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Abundance of juveniles of commercial species in coastal habitats. The case of the Ártabro Gulf (NW Spain)

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Summary: A wide variety of species use coastal habitats at some or all stages of their life cycle. These habitats are recognized as nurseries for many species. During their early life stages, most commercially exploited species rely on shallow coastal waters, which are heavily affected by anthropogenic influences. This study focuses on characterizing the habitats of juvenile fish of the main commercial species in the Ártabro Gulf (northwest Spain), through the analysis of trawl survey data collected on soft-bottom substrates between 2017 and 2024. We used generalized additive models to quantify the influence of environmental variables (exposure, type of substrate, bottom depth, zone and season) on the abundance of five ecologically and commercially important benthic species in their juvenile stage. Our results identified the Ares-Betanzos zone as the primary nursery ground due to its sheltered conditions, which resulted in the highest juvenile densities. Exposure and depth were found to be the most important determining factors: sheltered areas had densities eight times higher than exposed sites, and maximum abundance was recorded at depths of 30–40 m. Among the species analysed, the spider crab and solenette showed a preference for shallow waters (less than 20 m deep), while the scaldfish preferred muddy sediments. These findings provide a scientific basis for establishing conservation measures, such as seasonal fishing closures or the designation of marine protected areas in shallow waters. This will ensure the sustainability of the region's fishery resources.

Keywords: nursery grounds; juveniles; commercial species; coastal habitats; Ártabro Gulf; northwest Iberian Peninsula.

Abundancia de juveniles de especies comerciales en hábitats costeros. El caso del golfo Ártabro (NO España)

Resumen: Una amplia variedad de especies utiliza los hábitats costeros en alguna o todas las etapas de su ciclo de vida. Estos hábitats se reconocen como criaderos para muchas especies. Durante las primeras etapas de vida, la mayoría de las especies explotadas comercialmente dependen de aguas costeras poco profundas, las cuales están fuertemente afectadas por influencias antropogénicas. Este estudio se centra en caracterizar los hábitats de los peces juveniles de las principales especies comerciales del golfo de Ártabro (NO España), mediante el análisis de datos de campañas de arrastre realizadas sobre sustratos blandos entre 2017 y 2024. Se emplearon modelos aditivos generalizados para cuantificar la influencia de variables ambientales (exposición, tipo de sustrato, profundidad del fondo, zona y estación) en la abundancia de cinco especies bentónicas de importancia ecológica y comercial en su etapa juvenil. Nuestros resultados identificaron la zona de Ares-Betanzos como la principal zona de cría debido a sus condiciones protegidas, lo que dio lugar a mayores densidades de juveniles. La exposición y la profundidad fueron los factores determinantes más importantes: las áreas protegidas tenían densidades ocho veces superiores a las de las zonas expuestas, y la máxima abundancia se registró a profundidades de 30-40 m. Entre las especies analizadas, el centollo y el tambor mostraron preferencia por aguas someras (menos de 20 m de profundidad), mientras que la peluda prefirió los sedimentos fangosos. Estos hallazgos proporcionan una base científica para el establecimiento de medidas de conservación, como vedas estacionales o la designación de áreas marinas protegidas en aguas poco profundas. Esto garantizará la sostenibilidad de los recursos pesqueros de la región.

Palabras clave: zonas de cría; juveniles; especies comerciales; hábitats costeros; Golfo Ártabro; noroeste Península Ibérica.

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INTRODUCTION

Coastal and estuarine areas are of significant ecological and socioeconomic importance, functioning as vital nursery habitats for numerous species of fish and crustaceans, many of which are of considerable commercial value. The high primary productivity of these areas, coupled with their critical role in supporting fisheries production (Beck et al. 2001, Seitz et al. 2014, Day et al. 2021, Nodo et al. 2023), underscores both their vulnerability and their significant ecological and economic value.

These nursery areas provide optimal conditions for the settlement, survival and growth of juvenile marine species, offering a high diversity of habitats (e.g. sandbanks and macroalgal beds), shelter from predators and high food availability (Manderson et al. 2004, Freeman et al. 2024). Many coastal marine species with complex life cycles depend on these areas to successfully complete their development (Cabral et al. 2007, Primo et al. 2013). Therefore, the availability of these nursery habitats can be a key factor in population turnover and a determinant of adult assemblage composition (Cheminee et al. 2011).

The integrity of these essential ecosystems is increasingly under threat. Over 60% of the world's population is concentrated in coastal and estuarine areas (Ray and McCormick-Ray 2009), making these ecosystems increasingly vulnerable to the impact of anthropogenic disturbances (Lindeboom 2002, Courrat et al. 2009) such as habitat destruction (Kaiser et al. 2002), chemical pollution (Islam and Tanaka 2004, Vikas and Dwarakish 2015) and overfishing (Blaber et al. 2000). Such impacts contribute to the degradation and loss of essential habitats, which can significantly affect the recruitment and stability of exploited populations (Le Pape et al. 2007, Rochette et al. 2010). Ultimately, disturbances to the dynamics of exploited stocks may threaten their viability and the livelihoods of the local communities that depend on them.

This study analyses the occurrence and abundance patterns of the juvenile stages of five ecologically and commercially important species in the Ártabro Gulf, a coastal habitat in Galicia, northwest Spain, in relation to environmental and temporal factors. The species selected were the scaldfish, *Arnoglossus laterna* (Walbaum, 1792), the solenette, *Buglossidium luteum* (Risso, 1810), the sand sole, *Pegusa lascaris* (Risso, 1810), the pouting, *Trisopterus luscus* (Linnaeus, 1758), and the spider crab *Maja brachydactyla* (Balss, 1922). The aim of this study is to evaluate the spatio-temporal distribution of juveniles of the target species to determine the role of this coastal habitat as a nursery area for commercial species. This will help to develop appropriate conservation and fisheries management strategies for these valuable ecological and economic resources.

MATERIAL AND METHODS

Study area

The study was conducted in the Ártabro Gulf, a dynamic coastal system located in northwest Galicia on the northwest Iberian Peninsula (Fig. 1). This semi-enclosed gulf covers an area of around 1500 km², forming a 46 km-long arc between the Sisargas Islands and Cape Prior (Prego and Varela 1998). It is made up of the rias of Ares-Betanzos, Ferrol and A Coruña, which form part of the so-called intermediate Galician rias (Torre Enciso 1958) and it is characterized by depths ranging from 32 to 36 m at their mouths to >100 m offshore (Prego et al. 1999).

The Ártabro Gulf is a biologically productive region influenced by seasonal upwelling, which drives high primary production (Bode and Varela 1998). The seafloor encompasses diverse habitats, including rocky, sandy and mixed substrates, which support rich decapod communities and serve as nursery and recruitment areas for commercially important species such as rays (*Raja* spp.) and spider crab (*Maja brachydactyla*) (Pallas et al. 2006, Pita 2011). Due to its ecological and socioeconomic significance, the gulf is a representative model of Galician coastal ecosystems in which multi-gear fisheries such as gillnets, pots and longlines are operative (Freire et al. 2002).

Study species

This study focuses on five species that were selected due to their ecological dependence on coastal nursery habitats, as well as their commercial importance to the artisanal fleets operating in the Ártabro Gulf (northwest Iberian Peninsula). These species exhibit different distributions according to depth and substrate preference. *A. laterna* inhabits mixed or muddy bottoms at depths of between 10 and 100 m (Muus and Nielsen 1999). *B. luteum* is commonly found from the intertidal zone to depths of 40 m (Déniel 1981). *P. lascaris* prefers habitats with a gravel, sandy or muddy bottom at depths of between 20 and 50 m (Sanches 1991). *T. luscus* inhabits rocky and sandy bottoms at depths of between 30 and 100 m (Whitehead et al. 1986) and exhibits ontogenetic habitat segregation: juveniles prefer shallow coastal and estuarine areas, while adults occupy deeper offshore habitats (Tanner et al. 2009, Felício et al. 2021). Finally, *M. brachydactyla* inhabits depths ranging from the intertidal zone to 100 m (Corgos and Freire 2006) and also exhibits ontogenetic habitat segregation: juveniles inhabit shallow (less than 20 m) rocky, sandy and mixed bottoms (Sampedro and González-Gurriarán 2004), while adults undergo seasonal migrations, remaining in shallow coastal zones with various substrates in spring and summer and moving to deeper, soft sandy bottoms (30-100 m) in autumn and winter (Corgos and Freire 2006).

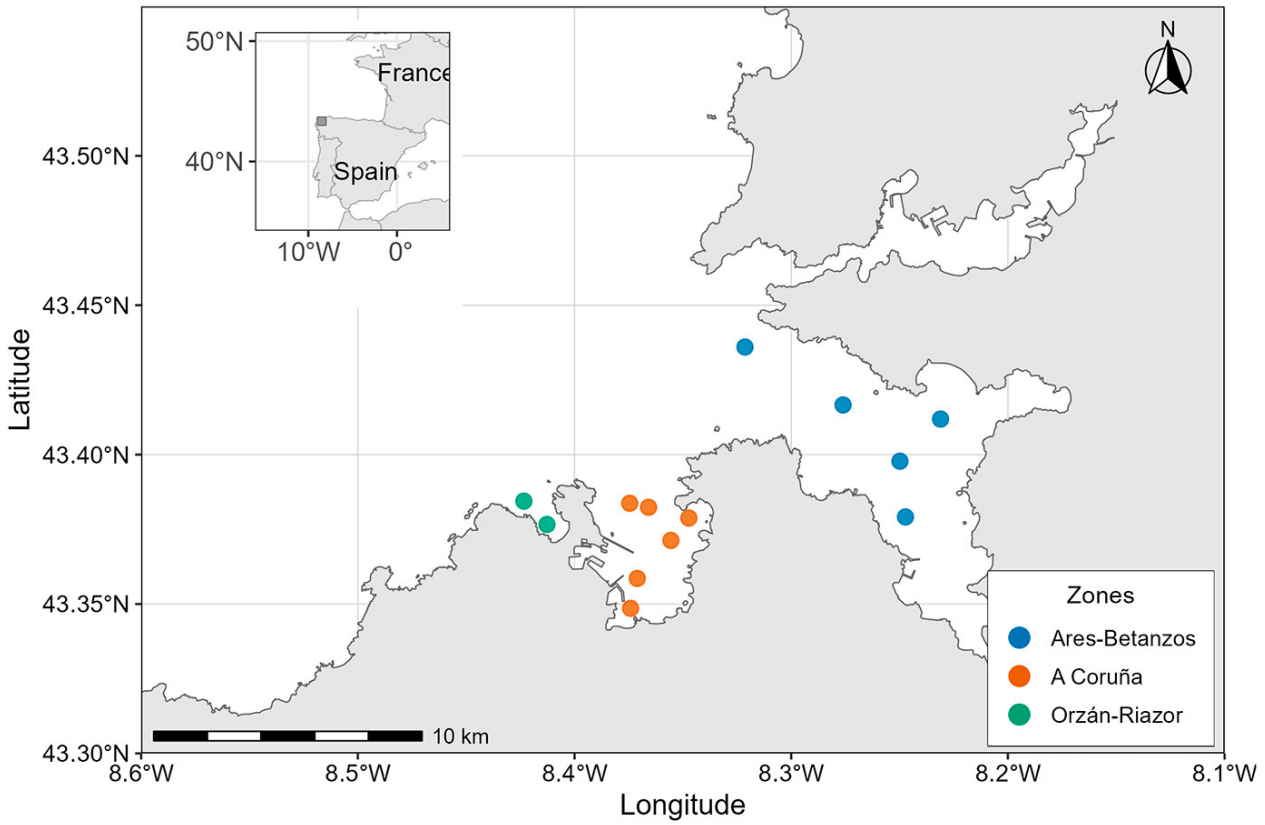

Fig 1. – Map showing the sampling sites analysed in the Ártabro Gulf (Galicia, NW Spain) divided by zones: Ares-Betanzos (blue dots), A Coruña (orange dots) and Orzán-Riazor (green dots).

Commercially, these species represent a diverse group of taxa, ranging from high-value target species such as *M. brachydactyla* and *P. lascaris* to species traditionally considered bycatch such as *A. laterna* and *B. luteum*. Although they have little commercial value, *T. luscus* are an important resource for artisanal fleets in several European countries, including France, Portugal and Spain (Alonso-Fernández et al. 2008).

Sampling

For this study, a stratified random sampling approach covered a depth range of up to 40 m. Sampling was conducted during two periods, 2017–2018 and 2022–2024, through quarterly surveys, resulting in a total of 209 bottom trawl hauls. Thirteen sampling stations were set up, stratified by depth intervals (10–20 m and 20–40 m) and geographical zones (Orzán-Riazor, an exposed coastal area; Ría de A Coruña, an inner ria environment; and Ría de Ares-Betanzos, which includes the adjacent Ferrol area (Fig. 1). All stations were located in shallow coastal waters with a soft seabed, targeting areas that are usually inaccessible to regular oceanographic surveys. Each haul consisted of a 10-min bottom trawl at a speed of approximately two knots using a beam-trawl gear. Abiotic variables (bottom depth and surface water temperature) were recorded for all hauls, alongside latitude-longitude position. All captured individuals were identified to the species level, and their total length (TL), was measured to the nearest mm. Juveniles were defined as specimens with a TL below the species-specific maturity size, as derived from the literature.

Data analysis

The response variable was the density of juveniles per haul (ind. km^{-2}), calculated from the area of seabed swept by each haul (the distance covered by the length of the beam-trawl's mouth). The substrate of the sampling sites, all of which were on soft bottoms, was classified as fine sand, coarse sand or gravel sediment (Medialdea et al. 2021). Exposure was defined as the combined physical disturbance on the bottom sediment caused by tidal and wind-induced waves and currents, and it was categorized as either 0 or 1. Sampling time was categorized into two seasons: warm (April to September) and cold (October to March).

Generalized additive models (GAMs) using the *mgcv* R package (version 1.9-1; Wood 2011) were employed to evaluate the environmental drivers influencing the abundance of juvenile fish, for both (1) all commercial species combined and (2) the five most frequent commercial species (Table 1). The models included the Ártabro Gulf zone, the season, exposure, substrate and bottom depth. For the five selected species, the response variable exhibited a significant proportion of zeros (45%–70%), indicating zero inflation, combined with positive continuous values (Table 2). Descriptive statistics revealed a positively skewed distribution with variance exceeding the mean and indicating overdispersion. These characteristics support the use of GAMs to accommodate the zero-inflated continuous density data (ind. km^{-2}) (Dunn and Smyth 2005, 2008).

The best models were selected from the following equation:

$$Ji=\beta0+\beta1\cdot Zonei+\beta2\cdot Exposurei+\beta3\cdot Substratei+\beta4\cdot Seasoni+f(Depth)i)+\epsilon i$$

where *Ji,* the juveniles' density, is the response variable (assumed to follow a Tweedie distribution with a log link function), Zone, Exposure, Substrate and Season are categorical/fixed effects (linear predictors), Depth is a smooth (non-linear) function of the bottom depth of each haul (with four knots), and ϵ is the error term. The number of knots for the smooth term was determined by evaluating different models with varying numbers of knots (ranging from two to five) and selecting the model that minimized the Akaike information criterion. This ensured the best balance between model fit and complexity. When sample sizes were inadequate to support estimation for specific variables, those terms were omitted from the model. Residual diagnostics were employed to evaluate the suitability of the fitted model and to detect any deviations from the model assumptions or patterns in the residuals. For each model, post-hoc pairwise comparisons of estimated marginal means were performed for the categorical variables using Tukey's honestly significant difference (HSD) with the *emmeans* R package (version 1.10.7). All statistical analyses were conducted with R software version 4.4.2 (R Core Team 2024), using a significance level of $p<0.05$.

Table 1. – Top 10 most frequently caught commercial species on soft bottoms of the Ártabro Gulf. Total number of individuals (n), number of hauls with presence (nHauls), relative abundance in percentage and occurrence in percentage.

	n	nHauls	Abundance (%)	Ocurrence (%)
Arnoglossus laterna	988	151	15.33	72.25
Buglossidium luteum	1742	128	27.04	61.24
Pegusa lascaris	598	120	9.28	57.42
Trisopterus luscus	1329	59	20.63	28.23
Maja brachydactyla	215	55	3.34	26.32
Chelidonichthys lucerna	85	50	1.32	23.92
Sepia officinalis	83	39	1.29	18.66
Solea solea	64	36	0.99	17.22
Raja undulata	56	36	0.87	17.22
Chelidonichthys obscurus	55	30	0.85	14.35

RESULTS

A total of 12864 individuals were sampled from the 209 hauls. Of the 103 species identified in Ártabro Gulf, 62 were commercially exploited. This group comprised 50 fish species from 22 different families, six cephalopod species from five families, and six crustacean species from six families (Table S1). The density of juveniles showed a high variability between hauls, ranging from 311 to 94605 juv. km^{-2} with a median of 3109 juv. km^{-2}.

Analysis of trawl hauls revealed that ten commercial species were the most prevalent in the soft-bottom habitats of the Ártabro Gulf in terms of occurrence (Table 1). The three most frequent species were flatfishes: scaldfish (*A. laterna*), solenette (*B. luteum*) and sand sole (*P. lascaris*) accounted for 72.25%, 61.24% and 57.42% of occurrences, respectively, exhibiting high relative abundances of 15.33%, 27.04% and 9.28%, respectively. Pouting (*T. luscus*) exhibited a lower but consistent presence, accounting for 28.23% of occurrences and 20.63% of abundance, while spider crab (*M. brachydactyla*) was caught in 26.23% of the hauls, with low abundance (3.34%).

Table 2. – Descriptive statistics for the abundance of juveniles of the five species across 182 hauls, reporting the mean, standard deviation (SD), variance, proportion of zero counts, skewness, and assessment of overdispersion (defined as variance exceeding the mean).

	N	Mean	SD	Variance	Proportion of zeros	Skewness	Overdispersion (var > mean)
Arnoglossus laterna	182	981	2066	4270391	45%	4.99	yes
Buglossidium luteum	182	716	2057	4231913	65%	5.65	yes
Pegusa lascaris	182	318	590	348390	61%	3.26	yes
Trisopterus luscus	182	2449	9568	91552835	70%	6.73	yes
Maja brachydactyla	182	316	1009	1018218	61%	5.09	yes

All species

The GAM analysis revealed significant spatial and environmental influences on juvenile abundance, explaining 17.7% of the observed variability (Fig. 2 and Table 3). Spatial analysis revealed different zone preferences, with the Ares-Betanzos zone supporting significantly higher juvenile densities than the Orzán-Riazor zone (Tukey's HSD test: $p<0.005$; Tables S2 and 5). Post-hoc Tukey HSD comparisons revealed that the mean response differed substantially between exposure categories. Sheltered areas supported densities eight times higher than those supported in exposed sites (mean ratio = 7.68, $p<0.001$; Table 5). There was a significant non-linear relationship between depth and juvenile density ($p<0.001$), with peak densities occurring at depths of 30–40 m.

Table 3. – Summary of parameter estimates and smooth term diagnostics of generalized additive model results for total juvenile density. The table includes estimates, standard errors (SE), z-values, p-values for parametric terms, as well as effective degrees of freedom (edf) and reference degrees of freedom (Ref.df) for the smooth term.

Term	Estimate	SE	z value	p-value	edf	Ref.df
Intercept	9.31	0.173	53.8	p<0.001	-	-
ZoneAres-Betanzos	0.447	0.319	1.4	p=0.164	-	-
ZoneOrzan-Riazor	–0.734	0.361	–2.03	p<0.05	-	-
Exposure 1	–2.04	0.464	–4.4	p<0.001	-	-
SubstrateFineSand	0.386	0.258	1.49	p=0.137	-	-
SubstrateGravel	0.188	0.282	0.665	p=0.507	-	-
s(Depth_mean)	-	-	6.36	p<0.001	2.85	2.98

By species

The abundance of juveniles of the five most frequent species (*A. laterna*, *B. luteum*, *P. lascaris, T. luscus* and *M. brachydactyla*) was analysed through GAMs, with exposure, type of substrate, bottom depth, zone and season acting as explanatory variables.

Scaldfish

Scaldfish was the most frequently encountered species in the study, appearing in 72% of the samples, and it acts as a representative flatfish in demersal fish assemblages, contributing to the overall diversity and biomass of these benthic ecosystems. The GAM for juvenile scaldfish explained 14.6% of the deviance. Two tested environmental descriptors were found to significantly affect the density of scaldfish (p-values of less than 5%) (Fig. 3 and Table 4). Substrate type was the most significant predictor ($p<0.001$), with an estimated mean abundance of 1291 ind. km^{-2} in fine sand habitats and 338 ind. km^{-2} in coarse sand habitats (Tukey's HSD test: $p<0.05$) (Tables S2 and 5). Depth had a significant non-linear effect ($p<0.01$), with peak abundances occurring at depths between 30 and 40 m. Exposure was not statistically significant ($p=0.055$), nor were and differences in spatial zones ($p>0.1$). Seasonal variation was negligible ($p=0.42$).

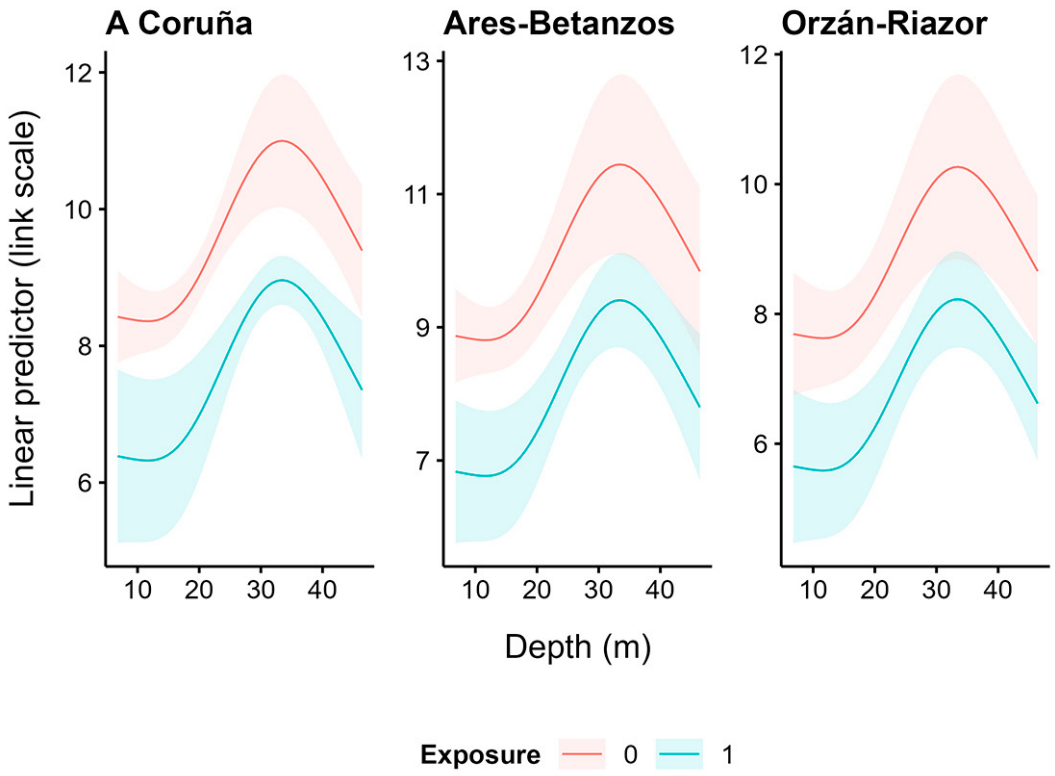

Fig 2. – Predicted total juvenile density from the generalized additive model as a function of depth in three zones (A Coruña, Ares-Betanzos, Orzán-Riazor), shown separately by exposure category (0/1). Solid lines represent the predicted smooth functions, and shaded areas indicate 95% confidence intervals.

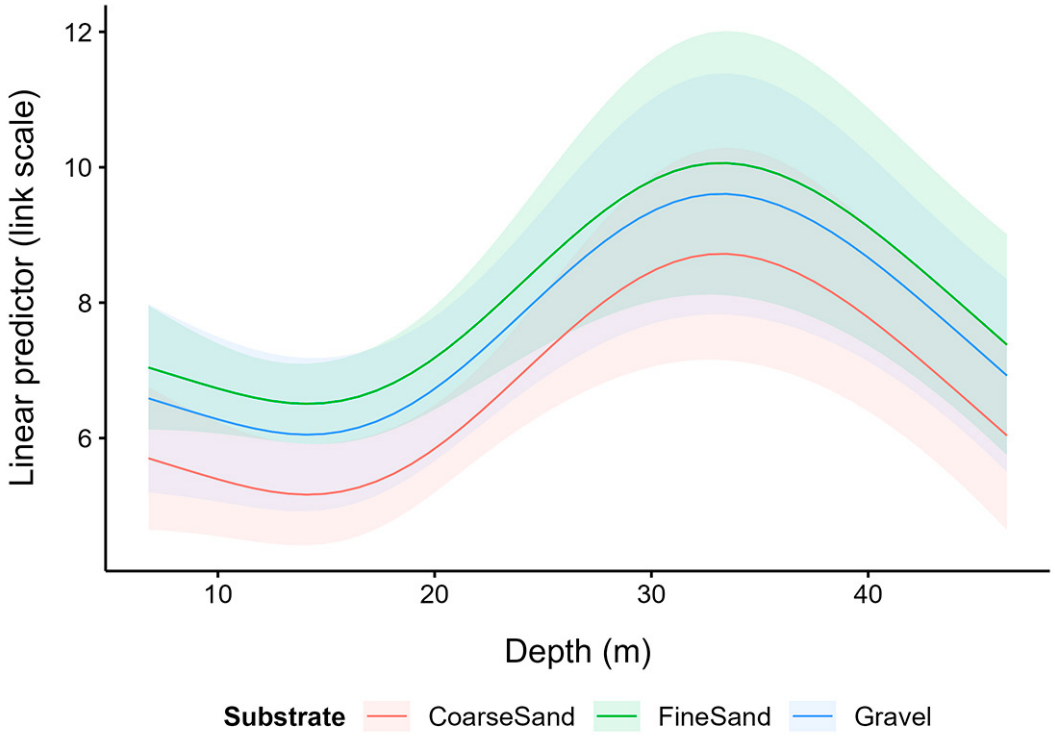

Fig 3. – Predicted density of scaldfish juveniles from the generalized additive model as a function of depth across three substrate types. Solid lines represent the predicted smooth functions, and shaded areas indicate 95% confidence intervals.

Table 4. – Summary of parameter estimates and smooth term diagnostics of generalized additive model assessing juvenile density for the five species with the highest occurrences in the Ártabro Gulf (NW Spain). The table includes estimates, standard errors (SE), z-values, p-values for parametric terms, as well as effective degrees of freedom (edf) and reference degrees of freedom (Ref.df) for the smooth term.

Arnoglossus laterna						
Term	Estimate	SE	z value	p-value	edf	Ref.df
Intercept	6.16	0.339	18.2	p<0.001	–	–
ZoneAres-Betanzos	0.884	0.527	1.68	p=0.096	–	–
ZoneOrzan-Riazor	–0.0971	0.513	–0.189	p=0.85	–	–
SeasonWarm	0.222	0.274	0.809	p=0.42	–	–
SubstrateFineSand	1.34	0.408	3.28	p<0.01	–	–
SubstrateGravel	0.885	0.454	1.95	p=0.053	–	–
Exposure1	–1.45	0.751	–1.93	p=0.055	–	–
s(Depth_mean)	–	–	4.78	p<0.01	2.86	2.98
Buglossidium luteum						
Term	Estimate	SE	z value	p-value	edf	Ref.df
Intercept	7.13	0.166	43.1	p<0.001	–	–
ZoneAres-Betanzos	0.503	0.24	2.09	p<0.05	–	–
s(Depth_mean)	–	–	12.8	p<0.001	2.34	2.69
Pegusa lascaris						
Term	Estimate	SE	z value	p-value	edf	Ref.df
Intercept	4.95	0.348	14.2	p<0.001	–	–
ZoneAres-Betanzos	1.37	0.431	3.18	p<0.01	–	–
ZoneOrzan-Riazor	0.452	0.506	0.892	p=0.374	–	–
SeasonWarm	0.79	0.32	2.47	p<0.05	–	–
SubstrateFineSand	–0.271	0.415	–0.654	p=0.514	–	–
SubstrateGravel	–1.15	0.371	–3.1	p<0.01	–	–
Exposure1	–0.194	0.589	–0.329	p=0.742	–	–
s(Depth_mean)	–	–	3.16	p=0.068	2.4	2.73
Trisopterus luscus						
Term	Estimate	SE	z value	p-value	edf	Ref.df
Intercept	8.08	0.595	13.6	p<0.001	–	–
ZoneAres-Betanzos	1.38	1.07	1.29	p=0.198	–	–
ZoneOrzan-Riazor	–1.89	1.25	–1.51	p=0.132	–	–
SeasonWarm	0.287	0.506	0.567	p=0.572	–	–
SubstrateFineSand	0.97	0.78	1.24	p=0.215	–	–
SubstrateGravel	1.2	0.913	1.31	p=0.191	–	–
Exposure1	–5.21	1.5	–3.48	p<0.001	–	–
s(Depth_mean)	–	–	6.47	p<0.001	2.73	2.94
Maja brachydactyla						
Term	Estimate	SE	z value	p-value	edf	Ref.df
Intercept	4.88	0.508	9.6	p<0.001	–	–
SeasonWarm	0.432	0.42	1.03	p=0.305	–	–
SubstrateFineSand	0.0256	0.44	0.0582	p=0.954	–	–
SubstrateGravel	–0.543	0.439	–1.24	p=0.218	–	–
Exposure1	0.325	0.756	0.43	p=0.668	–	–
s(Depth_mean)	–	–	5.23	p<0.01	1.61	1.94

Solenette

For juvenile solenette, the model explained 53% of the deviance. Abundance patterns were strongly influenced by spatial zonation ($p<0.05$) (Fig. 4 and Table 4), with the Ares-Betanzos zone supporting significantly higher densities (estimated mean: 1533 ind. km^{-2}) than the A Coruña zone (estimated mean: 927 ind. km^{-2}) (Tukey's HSD test: $p<0.05$; Tables S2 and 5). The species exhibited a pronounced non-linear relationship with depth ($p<0.001$), showing the highest abundances at shallow depths and declining abundances at greater depths. Seasonal effects were not considered, due to insufficient data in some sectors.

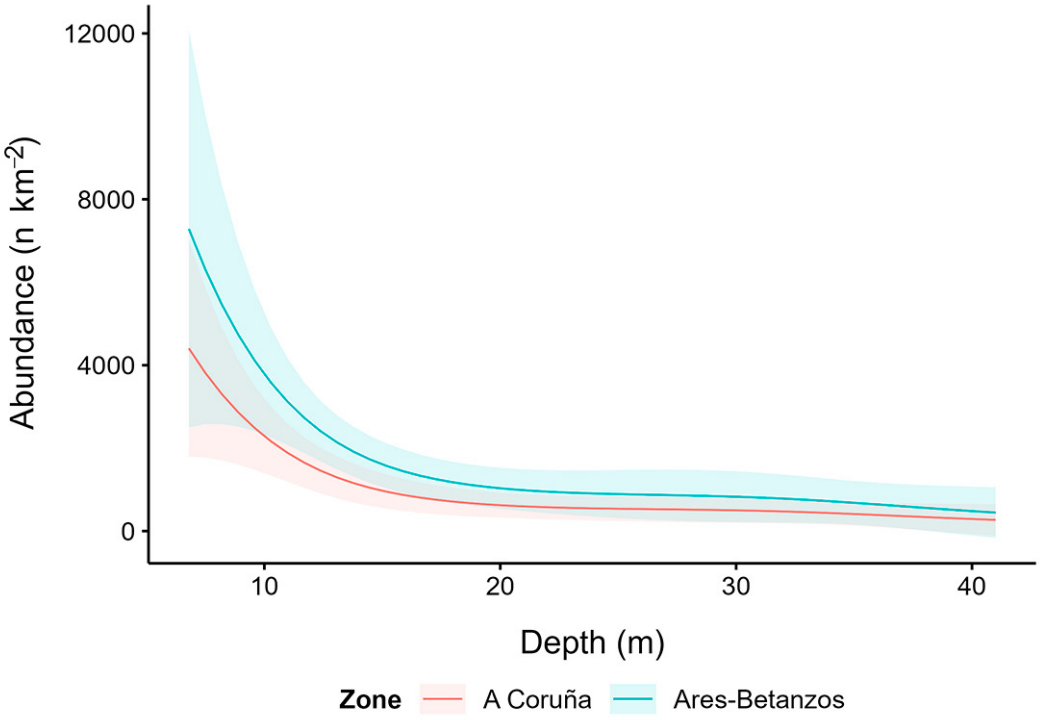

Fig 4. – Predicted density of solenette juveniles from the generalized additive model as a function of depth across two zones of the Ártabro Gulf (A Coruña and Ares-Betanzos). Solid lines represent the predicted smooth functions, and shaded areas indicate 95% confidence intervals.

Sand sole

The model for juvenile sand sole explained 15% of the total deviance (Fig. 5 and Table 4). Substrate type significantly influenced the distribution, with lower densities in gravel habitats than in coarse sand (Tukey's HSD test: $p<0.01$; Table 5). Spatial zonation was also a strong factor ($p<0.01$), with the Ares-Betanzos zone showing significantly higher abundances (estimated mean: 753 ind. km^{-2}) than the A Coruña zone (estimated mean: 191 ind. km^{-2}) (Tukey's HSD test: $p<0.01$). The Orzán-Riazor zone showed intermediate values and was not significantly different to the other sectors (Tables S2 and 5). Seasonal variation was pronounced, with higher densities observed during warm periods ($p<0.05$). The depth effect was marginal ($p=0.068$), and exposure had no impact on abundance ($p=0.74$).

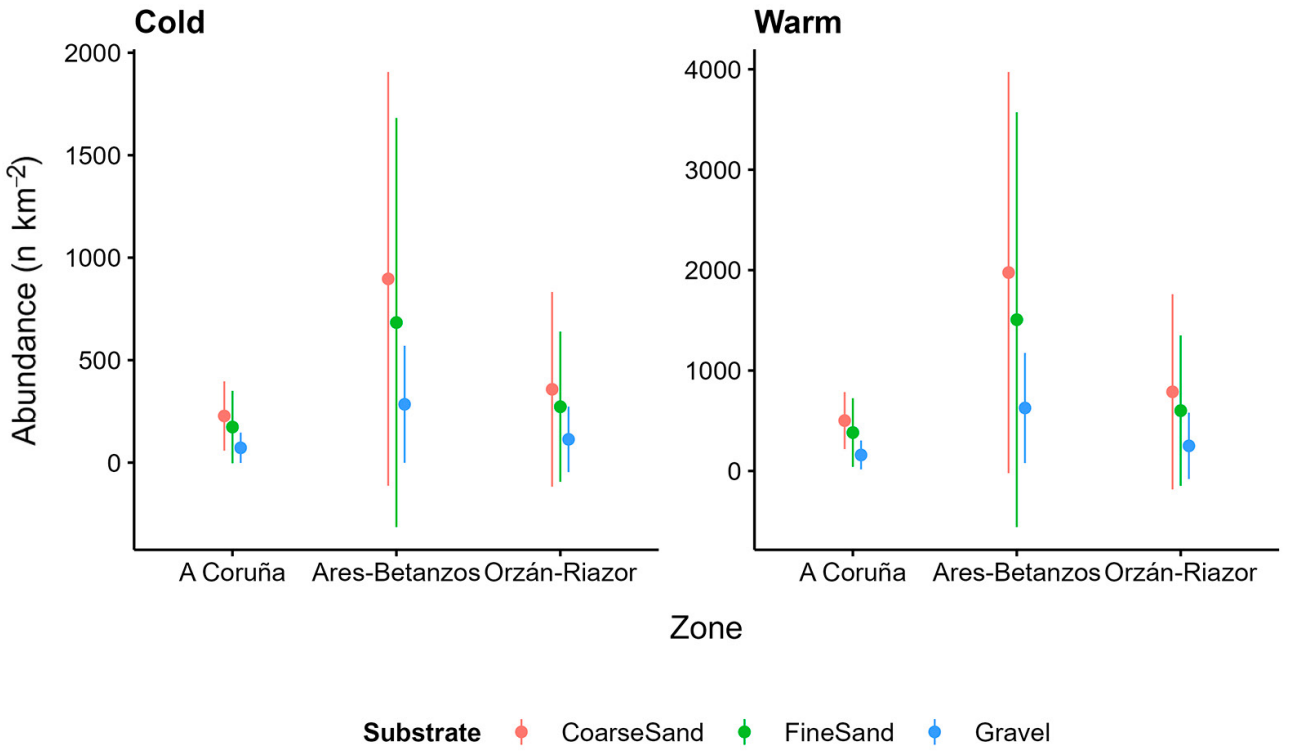

Fig 5. – Predicted density of sand sole juveniles from the generalized additive model across three zones and substrate types, shown separately by cold and warm season. Points represent model estimates, with error bars indicating 95% confidence intervals.

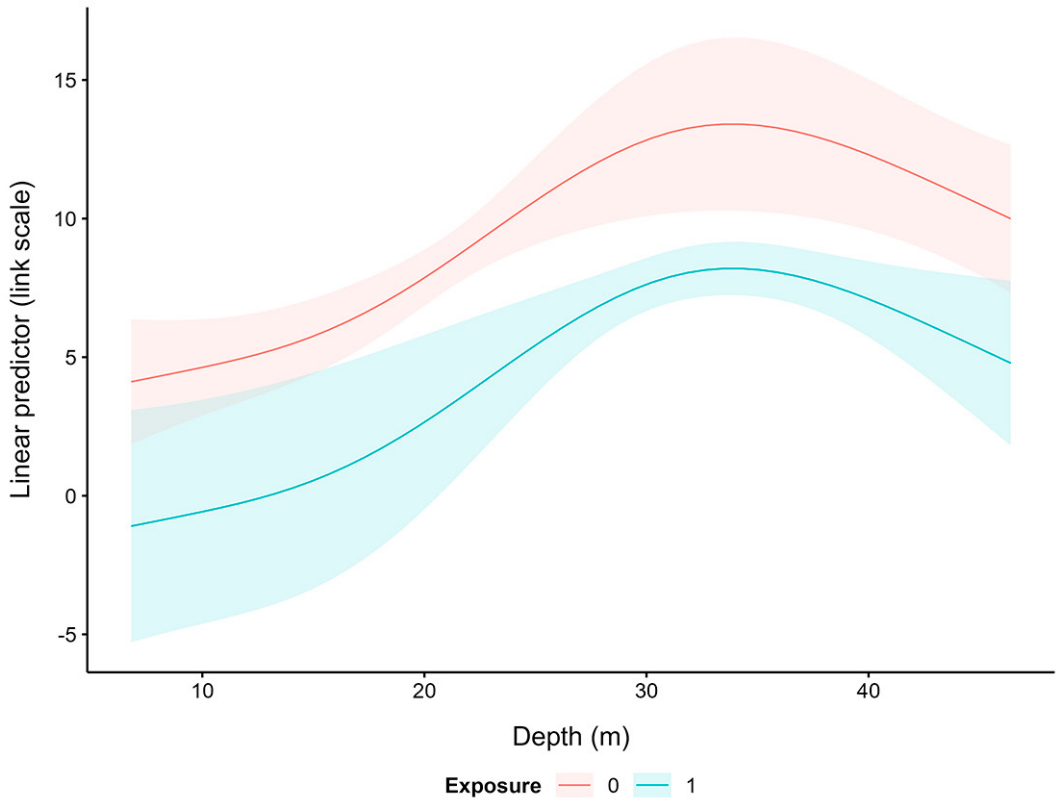

Fig 6. – Predicted density of pouting juveniles from the generalized additive model as a function of depth across exposure categories. Solid lines represent the predicted smooth functions, and shaded areas indicate 95% confidence intervals.

Pouting

The abundance of juvenile pouting could be best explained by exposure and depth, with the GAM accounting for 19% of the deviance (Fig. 6 and Table 4). Sheltered locations supported significantly higher densities (estimated mean: 12601 ind. km^{-2}) than exposed ones (estimated mean: 69 ind. km^{-2}) (Table S2). Tukey's HSD test revealed high significance for the exposure comparison ($p<0.001$) (Table 5). Depth exerted a strong non-linear influence ($p<0.001$), with maximal abundance at intermediate depths (25-35 m).

The GAM did not identify a significant effect of the type of substrate, zone or season. However, the post-hoc Tukey test identified a significant difference in predicted mean abundance between the Ares-Betanzos and Orzán-Riazor zones ($p<0.01$; Table 5).

Spider crab

The GAM explained 24.7% of the deviance for juvenile spider crab. Depth was the only significant variable ($p<0.001$), with peak densities occurring at shallow depths and decreasing with increasing depth (Fig. 7). Substrate type, exposure, and seasonal effects were non-significant ($p=0.31$), indicating relatively uniform use of available habitats across the substrate, exposure, and seasonal categories (Fig. 7 and Table 4).

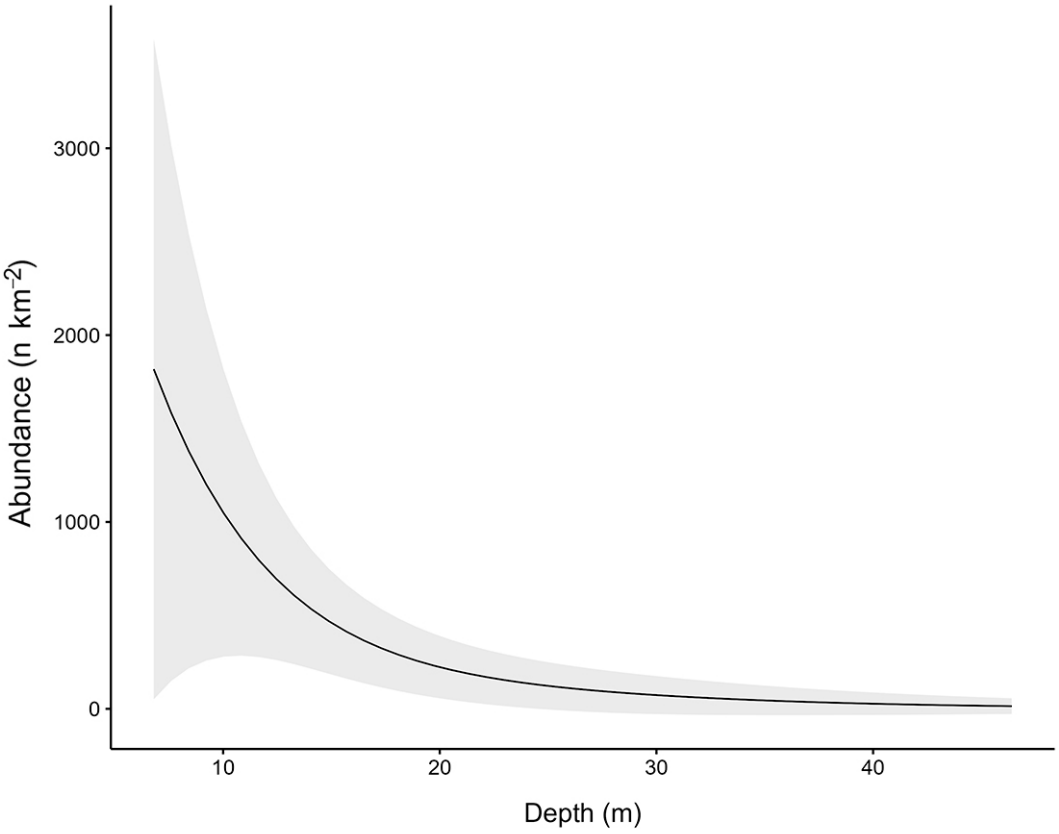

Fig 7. – Predicted density of spider crab juveniles from the generalized additive model as a function of depth. Solid lines represent the predicted smooth function, and the shaded area indicates 95% confidence intervals.

Table 5. – Pairwise comparisons from Tukey's HSD test for factor covariables in the generalized additive models across all species and the five selected species. The table shows the ratio of group means being compared (Ratio), the standard error of the ratio (SE), the test statistic value (t-value), and the significance of the difference (sig). Significant differences indicate pairs of groups with statistically distinct mean responses after adjustment for multiple comparisons.

	Comparisons	Ratio	SE	t-value	sig
All species					
Zone	A Coruna / Ares-Betanzos	0.64	0.204	–1.399	NO
	A Coruna / Orzan-Riazor	2.083	0.753	2.031	NO
	Ares-Betanzos / Orzan-Riazor	3.256	1.117	3.441	YES
Exposure	Exposure0 / Exposure1	7.681	3.562	4.396	YES
Substrate	CoarseSand / FineSand	0.68	0.176	–1.495	NO
	CoarseSand / Gravel	0.829	0.234	–0.665	NO
	FineSand / Gravel	1.22	0.446	0.543	NO
Arnoglossus laterna					
Zone	A Coruna / Ares-Betanzos	0.413	0.218	–1.676	NO
	A Coruna / Orzan-Riazor	1.102	0.566	0.189	NO
	Ares-Betanzos / Orzan-Riazor	2.668	1.311	1.997	NO
Season	Cold / Warm	0.801	0.22	–0.809	NO
Exposure	Exposure0 / Exposure1	4.27	3.21	1.93	NO
Substrate	CoarseSand / FineSand	0.262	0.107	–3.284	YES
	CoarseSand / Gravel	0.413	0.187	–1.95	NO
	FineSand / Gravel	1.577	0.882	0.815	NO
Buglossidium luteum					
	A Coruna - Ares-Betanzos	0.605	0.145	–2.09	YES
Pegusa lascaris					
Zone	A Coruna / Ares-Betanzos	0.254	0.11	–3.178	YES
	A Coruna / Orzan-Riazor	0.637	0.322	–0.892	NO
	Ares-Betanzos / Orzan-Riazor	2.507	1.298	1.776	NO
Season	Cold / Warm	0.454	0.145	–2.47	YES
Exposure	Exposure0 / Exposure1	1.21	0.715	0.329	NO
Substrate	CoarseSand / FineSand	1.31	0.544	0.654	NO
	CoarseSand / Gravel	3.15	1.168	3.096	YES
	FineSand / Gravel	2.4	1.284	1.64	NO
Trisopterus luscus					
Zone	A Coruna / Ares-Betanzos	0.252	0.269	–1.29	NO
	A Coruna / Orzan-Riazor	6.638	8.302	1.51	NO
	Ares-Betanzos / Orzan-Riazor	26.317	29.04	2.96	YES
Season	Cold / Warm	0.751	0.38	–0.567	NO
Exposure	Exposure0 / Exposure1	0.454	0.145	3.48	YES
Substrate	CoarseSand / FineSand	0.379	0.296	–1.243	NO
	CoarseSand / Gravel	0.302	0.275	–1.312	NO
	FineSand / Gravel	0.796	0.926	–0.196	NO
Maja brachydactyla					
Season	Cold / Warm	0.649	0.273	–1.03	NO
Exposure	Exposure0 / Exposure1	0.723	0.546	–0.43	NO
Substrate	CoarseSand / FineSand	0.975	0.428	–0.058	NO
	CoarseSand / Gravel	1.722	0.756	1.237	NO
	FineSand / Gravel	1.766	0.825	1.218	NO

DISCUSSION

Coastal and estuarine zones play a vital role as nursery habitats, supporting marine biodiversity and sustaining fisheries. However, their ecological function remains understudied in many regions. The different ecosystems within these zones are interconnected both hydrologically and ecologically and are of key importance in maintaining offshore populations of commercial fish and crustacean species (Beck et al. 2001, Nagelkerken 2009). Therefore, a deeper understanding of these ecosystems is crucial to ensure their long-term conservation and the sustainability of the fisheries that depend on them.

Our study shed new light on the composition, abundance and habitat preferences of juveniles of commercial species in the Ártabro Gulf, revealing the environmental and spatial drivers that influence their distribution. Sixty per cent of the species found in the habitats of the Ártabro Gulf soft bottom are exploited commercially and targeted by local artisanal fisheries (Freire and García-Allut 2000, Freire et al. 2002). Notable among these species are the pouting fish, various species of flatfish and the spider crab, which are of particular ecological and commercial importance.

Previous studies have documented the distribution and density patterns of juveniles in several Galician coastal ecosystems (Freire et al. 2002). Our findings reveal that the Ares-Betanzos zone has the highest juvenile densities and functions as the primary nursery ground in the Ártabro Gulf. This is likely due to the area's sheltered conditions, which provide optimal conditions for the survival and growth of juveniles, such as food availability and refuge from predators (Gibson 1994), combined with the prevalence of favourable coarse sand substrates. The stark difference in abundance between the sheltered Ares-Betanzos zone and the more exposed Orzán-Riazor zone strongly supports the hypothesis that the Ártabro Gulf´s sheltered regions constitute essential nursery habitats

Juveniles on soft bottoms did not exhibit a clear substrate preference, contrasting with the findings of other studies reporting differences in species and/or stage distributions between rocky and sandy substrates (Pita 2011). Juvenile density also varies with depth, with some species preferring shallower waters and others being more abundant at greater depths. For example, the pouting—one of the most abundant species in the Ártabro Gulf—shows a strong preference for depths between 30 and 40 m. This trend was consistent in the analysis of all species combined, in which depth was a significant variable with the highest juvenile densities recorded at 30–40 m.

A consistent finding across all species analysed was the dominant role of depth in shaping juvenile distribution. Flatfishes such as scaldfish and solenette, as well as the spider crab, showed marked bathymetric constraints, with juveniles concentrated at shallow or intermediate depths. Pouting displayed a similar ontogenetic habitat shift, with peak densities at intermediate depths (25–35 m), which further highlights the role of bathymetric gradients in reducing competition between life stages. In contrast, sand sole showed little response to depth, likely due to lower densities in the area; however, they shared a general preference for coastal nursery habitats. These consistent bathymetric patterns across different taxa support the idea that depth-related ontogenetic segregation is a key mechanism that structures early life stages in the Ártabro Gulf.

The characteristics of the habitats also shaped the distributions of the juveniles. Scaldfish strongly preferred fine sands, while sand soles were more associated with coarse sands and solenette with muddy sediments near river estuaries. Despite these differences, juveniles were concentrated in the Ares-Betanzos zone, where the sheltered conditions and several types of sediment could accommodate the habitat needs of multiple species. Pouting juveniles also favoured sheltered locations, indicating that protection from hydrodynamic stress and predation is a benefit common to these zones. The spider crab showed high plasticity in response to different substrate types, but remained closely tied to shallow waters, highlighting its sensitivity to coastal anthropogenic pressures. Overall, these results emphasize that the diversity of substrates within sheltered zones such as Ares-Betanzos provides suitable conditions for multiple species, supporting high juvenile densities and confirming the Ártabro Gulf's status as a nursery hotspot.

Of the flatfishes, the scaldfish had the highest occurrence, appearing in over 70% of hauls conducted in the rias of A Coruña and Ares-Betanzos. Our findings revealed a strong association between scaldfish juveniles and fine sediments, with a fourfold higher abundance observed in fine sand habitats than in coarse sand substrates. This preference likely reflects the species' reliance on unconsolidated sediments for burrowing purposes as a means of camouflage, as has been observed in another flatfish species, *Pleuronectes platessa* (Gibson and Robb 2000). In addition to substrate type, depth also played a key role in the distribution of juveniles.

Although scaldfish juveniles were found at depths as shallow as 10 m, their maximum abundance was recorded between 30 and 40 m. By contrast, the other variables, such as exposure, zone and season, had no significant impact on the abundance of scaldfish juveniles. However, previous studies in other zones reported that the main factors influencing the distribution of flatfish juveniles were not only depth and substrate type but also salinity and temperature (Amara et al. 2004), which were not included as explanatory variables in the present study.

Like the scaldfish, the solenette is a prevalent species in the coastal ecosystems of northwest Spain and is the most abundant species in our study area. Solenette juveniles accounted for almost 30% of the total abundance and were present in over 60% of hauls. They showed marked spatial segregation, with significantly higher densities in the Ares-Betanzos zone. This zonation may be related to the environmental differences in these zones, particularly the prevalence of muddy sediments and the greater influence of river inputs. Such conditions are consistent with previous findings showing that solenette juveniles are especially abundant in muddy sand bottoms near river outflows, which are also associated with lower salinity values (Amara et al. 2004). These zones are enriched with organic

matter and likely support a higher availability (Fernández-Zapico et al. 2017). The preference for these soft-bottom habitats is probably due to the advantages they offer for feeding, as the high organic content may favour the presence of diverse benthic prey, and to better camouflage against predators, as the flat morphology of their body allows them to blend in with the muddy substrate.

Additionally, solenette juveniles exhibited a distinct preference for shallow waters, likely reducing intraspecific competition with adults inhabiting deeper waters (10–100 m) (Fernández-Zapico et al. 2017). This pattern of ontogenic segregation by depth has also been observed in other areas (Sell and Kröncke 2013, Fernández-Zapico et al. 2017), confirming this feature of the species' life-history.

The sand sole was the third most frequently observed flatfish in the Ártabro Gulf, accounting for 60% of the samples. However, its abundance remained relatively low, at under 10%. The spatial distribution pattern of sand sole juveniles was similar to that of solenette juveniles, with higher densities observed in the Ares-Betanzos zone and a preference for coarse sand substrates. This is consistent with the findings of Fernández-Zapico et al. (2017), who reported the species' preference for moderately thick sands (>150 μm) and its avoidance of both very fine sediments and coarser gravel bottoms. Our results reveal higher densities of sand sole juveniles during the warm period, which is likely linked to autumn recruitment preceding this period and matching the seasonal patterns described by Quillien et al. (2018).

For *P. lascaris*, our models did not detect a significant relationship with depth or exposure in terms of density. The lack of statistical significance contrasts with the findings of other studies, which reported a clear ontogenetic migration of adults from flatfish to deeper waters (Fernández-Zapico et al. 2017), the presence of recruits in shallow areas (Quillien et al. 2018) and a preference for exposed areas, particularly high-energy surfing areas in southern Spain (Rodríguez-García et al. 2024). These results could be a consequence of the low density of juvenile sandy sole in the study area, so they should be interpreted with caution.

After solenette, the pouting was the most abundant commercial species in the Ártabro Gulf, accounting for 21% of the total abundance of commercial species. Juveniles were present in 28% of the hauls. The spatial distribution patterns of pouting juveniles observed in this study are consistent with previous literature on the species' nursery habitat preferences. The significantly higher densities in sheltered zones than in exposed zones are also consistent with the findings of Hamerlynck and Hostens (1993) and Fowler et al. (1999), who documented the active coastal migration of individuals in the 0-group to sheltered, shallow nursery areas. Such environments are likely to provide reduced hydrodynamic stress and predation risk, thereby increasing juvenile survival (França et al. 2004, Vasconcelos et al. 2008). In the Ártabro Gulf, juvenile pouting showed the highest densities at intermediate depths (25–35 m), which supports the importance of shallow coastal areas as nursery grounds for this species (Castro et al. 2013, Guerreiro et al. 2021). This depth pattern coincides with the findings of previous studies that have reported concentrations of juveniles in areas shallower than 50 m (El Omrani et al. 2021), and that adults typically occupy deeper habitats depths between 30 and 100 m (Silva et al. 2011). Such bathymetric segregation may reflect an ontogenic shift in habitat that reduces competition between life stages and ensures access to suitable food and refuge.

Differences in abundance between zones (Ares-Betanzos vs. Orzán-Riazor) may reflect interactions with different environmental variables such as substrate composition or hydrographic conditions. While the type of substrate did not significantly influence juvenile densities in our study, the trend towards higher abundances in fine sand is consistent with Ballerstedt's (2008) observations that pouting juveniles often form schools on sandy bottoms. This lack of strong substrate specificity, together with its bathymetric segregation from adults, may indicate behavioural and ecological plasticity of this species. This plasticity could explain its adaptability to a wide range of coastal habitats in sheltered areas within the Ártabro Gulf. This generalist strategy contrasts with the more specific habitat requirements of flatfish species also present in the Ártabro Gulf.

Finally, our observations indicate that juvenile pouting use these nursery areas throughout the year. This could be related to the more stable environmental conditions there and/or indicate that the species has multiple recruitment pulses per year, a hypothesis that can be confirmed in future studies with age classes. This differs from observations of other coastal species, in which temperature-driven seasonality strongly influences distribution (Power et al. 2002).

The spider crab, the species of highest commercial value in the Ártabro Gulf, showed a marked preference for shallow waters. This is in line with its life-history strategy, in which the post-settlement stages occupy nearshore areas. Post-larval stages settle on very shallow rocky substrates (at depths of around 5 m) before moving to slightly deeper (5–15 m) sandy or mixed bottoms as they grow (Freire et al. 2009). The spider crab spends two or three years in shallow areas during its juvenile stage, as has been observed in the Ría of A Coruña (Bernárdez et al. 2000, Corgos et al. 2011). This prolonged juvenile stage in shallow waters could be a good reason to establish technical management measures in the Ártabro Gulf in order to protect this critical phase of the species' life cycle and ensure suitable recruitment.

The decrease in juvenile abundance with increasing depth probably reflects individuals migrating to deeper, offshore habitats as they mature (Hines et al. 1995, González-Gurriarán et al. 2002). In fact, the absence of juveniles in the deeper Orzán-Riazor zone also supports the bathymetric limitation of this species.

Unlike flatfishes or pouting, spider crabs exhibit little discrimination in terms of substrate or exposure, suggesting an ecological plasticity that transcends depth constraints. Isotopic studies have revealed frequent movements between rocky (feeding) and sandy (refuge from predation) areas (Freire et al. 2009, Corgos et al. 2011). The habitats

of juveniles are therefore bottoms that may be soft, hard or mixed (González-Gurriarán and Freire 1994, Sampedro and González-Gurriarán 2004). In contrast, adult populations exhibit different habitat preferences such as rocky substrates in sheltered areas (e.g. Ría de Arousa; González-Gurriarán and Freire 1994) and soft bottoms in exposed areas (e.g. Ría de A Coruña and the English Channel; Meyer 1993). However, this affinity for shallow waters also makes them highly sensitive to human pressures in coastal areas, such as habitat alteration, contamination and the concentration of artisanal fishing activities.

The low deviation explained by the GAM for juvenile density in all species probably reflects the high natural variability of early life stages in coastal ecosystems, as well as the limitations of our study. To address these limitations and better understand the drivers of nursery habitat use, future studies should be included to quantify prey availability and trophic relationships in different areas of the Ártabro Gulf using stable isotopes, analyse the influence of abiotic variables such as temperature, salinity and dissolved oxygen on juvenile abundance, and increase the sampling effort in species of low occurrence and abundance.

From a management and conservation perspective, the shared reliance on shallow, sheltered coastal habitats highlights their high ecological and socioeconomic value. Conserving these nursery grounds is essential for protecting the recruitment of high-value resources such as spider crabs, pouting and flatfishes. At the same time, the observed variability in species-specific responses to substrate and depth necessitates fine-scale characterization in order to design effective, multi-species conservation strategies in the face of increasing anthropogenic pressures across the Ártabro Gulf.

SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article:

Table S1. – List of commercial species identified on soft bottoms of the Artabro Gulf.

Table S2. – Estimated means, adjusted for the levels of the model covariates ‘zone‘, ‘season’, ‘exposure’ and ‘substrate’, were obtained from generalised additive models for the ‘all species’ model and for each of the ‘five selected species’ models. Estimated marginal means, along with their standard errors (SE), degrees of freedom (df) and 95% confidence intervals (CI), are shown.

CODE AVAILABILITY

Scripts for the main analyses are published at: https://github.com/pazsamp/juvenilesArtabro

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DECLARATION OF COMPETING INTERESTS

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

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AUTHORSHIP CONTRIBUTION STATEMENT

Patricia Verísimo: Formal analysis, Investigation, Writing – original draft. **Cristina García-Fernández:** Data curation, Formal analysis, Writing – original draft. **Raúl Soria:** Data curation, Formal analysis, Writing – review & editing. **Urbano Autón:** Writing – review & editing. **Juan Fernández-Feijoo:** Writing – review & editing. **Dolores Garabana:** Writing – review & editing. **Paz Sampedro:** Conceptualization, Formal analysis, Investigation, Project administration, Writing – original draft.

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