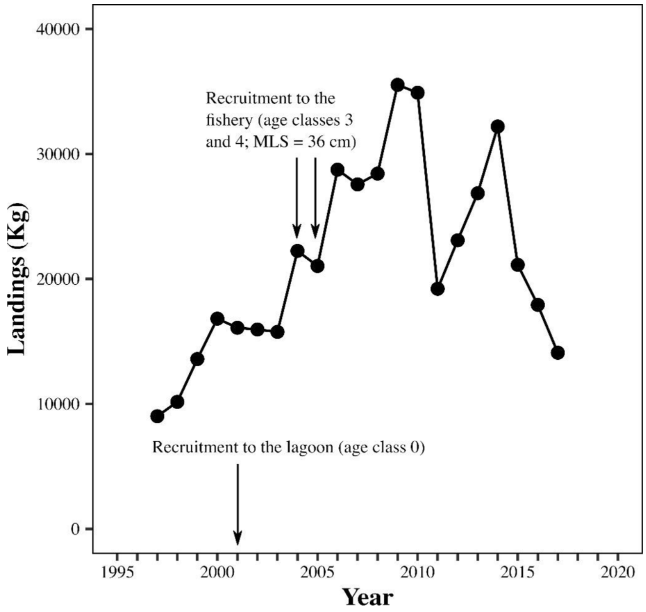

Fig. 5. Total annual landings of the European sea bass, *D. labrax* sold at auction in southern Portugal (Algarve). MLS = minimum legal landing size. Source of data: DGRM (Direção-Geral de Recursos Naturais, Segurança e Serviços Marítimos).

increased food supply but also with shelter from strong tidal currents and protection from predators, which in the Ria Formosa lagoon include cuttlefish (*Sepia officinalis*), larger sea bass (*D. labrax*) and diving birds such as the great cormorant (*Phalacrocorax carbo*). In contrast, Franco et al. (2006) reported a minor nursery role of seagrass habitat in Venice lagoon, Italy, compared to other lagoon habitats, attributing this in part to a higher abundance of predators in seagrass meadows and a juvenile preference for patches of unvegetated habitat near seagrass.

Fish survival rates were also higher in seagrass than in unvegetated habitats for 6 out of 8 species, with survival enhanced by up to 72 % in the case of *D. sargus*. These findings are in line with the meta-analysis of survivorship data of Heck et al. (2003) who reported significant differences between seagrass habitat and unstructured habitat, but not between seagrass and other structured habitat, and of Lefcheck et al. (2019) who reported that submersed aquatic vegetation (SAV) enhanced survival. Anomalously low mortality values for *S. porcus* are probably due to its cryptic, spiny and venomous characteristics, in common with other Scorpaenidae (Santhanam, 2019).

Analysis of differences in growth between habitats were inconclusive, suggesting that the species that prefer the seagrass habitat also use the unvegetated habitat but in lower numbers, despite a certain degree of site fidelity as indicated by the tagging study. High site fidelity and relatively small home ranges of juveniles within the Ria Formosa are in line with other studies such as those of Potthoff and Allen (2003) who reported strong site fidelity within salt marsh creeks of juveniles of the pinfish, *Lagodon rhomboides* (Sparidae) and of Ventura et al. (2015) for four Sparids from a rocky coastline in Italy, three of which are among the 12 of the present study (*D. puntazzo*, *D. sargus* and *D. vulgaris*). However, expansion of the home ranges of juveniles, reflected in the mark-recapture data and the acoustic telemetry studies of Abecasis and Erzini (2008), Abecasis et al. (2012), is to be expected as the fish grow (Ventura et al., 2015) and move towards the inlets and eventually out of the Ria Formosa lagoon in the autumn. The patchy distribution of vegetated habitat and information on the movement ecology of juveniles derived from tagging and acoustic telemetry studies supports the "seascape nursery" approach advocated by Nagelkerken et al. (2015), with species strongly associated with vegetated habitat, but using a mosaic of habitats (Sheaves, 2009; Whitfield, 2017) as they expand their range within the lagoon.

We showed here that seagrass meadows contribute to fish provisioning of Ria Formosa through their role as nurseries or in terms of food production as habitat for exploitable life history stages (Almeida et al., 2008; Baker et al., 2020; Dewsbury et al., 2016; Costanza et al., 2017; Nordlund et al., 2018; Unsworth et al., 2019). The Ria Formosa lagoon is by far the most extensive vegetated transitional zone and juvenile fish nursery in southern Portugal, where most of the coast consists of exposed, sandy beaches that are not a suitable habitat for young-of-the-year of most of the commercial fish species assessed in this study. The importance of the Ria Formosa lagoon and its vegetated habitat as a nursery are clear from the high site fidelity, high density and biomass, evidence for growth, low mortality, and high production. In combination, our results support classifying the vegetated subtidal habitat of the Ria Formosa lagoon as Nursery Role Habitat (NRH), Effective Juvenile Habitat (EJH) and Essential Fish Habitat (EFH) for the majority of the species, following the criteria of Beck et al. (2001), Dahlgren et al. (2006) and Litvin et al. (2018).

5. Conclusion

The landscape approach used here to assess the fish nursery ecosystem service of Ria Formosa lagoon, as advocated by Sheaves (2009), Nagelkerken et al. (2015) and Whitfield (2017), combined with the first-time evaluation of fish provisioning services based on individual cohorts revealed the highly relevant economic contribution of Ria Formosa to local coastal fisheries. As well, our study highlighted the role of subtidal seagrass meadows that enhance density, biomass, survival and production of the majority of the species, which emphasizes the importance of preserving and restoring this habitat in the Ria Formosa lagoon. In fact, seagrasses have been declining in Ria Formosa, especially in the inter-tidal zone, due to meadow destruction and fragmentation caused by the cultivation of bivalves and harvesting of invertebrates for consumption and bait (Cunha et al., 2013).

On the other hand, some important commercial species are more dependent on unvegetated habitat than vegetated habitat. A recent threat to this ecosystem service of the unvegetated sub-tidal habitat of the Ria Formosa is the aggressive takeover by the green algae *Caulerpa prolifera* which may alter the structure of native faunal communities, with likely negative implications for fisheries (Parreira et al., 2021). Given there are threats to all habitats in the Ria Formosa supports the importance of using a whole lagoon landscape approach to assess nurseries and sources of recruits to coastal fisheries.

We hope that this study will contribute to improving the conservation and management of the Ria Formosa lagoon, the largest and most important in Portugal, and to the sustainability of the small-scale coastal fisheries of southern Portugal.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2022.101490.

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