



Shallow waters as critical habitats for fish assemblages under eutrophication-mediated events in a coastal lagoon

Antonio Zamora-López^{a,*}, Adrián Guerrero-Gómez^a, Mar Torralva^a, José Manuel Zamora-Marín^{b,a}, Antonio Guillén-Beltrán^a, Francisco José Oliva-Paterna^a

^a Department of Zoology and Physical Anthropology, Faculty of Biology, University of Murcia, Spain

^b Department of Applied Biology, Centro de Investigación e Innovación Agroalimentaria (CIAGRO-UMH), Miguel Hernández University of Elche, Elche, Spain

ARTICLE INFO

Keywords:

Shorelines
Eutrophic waters
Fish index
Aquatic communities
Fish kill
Refuges
Mar Menor

ABSTRACT

Eutrophication is a major driver of the degradation of transitional waters worldwide, especially in environments with a restricted connection to the sea, such as coastal lagoons. In recent decades, intensive agriculture and urban water inputs around the Mar Menor coastal lagoon (Western Mediterranean) have disturbed this originally oligotrophic aquatic system. The nutrient input into the lagoon has triggered its eutrophication, leading to dystrophic crises and mass mortality events for aquatic biota, transforming it into one of the most eutrophication-impacted transitional waters in the Mediterranean basin. In this study, we applied a fish-based indicator to assess the ecological quality of shallow waters under different eutrophication-mediated environmental stress scenarios (from pre-eutrophic reference periods to critical eutrophic periods), as well as to explore the role of confinement (i.e., water renewal time) and shoreline anthropogenic pressure as factors modulating the indicator response. Despite the high magnitude of the eutrophication impact on the lagoon, the ecological quality of the shallow waters decreased only slightly after the mass mortality events. The level of confinement also had slight effects on the ecological quality of the most confined shallow areas in the summer during eutrophic periods. Hence, shallow waters could play a critical role as refuge habitats, both for fish assemblages and other aquatic taxa, by buffering eutrophic conditions during eutrophication processes. In fact, shallow waters could act as critical habitats, allowing for the recolonisation of aquatic biota from more impacted areas in the lagoon. This attribute further reinforces the need to properly manage and protect the shoreline areas of transitional waters, particularly under eutrophication scenarios.

1. Introduction

Transitional waters have been widely acknowledged as key ecosystems supporting biodiversity and providing diverse ecosystem services (Elliott and Whitfield, 2011; Newton et al., 2018). Among the representative taxa of transitional environments, fish are particularly interesting because they often show notably diversified assemblages, which include a wide array of life-history traits (e.g., functional groups). Consequently, fish are involved in multiple ecological processes of paramount importance for estuarine ecosystem functioning (Elliott, 2007). Moreover, they are highly appreciated by local economies due to their high value in recreational and commercial fisheries (Lewis et al., 2021). In this context, the nutrient input delivered by adjacent flowing waters (i.e., rivers, streams and watercourses) places transitional waters as one of the most productive ecosystems worldwide (Marcos et al.,

2015; Sheaves et al., 2014), thus directly or indirectly supporting global fisheries (Jordan and Peterson, 2012).

Within coastal lagoons, shallow waters are considered key habitats for fish not only due to the provision of feeding, reproduction and nursery grounds but also due to their role as pathways for fish migration, thus harbouring widely diversified fish assemblages, which often include threatened species (Franco et al., 2006; Verdiell-Cubedo et al., 2013a). However, these aquatic habitats are especially vulnerable to impacts derived from increasing human activities, which may impair their ecological status through abiotic and biotic homogenisation (Ferrarin et al., 2014), ultimately disrupting key ecological process and the provision of ecosystem services (Limburg et al., 2015; Worm et al., 2006). In fact, coastal lagoons are exposed to multiple anthropogenic stressors usually associated with different human activities occurring both within their waters and in their adjacent landscape (i.e., drainage

* Corresponding author.

E-mail address: antonio.zamora2@um.es (A. Zamora-López).

<https://doi.org/10.1016/j.ecss.2023.108447>

Received 13 March 2023; Received in revised form 17 July 2023; Accepted 23 July 2023

Available online 24 July 2023

0272-7714/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

basins) (Elliott and Whitfield, 2011).

Due to the increasing and varied impacts, the effective management and conservation of coastal lagoons requires the implementation of monitoring programs aimed at assessing their ecological status. Fish-based indicators are frequently used to assess the ecological quality of these environments and to inform management actions (Marcos et al., 2015; Hallett et al., 2012). The use of fish assemblages as bioindicators in transitional waters is supported by the wide array of life strategies, trophic levels and functional traits displayed by different fish species (Whitfield and Elliott, 2002). In addition, fish communities in coastal lagoons often include both resident and migratory species, thus allowing not only for an assessment of the effects of local stressors but also of other factors acting on a regional scale. Furthermore, fish represent a highly visible biological component and are easy to identify in the field, and cost-effective survey methods are available to standardised monitoring (Roset et al., 2007). Lastly, most fish species are of a high economic and conservation interest, which allows one to quantify the socioeconomic costs associated with environmental degradation. In fact, the development and application of fish-based indicators to assess the health of transitional waters have recently intensified (Lepage et al., 2015; Sapounidis and Koutrakis, 2021). Most of these indicators correspond to multimetric fish-based indices on an integrative approach accounting for several parameters associated with the structure, composition and functionality of fish assemblages (Pérez-Domínguez et al., 2012).

Eutrophication is currently a major driver of the degradation of transitional waters, affecting their ecological integrity and health status (Lemley et al., 2017). In particular, coastal lagoons are probably the transitional ecosystems most vulnerable to eutrophication, mostly due to the strong influence of adjacent terrestrial ecosystems, which provide an important amount of nutrients and organic matter, as well as their restricted connectivity with the open sea (Newton et al., 2014). Thus, the community-level ecological effects of eutrophic processes and dystrophic crises in coastal lagoons have been increasingly assessed in recent years (Ménesguen and Lacroix, 2018; Pérez-Ruzafa et al., 2019a). The Mar Menor coastal lagoon (Western Mediterranean Sea) is a transitional ecosystem highly impacted by nutrient overload, which has recently promoted changes in its capacity of self-regulation and triggered dystrophic crises (Fernández-Álías et al., 2022). Historically, this coastal environment was an oligotrophic system, characterised by a high productivity, complex food webs, prolific fisheries, regular energy exchange with the open sea and the accumulation of surplus organic matter in the sediment (Pérez-Ruzafa et al., 2020). Nevertheless, human pressures impacting the Mar Menor have notably increased in recent decades, mainly due to rising intensive farming practices and growing urbanisation, thus promoting the discharge of nutrient-rich waters into the lagoon (Álvarez-Rogel et al., 2020). In addition, the rise in groundwater levels due to excessive irrigation practices and intense rainfall periods triggered this influx. However, adjacent coastal wetlands have strongly been disturbed during the last two decades (Martínez-López et al., 2015), thus diminishing their function as natural green filters buffering the eutrophication of the lagoon. A highly visible episode in the eutrophication process of the Mar Menor was documented in 2015 through the occurrence of phytoplankton blooms and an acute reduction in water transparency, leading to the loss of about 86% of benthic macrophyte coverage (Belando et al., 2019). Though varying in intensity, this eutrophic situation has been maintained until today, and it has led to mass mortality events of aquatic fauna driven by algal blooms and hypoxic conditions (Ruiz-Fernández et al., 2019), with two critical events occurring in autumn 2019 and summer 2021. These acute eutrophic events may disrupt natural dynamics and strongly impact multiple facets of fish assemblages. However, a comprehensive assessment encompassing a comparative analysis of aquatic biota between reference pre-eutrophic conditions and eutrophic periods has not been conducted to date.

In this study, we assessed the ecological status of the Mar Menor

coastal lagoon under different eutrophication-mediated environmental stress scenarios by using a fish-based multimetric index. We performed a temporal comparison between a pre-eutrophic reference period (2002–2004) and critical eutrophic periods (2018–2021), and we assessed the roles of anthropogenic pressure (i.e., regular dredging and artificial sand supply) and site-level confinement (i.e., water renewal time) as spatial factors affecting the response of fish assemblages at the local scale. Shallow waters in nearshore areas are probably the most affected by human activities in coastal lagoons (Bilkovic and Roggero, 2008; Verdiell-Cubedo et al., 2012), and the ecological status of these shallow areas is frequently expressed as changes in fish assemblage composition and structure. We hypothesised that critical eutrophic periods have a significant impact on the ecological quality of shallow waters and that the extent of this disturbance is mediated by the degree of anthropogenic pressure and the water renewal time. In this context, more naturalised shallow areas should present a higher ecological integrity and resilience against eutrophication-mediated impacts, whereas more confined areas should be more strongly impacted by eutrophic periods due to their lower water renewal rates.

2. Material and methods

2.1. Study area

The Mar Menor, located in southeastern Spain, was originally a hypersaline and oligotrophic coastal lagoon (Fig. 1). With a surface of 136.5 km², the Mar Menor represents one of the largest coastal lagoons in the Mediterranean basin, and it is separated from the Mediterranean Sea by a 21 km long sand bar, which presents three major water exchange inlets (i.e., channels or tidal areas) (Álvarez-Rogel et al., 2020). The Mar Menor is characterised by a low mean depth (4.5 m) and particular water temperature and salinity conditions, ranging between 11 and 30 °C and 39 and 51, respectively (Pérez-Ruzafa et al., 2020). In the early 2000s the salinity was slightly higher than that observed at present (43–48 in period 2002–2004; 40–45 in period 2018–2021) due to the increasing input of fresh waters into the lagoon. Moreover, the hydrodynamic regime of this coastal lagoon is strongly influenced by prevailing winds and the water level difference with the Mediterranean Sea, which lead to dissimilar water renewal rates between (see confinement levels in Fig. 1) (García-Oliva et al., 2018).

Strong human pressures have historically affected this transitional ecosystem. Important urban and tourist areas have developed along the perimeter of the lagoon, and they support high population densities during the summer season. Consequently, the shoreline morphology and integrity have been modified by management actions (e.g., dredging, algal removal and sand supply) and the construction of marinas and rocky breakwaters (Pérez-Ruzafa et al., 2005). In contrast, the lagoon still has natural shores associated with adjacent wetlands with a high ecological value, and they are legally protected under international figures (Natura 2000 Network and the Ramsar Convention) (see urbanised areas and natural saltmarshes in Fig. 1).

Currently, the major impact on the Mar Menor coastal lagoon is derived from the agricultural intensification within the adjacent drainage basin, which has experienced a steep land-use change from traditional rainfed farming to intensive irrigation crops in recent decades (Álvarez-Rogel et al., 2020). This issue has led to an increased surface input of sediments, nutrients and terrestrial organic matter into the lagoon through seasonal watercourses (Álvarez-Rogel et al., 2020). The Mar Menor also receives urban wastewater and nutrient-rich groundwater discharges from excessive irrigation practices developed over decades. Hence, this ongoing nutrient input has triggered important changes in the original lagoon conditions, increasing nutrient levels and leading to eutrophic processes (Fernández-Álías et al., 2022).

Before the occurrence of eutrophic events, this coastal lagoon was characterised by muddy bottoms predominantly dominated by large meadows of the invasive macroalga *Caulerpa prolifera* (Pérez-Ruzafa

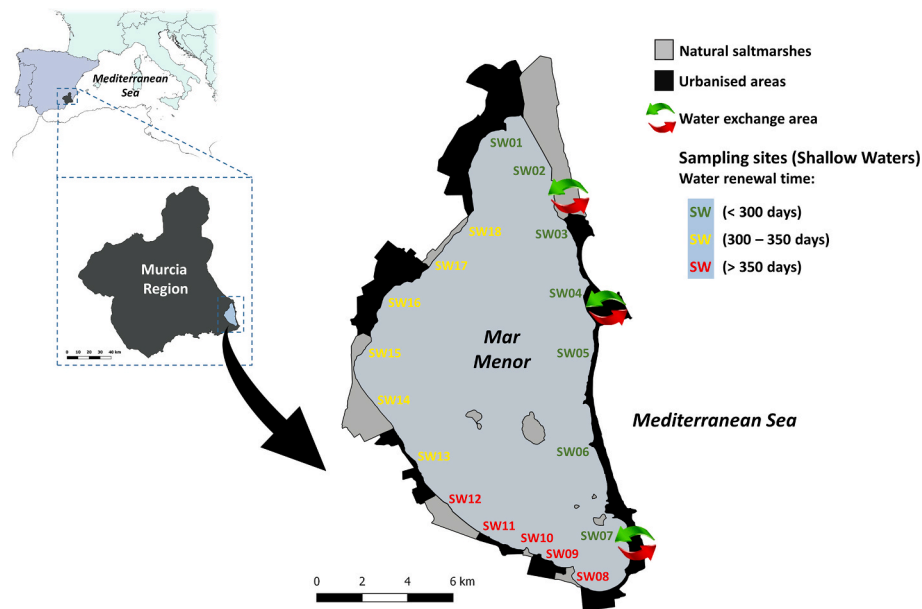


Fig. 1. Location of the Mar Menor coastal lagoon and distribution of sampling sites targeting fish assemblages in shallow areas. Degree of anthropogenic pressure on the shoreline (urbanised areas and natural saltmarshes) and confinement levels (water renewal time at sampling sites) are represented: confinement 1 (<300 days); confinement 2 (300–350 days); and confinement 3 (>350 days). Main water exchange areas (inlets) with the Mediterranean Sea are also indicated.

et al., 2005, 2012). In contrast, rocky bottoms are very scarce across the coastal lagoon and almost exclusively spatially restricted to the surroundings of the five islands located within the lagoon, whereas sandy bottoms are distributed along the littoral shallow areas and mostly occupied by monospecific meadows of the native seagrass *Cymodocea nodosa* or mixed meadows of this species together with *C. prolifera* or *Ruppia cirrosa*. Previous research in the study area has already revealed that different meadows support dissimilar fish communities, discussing the bottom characteristics generated by *C. prolifera* are less attractive to certain species (Marcos et al., 2015; Pérez-Ruzafa et al., 2006). Overall, the high importance of vegetated shallow waters to some fish species of commercial and conservation interest has been previously acknowledged, particularly their role as critical habitats for fish settlement (Guerrero-Gómez et al., 2022). However, the original distribution of meadows within the lagoon has notably changed as a result of recent eutrophic events, even causing the loss of 86% of meadows cover, affecting mostly the macroalga *C. prolifera* (Belando et al., 2019).

2.2. Fish sampling

Fish samples were collected using a 10 m long beach seine net (8 m of effective catching width) with a 0.5 mm mesh size, being this technique considered one of the most effective sampling method for fish in shallow waters, especially in coastal lagoon ecosystems (Ríha et al., 2008). We selected 18 sampling sites across shallow waters covering the whole perimeter of the Mar Menor, and such sites were classified into two contrasting classes according to the degree of anthropogenic pressure: (1) highly urbanised areas under regular dredging and sand supply actions; and (2) natural saltmarshes without these human-mediated disturbances (Fig. 1). Moreover, three progressive levels of water renewal time were assigned to the sampling sites (*sensu* García-Oliva et al., 2018): confinement 1, less than 300 days; confinement 2, between 300 and 350 days; and confinement 3, more than 350 days (Fig. 1). In each sampling site, three 20 m long quantitative sampling replicates were carried out along the coastline, covering all representative habitats (160 m² of sampling area per replicate; 480 m² per sampling site). This sampling method has previously been shown to be the most effective for monitoring fish assemblages in all available habitats of shallow waters in the study area (Franco et al., 2012).

In this context, all shoreline habitats were equally surveyed to ensure an adequate sampling completeness and to collect reliable data on species richness and fish abundance at a given sampling site. The sampling sites were mainly represented by shallow habitats (40 cm of average water depth) and mostly sandy and muddy bottoms (these fine substrates represented 84% of the sampled bottoms). Overall, about 31% of the total surface of the sampling sites was covered by meadows, mainly monospecific meadows of *C. nodosa* and mixed meadows of *C. nodosa* and *C. prolifera*. Detailed information for each sampling site and study period is provided in Table 1.

Fish surveys were conducted on a seasonal basis during three two-years study periods: (1) a reference period (from summer 2002 to spring 2004), (2) the first critical eutrophic period (2018–2019) (hereafter, CEP-1), and (3) the second critical eutrophic period characterised by multispecies mass mortality events (2020–2021) (hereafter, CEP-2). Although eutrophic events occurred prior to the ones considered in the present work, no data are available on fish assemblages in the shallow areas before 2018, and therefore the period 2018–2019 is considered here as the first critical eutrophic period. Within each period, the 18 selected sampling sites were surveyed once for each season of the year (winter, spring, summer and autumn). Captured fish were identified in the field at species level immediately after catching, but a representative sample of cryptic species (e.g., mugilids) was taken to the laboratory for their later identification using reference literature. After processing, all captured fish were released back into the sampling sites.

2.3. Application of fish-based index

The Estuarine Multimetric Fish Index (EMFI) was slightly adapted for application in our study system (Appendix A). The EMFI was developed by Harrison and Kelly (2013) and firstly applied in Irish transitional waters to assess their ecological status as required by the EU Water Framework Directive (hereafter, WFD). The EMFI has been proven to be a robust and integrated measure of the ecological status of transitional waters, being a useful tool for rapid assessment and being sensitive to anthropogenic disturbances (Harrison and Kelly, 2013). Our adapted version of the EMFI (hereafter, EMFI*) includes 14 metrics of ecological relevance and easy measurement (Table 2). The EMFI* is applied at the sampling site level. Some metrics included in this index require

Table 1

Average and maximum values (indicated in parentheses) of habitat descriptor variables at sampling site level for each of the study periods. % Fine substrate: average percentage of the sampled bottoms which are composed by sand and mud. % Meadow cover: average percentage of the sampled bottoms occupied by meadows.

Sampling site	Reference period (2002–2004)			CEP-1 (2018–2019)			CEP-2 (2020–2021)		
	Water Depth (cm)	% Fine substrate	% Meadow cover	Water Depth (cm)	% Fine substrate	% Meadow cover	Water Depth (cm)	% Fine substrate	% Meadow cover
SW01	42 (63)	93 (97)	19 (37)	52 (62)	95 (100)	35 (72)	49 (55)	98 (100)	42 (72)
SW02	47 (63)	73 (82)	36 (48)	41 (47)	70 (90)	49 (77)	37 (44)	62 (72)	59 (73)
SW03	33 (48)	90 (90)	16 (33)	30 (37)	76 (98)	10 (30)	26 (31)	84 (95)	28 (65)
SW04	51 (69)	89 (95)	16 (38)	44 (64)	95 (100)	31 (63)	38 (49)	91 (100)	39 (83)
SW05	57 (72)	85 (93)	8 (28)	58 (84)	86 (98)	17 (33)	56 (77)	80 (90)	31 (50)
SW06	45 (58)	85 (90)	4 (7)	44 (57)	90 (100)	6 (10)	40 (49)	85 (93)	26 (43)
SW07	29 (39)	82 (92)	14 (45)	39 (57)	77 (92)	37 (73)	35 (48)	85 (95)	59 (92)
SW08	38 (45)	78 (88)	25 (45)	31 (43)	96 (100)	55 (67)	26 (33)	90 (95)	48 (92)
SW09	65 (83)	79 (90)	7 (33)	58 (71)	74 (93)	11 (42)	54 (68)	77 (90)	16 (55)
SW10	66 (66)	22 (22)	37 (37)	39 (56)	83 (93)	66 (77)	36 (46)	95 (98)	57 (85)
SW11	53 (67)	80 (92)	11 (42)	42 (56)	86 (97)	42 (63)	39 (51)	90 (97)	54 (78)
SW12	40 (44)	90 (97)	25 (43)	41 (55)	90 (95)	67 (87)	41 (48)	94 (97)	67 (78)
SW13	36 (67)	88 (93)	30 (67)	33 (39)	86 (98)	38 (53)	31 (41)	90 (100)	36 (48)
SW14	29 (41)	90 (100)	16 (45)	26 (34)	97 (100)	34 (50)	21 (26)	92 (97)	15 (52)
SW15	37 (48)	87 (95)	38 (78)	38 (51)	68 (87)	12 (27)	37 (49)	69 (78)	17 (33)
SW16	53 (76)	90 (97)	17 (33)	39 (51)	79 (100)	8 (22)	38 (51)	86 (92)	11 (27)
SW17	29 (45)	94 (100)	28 (75)	34 (48)	77 (82)	28 (37)	28 (32)	79 (93)	19 (30)
SW18	40 (52)	84 (90)	24 (53)	38 (58)	68 (80)	46 (65)	35 (41)	74 (80)	57 (75)
All sampling sites	43 (83)	85 (100)	20 (78)	41 (84)	83 (100)	32 (87)	37 (77)	85 (100)	38 (92)

Table 2

Description of metrics and fish assemblage attributes used to the application of the Estuarine Multi-metric Fish Index (EMFI*) -modified from [Harrison and Kelly \(2013\)](#)- in shallow waters of the Mar Menor coastal lagoon (SE Spain).

Fish assemblage attribute and metrics		Description
Species diversity and composition		
M1	Species richness	Proportion of the number of species detected as compared to the expected richness
M2	Conservation value of the fish assemblage	Number of species included in conservation catalogues and red lists (threatened at regional, national, European or global scale).
M3	Species composition	% Similarity (presence/absence) to the reference fish assemblage
Species abundance		
M4	Species abundance	% Numerical similarity to the reference fish assemblage
M5	Dominance	Number of taxa that make up 90% of the site-level fish abundance
Estuarine use		
M6	Number of diadromous species	Number of anadromous and catadromous species
M7	Resident species richness	Representativeness of the number of resident species detected respect to the expected resident richness
M8	Marine migrant species richness	Representativeness of the number of marine migrant species detected respect to expected marine migrant richness
M9	Resident species abundance	Relative numerical abundance (%) of resident species
M10	Marine migrant species abundance	Relative numerical abundance (%) of marine migrant species
Trophic integrity		
M11	Zoobenthivorous species richness	Representativeness of the number of zoobenthivorous species detected respect to expected zoobenthivorous richness
M12	Piscivorous species richness	Representativeness of the number of piscivorous species detected respect to expected piscivore richness
M13	Zoobenthivores abundance	Relative abundance (%) of zoobenthivores to the total abundance
M14	Piscivores abundance	Relative abundance (%) of piscivores to the total abundance

reference values from fish assemblages to assess the extent of deviation according to the reference conditions. The reference conditions for the EMFI* metrics were established based on historical data, the best available information and expert consensus. Hence, a putative category of abundance was assigned to each species ([Tables A1 and A2; Appendix A](#)), and it represents the expected abundance value of each species under reference conditions. The EMFI* metric thresholds and scoring criteria are available in [Table A3 \(Appendix A\)](#).

Following [Harrison and Kelly \(2013\)](#), the EMFI* values obtained using the indicator were rescaled to an ecological quality ratio (EQR), thus yielding values from 0 (worst ecological status) to 1 (best ecological status) ([Table 3](#)).

$$EMFI^* - EQR = (EMFI^* - EMFI^*_{min}) / (EMFI^*_{max} - EMFI^*_{min})$$

where EMFI* is the site-specific index value, and $EMFI^*_{max}$ and $EMFI^*_{min}$ are the potential maximum (70) and minimum (14) EMFI values, respectively.

2.4. Statistical analysis

The inter-relationships between the metric scores and the EMFI* values were examined using Spearman rank correlations. Temporal and spatial variations in the EMFI* values between the study periods (reference period; CEP-1; CEP-2) were assessed using a permutational analysis of variance (PERMANOVA), accounting for 5999 permutations with Euclidean distances ([Anderson, 2017](#)) and using the `adonis2` function implemented in the R environment through the `vegan` package ([Oksanen et al., 2019](#)). Euclidean distances were chosen given the univariate character of the response variable ([Anderson, 2017](#)). Temporal

Table 3

Scoring criteria for assessing the ecological status of Mar Menor shallow areas according to a modified version of the Estuarine Multi-metric Fish Index (EMFI*). Five potential categories of ecological status can be assigned according to the EMFI* and the Ecological Quality Ratio (EQR) scores.

Ecological status category	EMFI* - EQR	EMFI* score
High	≥0.80	≥58.8
Good	≥0.60 to <0.80	≥47.2 to <58.8
Moderate	≥0.40 to <0.60	≥36.4 to <47.2
Poor	≥0.20 to <0.40	≥25.2 to <36.4
Bad	<0.20	<25.2

factors were season, study period and sampling-year nested in study period. The effects of shoreline type and confinement on the ecological quality of the sampling sites were studied through their inclusion in the model. All were considered as fixed factors and included in the model with the interaction between the temporal factors and each spatial factor.

3. Results

3.1. Fish assemblages

A total of 55 fish species belonging to 20 families were collected along the shallow waters of the Mar Menor coastal lagoon during the three study periods (Table 4). Overall, we captured 254,515 individuals and recorded a mean density of 137.4 fish per 100 m². Four families accounted for 87.7% of the total abundance: Mugilidae (49.5%), Gobiidae (16.2%), Atherinidae (13.6%) and Syngnathidae (8.4%). Moreover, almost 99% of the total abundance was represented by these families and four additional ones: Sparidae (4.4%), Engraulidae (2.7%), Labridae (2.3%) and Cyprinodontidae (1.6%). Mugilidae was the dominant family in terms of abundance over the three study periods. The density of Gobiidae was higher during the reference period than during both eutrophic periods, whereas Syngnathidae and Atherinidae showed the highest values of density in the CEP-1. Sparidae was the family with the greatest species richness in the Mar Menor shallow waters (10 species), followed by Mugilidae (6 species), Gobiidae (6 species) and Syngnathidae (5 species).

3.2. Metrics of EMFI*

The abundance of resident species (M9), the abundance of marine migrant species (M10), the abundance of zoobenthivorous species (M13) and species richness (M1) were the metrics most correlated with EMFI* (Table B1; Appendix B). The contribution of these metrics to the index values differed slightly across seasons, alternating in order of the highest correlation (Tables B2; Appendix B). The seasonal correlations also showed a high contribution of dominance (M5) and species

composition (M3) to EMFI* in the winter and spring seasons. In contrast, diadromous species richness (M6), piscivorous species richness (M12) and piscivorous abundance (M14) were the metrics most poorly correlated with the index values.

The contribution of the metrics to the EMFI* values (Fig. 2) showed a great similarity between the winter and summer seasons, with no major changes observed across the three different study periods. However, zoobenthivorous species richness (M11), resident species richness (M7), marine migrant species richness (M8), resident species abundance (M9) and marine migrant species abundance (M10) showed changes in their average contribution to the EMFI*, with all of them being higher during the reference period. Species richness (M1), species composition (M3) and the abundance of zoobenthivorous species (M13) also showed some slight differences (change <10%) among the autumn season across the three periods. A similar pattern of metric contribution was observed in the autumn and spring seasons, although the average contribution of M13, M10 and M9 was notably higher in the CEP-1 than in the mortality-associated second period.

3.3. Spatio-temporal changes in ecological quality

The EMFI* values at the sampling sites ranged between 23 and 57 points for the whole study period, so the ecological status varied from bad to good quality (Table B3; Appendix B). The average EMFI* values ($\pm$ standard deviation) per period were 41.0 ± 5.70 for the reference period, 40.5 ± 5.93 for the CEP-1 and 39.0 ± 5.90 for the CEP-2 (Table 5; Fig. 3). Therefore, the overall ecological status of the Mar Menor shallow areas remained moderate across the whole study period.

A temporal analysis showed significant changes in the EMFI* values associated with the study periods (Fig. 3; Table 6). The EMFI* values obtained in the CEP-2 were significantly lower than those obtained in the reference period and in the CEP-1, but no significant differences were found between these latter two periods. Furthermore, significant interannual differences in the EMFI* were observed within the study periods, as well as within-year changes associated with seasonality (Table 6). Overall, spring was the season with the highest average EMFI* values (Table 5; Fig. 4), although no seasonal differences were observed

Table 4

Descriptive results showing family-level species richness (S), rankings by ordered density (Rk), mean density (D, numbers of fish per 100 m²) and relative proportion of the total abundance (%) for the fish families detected in shallow areas of the Mar Menor coastal lagoon (SE Spain). Results are provided for each of the three study periods (reference period; First Critical Eutrophic Period “CEP-1”; Second Critical Eutrophic Period “CEP-2”) as well as for the whole study period. Values of the five most important families for each parameter are highlighted in bold.

Fish families	Reference period (2002–2004)				CEP-1 (2018–2019)				CEP-2 (2020–2021)				Whole study period			
	S	Rk	D	%	S	Rk	D	%	S	Rk	D	%	S	Rk	D	%
Anguillidae	1	18	<0.1	<0.1	1	14	<0.1	<0.1	1	14	<0.1	<0.1	1	18	<0.1	<0.1
Atherinidae	1	3	16.9	9.7	1	2	27.5	24.5	1	3	11.3	8.4	1	3	18.6	13.6
Belonidae	1	11	<0.1	<0.1	2	10	0.2	0.2	2	13	<0.1	<0.1	2	12	0.1	0.1
Blennidae	2	7	1.8	1	2	8	0.7	0.7	4	8	1.7	1.2	4	9	1.4	1.0
Callionymidae	1	10	<0.1	<0.1	0	20	–	–	0	20	–	–	1	17	<0.1	<0.1
Carangidae	1	19	<0.1	<0.1	2	13	<0.1	<0.1	0	18	–	–	2	10	0.0	<0.1
Clupeidae	2	14	<0.1	<0.1	2	15	<0.1	<0.1	1	11	0.2	0.1	3	13	0.1	0.1
Cyprinodontidae	1	6	2.8	1.6	1	5	3	2.6	1	9	1.0	0.7	1	8	2.2	1.6
Engraulidae	1	13	<0.1	<0.1	1	6	2.4	2.1	1	5	7.5	5.5	1	6	3.7	2.7
Gobiidae	4	2	40.4	23.1	5	4	11.3	10.1	4	2	19.7	14.6	6	2	22.2	16.2
Labridae	2	9	0.1	0.1	1	9	0.3	0.3	2	4	8.2	6.0	3	7	3.2	2.3
Moronidae	2	8	0.9	0.5	1	11	0.1	0.1	1	10	0.2	0.1	2	11	0.3	0.2
Mugilidae	5	1	93	53.2	6	1	41.4	36.9	6	1	75.6	56.0	6	1	67.9	49.5
Mullidae	1	15	<0.1	<0.1	1	17	<0.1	<0.1	1	12	<0.1	<0.1	1	15	<0.1	<0.1
Poeciliidae	1	17	<0.1	<0.1	0	19	–	–	1	17	<0.1	<0.1	1	19	<0.1	<0.1
Pomatomidae	1	16	<0.1	<0.1	1	12	<0.1	<0.1	1	16	<0.1	<0.1	1	14	<0.1	<0.1
Serranidae	0	20	–	–	1	18	<0.1	<0.1	0	19	–	–	1	20	<0.1	<0.1
Soleidae	3	12	<0.1	<0.1	1	16	<0.1	<0.1	1	15	<0.1	<0.1	3	16	<0.1	<0.1
Sparidae	6	4	14.2	8.1	8	7	1.6	1.5	7	7	4.6	3.4	10	5	6.1	4.4
Syngnathidae	5	5	4.6	2.6	4	3	23.5	21	2	6	5.1	3.8	5	4	11.6	8.4
Species richness	41				41				37				55			
Total catches	86,371				74,759				93,385				254,515			
Mean density	174.7				112.0				135.1				137.4			

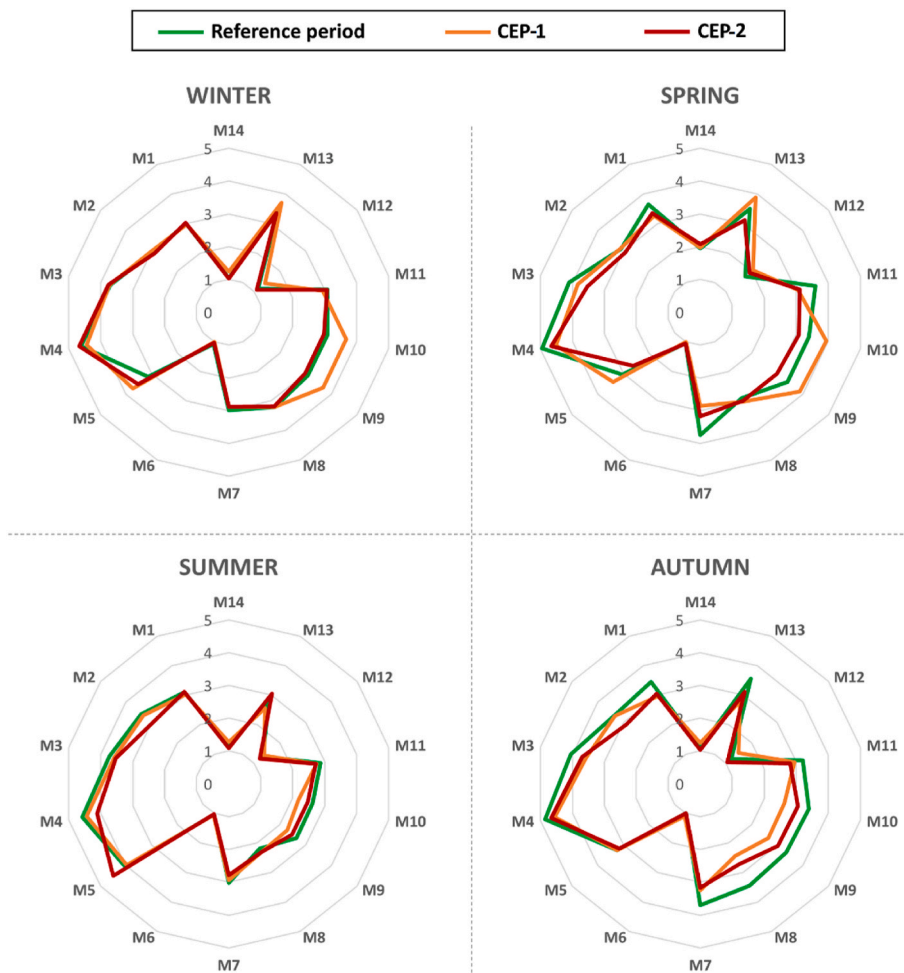


Fig. 2. Radar plots representing the seasonal contribution of the 14 metrics comprising the modified Estuarine Multi-metric Fish Index (EMFI*). Metric scores range from 1 to 5. Within each radar plot, the three assessed periods (reference period; First Critical Eutrophic Period “CEP-1”; Second Critical Eutrophic Period “CEP-2”) are represented through coloured polygons. M1 = Species richness; M2 = Conservation value of the fish assemblage; M3 = Species composition; M4 = Species abundance; M5 = Dominance; M6 = Number of diadromous species; M7 = Resident species richness; M8 = Marine migrant species richness; M9 = Resident species abundance; M10 = Marine migrant species abundance; M11 = Zoobenthivorous species richness; M12 = Piscivorous species richness; M13 = Zoobenthivores abundance; M14 = Piscivores abundance.

Table 5

Mean EMFI* values per season for each study period (reference period; First Critical Eutrophic Period “CEP-1”; Second Critical Eutrophic Period “CEP-2”) across shallow waters from the Mar Menor coastal lagoon. Standard deviation is included. The colour indicates the conservation status category assigned according to the EMFI*-EQR rescaling.

Seas	Reference period	CEP-1	CEP-2
Winter	40.3 ± 4.16	41.6 ± 4.68	39.5 ± 6.79
Spring	44.7 ± 4.80	43.8 ± 6.24	40.6 ± 5.03
Summer	38.9 ± 6.51	37.1 ± 5.42	37.4 ± 4.89
Autumn	43.1 ± 5.48	39.4 ± 5.24	38.4 ± 6.40
EMFI* (mean)	41.0 ± 5.70	40.5 ± 5.93	39.0 ± 5.90

for the CEP-2. Mean values of those EMFI* metrics with a relevant contribution to the final scores are provided in [Tables B4 and B5 – Appendix B](#).

Changes in the ecological quality of the shallow areas among the periods unevenly affected the sites with different levels of confinement (water renewal rates), as shown by the significant interaction between these two factors ([Fig. 5; Table 6](#)). In this context, the partially confined sites (confinement class 2, with a water renewal time between 300 and 350 days) showed a progressively steeper decrease in the EMFI* values, reaching the greatest differences during the CEP-2. During the summer season of both eutrophic periods, a slight decrease in the EMFI* values was observed in the more confined sites as compared to in other seasons. Furthermore, sites with higher water renewal rates obtained better ecological quality values during the winter and spring seasons. Finally,

the degree of anthropogenic pressure (represented by the shoreline type, urbanised areas *versus* natural saltmarshes) at the sampling sites did not appear to influence the EMFI* values. This factor also showed no interaction with the other temporal factors or the confinement level, so artificial and natural sites displayed similar patterns in their ecological quality ([Fig. B1; Appendix B; Table 6](#)).

4. Discussion

4.1. Metric response

Species richness and abundance were the most important metrics explaining variability in our fish-based multimetric index (EMFI*), with both showing the temporal stability of the fish community structure



Fig. 3. Overall temporal variation into the ecological status of the Mar Menor shallow waters based on an adapted version of the Estuarine Multimetric Fish Index (EMFI*). The bar chart shows the percentage of sampling sites included in each category of ecological status across the different study periods (reference period (2002–2004); First Critical Eutrophic Period “CEP-1” (2018–2019); and Second Critical Eutrophic Period “CEP-2” (2020–2021)).

Table 6

Parameters resulted from the five factors PERMANOVA tests based on the Estuarine Multi-metric Fish Index (EMFI*) values of the Mar Menor shallow areas. Factors are study period, season, confinement, anthropogenic pressure (shoreline type) and sampling-year (nested into the study period). Mean squares (MS), F-values (F), coefficient of determination (R^2) and degrees of freedom (df). Significance levels (P): * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Main factors	df	MS	R^2	F	P
Study Period	2	291	0.02	4.9	0.007**
Season	3	1245.3	0.09	13.9	<0.001***
Confinement	2	33.2	0.00	0.6	0.572
Shoreline type	1	1	0.00	0.0	0.855
Sampling-year (Study Period)	3	783.2	0.06	8.7	<0.001***
Interactions					
Study Period X Season	6	184.1	0.14	1.1	0.414
Study Period X Confinement	4	404	0.03	3.4	0.013*
Season X Confinement	6	432.2	0.03	2.4	0.024*
Study Period X Shoreline type	2	18.8	0.00	0.3	0.731
Season X Shoreline type	3	89.9	0.01	1.0	0.403
Sampling-year (Study Period) X Season	7	88.6	0.01	0.4	0.883
Sampling-year (Study Period) X Confinement	6	81.4	0.01	0.5	0.847
Study Period X Season X Confinement	12	381.9	0.03	1.1	0.381
Sampling-year (Study Period) X Shoreline type	3	47.4	0.00	0.5	0.662
Study Period X Season x Shoreline type	6	94.3	0.01	0.5	0.791
Sampling-year (Study Period) X Season X Confinement	14	263.5	0.02	0.6	0.843
Sampling-year (Study Period) X Season X Shoreline type	7	187.8	0.01	0.9	0.509
Residuals	300	8974.9	1.00		

associated with shallow areas despite changing environmental scenarios during the whole study period. Conversely, diadromous species richness was the metric with the lowest contribution to the EMFI*, which is attributed to the scarce occurrence of migratory species in our study area. In fact, a relatively low importance of diadromous fish has also been reported for other European estuaries and coastal lagoons, where migratory taxa account for only 9% of the overall species richness (Franco et al., 2008). Similarly, the metrics on the richness and abundance of piscivorous species also made a marginal contribution to the overall EMFI* score, as this trophic group of fish is scarcely represented

in coastal lagoons (Franco et al., 2008).

A recent multimetric fish-based index developed to assess the ecological status of coastal lagoons in Greece selected metrics associated with the life cycle of species (e.g., resident or marine migrant species abundance) as the most important contributors to the overall index score (Sapounidis and Koutrakis, 2021). As stated by these authors, fish species strongly rely upon shallow waters as feeding, reproduction and nursery grounds, so the environmental degradation of these habitats could greatly affect their abundance. Our results are in line with those of previous studies because the metrics on resident and marine migrant abundances were highly correlated with the index values, and these metrics also showed the highest variation among the study periods (Table B1; Appendix B; Fig. 2). These metrics increased in the winter and spring seasons in the CEP-1, probably as a response to forced movements of some fish from deeper and impaired habitats (Belando et al., 2019) to shallow waters whose less impacted bottoms may have acted as alternative habitats. However, the critical situation experienced during the warmer seasons in the CEP-2 period (algal blooms and mass mortality events) resulted in these metrics having decreased scores as compared to those of the reference period. This result is consistent with the worsening of eutrophic conditions due to the rising water table and the greater dispersion of nutrient inputs along the inner coast (Fernández-Alfás et al., 2022). Therefore, fish assemblages from Mar Menor shallow areas could be notably impaired if these critical eutrophic events become regular over time, impacting the ecosystem services provided by this coastal lagoon and leading to evident ecological and socioeconomic consequences.

4.2. Ecological status of shallow waters

Although fish-based multimetric indicators are widely applied to assess the ecological status of different aquatic environments, their use is continuously under debate (Puig-Girones and Real, 2022; Souza and Vianna, 2020). Some multimetric indices based on community structure may be too robust and not sensitive enough to reflect changes in fish assemblages, thus placing constraints on their ability to provide an early warning of certain anthropogenic impacts (Fonseca et al., 2013; Pérez-Ruzafa et al., 2019a). Moreover, transitional environments are particularly characterised by natural fluctuations in habitat conditions (the so-called “estuarine quality paradox”) (Dauvin and Ruellet, 2009), thus making pristine conditions difficult to distinguish from stressed conditions.

In this study, we found no drastic temporal changes in the ecological quality (i.e., the EMFI* values) of the Mar Menor shallow waters, despite the occurrence of critical eutrophic periods in recent years, including mortality events of aquatic fauna and meadows (Belando et al., 2019; Ruiz-Fernández et al., 2019). This result might be explained by the buffering role of the shallow waters under a generalised eutrophication process, providing alternative refuge habitats to fish moving from more impaired deeper waters. Though empirical evidence is required, this argument is supported by the following assumptions: Firstly, the massive mortality of meadows (macroalgae and seagrass) associated with eutrophic processes had no significant effects on the meadows in shallow perimeter areas (less than 2 m depth) (Belando et al., 2019; Mercado et al., 2021). Secondly, the bottom surface of shallow areas covered by seagrass meadows (mostly *C. nodosa*) increased during eutrophic periods and even expanded towards the coastline (Table 1). This fact could be due to a greater nutrient availability. Furthermore, lower incidence of sunlight reaching the bottom (promoted by a higher water turbidity), could have facilitated the spread of sunlight-sensitive macroalgae species (e.g., *C. prolifera*), as suggested by previous studies (García-Sánchez et al., 2012; Pérez-Ruzafa et al., 2012). Hence, this situation promoted the spread of seagrass meadows dominated by *C. nodosa* in shallow littoral areas, with these vegetated bottoms having already been reported to support a higher fish richness, abundance and biomass than unvegetated bottoms (Scapin et al., 2018; Verdiell-Cubedo

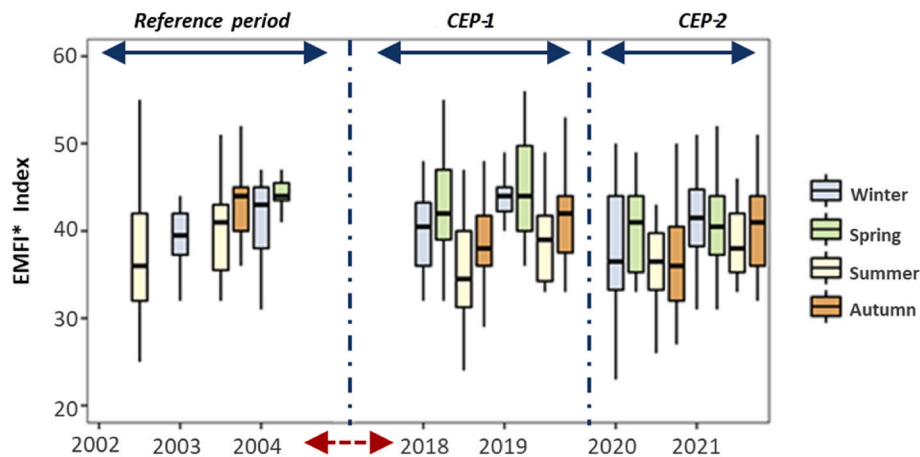


Fig. 4. Boxplot showing temporal changes in the ecological status of the Mar Menor shallow areas based on the Estuarine Multi-metric Fish Index (EMFI*) score. Data are represented on a seasonal time scale and divided into three study periods (reference period; First Critical Eutrophic Period “CEP-1”; Second Critical Eutrophic Period “CEP-2”).

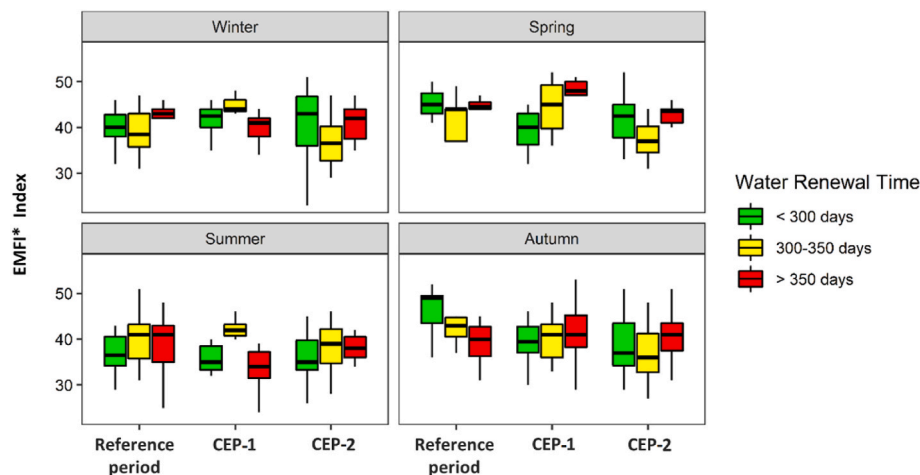


Fig. 5. Boxplots comparing the ecological status of the Mar Menor shallow areas in relation to the water renewal rate (confinement levels). The ecological status is measured through the modified Estuarine Multi-metric Fish Index (EMFI*). Boxplots are grouped in the study periods (reference period; First Critical Eutrophic Period “CEP-1”; Second Critical Eutrophic Period “CEP-2”), and each plot represents a season.

et al., 2007). Finally, the higher photosynthetic activity of these vegetated shallow areas, as compared to that of unvegetated deeper bottoms, resulted in a higher availability of dissolved oxygen. Therefore, our results together with the available evidence from the study area support the role of Mar Menor shallow waters as alternative refuge habitats for fish during the occurrence of critical eutrophic events impacting deeper bottoms.

Our analyses highlight the stability of the ecological quality of the shallow areas of the Mar Menor during the whole study period (the EMFI* values were similarly moderate across the three study periods), in contrast to the critical state observed in deeper bottoms of this coastal lagoon (Ruiz-Fernández et al., 2019). This result was not expected, as the strong and direct relationship between fish assemblages and submerged habitats suggested that fish-based indicators should respond negatively to meadow deterioration and bottom disturbance (Whitfield and Elliott, 2002). The loss of structural complexity and the homogenisation of aquatic habitats resulting from long-term eutrophication processes should have a direct impact on fish assemblages, since habitat heterogeneity has been identified as one of the main drivers of species diversity in lagoon communities (Bennett et al., 2001; Pelletier et al., 2020). A recovery in the ecological status of the Mar Menor coastal lagoon was suggested in 2018 following an assessment of long-term

dynamics of several parameters related to water quality (e.g. nutrients, chlorophyll *a* and others) (Pérez-Ruzafa et al., 2019a). However, this presumed improvement in the ecological quality contrasts with our results obtained from the fish-based index, since the lowest EMFI* values (i.e., poorest ecological quality) obtained here for the whole study period were just recorded in summer 2018. Hence, as compared to fish assemblages in shallow areas, water-quality parameters in deeper areas seem to respond dissimilarly to eutrophic events. These differences may be explained by the two following non-exclusive arguments, which could act synergistically: the existence of divergent dynamics between shallow areas and the rest of the lagoon (e.g., delayed eutrophication-related effects in shallow areas) or a dissimilar response of the assessed metrics (e.g., fish response later to eutrophication-related effects as compared to chlorophyll or nutrients).

4.3. Effects of confinement and anthropogenic pressure

The confinement or isolation of transitional environments has already been identified as a major factor affecting fish assemblage composition (Sheaves, 2016). In this context, the Mar Menor shows a lower water renewal time as compared to other larger coastal lagoons, so it would be expected a non-diverse community restricted by already

described low colonisation rates of individuals and species (García-Oliva et al., 2018; Pérez-Ruzafa et al., 2019a). However, a total of 55 fish species have been detected in the Mar Menor shallow waters. This relatively high fish diversity could be explained by the wide range of geomorphological and hydrographic variabilities characterising the Mar Menor, as well as the high environmental heterogeneity (Pérez-Ruzafa et al., 2019b), thus offsetting the isolation of their biological communities.

Although previous studies in this lagoon have already confirmed the effects of confinement on species richness, abundance and diversity of benthic fish assemblages, with highest values for these descriptors being observed in least confined areas (Pérez-Ruzafa et al., 2007), the ecological quality values obtained here using the fish-based indicator EMFI* showed a similar pattern regardless of the confinement degree. Despite several taxa of migrant fish (e.g., *Sparus aurata* and *Chelon auratus*) show patterns of spatial abundance associated with proximity to water exchange inlets (Verdiell-Cubedo et al., 2013b), these patterns were not sufficiently marked to affect the EMFI* scores, probably because most of the migrant fish species (as well as some resident fish) display routine colonisation movements between different shallow areas. This fact may also be explained by the important role of the currents and dynamics within the lagoon, as these factors seem to play a more important role for the ichthyoplankton structure and population genetic structure of some species as compared to the connectivity between the coastal lagoon and the Mediterranean sea (Pérez-Ruzafa et al., 2019b). However, the confinement regime seemed to have become more relevant in our seasonal analysis (Table 6; Fig. 5). For instance, the less confined areas obtained higher ecological quality values in the winter and spring seasons. These better scores are likely associated with their proximity to water exchange inlets, which promotes more diversified fish communities by incorporating migrant species with a more temporally concentrated recruitment phenology in these seasons, such as species from Mugilidae and Sparidae families (Verdiell-Cubedo et al., 2013a). These findings are also supported by previous studies of ichthyoplankton in the lagoon, which described highest species and family richness in areas with a greater connection to the Mediterranean sea (Pérez-Ruzafa et al., 2004). Moreover, we observed a decrease in the ecological quality of the most confined areas in summer under eutrophic conditions. An increasing water temperature triggers the depletion of dissolved oxygen (Brauko et al., 2020), which may force several fish species to move and seek refuge in more oxygenated areas (i.e., less confined sampling sites). Interestingly, our results are in contrast with those reported in other coastal lagoons and estuaries from tropical and subtropical regions, which are characterised by more stable water temperatures (warm conditions all throughout the year), and no seasonal effects of eutrophic and dissolved oxygen drops events have been observed to affect fish assemblages in these regions (Cabrera-Páez et al., 2021; James et al., 2008).

Unexpectedly, natural saltmarshes showed an ecological status similar to that observed in urbanised areas (recreational beaches), in contrast with previous studies conducted in the study area (Verdiell-Cubedo et al., 2012) and other transitional waters (Viana et al., 2010). In our case, this could be because the structural diversity and hard substrates provided by breakwaters and marine structures frequent on urban beaches, factors that promote the richness and diversity of benthic fish communities, as some authors suggest (Pérez-Ruzafa et al., 2006). The absence of differences in ecological quality across shallow waters dissimilarly impacted by anthropogenic pressures could also be attributed to the recent homogenisation of local habitat conditions caused by the increased input of nutrients and organic matter, which is much more marked in unmodified sites than in urbanised areas. Though human settlements are evenly distributed along the whole lagoon perimeter, our urbanised sampling sites were mostly concentrated in the eastern sector and close to the Mediterranean inlets, so the arrival of nutrients and organic matter is notably low due to the absence of agriculture fields in the drainage basin from this lagoon sector. However, some gregarious

species are often attracted to shallow waters receiving inputs of nutrients and organic matter (highly productive areas), as reported for *Engraulis encrasicolus* and Mugilidae species (Zorica et al., 2013), with the consequent effects of some metrics (e.g., dominance or marine migrant abundance) and a reduction in indicator values at natural sampling sites.

Overall, the spatial factors analysed in our study (the confinement regime and the degree of anthropogenic pressure) did not explain the major changes in the ecological quality of the Mar Menor shallow waters. This result highlights that the shallow areas of coastal lagoons, regardless of their confinement regime and degree of anthropogenic pressure, are equally important for fish assemblages during critical eutrophic periods, as they provide an alternative habitat for estuarine biota.

4.4. Shallow areas as critical refuge for fish

Eutrophication effects do not always lead to the rapid loss of ecological quality in coastal lagoons or the impairment of fish assemblages, though this human-derived disturbance often affects the bottom composition and benthic communities (Ishitobi et al., 2000). However, the long-term persistence of this threat may have particularly negative effects on the ecological integrity of shallow areas because bottom conditions (e.g., vegetation cover or substrate coarseness) have been reported to be major drivers of fish assemblage structures and species distributions (Becheker et al., 2022), being even more important than other abiotic variables, such as salinity, water temperature and dissolved oxygen. In our study area, the most frequent resident fish families (Atherinidae, Gobiidae and Syngnathidae) are also the most affected by anoxic conditions. Continued and mass mortality events occurred during the CEP-2, leading to evident changes in the fish densities of these families (Fig. 6). Despite some of these families showing high densities before the mass mortality events (i.e., Syngnathidae), their populations experienced a steep decline after these critical eutrophic events. Among this resident families, only Gobiidae showed occasional high density values in summer 2021, related to the peak of catches of *Gobius niger*, a species characteristic of deeper areas and which found refuge in shallow areas before the mortality that happened weeks later. In contrast, marine migrant fish families (Mugilidae and Sparidae) continued to display their usual inter-annual fluctuations with an erratic unclear pattern. The life-history traits of resident species make them particularly vulnerable to eutrophic events, and recolonisation processes and the establishment of new species in previously impacted shallow areas can be really difficult (Pollom et al., 2021). Most of these species are exclusive to coastal lagoons or estuarine environments, and they are rare in offshore waters, thus hampering recolonisation from adjacent coastal wetlands or streams. In fact, the limited connectivity between the Mar Menor coastal lagoon and the Mediterranean sea, as well as the low dispersal ability of these species during the larval stage, does not facilitate the influx of these species (Pérez-Ruzafa et al., 2019b). Conversely to coastal lagoons, recovery post-eutrophication process can be faster in freshwater lotic ecosystems. For example, some authors have assessed the ecological resilience of rivers after pollution or defaunation events, reporting recolonisation processes of fish communities in a few months or even weeks (Erős et al., 2015; Piller and Geheber, 2015). Fast recolonisation rates have also been reported in lentic environments, such as lakes, although recolonisation success was hindered by the low reproduction of some freshwater species (Kristensen et al., 2020). This high resilience of freshwater fish assemblages is mostly linked to morphological and ecological traits that provide them with the ability to disperse and migrate along the watercourse and to even use other adjacent aquatic ecosystems, such as tributaries or small streams, that can act as alternative refuge habitats (source areas) and assist subsequent recolonisation (Piller and Geheber, 2015).

Previous studies have also reported the movement of fish in search of refuge areas during hypoxic situations (Thiem et al., 2020). In our study



Fig. 6. Bar charts represent the interannual and seasonal changes in average fish density (number of fish per 100 m²) and standard error of the most relevant families (Mugilidae, Sparidae, Atherinidae, Gobiidae, Syngnathidae and Labridae) in shallow waters of the Mar Menor coastal lagoon across the study period.

case, high scores on some EMFI* metrics (e.g. species richness) were maintained in shallow waters due to the arrival of fish species that usually inhabit deeper waters (e.g. *Gobius niger* and *Symphodus cinereus*). This movement could be triggered by hypoxic processes generated by the eutrophication of the lagoon. The peaks in the density of Gobiidae and Labridae species, not typically from shallow waters, that occurred just before the mortality events of autumn 2019 and summer 2022 suggest that shallow oxygenated areas played a key role as a refuge habitat for these taxa (Fig. 6). This assumption is also supported by field observations concerning the aquatic surface respiration of these species during severe hypoxia periods, as well as their higher eutrophication-mediated mortality rates recorded in prospective transects conducted along impacted sampling sites during critical hypoxia events (unpublished results). Moreover, further studies carried out in the Mar Menor coastal lagoon during recent eutrophic periods found a negative correlation between ichthyoplankton abundance and chlorophyll and nutrient concentrations in the water column (Pérez-Ruzafa et al., 2019a). Hence, the higher density of these species in shallow

waters during eutrophic events was mediated by fish movement from deeper waters instead of a greater juvenile recruitment due to potential reproductive pulses of these species. Depth and vegetation cover have been ranked as important drivers in structuring fish assemblages in mediterranean coastal lagoons with similar fish communities (Selfati et al., 2019). In this context, recurrent eutrophication processes may promote the prolonged occurrence of typically deeper-water fish species (e.g., *Symphodus cinereus* and *Gobius niger*) in shallow areas, thus leading to increased interspecific interactions with typically shallow-water fish (e.g., *Syngnathus abaster* and *Pomatoschistus marmoratus*). The coexistence in shallow areas of species with different functional traits and habitat selection could threaten the community structure and the survival of less competitive species. Further research should assess the potential effects of these increased interactions (e.g., resource competition) on the structure and composition of fish assemblages in shallow waters.

Future management actions targeting this coastal lagoon, which is highly impacted by eutrophication processes, should consider shallow

areas to be critical habitats for aquatic biota. Such littoral waters provide multiple ecosystem services, including the recruitment and fattening of fish with a high economic value (Guerrero-Gómez et al., 2022). Moreover, shallow waters could play a pivotal role as buffers and refuge habitats during eutrophication processes not only for fish assemblages but also for other aquatic taxa (e.g., crustaceans, molluscs and echinoderms). Likewise, shallow littoral waters could be considered source sites for assisting natural recolonisation processes after eutrophic events, thus facilitating the ecological restoration of deeper lagoon waters. Therefore, the effective management of these critical habitats and their associated biotic communities requires an adequate surveillance of points of pollution and nutrient discharge, as well as the implementation of nature-based solutions for restoring adjacent salt-marshes (Álvarez-Rogel et al., 2020). Some of these actions have already been successfully implemented in other coastal lagoons to safeguard threatened fish species and valuable fish habitats (De Villiers et al., 2019).

5. Conclusions

The slight decrease in the ecological quality of the Mar Menor shallow areas observed during the recent eutrophic episodes, even after the mass mortality events, indicates that shallow littoral habitats have a great buffering ability to cope with high turbidity and euxinic conditions. However, the intensification of eutrophic conditions during the warmer seasons promoted the water renewal rate to act as an important driver of seasonal changes in the ecological status. In addition to the ecosystem services already known to be provided by shallow areas, these nearshore habitats could play an alternative role as refuge areas for fish assemblages during euxinic crises in the Mar Menor. This attribute further reinforces the need to properly manage and protect these critical habitats, not only for their key role as source and recruitment areas for the short-term recovery of fish assemblages in the lagoon ecosystem as a whole but also for the benefit of other biotic components. However, it should be considered that the long-term persistence of eutrophic episodes may undermine the resilience of the coastal lagoon and hamper natural recolonisation processes by fish communities. In addition, it should be noted that the seasonal dynamism of fish assemblages observed in shallow areas and the holistic approach characteristic of fish-based indices could be masking taxonomic-level impacts, thus hindering the detection of fish community simplification processes or the loss of functional integrity that may be occurring in the Mar Menor coastal lagoon.

CRedit authorship contribution statement

Antonio Zamora-López: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Adrián Guerrero-Gómez:** Methodology, Formal analysis, Data curation. **Mar Torralva:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **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.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgement

The authors are grateful to other members of the Department of Zoology and Physical Anthropology of the University of Murcia for their help in field sampling and laboratory processing. Part of this research was supported by the Environmental Service and Mar Menor Service of the Government of the Autonomous Community of Murcia (CARM, Spain) and the contract “Estudio del estado de la ictiofauna indicadora de zonas someras, mejora de la información y aplicación en la redacción de proyectos en zona sumergida del Mar Menor” (TRAGSATEC). J.M. Z.-M. is supported by a postdoctoral grant funded by the Spanish Ministry of Science and Innovation and the European Union NextGeneration EU/PRTR (FJC 2021-046923-I).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2023.108447>.

References

- Álvarez-Rogel, J., Barberá, G.G., Maxwell, B., Guerrero-Brotóns, M., Díaz-García, C., Martínez-Sánchez, J.J., Sallent, A., Martínez-Ródenas, J., González-Alcaraz, M.N., Jiménez-Cárceles, F.J., Tercero, C., Gómez, R., 2020. The case of Mar Menor eutrophication: state of the art and description of tested Nature-Based Solutions. *Ecol. Eng.* 158, 106086 <https://doi.org/10.1016/j.ecoleng.2020.106086>.
- Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). *Wiley StatsRef Stat.* <https://doi.org/10.1002/9781118445112.stat07841>. Ref. Online 1–15.
- Becheker, A., Chaoui, L., Kara, M.H., 2022. The profiles of occupancy by fish fauna of four shallow coastal habitats at a limited regional scale in the south-western Mediterranean. *Reg. Stud. Mar. Sci.* 51, 102195 <https://doi.org/10.1016/j.rsma.2022.102195>.
- Belando, M.D., Ruiz, J.M., Muñoz, R., Segura, A., Esteller, J., Casero, J., Guirao, L., Moreno, P., Navarro, I., Nuez, E., Mercado, J., 2019. Collapse of macrophytic communities in a eutrophicated coastal lagoon. *Front. Mar. Sci. Conference Abstract: XX Iberian Symposium on Marine Biology Studies (SIEBM XX)*. <https://doi.org/10.3389/conf.fmars.2019.08.00192>.
- Bennett, E., Carpenter, S., Caraco, N., 2001. Human impact on erodable phosphorus and eutrophication: a global perspective. *Bioscience* 51, 227–234. [https://doi.org/10.1641/0006-3568\(2001\)051](https://doi.org/10.1641/0006-3568(2001)051).
- Bilkovic, D.M., Roggero, M.M., 2008. Effects of coastal development on nearshore estuarine nekton communities. *Mar. Ecol. Prog. Ser.* 358, 27–39. <https://doi.org/10.3354/meps07279>.
- Brauko, K.M., Cabral, A., Costa, N.V., Hayden, J., Dias, C.E.P., Leite, E.S., Westphal, R.D., Mueller, C.M., Hall-Spencer, J.M., Rodrigues, R.R., Röhr, L.R., Pagliosa, P.R., Fonseca, A.L., Alarcon, O.E., Horta, P.A., 2020. Marine heatwaves, sewage and eutrophication combine to trigger deoxygenation and biodiversity loss: a SW Atlantic case study. *Front. Mar. Sci.* 7, 1–11. <https://doi.org/10.3389/fmars.2020.590258>.
- Cabrera-Páez, Y., Aguilar-Betancourt, C.M., González-Sansón, G., Hinojosa-Larios, A., 2021. Spatial and seasonal variation in littoral fish assemblages of four estuarine lagoons on the Mexican Pacific coast. *Reg. Stud. Mar. Sci.* 48 <https://doi.org/10.1016/j.rsma.2021.102000>.
- Dauvin, J.C., Ruellet, T., 2009. The estuarine quality paradox: is it possible to define an ecological quality status for specific modified and naturally stressed estuarine ecosystems? *Mar. Pollut. Bull.* 59, 38–47. <https://doi.org/10.1016/j.marpolbul.2008.11.008>.
- De Villiers, N.M., Barker, C., Claassens, L., Hodgson, A.N., 2019. Conservation value of Codium tenue habitat for the endangered Knysna seahorse Hippocampus capensis. *J. Fish. Biol.* 95, 1457–1464. <https://doi.org/10.1111/jfb.14165>.
- Elliott, M., 2007. An overview of the status, study and management of fishes in estuaries. *Fishes in Estuaries* 555–575. <https://doi.org/10.1002/9780470995228.ch10>.
- Elliott, M., Whitfield, A.K., 2011. Challenging paradigms in estuarine ecology and management. *Estuar. Coast Shelf Sci.* 94, 306–314. <https://doi.org/10.1016/j.ecss.2011.06.016>.
- Erős, T., Takács, P., Czeglédi, I., Sály, P., Specziár, A., 2015. Taxonomic- and trait-based recolonization dynamics of a riverine fish assemblage following a large-scale human-mediated disturbance: the red mud disaster in Hungary. *Hydrobiologia* 758, 31–45. <https://doi.org/10.1007/s10750-015-2262-9>.
- Fernández-Alfás, A., Montaña-Barroso, T., Conde-Caño, M.R., Manchado-Pérez, S., López-Galindo, C., Quispe-Becerra, J.I., Marcos, C., Pérez-Ruzafa, A., 2022. Nutrient overload promotes the transition from top-down to bottom-up control and triggers dystrophic crises in a Mediterranean coastal lagoon. *Sci. Total Environ.* 846, 157388 <https://doi.org/10.1016/j.scitotenv.2022.157388>.
- Ferrarin, C., Bajo, M., Bellafiore, D., Cucco, A., De Pascalis, F., Ghezzi, M., Umgieser, G., 2014. Toward homogenization of Mediterranean lagoons and their loss of hydrodiversity. *Geophys. Res. Lett.* 41, 5935–5941. <https://doi.org/10.1002/2014GL060843>.
- Fonseca, V.F., Vasconcelos, R.P., Gamito, R., Pasquaud, S., Gonçalves, C.I., Costa, J.L., Costa, M.J., Cabral, H.N., 2013. Fish community-based measures of estuarine

- ecological quality and pressure-impact relationships. *Estuar. Coast Shelf Sci.* 134, 128–137. <https://doi.org/10.1016/j.ecss.2013.02.001>.
- Franco, A., Franzoi, P., Malavasi, S., Riccato, F., Torricelli, P., Mainardi, D., 2006. Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. *Estuar. Coast Shelf Sci.* 66, 67–83. <https://doi.org/10.1016/j.ecss.2005.07.020>.
- Franco, A., Elliott, M., Franzoi, P., Torricelli, P., 2008. Life strategies of fishes in European estuaries: the functional guild approach. *Mar. Ecol. Prog. Ser.* 354, 219–228. <https://doi.org/10.3354/meps07203>. %W <Go.
- Franco, A., Pérez-Ruzafa, A., Drouineau, H., Franzoi, P., Koutrakis, E.T., Lepage, M., Verdiell-Cubedo, D., Bouchouca, M., López-Capel, A., Riccato, F., Sapounidis, A., Marcos, C., Oliva-Paterna, F.J., Torralva-Forero, M., Torricelli, P., 2012. Assessment of fish assemblages in coastal lagoon habitats: effect of sampling method. *Estuar. Coast Shelf Sci.* 112, 115–125. <https://doi.org/10.1016/j.ecss.2011.08.015>.
- García-Oliva, M., Pérez-Ruzafa, A., Umgieser, G., McKiver, W., Ghezzi, M., De Pascalis, F., Marcos, C., 2018. Assessing the hydrodynamic response of the Mar Menor lagoon to dredging inlets interventions through numerical modelling. *Water* 10, 1–33. <https://doi.org/10.3390/w10070959>.
- García-Sánchez, M., Korb, N., Pérez-Ruzafa, I.M., Marcos, C., Domínguez, B., Figueroa, F.L., Pérez-Ruzafa, A., 2012. Physiological response and photoacclimation capacity of *Caulerpa prolifera* (forsskål) J.V. Lamouroux and *Cymodocea nodosa* (ucris) ascherson meadows in the mar menor lagoon (SE Spain). *Mar. Environ. Res.* 79, 37–47. <https://doi.org/10.1016/j.marenvres.2012.05.001>.
- Guerrero-Gómez, A., Zamora-López, A., Guillén-Beltrán, A., Zamora-Marín, J.M., Sánchez-Pérez, A., Torralva, M., Oliva-Paterna, F.J., 2022. An updated checklist of YOY fish occurrence in the shallow perimetral areas of the Mar Menor (Western Mediterranean Sea). *Limnética* 41, 101–106. <https://doi.org/10.23818/limn.41.08>.
- Hallett, C.S., Valesini, F.J., Clarke, K.R., Hesp, S.A., Hoeksema, S.D., 2012. Development and validation of fish-based, multimetric indices for assessing the ecological health of Western Australian estuaries. *Estuar. Coast Shelf Sci.* 104–105, 102–113. <https://doi.org/10.1016/j.ecss.2012.03.006>.
- Harrison, T.D., Kelly, F.L., 2013. Development of an estuarine multi-metric fish index and its application to Irish transitional waters. *Ecol. Indic.* 34, 494–506. <https://doi.org/10.1016/j.ecolind.2013.06.018>.
- Ishitobi, Y., Hiratsuka, J.-I., Kuwabara, H., Yamamuro, M., 2000. Comparison of fish fauna in three areas of adjacent eutrophic estuarine lagoons with different salinities. *J. Mar. Res.* 26, 171–181.
- James, N.C., Whitfield, A.K., Cowley, P.D., 2008. Long-term stability of the fish assemblages in a warm-temperate South African estuary. *Estuar. Coast Shelf Sci.* 76, 723–738. <https://doi.org/10.1016/j.ecss.2007.07.036>.
- Jordan, S.J., Peterson, M.S., 2012. Contributions of estuarine habitats to major fisheries. *Estuaries Classif. Ecol. Hum. Impacts* 75–91.
- Kristensen, E., Sand-Jensen, K., Kristensen, J.S.B., Pedersen, M.E., Baastrup-Spohr, L., Kragh, T., 2020. Early fish colonization and community development in a shallow re-established lake. *Ecol. Eng.* 155, 105956. <https://doi.org/10.1016/j.ecoleng.2020.105956>.
- Lemley, D.A., Adams, J.B., Strydom, N.A., 2017. Testing the efficacy of an estuarine eutrophic condition index : does it account for shifts in flow conditions. *Ecol. Indic.* 74, 357–370. <https://doi.org/10.1016/j.ecolind.2016.11.034>.
- Lepage, M., Harrison, T., Breine, J., Cabral, H., Coates, S., Galván, C., García, P., Jager, Z., Kelly, F., Mosch, E.C., Pasquaud, S., Scholle, J., Uriarte, A., Borja, A., 2015. An approach to intercalibrate ecological classification tools using fish in transitional water of the North East Atlantic. *Ecol. Indic.* 67, 318–327. <https://doi.org/10.1016/j.ecolind.2016.02.055>.
- Lewis, D.M., Thompson, K.A., MacDonald, T.C., Cook, G.S., 2021. Understanding shifts in estuarine fish communities following disturbances using an ensemble modeling framework. *Ecol. Indic.* 126, 107623. <https://doi.org/10.1016/j.ecolind.2021.107623>.
- Limburg, K.E., Hughes, R.M., Jackson, D.C., Czech, B., 2015. Human population increase, economic growth, and fish conservation: collision course or savvy stewardship? *Fisheries* 36, 27–35. <https://doi.org/10.1577/03632415.2011.10389053>.
- Marcos, C., Torres, I., López-Capel, A., Pérez-Ruzafa, A., 2015. Long term evolution of fisheries in a coastal lagoon related to changes in lagoon ecology and human pressures. *Rev. Fish Biol. Fish.* 25, 689–713. <https://doi.org/10.1007/s11160-015-9397-7>.
- Martínez-López, J., Martínez-Fernández, J., Naimi, B., Carreño, M.F., Esteve, M.A., 2015. An open-source spatio-dynamic wetland model of plant community responses to hydrological pressures. *Ecol. Model.* 306, 326–333. <https://doi.org/10.1016/j.ecolmodel.2014.11.024>.
- Ménesguen, A., Lacroix, G., 2018. Modelling the marine eutrophication: a review. *Sci. Total Environ.* 636, 339–354. <https://doi.org/10.1016/j.scitotenv.2018.04.183>.
- Mercado, J.M., Cortés, D., Gómez-Jakobsen, F., García-Gómez, C., Ouaissa, S., Yebra, L., Ferrera, I., Válcárcel-Pérez, N., López, M., García-Muñoz, R., Ramos, A., Bernardeau, J., Belando, M.D., Fraile-Nuez, E., Ruíz, J.M., 2021. Role of small-sized phytoplankton in triggering an ecosystem disruptive algal bloom in a Mediterranean hypersaline coastal lagoon. *Mar. Pollut. Bull.* 164. <https://doi.org/10.1016/j.marpolbul.2021.111989>.
- Newton, A., Icely, J., Cristina, S., Brito, A., Cardoso, A.C., Colijn, F., Riva, S.D., Gertz, F., Hansen, J.W., Holmer, M., Ivanova, K., Leppäkoski, E., Canu, D.M., Mocenni, C., Mudge, S., Murray, N., Pejrup, M., Razinkovas, A., Reizopoulou, S., Pérez-Ruzafa, A., Schernewski, G., Schubert, H., Carr, L., Solidoro, C., Viaroli, P., Zaldivar, J.M., 2014. An overview of ecological status, vulnerability and future perspectives of European large shallow, semi-enclosed coastal systems, lagoons and transitional waters. *Estuar. Coast Shelf Sci.* 140, 95–122. <https://doi.org/10.1016/j.ecss.2013.05.023>.
- Newton, A., Brito, A.C., Icely, J.D., Derolez, V., Clara, I., Angus, S., Schernewski, G., Inácio, M., Lillebø, A.I., Sousa, A.I., Béjaoui, B., Solidoro, C., Tosic, M., Cañedo-Argüelles, M., Yamamuro, M., Reizopoulou, S., Tseng, H.C., Canu, D., Roselli, L., Maanan, M., Cristina, S., Ruiz-Fernández, A.C., Lima, R.F.d., Kjerfve, B., Rubio-Cisneros, N., Pérez-Ruzafa, A., Marcos, C., Pastres, R., Pranovi, F., Snoussi, M., Turpie, J., Tuckhovenko, Y., Dyack, B., Brookes, J., Povilanskas, R., Khokhlov, V., 2018. Assessing, quantifying and valuing the ecosystem services of coastal lagoons. *J. Nat. Conserv.* 44, 50–65. <https://doi.org/10.1016/j.jnc.2018.02.009>.
- Oksanen, J., Guillaume Blanchet, F., Friendly, Michael, Kindt, Roeland, Legendre, Pierre, McGinn, Dan, Peter, R., Minchin, R., O'Hara, B., Simpson, Gavin L., Peter, Solymos, Henry, M., Stevens, E.S., 2019. *Vegan: Community Ecology Package*. R Package Version 2.5-4.
- Pelletier, D., Selmaoui-Folcher, N., Bockel, T., Schohn, T., 2020. A regionally scalable habitat typology for assessing benthic habitats and fish communities: application to New Caledonia reefs and lagoons. *Ecol. Evol.* 10, 7021–7049. <https://doi.org/10.1002/ece3.6405>.
- Pérez-Domínguez, R., MacÍ, S., Courrat, A., Lepage, M., Borja, A., Uriarte, A., Neto, J.M., Cabral, H., Straykov, V., Franco, A., Alvarez, M.C., Elliott, M., 2012. Current developments on fish-based indices to assess ecological quality status of estuaries and lagoons. *Ecol. Indic.* 23, 34–45. <https://doi.org/10.1016/j.ecolind.2012.03.006>.
- Pérez-Ruzafa, A., Quispe-Becerra, J.I., García-Charton, J.A., Marcos, C., Pérez-Ruzafa, A., Quispe-Becerra, J.I., García-Charton, J.A., Marcos, C., 2004. Composition, structure and distribution of the ichthyoplankton in a Mediterranean coastal lagoon. *J. Fish. Biol.* 64, 202–218. <https://doi.org/10.1111/j.1095-8649.2004.00301.x>.
- Pérez-Ruzafa, A., Marcos, C., Gilabert, J., 2005. *The ecology of the Mar Menor coastal lagoon: a fast changing ecosystem under human pressure*. In: Gönenç, I.E., Wolfli, J. P. (Eds.), *Coastal Lagoons. Ecosystem Processes and Modeling for Sustainable Use and Development*. CRC Press, Boca Raton, pp. 392–422.
- Pérez-Ruzafa, A., García-Charton, J.A., Barcala, E., Marcos, C., 2006. Changes in benthic fish assemblages as a consequence of coastal works in a coastal lagoon: the Mar Menor (Spain, Western Mediterranean). *Mar. Pollut. Bull.* 53, 107–120. <https://doi.org/10.1016/j.marpolbul.2005.09.014>.
- Pérez-Ruzafa, A., Marcos, C., Pérez-Ruzafa, I.M., Barcala, E., Hegazi, M.I., Quispe, J., 2007. Detecting changes resulting from human pressure in a naturally quick-changing and heterogeneous environment: spatial and temporal scales of variability in coastal lagoons. *Estuar. Coast Shelf Sci.* 75, 175–188. <https://doi.org/10.1016/j.ecss.2007.04.030>.
- Pérez-Ruzafa, A., Marcos, C., Bernal, C.M., Quintino, V., Freitas, R., Rodrigues, A.M., García-Sánchez, M., Pérez-Ruzafa, I.M., 2012. *Cymodocea nodosa* vs. *Caulerpa prolifera*: causes and consequences of a long term history of interaction in macrophyte meadows in the Mar Menor coastal lagoon (Spain, southwestern Mediterranean). *Estuar. Coast Shelf Sci.* 110, 101–115. <https://doi.org/10.1016/j.ecss.2012.04.004>.
- Pérez-Ruzafa, A., Campillo, S., Fernández-Palacios, J.M., García-Lacunza, A., García-Oliva, M., Ibañez, H., Navarro-Martínez, P.C., Pérez-Marcos, M., Pérez-Ruzafa, I.M., Quispe-Becerra, J.I., Sala-Mirete, A., Sánchez, O., Marcos, C., 2019a. Long-term dynamic in nutrients, chlorophyll a, and water quality parameters in a coastal lagoon during a process of eutrophication for decades, a sudden break and a relatively rapid recovery. *Front. Mar. Sci.* 6, 1–23. <https://doi.org/10.3389/fmars.2019.00026>.
- Pérez-Ruzafa, A., De Pascalis, F., Ghezzi, M., Quispe-Becerra, J.I., Hernández-García, R., Muñoz, I., Vergara, C., Pérez-Ruzafa, I.M., Umgieser, G., Marcos, C., 2019b. Connectivity between coastal lagoons and sea: asymmetrical effects on assemblages' and populations' structure. *Estuar. Coast Shelf Sci.* 216, 171–186. <https://doi.org/10.1016/j.ecss.2018.02.031>.
- Pérez-Ruzafa, A., Morkune, R., Marcos, C., Pérez-Ruzafa, I.M., Razinkovas-Baziukas, A., 2020. Can an oligotrophic coastal lagoon support high biological productivity? Sources and pathways of primary production. *Mar. Environ. Res.* 153. <https://doi.org/10.1016/j.marenvres.2019.104824>.
- Piller, K.R., Geheber, A.D., 2015. Black liquor and the hangover effect: fish assemblage recovery dynamics following a pulse disturbance. *Ecol. Evol.* 5, 2433–2444. <https://doi.org/10.1002/ece3.1530>.
- Pollom, R.A., Ralph, G.M., Pollock, C.M., Vincent, A.C.J., 2021. Global extinction risk for seahorses, pipefishes and their near relatives (Syngnathiformes). *Oryx* 55, 497–506. <https://doi.org/10.1017/S0030605320000782>.
- Puig-Girones, R., Real, J., 2022. A comprehensive but practical methodology for selecting biological indicators for long-term monitoring. *PLoS One* 17, 1–19. <https://doi.org/10.1371/journal.pone.0265246>.
- Říha, M., Kubečka, J., Mrkvička, T., Prchalová, M., Čech, M., Draštil, V., Frouzová, J., Hladík, M., Hohašová, E., Jarolím, O., Jůza, T., Kratochvíl, M., Peterka, J., Tušer, M., Vašek, M., 2008. Dependence of beach seine net efficiency on net length and diel period. *Aquat. Living Resour.* 21, 411–418. <https://doi.org/10.1051/alr:2008061>.
- Roset, N., Grenouillet, G., Goffaux, D., Pont, D., Kestemont, P., 2007. A review of existing fish assemblage indicators and methodologies. *Fish. Manag. Ecol.* 14, 393–405. <https://doi.org/10.1111/j.1365-2400.2007.00589.x>.
- Ruiz-Fernández, J., León, V., Marín-Guirao, L., Giménez-Casado, F., Rogel, J., Esteve-Selma, M., Gómez-Cerezo, R., Robledano-Aymerich, F., González-Barberá, G., Martínez-Fernández, J., 2019. *Synthesis Report of the Current State of Mar Menor Lagoon and its Causes in Relation to the Nutrient Contents*. Murcia.
- Sapounidis, A.S., Koutrakis, E.T., 2021. Development of a fish-based multimetric index for the assessment of lagoons' ecological quality in northern Greece. *Water (Switzerland)* 13. <https://doi.org/10.3390/w13213008>.
- Scapin, L., Zucchetto, M., Sfriso, A., Franzoi, P., 2018. Local habitat and seascape structure influence seagrass fish assemblages in the venice lagoon: the importance of conservation at multiple spatial scales. *Estuar. Coast* 41, 2410–2425. <https://doi.org/10.1007/s12237-018-0434-3>.

- Selfati, M., El Ouamari, N., Franco, A., Lenfant, P., Lecaillon, G., Mesfioui, A., Boissery, P., Bazairi, H., 2019. Fish assemblages of the Marchica lagoon (Mediterranean, Morocco): spatial patterns and environmental drivers. *Reg. Stud. Mar. Sci.* 32 <https://doi.org/10.1016/j.rsma.2019.100896>.
- Sheaves, M., 2016. Simple processes drive unpredictable differences in estuarine fish assemblages: baselines for understanding site-specific ecological and anthropogenic impacts. *Estuar. Coast Shelf Sci.* 170, 61–69. <https://doi.org/10.1016/j.ecss.2015.12.025>.
- Sheaves, M., Baker, R., Nagelkerken, I., Connolly, R.M., 2014. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. *Estuar. Coast* 38, 401–414. <https://doi.org/10.1007/s12237-014-9846-x>.
- Souza, G.B.G., Vianna, M., 2020. Fish-based indices for assessing ecological quality and biotic integrity in transitional waters: a systematic review. *Ecol. Indic.* 109, 105665 <https://doi.org/10.1016/j.ecolind.2019.105665>.
- Thiem, J.D., Wooden, L.J., Baumgartner, L.J., Butler, G.L., Taylor, M.D., Watts, R.J., 2020. Hypoxic conditions interrupt flood-response movements of three lowland river fish species: implications for flow restoration in modified landscapes. *Ecohydrology* 13, 1–10. <https://doi.org/10.1002/eco.2197>.
- Verdiell-Cubedo, D., Oliva-Paterna, F.J., Torralva-Forero, M., 2007. Fish assemblages associated with *Cymodocea nodosa* and *Caulerpa prolifera* meadows in the shallow areas of the Mar Menor coastal lagoon. *Limnética* 26, 341–350.
- Verdiell-Cubedo, D., Torralva, M., Andreu-Soler, A., Oliva-Paterna, F.J., 2012. Effects of shoreline urban modification on habitat structure and fish community in littoral areas of a mediterranean coastal lagoon (Mar Menor, Spain). *Wetlands* 32, 631–641. <https://doi.org/10.1007/s13157-012-0296-6>.
- Verdiell-Cubedo, D., Oliva-Paterna, F.J., Ruiz-Navarro, A., Torralva, M., 2013a. Assessing the nursery role for marine fish species in a hypersaline coastal lagoon (Mar Menor, Mediterranean Sea). *Mar. Biol. Res.* 9, 739–748. <https://doi.org/10.1080/17451000.2013.765580>.
- Verdiell-Cubedo, D., Torralva, M., Ruiz-Navarro, A., Oliva-Paterna, F.J., 2013b. Fish assemblages in different littoral habitat types of a hypersaline coastal lagoon (Mar Menor, Mediterranean Sea). *Ital. J. Zool.* 80, 104–116. <https://doi.org/10.1080/11250003.2012.686525>.
- Viana, A.P., Lucena Frédou, F., Frédou, T., Torres, M.F., Bordalo, A.O., 2010. Fish fauna as an indicator of environmental quality in an urbanised region of the Amazon estuary. *J. Fish. Biol.* 76, 467–486. <https://doi.org/10.1111/j.1095-8649.2009.02487.x>.
- Whitfield, A.K., Elliott, M., 2002. Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. *J. Fish. Biol.* 61, 229–250. <https://doi.org/10.1006/jfbi.2002.2079>.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790. <https://doi.org/10.1126/science.1132294>.
- Zorica, B., Vilibić, I., Keč, V.Č., Šepić, J., 2013. Environmental conditions conducive to anchovy (*Engraulis encrasicolus*) spawning in the Adriatic Sea. *Fish. Oceanogr.* 22, 32–40. <https://doi.org/10.1111/fog.12002>.