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Population dynamics of resident fish in a coastal lagoon under eutrophication-mediated habitat changes

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Abstract

Coastal lagoons, as transitional ecosystems, are crucial for providing ecosystem services and preserving fish communities, yet they face increasing pressures from anthropogenic activities. The Mar Menor coastal lagoon in the western Mediterranean exemplifies this challenge, as it suffers from severe eutrophication driven by agricultural and urban influences. In this study, we assess changes in the population dynamics of three resident fish species (*Apricaphanius iberus*, *Pomatoschistus marmoratus*, and *Syngnathus abaster*) in the context of human-induced impacts in the Mar Menor. Using long-term monitoring data (the reference period of 2002-2004 vs. the eutrophication period of 2015-2019), we analyze temporal variations in their population dynamics and their relationships with eutrophication-mediated structural changes in shallow waters. Our results suggest that these resident species, which are closely associated with shallow areas, show population dynamics that reflect habitat alterations, underscoring their potential as indicators of eutrophication impacts. This study enhances our understanding of the dynamics within transitional ecosystems and provides a basis for integrated management strategies aimed at promoting effective fish conservation.

Keywords: anthropogenic impacts; ecological indicators; transitional waters; shallow areas; Mar Menor.

Introduction

Coastal lagoons are transitional water ecosystems that exhibit high environmental variability and often experience extreme fluctuations in physicochemical conditions (Pérez-Ruzafa *et al.*, 2020a). They play a crucial role in providing essential ecosystem services to local societies, including resource provisioning, flood control, and recreational opportunities (Franco *et al.*, 2008; Pérez-Ruzafa & Marcos, 2012). Particularly, these ecosystems are pivotal for conserving fish communities, as they act as key areas for spawning, feeding, and migration (Elliott *et al.*, 2007), thus contributing substantially to global biodiversity (Pérez-Ruzafa *et al.*, 2011). Despite their importance, transitional water ecosystems are under increasing pressure from human activities such as agricultural intensification, industrial resource extraction, and overexploitation of natural resources (El Mahrad *et al.*, 2020), which impact natural nutrient dynamics and sedimentation processes (Badosa *et al.*, 2007). At the European level, both the European Water Framework Directive and the European Marine Strategy Framework Directive con-

sider fish as an important biological component, requiring regular monitoring to assess the ecological integrity of transitional waters. Furthermore, coastal lagoons are classified as conservation-priority habitats by the Habitat Directive (Directive 92/43/ECC), thus highlighting the need for targeted surveillance programs for effective knowledge-based management. In turn, the development and application of fish-based indices in coastal lagoons is being globally scaled up (Whitfield & Elliott, 2002; Hallett *et al.*, 2019; Zamora-López *et al.*, 2023). The ability of fish to serve as monospecific indicators of ecological integrity in transitional ecosystems has been scarcely explored (Facca *et al.*, 2020; Almeida *et al.*, 2023), although it could comprise a useful tool for understanding impacts of human activities and promoting successful restoration initiatives (Souza & Vianna, 2020; Olsson *et al.*, 2023).

In recent decades, agricultural intensification and urban development around coastal lagoons have resulted in increased nutrient input to inshore waters, making these ecosystems particularly vulnerable to eutrophication processes (Viaroli *et al.*, 2015). Ultimately, these processes can trigger seagrass meadow mortalities (Hughes *et al.*,

2002) and lead to critical hypoxia episodes that promote mass fish kills (Ram *et al.*, 2014). Under eutrophic conditions in coastal lagoons, shallow waters can act as critical areas for fish assemblages by buffering impacts from hypoxia and can provide eutrophic-displaced deep-water organisms with suitable habitats (Zamora-López *et al.*, 2023), such as seagrass meadows, which are often rapidly depleted in less-oxygenated, deeper waters (Bernardeau-Esteller *et al.*, 2023). Progressive eutrophication of lagoons may strongly impact fish populations and, ultimately, lead to community-level effects such as trophic cascades (Sayer *et al.*, 2016). Nevertheless, fish response to eutrophic conditions is species-specific and relies upon hypoxia tolerance, habitat preferences, and dispersal ability (Jacobson *et al.*, 2017), among other traits. Fish species may largely differ in their life-spans and generation times and may show contrasting habitat preferences, leading them to respond dissimilarly to eutrophic episodes. However, the potential of indicator fish species to track eutrophication-mediated changes in habitat structure has not been explored.

The Mar Menor (western Mediterranean Sea) is a paradigmatic case of a coastal lagoon highly disturbed by eutrophication resulting from intensive agricultural practices and excessive urban development in its adjacent basin (Álvarez-Rogel *et al.*, 2020). From 2015 onwards, these activities led to extensive lagoon habitat degradation and triggered a critical situation of seagrass meadow mortalities and fish kills (Ruiz-Fernández *et al.*, 2019). Despite these disturbances, shallow littoral areas of the Mar Menor coastal lagoon have retained patches of vegetated bottoms (i.e., seagrass meadows) due to continuous sunlight exposure (Pérez-Ruzafa *et al.*, 2018), which points to the high resilience of these areas to eutrophication-mediated processes. In fact, shallow littoral areas have played a pivotal role in the recovery process of the seagrass meadow within the lagoon (Bernardeau-Esteller *et al.*, 2023) and continue to serve as crucial recruitment areas for fish (Guerrero-Gómez *et al.*, 2022). Additionally, they act as key refuge habitats for fish assemblages and other aquatic taxa, mitigating euxinic conditions during eutrophic episodes (Zamora-López *et al.*, 2023). Nevertheless, the impact of these episodes on estuarine fish assemblages, including potential alterations in their structure, composition, and population dynamics, remains poorly understood and warrants further investigation.

The fish fauna of Mar Menor exhibits a rich diversity, comprising a total of 43 species from 19 families, including resident, marine migrant, marine straggler, and diadromous species (Guerrero-Gómez *et al.*, 2022). Among the species that complete their entire life cycle within the lagoon environment (i.e., resident species), we targeted three representative taxa: the marbled goby *Pomatoschistus marmoratus* (Risso 1810), the black-striped pipefish *Syngnathus abaster* Risso 1820, and the Spanish toothcarp *Apricaphanius iberus* (Valenciennes, 1846). All three species are small and short-lived benthic fish with different habitat preferences related to their reproductive and feeding strategies (Oliva-Paterna *et al.*, 2006; Verdiell-Cubedo *et al.*, 2007; Castro-Fernández *et al.*, 2020).

Despite these ecological differences, all three species exhibit a strong affinity for shallow areas along their entire life cycles.

In this study, we used long-term monitoring data collected during a reference period (2002-2004) and a period characterized by critical eutrophication events (2015-2019) to investigate the population dynamics (i.e., occurrence, abundance and population structure) of three representative resident fish species and to determine their relationships to the bottom habitat structure. Additionally, we evaluated the potential of these fish as indicators of eutrophication-mediated changes in shallow water habitats. Based on the assumption that the shallow littoral areas of coastal lagoons are critical habitats for aquatic biota (Zamora-López *et al.*, 2023), we hypothesize that these habitats undergo structural changes (e.g., changes in substrate and vegetation parameters) mediated by the eutrophication process, primarily associated with (1) the accumulation of fine particles (e.g., silt and mud) due to the continuous input of organic matter (Pérez-Ruzafa *et al.*, 2019) and (2) the expansion of macrophyte meadows, especially *C. prolifera*, probably mediated by the increased nutrient availability in shallow areas where sunlight is also not limited by reduced water transparency (Bernardeau-Esteller *et al.*, 2023). In addition, a slight reduction in shallow water transparency could also promote the spread of this alga as its photoinhibition would be limited (García-Sánchez *et al.*, 2012, Pérez-Ruzafa *et al.*, 2012). In this context, the three resident species exhibit alterations in their population dynamics that are consistent with their habitat preferences.

Material and Methods

Study area

The Mar Menor is an originally hypersaline and oligotrophic coastal lagoon located in the southeast of the Iberian Peninsula. This coastal lagoon covers an area of 136.5 km² and has an average depth of 3.6 m. It is separated from the Mediterranean Sea by a 21 km long sand bar named La Manga, although three inlets or connecting channels allow water to be exchanged between the lagoon and the Mediterranean Sea (Pérez-Ruzafa *et al.*, 2005). Salinity and temperature currently range from 39 to 51 psu and from 11 to 30 °C, respectively (Pérez-Ruzafa *et al.*, 2019). Its shallow areas (< 2 m in depth) are characterized mostly by three habitat types: vegetated bottoms dominated by seagrass meadows composed of *Cymodocea nodosa* and/or *Caulerpa prolifera*, unvegetated sandy bottoms, and unvegetated muddy bottoms. These shallow littoral areas play a key role for both commercial fishes and those that are species of conservation concern (Verdiell-Cubedo *et al.*, 2013). The Mar Menor is legally protected under several international, national, and regional designations, including Site of Community Importance and Special Protected Area for Birds (Natura 2000 network), Ramsar wetland (Ramsar Convention), Specially Protected Area of Mediterranean Importance (Barcelona

Convention), and natural protected area (regional network). Moreover, this coastal lagoon has recently become the first European ecosystem to be recognized as a legal entity with explicit rights (Jones, 2022). However, these conservation strategies have failed to mitigate anthropogenic impacts on the lagoon (Pérez-Ruzafa *et al.*, 2020a), which has experienced its most evident ecological consequences in recent years.

The increase in nutrient loads has transitioned the coastal lagoon from its originally oligotrophic condition to a eutrophic state (Pérez-Ruzafa *et al.*, 2019). The impact of increased nutrient load on coastal waters was initially buffered by self-regulatory mechanisms. However, this buffering capacity was exceeded between summer 2015 and spring 2016, when chlorophyll *a* levels increased from around 2 µg/L in the reference period (2002-2004) to peaks of 17 µg/L (Pérez-Ruzafa *et al.*, 2019). The algae blooms triggered a drastically reduced water transparency level during a 9-month period, thus preventing sunlight from reaching the bottom and causing a massive macrophyte mortality in water of 2 m and deeper (i.e., more the 80 % of the lagoon's vegetated surface) (Álvarez-Rogel *et al.*, 2020). After this first eutrophic episode, seagrass meadows were constrained in deep waters and remained almost exclusively associated with shallow waters. In autumn 2019, an intense rainfall event led to the discharge of about 70 hm³ of freshwater (which comprised about 10% of the lagoon water volume) containing a large amount of nutrients and sediments. A few days later, prevailing calm atmospheric conditions (i.e., windless days) prevented brackish surface waters and deep saline waters from mixing, promoting water column stratification and causing oxygen depletion in deeper waters, which ultimately led to hypoxia and subsequent marine fauna kills (Álvarez-Rogel *et al.*, 2020). According to the information recorded in Ruiz-Fernández *et al.* (2020), the fish and invertebrate fauna mortality event was massive at depths of more than 3 m and affected more than 70% of

the lagoon's surface area. In the perimeter areas, we were able to detect, through visual assessments, 3000 dead fish per 100 m² during a 48 h period in approximately 10 km of the north shoreline (unpublished data). At least 18 different fish taxa were identified, with a predominance of gobies. Several of these taxa were not abundant species in the shallow perimeter zones, according to our surveys.

Fish surveys

The perimeter of the Mar Menor coastal lagoon was sectorized into 18 sampling sites (Fig. 1) which were sampled in each season (winter, spring, summer and autumn) during most of the 7-year study period. We conducted fish surveys during two consecutive annual cycles (years 2002-2004) as part of a reference period (before widespread eutrophication episodes), and we repeated those surveys for five complete annual cycles (years 2015-2019) during a critical eutrophic period (Appendix – Table A1).

The fish surveys consisted of hauling a 10 m long beach seine net (8 m of effective catching width; 1.5 m height; 0.5 mm mesh size) along a 20 m section of shoreline (160 m² effective surface covered by each haul). This sampling technique has been reported as a very effective method targeting small-sized fish species in shallow waters of a coastal lagoon (Franco *et al.*, 2012). For a better habitat representativeness, three sampling replicates (i.e., 3 × 160 m², total hauled area = 480 m² per sampling site) were used at each sampling site. All captured fish were provisionally deposited into plastic containers, and abundance data of the target fish were recorded. In addition, during the years 2018-2019, all captured fish belonging to the target species were photographed on a millimeter-scaled plastic tray, allowing for the measurement of total body length (hereafter, TL) by using the ImageJ software (Schneider *et al.*, 2012). This measurement pro-

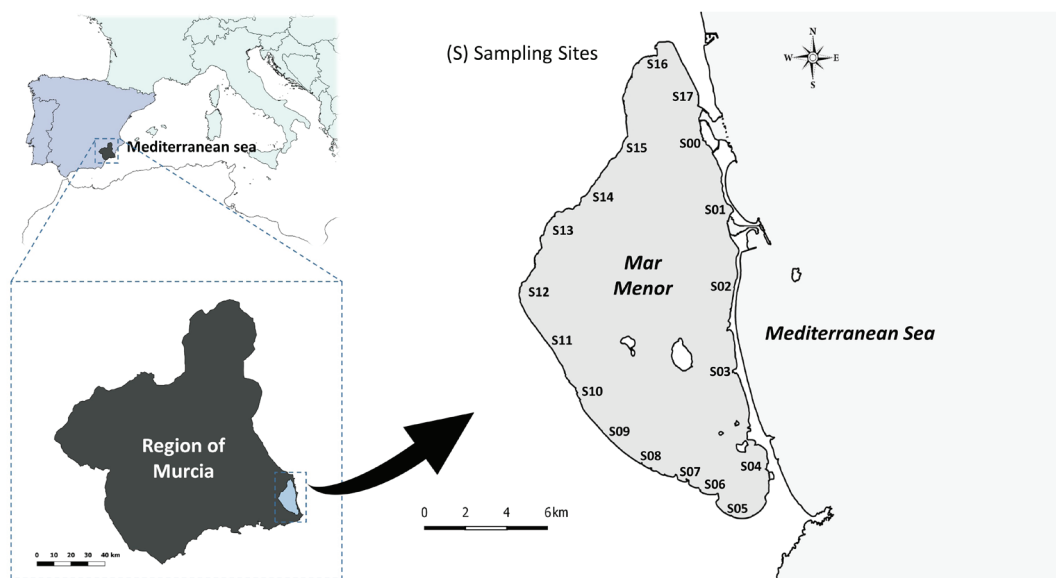


Fig. 1: Map of the study area showing the geographic location for the Mar Menor coastal lagoon (southeastern Spain, region of Murcia). Location of sampling sites is depicted with alphanumeric codes (S00-S17).

cedure allowed us to reduce handling time; thus, specimens were quickly released back into the surveyed habitat. Abundance data were computed by catches per unit effort (CPUE; catches per 160 m²) and, together with the frequency of occurrence (FO), were analyzed to assess population dynamics.

Following the same procedure as Verdiell-Cubedo *et al.* (2008) and Zamora-López *et al.* (2023), habitat structure was characterized in each spatial replicate of each sampling site according to the following variables: percentage of submerged vegetation cover (hereafter, SVC), average water depth (WD), substrate particle size (SPS), and substrate particle heterogeneity (SPH). SVC was visually assessed and computed as the percentage covered by submerged vegetation at the hauled bottom surface (i.e., sampling replicate). The particles of substrate were classified according to the qualitative scale provided by Bain (1999): mud (1), sand (2), gravel (3), pebble (4), and boulder (5). In addition, they were assessed through visual estimation at 10 survey squares (4 m² for square) randomly distributed to cover the hauled bottom surface. SPS was calculated as the mean value pondered with the assigned qualitative scores, whereas SPH was computed as the standard deviation of these mean values.

All habitats were surveyed equally to ensure representative and reliable data on abundance and population structure at a given sampling site. Sampling sites were mainly represented by shallow habitats (40 cm of average water depth) and mostly by sandy and muddy bottoms (e.g., fine substrate accounted for more than 80% of the sampled bottoms). Sampling sites showed a marked variation between bare bottoms and vegetated bottoms covered mostly by monospecific *C. nodosa* meadows and mixed *C. nodosa* and *C. prolifera* meadows.

Statistical analysis

To explore temporal variation in population metrics of the target species, we used generalized linear mixed models (GLMMs) with FO and CPUE values, including *Cycle* and *Season* as fixed factors and *Sampling site* as a random factor. This approach permitted the control of the spatiotemporal structure of the data despite the non-balanced number of replicates between the two periods. The CPUE values were categorized into ordinal abundance classes (Appendix – Table A2). Size-frequency distributions of TL were analyzed based on mean size, diversity, and evenness metrics, calculated on a seasonal basis for each species during cycles 2018 and 2019 and considering as juveniles the individuals with TL < 20 mm for *A. iberus* (Oliva-Paterna *et al.*, 2009), TL < 24 mm for *P. marmoratus* (Verdiell-Cubedo *et al.*, 2008) and TL < 60 mm for *S. abaster* (Tomasini *et al.*, 1991).

In order to explore the temporal variation of habitat structure, we also used GLMMs with *Cycle* and *Season* as fixed factors and *Sampling site* as a random factor. We used the data of Cycles 2002, 2003, 2018, and 2019, as these were the only cycles for which habitat data were available. Finally, the relationship between habitat struc-

ture and population parameters (FO and CPUE) was also tested with GLMMs, including the four environmental variables (SVC, WD, SPS, SPH). In this case, the levels of *Cycle* were grouped in two *Periods* (the cycles of 2002-2004 vs. the cycles of 2018-2019). Moreover, environmental variables were previously scaled to understand the effect of each one with its standardized model coefficient. Once the model was developed with all the variables, an automatic model selection procedure was performed to choose the best habitat relationship model for each population metric. Model ranking and selection were based on the estimate of the Akaike information criterion (AIC) (Burnham & Anderson, 2002). When model comparisons yielded an inadequate support for the identification of the best model (AIC difference lower than 2), then the most parsimonious formulation (i.e., the model retaining less predictors) was selected. Due to the fact that the number of sampling replicates was higher than 40, corrections for small sample size (AICc) were not necessary.

GLMMs were performed with the *lme4* package (Bates *et al.*, 2015), their analysis of deviance was conducted with the *Car* package (Fox & Weisberg, 2011), and post-hoc tests were conducted with the *lsmeans* function implemented into the *emmeans* package, with a Bonferroni adjustment (Lenth, 2020). The binomial error family was used for FO models, the negative binomial error family was used for CPUEs, SVC, and WD, and the Gaussian error family was used for SPS and SPH. Model ranking and selection were performed with the *dredge* function of the *MuMIn* package (Barton, 2015). All analyses were conducted in R software (Version 3.6.3) (R Core Team, 2020).

Ethical statement

All field procedures complied with the animal use and care regulations of Europe and Spain. Specific licenses were granted for scientific field research in Murcia (Spain). Fish were collected by trained researchers; therefore, no adverse effects were caused to the target wildlife and environment. Virtually all specimens recovered fully from the handling procedure and were released back after recovery at the same collection sites: the mortality rate was less than 1% for the three species.

Results

Temporal variation in population dynamics

FO values were moderately high for *S. abaster* (range of 0.36-1.00; mean of 0.72) and *P. marmoratus* (range of 0.19-0.97; mean of 0.67) throughout the entire study period (Fig. 2; Appendix – Table A3). Comparatively, *A. iberus* showed a much lower FO, with maximum values below 0.40 (mean 0.2) and more stable seasonal and interannual variation. Significant seasonal variations were observed in the FO for the three target fish, with *A. iberus*

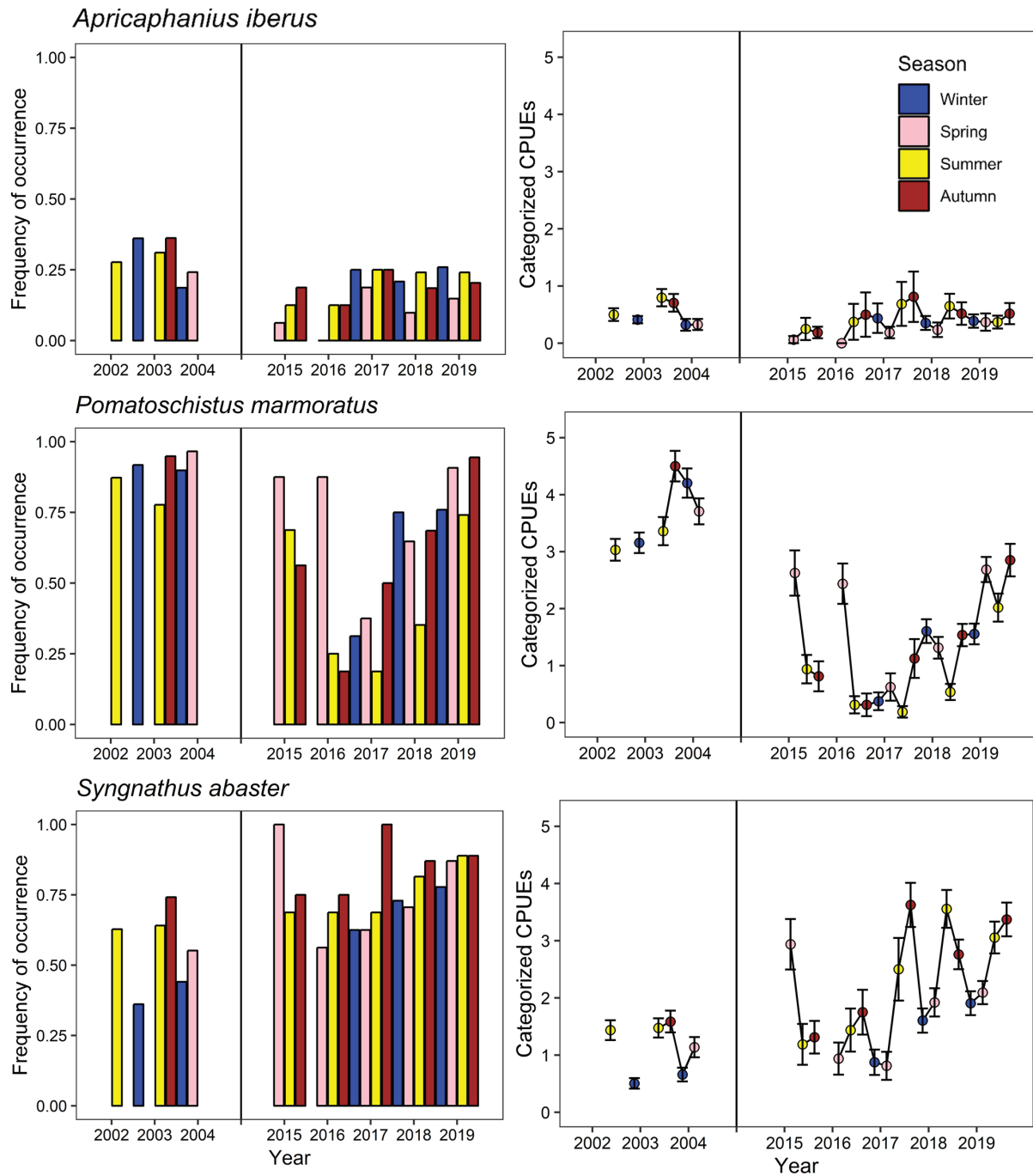


Fig. 2: Temporal variation of frequency of occurrence and abundance values (categorized catches per unit effort, CPUEs showing standard error; see Table A2) of the three target species (*Apricaphanius iberus*, *Pomatoschistus marmoratus*, and *Syngnathus abaster*) in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea). Data are divided according to two different periods: reference period (2002-2004) and critical eutrophic period (2015-2019).

showing less marked changes (Table 1). In terms of interannual variation, the FO of *P. marmoratus* dropped to minimum values in the 2016 and 2017 cycles. Nevertheless, the FO values exhibited a progressive increase thereafter, with levels during the last year (2019) resembling those observed during the reference period (2002-2004). By contrast, *A. iberus* and *S. abaster* remained relatively stable across the study periods, though *S. abaster* showed significantly higher FO values in the last cycles (2018-

2019) (Table 1).

Abundance in categorized CPUEs also showed significant seasonal and interannual differences for the three target species (Fig. 2; Appendix – Table A3). *A. iberus* was the species with the lowest CPUE values (range of 0-0.81; mean of 0.42) over the study period and showed lower variation in abundance between seasons and/or years. *P. marmoratus* and *S. abaster* presented comparatively higher CPUE values (range of 0.19-4.2; mean of

Table 1. Analysis of deviance of General Linear Mixed Models (GLMMs) performed with frequency of occurrence (FO) and abundance (categorized CPUEs) for the target species in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea). *Sampling site* was considered as random factor. *(P<0.05); **(P<0.001); DF (degree of freedom); Sum (summer), Aut (autumn), Win (winter) and Spr (spring).

Predicted variable	Fitted effect	Analysis of deviance (x ²)	DF	Pairwise
<i>Apricaphanius iberus</i>				
FO	Season	8.105*	3	-
	Cycle	20.381*	6	2002 > 2016
Abundance	Season	17.385*	3	(Sum = Aut) > Spr
	Cycle	23.775**	6	2003 > (2018 = 2019)
<i>Pomatoschistus marmoratus</i>				
FO	Season	45.438**	3	(Win = Spr = Aut) > Sum (2002= 2003= 2019) > 2018 > 2017;
	Cycle	146.269**	6	(2002= 2003= 2019) > 2016; (2002= 2003) > 2015 > 2017
Abundance	Season	38.319**	3	(Spr = Aut) > (Sum = Win)
	Cycle	401.688**	6	(2002= 2003) > 2019 > (2018 = 2015) > 2017; (2002= 2003) > 2019 > (2018 = 2016)
<i>Syngnathus abaster</i>				
FO	Season	35.503**	3	(Sum = Aut) > Win; Aut > Spr
	Cycle	68.058**	6	(2018 = 2019) > (2002= 2003); 2019 > 2016
Abundance	Season	102.18**	3	(Sum = Aut) > Spr > Win
	Cycle	165.52**	6	(2018 = 2019) > (2002= 2003= 2015 = 2016); 2017 > (2002= 2003)

1.91 and 0.51-3.56; mean of 1.85 respectively), as well as much more marked seasonal and interannual fluctuations (Fig. 2; Appendix – Table A3). Overall, *P. marmoratus* was less abundant in summer and autumn seasons, though this pattern was not congruent across all years, whereas *S. abaster* was most abundant during both warm seasons (summer and autumn). A steep decrease in *P. marmoratus* abundance was recorded between the pre-eutrophic period (2002-2004) and the eutrophic period (2015-2019). Despite CPUE values exhibiting a progressive increase since 2017, the average abundance showed a notable decrease of 73% between pre-eutrophic annual cycles and the eutrophic 2018-2019 annual cycles (Appendix – Table A4), with this declining trend particularly pronounced during summer and autumn seasons. Conversely, the average abundance of *S. abaster* experienced a substantial increase (838%) between the pre-eutrophic period and the eutrophic 2018-2019 annual cycles. Additionally, a distinct abundance peak was observed in spring 2015 before the progressive increase detected from 2017 onwards, mirroring the pattern observed for *P. marmoratus*.

Population size structure and recruitment

Size-frequency data indicated the presence of juve-

niles and breeding adult cohorts for the three target species in shallow waters across the study seasons (Fig. 3). For *A. iberus*, recruitment (i.e., incorporation of individuals in the mature population) was detected throughout the year, but the settlement of immature individuals showed some seasonal and interannual variation, with the detection of a distinct cohort in summer 2018 that is not as apparent in the 2019 cycle (Fig. 3). In the case of *P. marmoratus*, evident differences in size-frequency data were observed between the two assessed annual cycles (Fig. 3). Reproductive peaks were not evident during 2018, with immature gobies found across all seasons and smallest sizes (16 mm) detected exclusively in winter. However, a significant number of these immature gobies were detected during three seasons of the 2019 cycle (Fig. 3), which could indicate a significantly longer recruitment period for this last cycle. In addition, a significant increase in mature individuals was observed in autumn 2019, as well as a reduction of size diversity compared to the previous season. The proportion of mature gobies in the population remained remarkably stable throughout the annual cycle (Fig. 3). Finally, *S. abaster* population structure remained quite invariable between the two assessed annual cycles, and juvenile settlement was mostly observed in spring and summer seasons (Fig. 3). The recruitment of new adult pipefishes took place across the entire annual

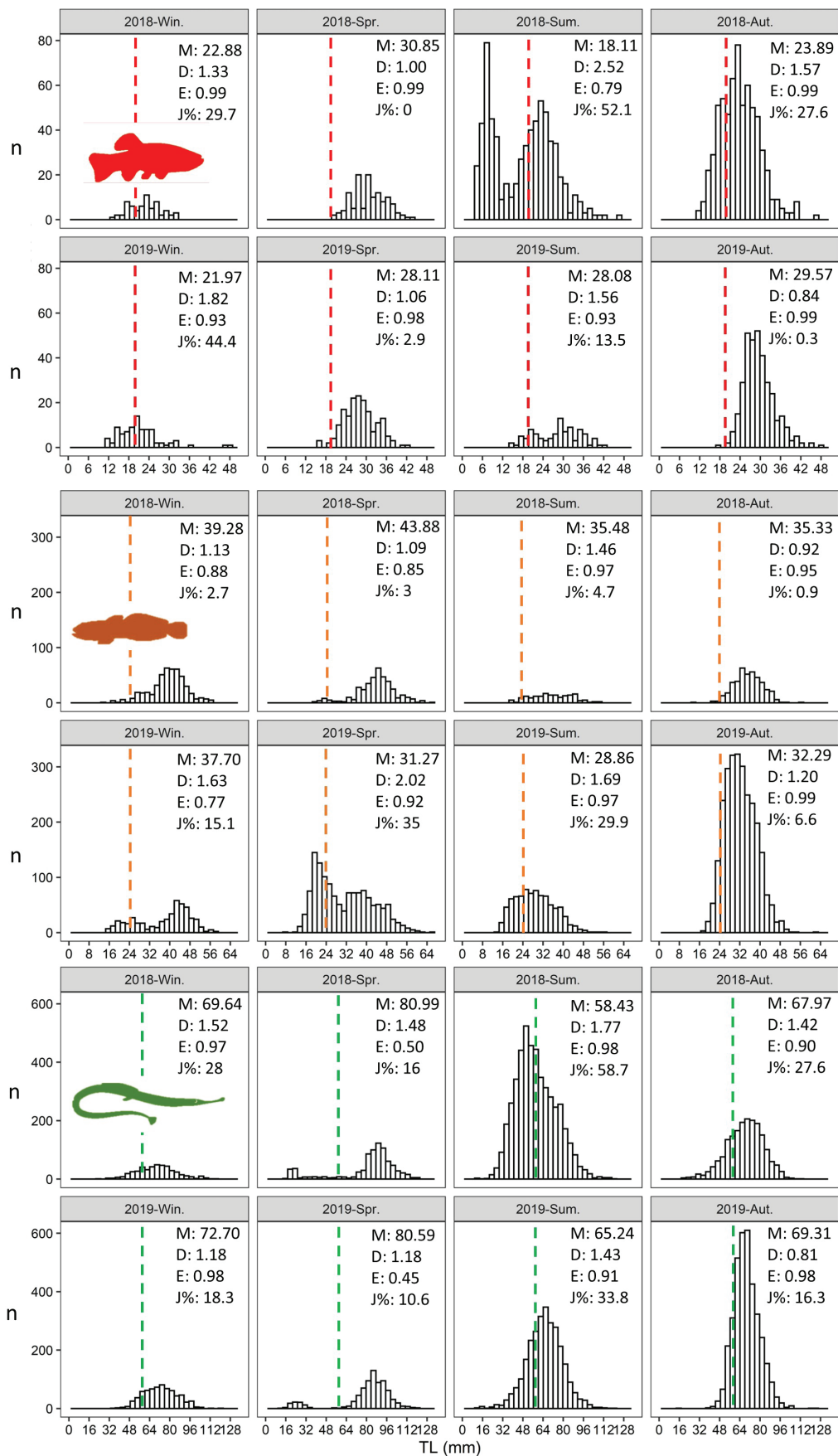


Fig. 3: Size frequency distribution of the three target species (*Apricaphanius iberus*, *Syngnathus abaster*, and *Pomatoschistus marmoratus*) in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea). Seasonal approach of the cycles 2018 and 2019 are presented: Sum (summer), Aut (autumn), Win (winter) and Spr (spring). Total captures per season (n) are indicated in the horizontal axis, whereas the following parameters are provided within graphs: M (mean size), D (size diversity), E (size evenness) and J% (percentage of juveniles). Dashed vertical lines represent the size at first maturity of the target species: 20 mm for *A. iberus*; 24 mm for *P. marmoratus*; and 60 mm for *S. abaster*.

cycle but mostly during warm seasons (summer and autumn). The observed pattern of *S. abaster* in autumn 2019 mirrored that of *P. marmoratus*, with a decrease in size diversity and an increase in mature individuals compared to the previous season (Fig. 3).

Temporal changes in habitat structure

The four selected habitat variables showed significant temporal variations (Fig. 4; Table 2; Appendix – Table A5). SPS and SPH did not undergo substantial changes on a seasonal basis, while SVC was generally higher in summer, and WD was generally lower in cold seasons (winter and spring). However, a significant change in habitat structure was observed between the reference period and the eutrophic period (2002-2004 vs. 2018-2019). In 2018-2019, SPS showed more uniform and significantly lower values compared to 2002-2004. Conversely, SPH and SVC showed an opposite trend, with higher values for the latter in the eutrophic period, which was consistent across all seasons. Additionally, WD had the lowest variation among the habitat variables. Therefore, this temporal variation in the assessed habitat variables supports a eutrophication-mediated change in the habitat structure of the shallow areas of the Mar Menor, which have become more vegetated and muddier in recent years compared to the reference period.

Habitat preferences by target species

The GLMM highlighted that both the FO and abundance of *A. iberus* were negatively associated with SPS and WD but positively associated with SVC and SPH (Table 3), which supports the conclusion that this species prefers habitats with shallow, muddy, and vegetated bottoms. In contrast, the models for *P. marmoratus* showed a positive relationship between FO and abundance with SPS but a negative relationship with SPH, SVC, and WD (Table 3). As sand comprises the vast majority of substrate particles, the results highlight that *P. marmoratus* selects habitats with shallow, unvegetated bottoms and sandy substrate. The models for *S. abaster* showed a positive relationship between FO and abundance with SVC and negative relationships with SPS and WD in some cases (Table 3). Therefore, *S. abaster* shows clear habitat preferences for shallow areas dominated by vegetated bottoms. Most models included both *Season* and *Cycle* as relevant predictors of species presence and abundance, indicating the importance of temporal factors.

Discussion

Long-term population dynamics

Our results indicate that shallow littoral areas are criti-

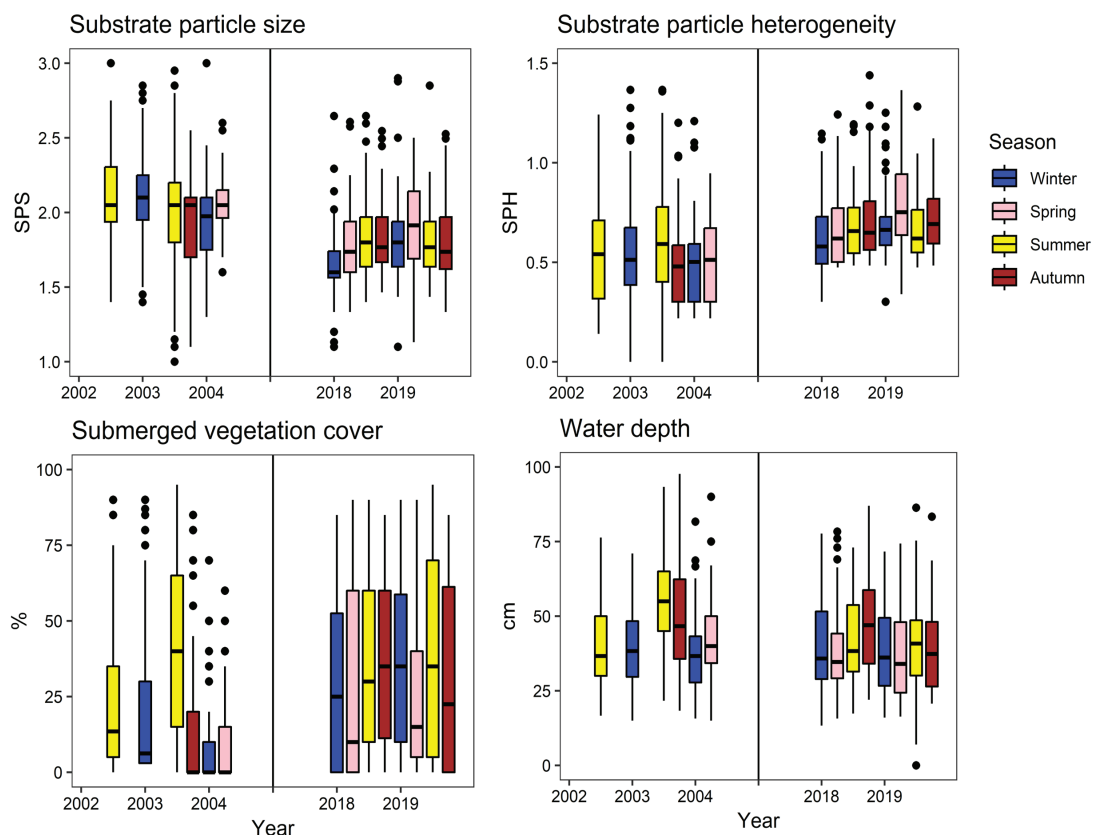


Fig. 4: Boxplot of temporal variation of habitat structure variables recorded in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea) between a pre-eutrophic reference period (2002-2004) and a critical eutrophic period (2018-2019). Average value of the assigned substrate particle size (1 mud; 2 sand; 3 gravel; 4 pebble; 5 boulder); average standard deviations of the substrate particle sizes; average of submerged vegetation cover (%); average of water depth (cm).

Table 2. Analysis of deviance of General Linear Mixed Models (GLMMs) performed with habitat variables in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea). *Sampling site* was considered as random factor. *(P<0.05); ***(P<0.001); DF (degree of freedom); Sum (summer), Aut (autumn), Win (winter) and Spr (spring).

Fitted effect	Analysis of deviance (x ²)	DF	Pairwise
Substrate particle size (SPS)			
Season	9.744*	3	Spr > Win
Cycle	143.28**	3	2002 > 2003 > (2018 = 2019)
Substrate particle heterogeneity (SPH)			
Season	5.917	3	-
Cycle	79.79**	3	(2018 = 2019) > (2002= 2003)
Submerged vegetation cover (SVC)			
Season	38.940**	3	Sum > (Win = Spr = Aut)
Cycle	26.368**	3	(2018 = 2019) > (2002= 2003)
Water depth (WD)			
Season	34.974**	3	(Sum = Aut) > (Win = Spr)
Cycle	43.265**	3	2003 > (2002 = 2018 = 2019)

Table 3. Generalized linear mixed models (GLMMs) of the target species frequency of occurrence (FO) and abundance in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea). Coefficients of the environmental variables are standardized. *Sampling site* was considered as random effect. The models with lowest AIC (within two units of ΔAIC) and the null model are presented (column “Model”). (SPS) substrate particle size; (SPH) substrate particle heterogeneity; (SVC) submerged vegetation cover; (WD) water depth; (P) period; (S) season; (+) factor considered in the model.

Model	(Int)	SPS	SPH	SVC	WD	P	S	R ² (adj.)	AIC	ΔAIC
<i>Apricaphanius iberus</i>										
FO										
1	-0.74	-0.97	0.37	0.63	-0.37	+		0.30	784.60	0
Null	-1.33							0.08	925.38	140.78
Abundance										
1	-0.07	-1.37	0.42	0.47	-0.56	+	+	0.42	2124.56	0
Null	0.23							0.26	2402.91	184.28
<i>Pomatoschistus marmoratus</i>										
FO										
1	2.4	0.45	-0.51	-0.26	-0.31	+	+	0.21	747.03	0
Null	1.50							0.03	838.2	91.21
Abundance										
1	3.53		-0.26	-0.38	-0.17	+	+	0.31	7285.41	0
Null	3.53							0.05	7548.85	263.43
<i>Syngnathus abaster</i>										
FO										
1	0.04	-0.22		0.95		+	+	0.30	885.42	0
2	-0.06			0.95	-0.21	+	+	0.30	885.80	0.38
Null	0.87							0.03	1067.63	183.50
Abundance										
1	0.87			0.88		+	+	0.50	5605.15	0
Null	2.93							0.09	6107.59	502.44

cal habitats for resident fish species, as evidenced by their frequency of occurrence, abundance, and size-frequency distribution. These species continue to complete their life cycles in these shallow littoral areas, even during the last eutrophic periods experienced by the Mar Menor lagoon. This is consistent with previous research in other Mediterranean and Atlantic estuaries (Franco *et al.*, 2006, 2008; Branco *et al.*, 2008) and in the studied coastal lagoon (Zamora-López *et al.*, 2023). However, the frequency of occurrence and abundance of the target species in the Mar Menor's shallow areas varied over the study period, indicating a stable population for *A. iberus*, a decreasing population for *P. marmoratus*, and an increasing population for *S. abaster*, all of them linked to changes in the habitat structure of these littoral zones.

Our analysis of the habitat species relationship revealed different responses to changes in habitat structure caused by eutrophication. *A. iberus* was found to be associated with shallow, muddy and vegetated bottoms, as previously noted by other authors in small saline wetlands (Alcaraz *et al.*, 2008; Oliva-Paterna *et al.*, 2009; Verdiell-Cubedo *et al.*, 2014), which comprise the most commonly inhabited environment across its current distribution range. Along the shallow littoral areas of the Mar Menor lagoon, vegetated environments are commonly

found in stagnant waters near port facilities and natural salt marshes where slow water flows allow for sediment accumulation and submerged vegetation development. At a lagoon scale, our results show an interannual stability in FO values and abundance of *A. iberus*. However, it is important to note that this lagoon-scale approach reflects the current scenario resulting from isolated populations with relatively low densities (Gonzalez *et al.*, 2018), which may mitigate the high variability typically exhibited by this species in confined environments (Oliva-Paterna *et al.*, 2009; Verdiell-Cubedo *et al.*, 2014). The study reveals that *A. iberus* experienced a narrower spatial distribution but higher occurrence frequency and abundance along the lagoon perimeter during the eutrophic period compared to the reference period (Fig. 5). This suggests a reduction in the lagoon's occupancy area but an increase in population stability in sites with available optimal habitats. As reported by García-Oliva *et al.* (2018), recent changes in the dynamics of shallow areas in the Mar Menor likely increased the surface area of stagnant waters, particularly in the southern basin, thereby enhancing habitat suitability for *A. iberus*. *P. marmoratus* exhibited evident seasonal and interannual changes in its occurrence, abundance, and even in its size-frequency distribution. Juvenile settlement was detected in all study seasons, although with

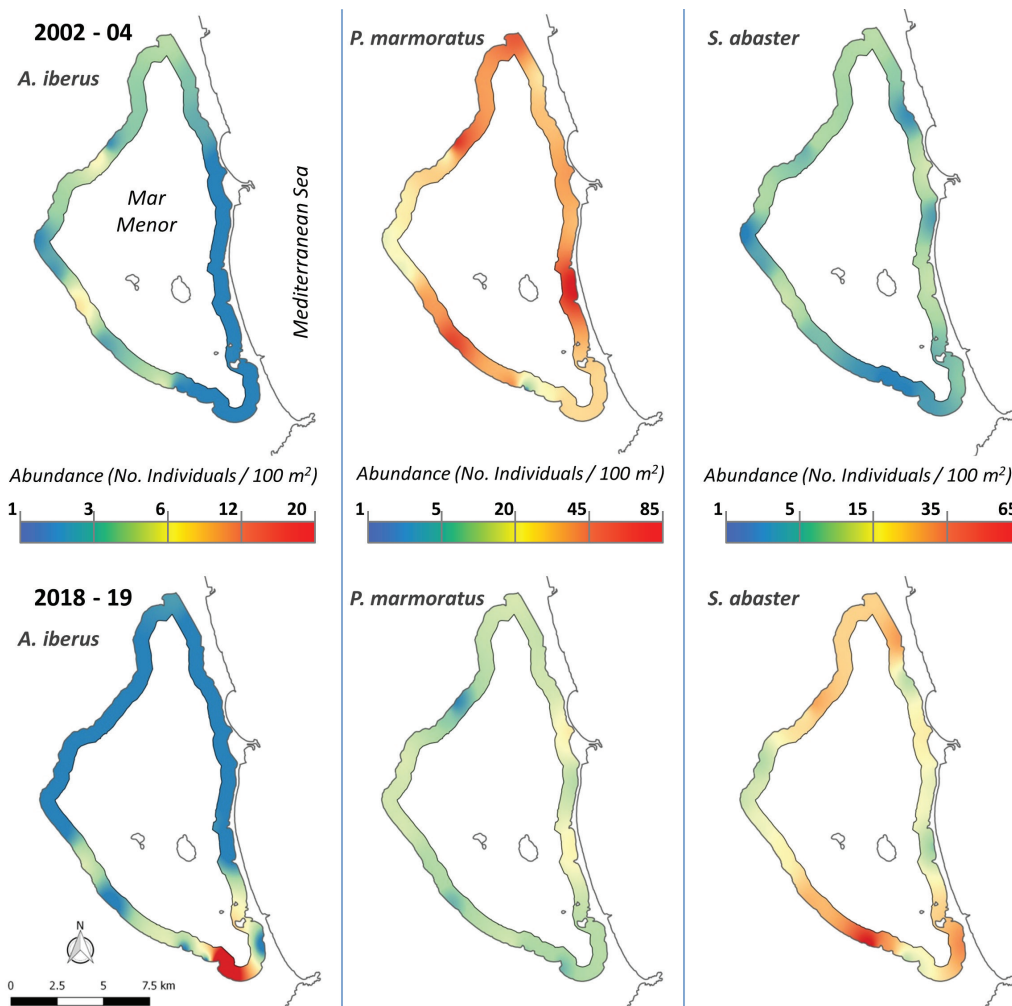


Fig. 5: Averaged abundance (no. of individuals/ 100m²) of the target species in the reference period (2002-2004 cycles) and the eutrophication period (2018-2019 cycles) in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea).

substantial changes in representativeness of size classes between the studied cycles. The temporal patterns of juvenile recruitment reported here differ from those found in 2003 (Verdiell-Cubedo *et al.*, 2008), where juvenile settlement was observed only in summer. The observed interannual difference in size structure could be related to factors such as annual variation in water temperature, which is one of the main drivers of goby reproduction (Parmanne & Lindström, 2003). However, several studies on the reproductive biology of *P. marmoratus* in Mediterranean transitional waters (Mazzoldi & Rasotto, 2001; Koutrakis & Tskliras, 2009) have shown a high phenotypic plasticity of the species, with significant differences related to the breeding season. This suggests that this species can show interannual variation, probably related to varying environmental conditions across years, although eutrophication could trigger changes in its breeding traits which differs from those expected under natural conditions. Thus, the current degradation process of the lagoon could also partially explain the observed changes in recruitment between 2018 and 2019. In this scenario, the species would respond to the population decline with greater reproductive investment. In this context, a compensatory density-dependent response could explain the increased juvenile settlement observed in the last annual cycle. Furthermore, this response would explain the recovery in occurrence and abundance shown by the species for 2019. Our study finished just before the massive fish kill that occurred in October 2019 (Ruiz-Fernández *et al.*, 2019), which could trigger a hypoxia-mediated fish movement from less-oxygenated, deeper waters to more-oxygenated, shallower areas (Zamora-López *et al.*, 2023). Hence, this situation could increase resource competition and predation in shallow areas, hampering the potential recovery in abundance of *P. marmoratus*. In addition, ongoing monitoring efforts support the reduced abundances of this species after that critical episode (unpublished data).

On the other hand, the relevance of the factor *Period* in habitat models supports the conclusion that other unassessed parameters could be determinants of the observed decline, beyond changes in shallow habitat. Thus, the strong habitat degradation in deep areas (Pérez-Ruzafa *et al.*, 2018) may have a cascading negative effect on *P. marmoratus* populations in the Mar Menor. Although the species is adapted to natural stress conditions related to water quality (e.g., changes in salinity), its strong association with bare bottoms could make it highly sensitive to recurrent hypoxia episodes, reducing survival rates and abundance in deep waters and, ultimately, leading to population declines in shallow littoral areas. In this context, changes in nest selection by females in response to varying oxygen levels have been reported for other *Pomatoschistus* species (Jones & Reynolds, 1999), showing nesting preferences for less secure (i.e., more exposed to predation) but more oxygenated sites. Hence, increased predation pressure on goby nests during hypoxic moments may also have influenced the population dynamics of *P. marmoratus*.

In relation to *S. abaster*, it is strongly associated with

vegetated substrates in shallow areas of the Mar Menor, and its occurrence is also correlated with muddy bottoms, which could be related to its burrowing behavior (Müller & Erzini, 2016). Probably, these habitats could also provide it with refuge from predator and/or food, although less efficiently than seagrass beds, since these vegetated habitats show a higher structural complexity. This habitat relationship for *S. abaster* would also be expected in deeper areas. In fact, the loss of seagrass meadows in deeper areas during recent eutrophication events (Mercado *et al.*, 2021) could have forced population movements mediated by habitat loss (Caldwell & Vincent, 2012), which were particularly evident in summer and autumn of the last study cycles. Furthermore, compared to the size of individuals present in shallow areas during the pre-eutrophication period (unpublished data), the proportion of mature specimens in shallow areas increased markedly in the 2019 cycle (66.2% compared to 49.1%), suggesting an even more important role of shallow areas as spawning grounds. This habitat-mediated movement is supported by the high abundances observed in cycles 2018-2019, where mean values of about 60 ind./100m² were recorded in sites with almost 100% vegetation cover. In the study area, *S. abaster* shows densities more than three times higher than those observed in other European transitional systems: 17.8 ind./100m² in the Venice lagoon (Franco *et al.*, 2006) or 17.9 ind./100m² in Ria Formosa (Ribeiro *et al.*, 2012). Furthermore, previous studies have not reported strong interannual fluctuations or population growth trends in this species (Araújo *et al.*, 2000; Pombo & Rebelo, 2002; Scapin *et al.*, 2018a). However, the increase in abundance in shallow areas, also mediated by changes in bottom habitat structure, was highly significant compared to the reference period.

Can populations of resident fish provide information about the structure of a shallow habitat?

The submerged habitat structure in shallow waters of the Mar Menor lagoon has undergone changes mediated by eutrophication that are consistent with trends in the occurrence and abundance of the populations of two of the target resident fish, *P. marmoratus* and *S. abaster* (Fig. 5; Fig. 6). An effect of this eutrophication process is the increase in mud in shallow areas, which has been constant and cumulative during the last decades (Álvarez-Rogel *et al.*, 2020). In our study, this effect is observed in the comparison between the reference period and the eutrophication period, with an increase in homogeneity and a significant decrease in grain size in the bottoms of shallow waters. Furthermore, submerged vegetation in the shallow littoral areas has increased its coverage due to the high amount of available nutrients and the greater sunlight exposure in these shallow environments (Hughes *et al.*, 2018; Mercado *et al.*, 2021). Additionally, a slight reduction in water transparency could facilitate the expansion of *C. prolifera*, preventing photoinhibition of its growth (García-Sánchez *et al.*, 2012). In turn, changes in habitat structure in shallow areas may not only be a consequence

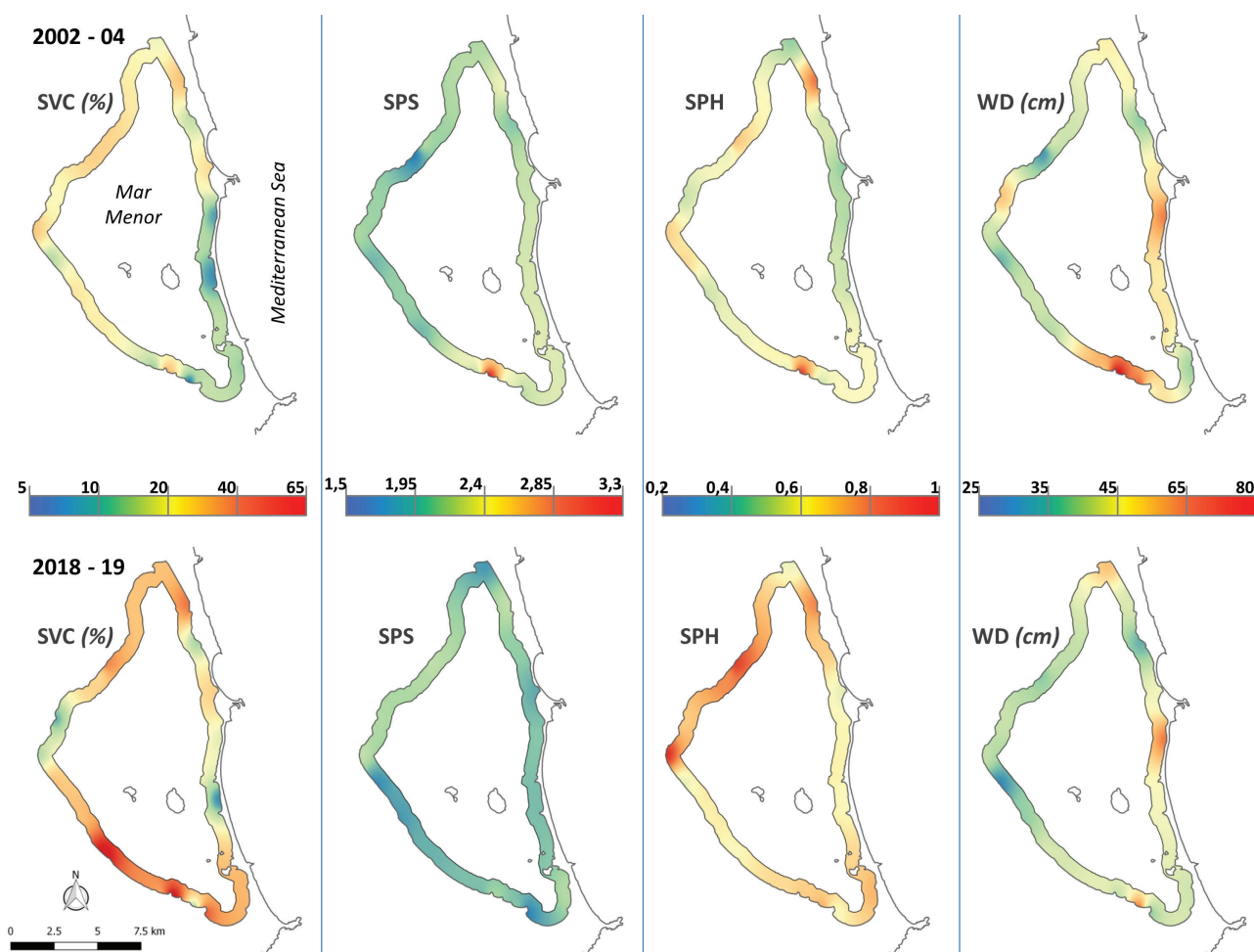


Fig. 6: Variation in habitat structure variables recorded in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea) between a pre-eutrophic reference period (2002-2004) and a critical eutrophic period (2018-2019). (SPS), average value of the assigned substrate particle size (1, mud; 2, sand; 3, gravel; 4, pebble; 5, boulder); (SPH), average standard deviations of the substrate particle sizes; [SVC (%)], average of submerged vegetation cover; [WD (cm)], average water depth.

of the long-term process of eutrophication. This process has shown a turning point since 2016, with the loss of self-regulating mechanisms of the lagoon (Pérez-Ruzafa *et al.*, 2020b) reflected in a significant impact in the deep areas, largely due to turbidity of the water column and mortality of seagrass meadows. However, shallow areas have previously been subject to dredging and shoreline regeneration actions (e.g., sand inputs) with significant impacts (Pérez-Ruzafa *et al.*, 2006). These types of actions generated habitat patchiness, which had already been identified as an important factor affecting fish communities in shallow areas (Verdiell-Cubedo *et al.*, 2012). Thus, beach management actions implemented before the 2016 crisis may have acted in synergy with the ongoing process of eutrophication, contributing to the observed temporal changes in shallow habitat structure.

The change in structural complexity of shallow water habitats resulting from long-term eutrophication processes should have a direct impact on fish populations, as bottom conditions (e.g., vegetation cover or substrate heterogeneity) have been reported to be a major driver of fish abundance and species distribution (Becheker *et al.*, 2022). In our study, we selected fish species that are potentially good candidates to reflect structural changes in shallow habitats, as they have a limited dispersal

capacity, complete their life cycles in these shallow environments, have a strong habitat dependency related to bottom structure, and present a short generation time (Caro & O'Doherty, 1999; Whitfield & Elliott, 2002; Verdiell-Cubedo *et al.*, 2013; Reis-Filho & Giarrizzo, 2016). However, in the case of *A. iberus*, despite its preference for muddy and vegetated habitats (Verdiell-Cubedo *et al.*, 2014), which have increased in area throughout the perimeter of the lagoon, the population dynamics of the species have not shown highly correlated changes with the temporal variation observed in habitat structure. Hence, though the availability of optimal habitats for *A. iberus* has increased, the species has not consequently increased its abundance and peripheral distribution. Instead, it appears to remain concentrated in more restricted areas. This could be explained by the following non-mutually exclusive arguments: the spatial structure of the species in the lagoon is characterized by isolation between its populations (Gonzalez *et al.*, 2018); the species tends to concentrate in highly productive areas (e.g., with inputs of nutrients and organic matter), which may reduce the colonization of other suitable habitats; and the possible increase in interspecific competition, which have been used to justify the isolation of some of its populations in saline wetlands (Oliva-Paterna *et al.*, 2009).

The species associated with unvegetated sandy bottoms, *P. marmoratus*, has undergone a decline in abundance and presence, which is consistent with the reduction of this preferred habitat type in favor of more vegetated and muddier substrates. Its short lifespan, egg-tending behavior and rapid larval settlement on the bottom (Mazzoldi & Rasotto, 2001) could make it highly sensitive to the observed changes in bottom habitat structure (Verdiell-Cubedo *et al.*, 2013). Substrate complexity is considered a key variable for the reproduction of different goby species (Reis-Filho & Giarrizzo, 2016; Koyama *et al.*, 2019; Facca *et al.*, 2020). In our study area, bottoms have become more homogeneous across shallow waters. For example, *P. marmoratus* could suffer from the loss of nesting microhabitats (e.g., available empty shells) due to mud accumulation. Additionally, increased resource competition in suboptimal habitats for the species could limit the use of these complex habitats. In fact, the ecological variable that accounted for most of the variation in the somatic condition of specimens of *P. marmoratus* was the abundance of potential competitor fish species, which was related to interspecific fish interactions (Verdiell-Cubedo *et al.*, 2007). In this scenario of high interspecific competition, substrate selection has also been observed as a relevant factor in the anti-predator behavior of *Pomatoschistus* taxa (Tallmark & Evans, 1986). Therefore, the increased prevalence of seagrass meadows in shallow areas could trigger higher rates of predation and competition, explaining part of the observed decline in their abundance. Finally, it is worth mentioning that the observed decline of this species is a trend shared with other taxa linked to unvegetated bottoms such as *Callionymus pusillus* and species of the Soleidae family (Guerrero-Gómez *et al.*, 2022), suggesting a surrogate value of the species to reflect trends in fish assemblages associated with unvegetated sandy bottoms, according to Caro & O'Doherty (1999).

The species associated with vegetated bottoms, *S. abaster*, has shown a significant increase in occurrence and abundance closely related to the increase in seagrass coverage in shallow areas observed from the reference period to the eutrophication period. Overall, meadows shaped and dominated by *C. nodosa* would have increased in shallow littoral areas due to nutrient enrichment and the maintenance of sunlight availability (Hughes *et al.*, 2018; Mercado *et al.*, 2021). Taxa from the Syngnathidae family mostly require the complexity of seagrass meadows, where they can find food and shelter from predators through camouflage behavior (Scapin *et al.*, 2018a). Comparing the reference period (2002-2004) with the eutrophication period (2018-2019), other less common syngnathid species in the Mar Menor lagoon (i.e., *Syngnathus typhle*, and *Hippocampus guttulatus*) have nearly doubled their detected frequency of occurrence in shallow areas (Guerrero-Gómez *et al.*, 2022). This aspect highlights the value of these vegetated shallow zones for representatives of this fish family. However, in the case of *H. guttulatus*, the decline shown by the species throughout the lagoon has been very significant as a consequence of eutrophication-mediated changes suffered in deeper

waters (Vivas *et al.*, 2023). Based on the demonstrated relevance of vegetation beds for the viability of *S. abaster* populations, we suggest that its population dynamic could be used in the future as an indicator of eutrophication-mediated changes in habitat structure, particularly when related to influences on seagrass meadows (Franco *et al.*, 2009). However, few studies have specifically assessed the potential indicator character of *S. abaster* (Scapin *et al.*, 2016, 2018b), while the value of other syngnathid species has more frequently been emphasized.

Management and conservation implications

Our results indicate that the population dynamics of certain resident fish in transitional water ecosystems may serve as indicators of eutrophication-mediated changes in habitat structure. Eutrophication is a currently widespread threat for coastal areas (Jiang *et al.*, 2019; Rose *et al.*, 2019), leading to significant modifications to their biotic component (Brauko *et al.*, 2020). Therefore, our results can be useful to develop management tools focused on monitoring the disturbances mediated by eutrophication processes. Additionally, the target species of our study are also included in national or regional red lists for the conservation of endangered species (Robledano *et al.*, 2006). Therefore, it is necessary to understand their population trends to design effective management measures. Thus, understanding their value as bioindicator taxa would enable their use in biological monitoring targeting eutrophicated transitional environments, allowing for two conservation purposes: (1) tracking population trends of protected fish species and (2) inferring changes in the shallow habitats of these transitional systems while simplifying conservation efforts. In this context, a recent study of *P. marmoratus* and *S. abaster* in the Mar Menor demonstrated the good performance of certain morphological and parasitological traits of these two taxa to be considered as robust ecological indicators of environmental health (Almeida *et al.*, 2023). This potential attribute further enhances the value of such species for assisting environmental managers and policy makers in the design of effective monitoring programs aimed at detecting impacts within transitional ecosystems of conservation-concern, such as the Mar Menor coastal lagoon.

On the other hand, the significant temporal variation observed in the population dynamics at the species level contrasts markedly with the temporal variation detected using fish-based multimetric indicators also developed in the Mar Menor shallow areas (Zamora-López *et al.*, 2023). The values of these multispecies indicators showed an unexpected stability even under critical eutrophic conditions. Therefore, our study highlights the sensitivity of resident species to long-term eutrophication-mediated effects, despite their adaptations to physicochemical fluctuations typical of transitional ecosystems (Dauvin & Ruellet, 2009). Although the plasticity of such species may make them tolerant to changes in water quality in estuarine systems (Facca *et al.*, 2020), their great fidelity to shallow areas makes them highly sensitive to

habitat structure changes. In contrast, an index based on a fish assemblage may be too robust and may not reflect changes at the temporal scale evaluated (Fonseca *et al.*, 2013; Pérez-Ruzafa *et al.*, 2019). Indeed, our current results highlight the usefulness of species-level metrics (e.g., population dynamics) as complementary indicators of habitat structural quality. However, there is still a profound lack of information on the ecological assessment of coastal lagoons using fish as indicators.

In order to provide more robust indicators for environmental assessment and to overcome the potential limitations of our study, future research could focus on other fish species with a wider range of ecological relationships (e.g., species associated with rocky substrates) or species from other functional guilds (e.g., piscivores). In terms of applicability to other regions, the surrogate value of species from the Aphaniidae, Syngnathidae and Gobiidae families could be explored in lagoons under eutrophication pressure throughout the Mediterranean basin, where resident taxa of these families are common (Pérez-Ruzafa *et al.*, 2007). However, it should be noted that these results should be extrapolated only to shallow areas (water depth < 2 m), as eutrophication has been observed to reduce macrophytes' surface in deeper areas (Bernardeau-Esteller *et al.*, 2023). Furthermore, future research should assess whether other stages that are more critical in eutrophication could also reduce macrophytes in shallow areas and whether these species would exhibit different responses. When biological or ecological patterns are shared with other Mediterranean lagoons, this regional information would be useful to establish a baseline for the design of specific indices applied to coastal lagoons on a wider scale, thus contributing to filling knowledge gaps related to fish-based indices for lagoons in other regions (Souza & Vianna, 2020).

Conclusions

In this study, we documented a significant temporal variation in the population dynamics of three representative resident fish species inhabiting shallow areas of one of the largest coastal lagoons in the Mediterranean Sea. Our dataset encompasses a robust time series that includes both a reference and a eutrophic period in a transitional ecosystem highly impacted by nutrient overload, which has recently induced changes in its self-regulation capacity and triggered dystrophic crises. We elucidated the strong relationships between fish population parameters (i.e., occurrence and abundance) and habitat structure in shallow littoral areas that have undergone eutrophication-mediated alterations. The observed congruence between changes in these population parameters and alterations in the habitat structure highlights their potential as indicators to identify eutrophication-mediated changes in the habitat quality of shallow waters and overall ecosystem health.

Future management strategies for transitional water ecosystems, which are commonly affected by eutrophication processes, should prioritize shallow areas as critical

habitats for aquatic biota, as recently highlighted for the Mar Menor coastal lagoon (Zamora-López *et al.*, 2023). However, it is worth noting that the holistic approach inherent to the fish-based indices frequently used for ecological quality assessment (i.e., multi-species indices) may mask species-level effects, making it difficult to detect habitat homogenization or simplification of fish communities mediated by eutrophication processes in coastal lagoons. Therefore, long-term monitoring of the population dynamics of focal species (e.g., resident fish) should be used as complementary indicator of habitat quality.

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CRedit authorship contribution statement: Adrián Guerrero-Gómez: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. Antonio Zamora-López: Writing – review & editing, Methodology, Investigation. Mar Torralva: Writing – review & editing, Supervision, Funding acquisition, Project administration. José Manuel Zamora-Marín: Writing – review & editing, Methodology, Investigation. Antonio Guillén-Beltrán: Methodology, Investigation. Francisco José Oliva-Paterna: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Appendix

Table A1. Summary table of the different fish surveys performed during the study period. (Win: winter; Spr: spring; Sum: summer; Aut: autumn). The value in brackets shows the number of the spatial sampling replicates performed in each monitoring season. Species density was calculated from sampling of 160 m².

Time cycle considered	Season and years included (Spatial replicates)	Available data
2002	Sum-2002 (94); Win-2003 (98)	Habitat variables; Species density; CPUEs; Occurrence
2003	Sum-2003 (103); Aut-2003 (58); Win-2004 (59); Spr-2004 (58)	Habitat variables; Species density; CPUEs; Occurrence
2015	Spr-2015 (16); Sum-2015 (16); Aut-2015 (16)	CPUEs; Occurrence
2016	Spr-2016 (16); Sum-2016 (16); Aut-2016 (16)	CPUEs; Occurrence
2017	Win-2017 (16); Spr-2017 (16); Sum-2017 (16); Aut-2017 (16)	CPUEs; Occurrence
2018	Win-2018 (48); Spr-2018 (51); Sum-2018 (54); Aut-2018 (54)	Habitat variables; Species density; CPUEs; Occurrence
2019	Win-2019 (54); Spr-2019 (54); Sum-2019 (54); Aut-2019 (54)	Habitat variables; Species density; CPUEs; Occurrence

Table A2. Equivalence between catches per 160 m² and categorized CPUEs (catches per unit effort; 160 m²).

Catches/160 m ²	Categorized CPUEs
1-5	1
6-10	2
11-20	3
21-50	4
51-100	5
101-300	6
301-500	7
> 500	8

Table A3. Temporal variation of frequency of occurrence and abundance values (categorized catches per unit effort, CPUEs showing standard error; see Table A2) of the target species (*A. iberus*, *P. marmoratus*, and *S. abaster*) in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea). Data are divided according to two different periods: reference period (2002-2004) and critical eutrophic period (2015-2019).

Species	Season	2002	2003	2015	2016	2017	2018	2019
<i>Apricaphanius iberus</i>	Winter	0.36 (0.41 ± 0.06)	0.19 (0.32 ± 0.1)			0.25 (0.44 ± 0.26)	0.21 (0.35 ± 0.12)	0.26 (0.39 ± 0.12)
	Spring		0.24 (0.33 ± 0.1)	0.06 (0.06 ± 0.06)	0 (0 ± 0)	0.19 (0.19 ± 0.1)	0.1 (0.24 ± 0.13)	0.15 (0.37 ± 0.15)
	Summer	0.28 (0.5 ± 0.11)	0.31 (0.8 ± 0.15)	0.13 (0.25 ± 0.19)	0.13 (0.38 ± 0.31)	0.25 (0.69 ± 0.38)	0.24 (0.65 ± 0.22)	0.24 (0.37 ± 0.11)
	Autumn		0.36 (0.71 ± 0.16)	0.19 (0.19 ± 0.1)	0.13 (0.5 ± 0.39)	0.25 (0.81 ± 0.44)	0.19 (0.52 ± 0.2)	0.2 (0.52 ± 0.18)
<i>Pomatoschistus marmoratus</i>	Winter	0.92 (3.15 ± 0.18)	0.9 (4.2 ± 0.26)			0.31 (0.38 ± 0.15)	0.75 (1.6 ± 0.21)	0.76 (1.56 ± 0.18)
	Spring		0.97 (3.71 ± 0.23)	0.88 (2.63 ± 0.4)	0.88 (2.44 ± 0.35)	0.38 (0.63 ± 0.24)	0.65 (1.31 ± 0.19)	0.91 (2.69 ± 0.22)
	Summer	0.87 (3.03 ± 0.19)	0.78 (3.36 ± 0.25)	0.69 (0.94 ± 0.25)	0.25 (0.31 ± 0.15)	0.19 (0.19 ± 0.1)	0.35 (0.54 ± 0.14)	0.74 (2.02 ± 0.25)
	Autumn		0.95 (4.5 ± 0.27)	0.56 (0.81 ± 0.26)	0.19 (0.31 ± 0.2)	0.5 (1.13 ± 0.34)	0.69 (1.54 ± 0.2)	0.94 (2.85 ± 0.29)
<i>Syngnathus abaster</i>	Winter	0.36 (0.51 ± 0.09)	0.44 (0.66 ± 0.12)			0.63 (0.88 ± 0.22)	0.73 (1.6 ± 0.21)	0.78 (1.91 ± 0.21)
	Spring		0.55 (1.14 ± 0.18)	1 (2.94 ± 0.44)	0.56 (0.94 ± 0.28)	0.63 (0.81 ± 0.25)	0.71 (1.92 ± 0.25)	0.87 (2.09 ± 0.2)
	Summer	0.63 (1.44 ± 0.17)	0.64 (1.48 ± 0.17)	0.69 (1.19 ± 0.36)	0.69 (1.44 ± 0.38)	0.69 (2.5 ± 0.55)	0.81 (3.56 ± 0.33)	0.89 (3.06 ± 0.28)
	Autumn		0.74 (1.59 ± 0.19)	0.75 (1.31 ± 0.28)	0.75 (1.75 ± 0.39)	1 (3.63 ± 0.39)	0.87 (2.76 ± 0.26)	0.89 (3.37 ± 0.29)

Table A4. Mean and confidence interval (95%) of the CPUEs (abundance/100m²) of the target species (*A. iberus*, *P. marmoratus*, and *S. abaster*) in the shallow littoral areas of the Mar Menor coastal lagoon (western Mediterranean Sea). Data are divided according to two different periods: reference period (2002-2004) and critical eutrophic period (2018-2019).

Species	Season	2002	2003	2018	2019
<i>Apricaphanius iberus</i>	Winter	0.7 ± 0.3	0.8 ± 0.7	0.8 ± 0.8	1.1 ± 0.9
	Spring	-	0.6 ± 0.6	1.5 ± 2.3	2 ± 2.6
	Summer	2.6 ± 2.5	7.4 ± 6.7	7.7 ± 7.5	1.1 ± 1.2
	Autumn	-	2.2 ± 1.4	7.6 ± 8.5	4 ± 4.1
<i>Pomatoschistus marmoratus</i>	Winter	22.3 ± 5.6	50.4 ± 13.5	6.3 ± 3.4	5.4 ± 2.1
	Spring	-	33.7 ± 10.6	4.9 ± 3.5	15.8 ± 6.5
	Summer	22.3 ± 6.2	52.4 ± 14.7	2 ± 2.4	9.5 ± 4.1
	Autumn	-	73.4 ± 23.9	4.9 ± 1.9	31 ± 17.1
<i>Syngnathus abaster</i>	Winter	1.2 ± 0.8	1.6 ± 0.8	5.9 ± 2.8	8 ± 2.8
	Spring	-	3.6 ± 1.7	9.8 ± 4.2	9 ± 3.6
	Summer	7.7 ± 3.7	8.2 ± 3.7	54.9 ± 21.9	32.2 ± 15.2
	Autumn	-	5.5 ± 2.2	21.9 ± 8.7	42.4 ± 20.3

Table A5. Temporal variation of the habitat structure variables (mean ± SE) in the shallow littoral areas of the Mar Menor coastal lagoon (Mediterranean Sea). (SPS) average value of the assigned substrate particle size (1 mud; 2 sand; 3 gravel; 4 pebble; 5 boulder); (SPH) average standard deviations of the substrate particle sizes; (%) average of submerged vegetation cover; (cm) average of water depth.

Habitat variables	Season	2002	2003	2018	2019
Submerged vegetation cover (SVC; %)	Winter	20.17 ± 2.58	14.74 ± 3.13	29.9 ± 4.39	35.83 ± 3.78
	Spring		9.74 ± 1.94	27.84 ± 4.28	24.96 ± 3.54
	Summer	21.91 ± 2.45	40.5 ± 2.9	34.35 ± 3.73	38.52 ± 4.56
	Autumn		9.81 ± 2.11	35.56 ± 3.78	30.37 ± 3.91
Substrate particle size (SPS)	Winter	2.11 ± 0.03	1.94 ± 0.04	1.66 ± 0.04	1.86 ± 0.05
	Spring		1.93 ± 0.04	1.78 ± 0.04	1.93 ± 0.04
	Summer	2.12 ± 0.04	2.07 ± 0.05	1.87 ± 0.04	1.8 ± 0.04
	Autumn		2.06 ± 0.03	1.87 ± 0.04	1.81 ± 0.04
Substrate particle heterogeneity (SPH)	Winter	0.59 ± 0.03	0.51 ± 0.03	0.65 ± 0.04	0.69 ± 0.02
	Spring		0.5 ± 0.03	0.72 ± 0.04	0.8 ± 0.03
	Summer	0.57 ± 0.03	0.63 ± 0.03	0.69 ± 0.03	0.68 ± 0.02
	Autumn		0.5 ± 0.03	0.72 ± 0.03	0.73 ± 0.02
Water depth (WD; cm)	Winter	39.16 ± 1.27	49.01 ± 2.3	40.51 ± 2.24	38.49 ± 1.95
	Spring		37.47 ± 1.79	38.4 ± 2.12	37.91 ± 2.07
	Summer	40.34 ± 1.69	54.46 ± 1.52	41.91 ± 2.07	40.31 ± 2.11
	Autumn		42.89 ± 2.08	47.38 ± 2.34	39.57 ± 2.06