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Season and seagrass: drivers of fish assemblage structure in the Banc d'Arguin, Mauritania☆

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ABSTRACT

The Banc d'Arguin is the most ecologically significant coastal wetland of West Africa, a UNESCO Marine World Heritage area with one of the most extensive seagrass areas on Earth, used by many marine species as breeding and/or feeding habitat. However, little is known about the subtidal biodiversity supported by these extensive seagrass meadows. This study aimed to assess the influence of subtidal seagrass vegetation on fish assemblages, using beach seines to compare vegetated and unvegetated habitat. Effects of season and site were also assessed. We sampled fish communities predominantly composed of juveniles (98.7 %). Specifically, we analyzed differences in abundance, species richness, diversity, evenness, and assemblage structure across these factors. Season was the most influential driver of fish assemblage structure, even more than habitat, as expected in a nursery area where fish reproduce seasonally. Notably, four species - *Atherina boyeri*, *Eucinostomus melanopterus*, *Mugil capurrii*, and *Chelon dumerili* - accounted for 53.7 % and 49.2 % of the variation in assemblages across habitat and season, respectively. Moreover, four times as many species were found exclusively in seagrass habitats compared to unvegetated areas, underscoring the critical role of seagrass meadows in the Banc d'Arguin in supporting species that depend on such shallow sheltered habitats, enhancing regional biodiversity, and contributing to the sustainability of fisheries.

1. Introduction

Seagrass habitats are widely recognized for their role in ecosystem services, including important ecological functions such as provision of food and shelter for fish and invertebrates (Heck et al., 1997; Nakamura et al., 2012). This nursery role for juveniles of commercial fish species among others extends beyond the extent of the seagrass, with the ability to support offshore fisheries, as shown in the Banc d'Arguin, Mauritania (Guénette et al., 2014; Trégarot et al., 2020).

This coastal wetland with extensive seagrass beds (Chefaoui et al., 2021) represents the most important fish nursery area in Mauritania and is essential to maintain sustainable fish stocks and support a magnitude of marine species (Jager, 1993; Campredon and Cuq, 2001; Schaffmeister et al., 2006; Correia et al., 2020). Several species of endangered turtles can be found in the Banc d'Arguin, most commonly the green turtle *Chelonia mydas* (Cardona et al., 2009) which is known to feed on the large seagrass beds covering the gulf (Godley et al., 2003; Catry et al., 2009). Moreover, many endangered species of rays and sharks are found in the Banc d'Arguin National Park (PNBA) (Leurs et al., 2021; De La Hoz Schilling et al., 2024). The PNBA contains dense seagrass meadows in the extensive subtidal shallow areas (Chefaoui et al., 2021), a type of habitat structure that provides protection and shelter from predators (Orth et al., 1984; Bell and Pollard, 1989). Seagrass habitats generally provide greater food diversity and availability for the juvenile individuals developing in these nursery zones compared to unvegetated habitats (Burchmore et al., 1984; Connolly, 1994; Nakamura et al., 2012). All these ecosystem functions of seagrass vegetated habitat are expected, but local quantitative estimates demonstrating the effects for the PNBA are not available.

Within the PNBA many species of fish of economic value occur (https://www.marafrica.net/pnba/). The only legal fishers are the Imraguen, allowed subsistence fishing, their techniques are focused on the

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use of nets and small non-motorized boats called “lanches” with a total of 114 of these sailing boats allowed access to fish in the PNBA (Correia et al., 2020; Trégarot et al., 2020). The diversity, community composition and nursery role for commercial and non-commercial species of the coastal shallow water habitat, composed of large seagrass beds and sand banks, remains largely unknown. These habitats are considered key to sustain the high biodiversity found in the Banc d’Arguin and its role in sustaining fisheries of Mauritania. It is important to have a better understanding of the importance of these habitats to manage and predict the consequences of potential future changes related to human activities, like offshore oil and gas exploration, coastal development, and fishing.

Although not targeting the effect of seagrass vegetation, a few studies have assessed fish species composition of the inshore habitats of the Banc d’Arguin. The fish community composition of five types of shallow littoral habitats within the PNBA and one external, sampled by beach seine from 2000 to 2004, found 91 fish species, with almost all the catch (97.9–99.7 %) classified as juveniles (Gushchin and Fall 2012). The juvenile fish assemblages of the Banc d’Arguin sampled by beam trawl in 50 locations (1–16 m depth) in September 1988, were dominated by only three taxa *Stephanolepsis hispidus*, *Diplodus bellottii* and Gobidae (Jager, 1993). Besides fish, three species of large crabs are reported abundant in the zone; *Afruca tangeri*, *Callinectes marginatus*, and *Panopeus africanus* (Wolf and Smit, 1990).

The specific location within the Banc d’Arguin played an important role in previous studies sampling the fish assemblages (Jager, 1993; Gushchin and Fall 2012). In these studies, the fish abundance as well as the species diversity varied considerably between locations and as a result it was important to sample different areas to assess any possible assemblage differences. Two distinct hydrographic regimes exist in the Banc d’Arguin. The upwelling-driven phytoplankton-based ecosystem present in the North (Berghuis et al., 1993) is different from the South-east intertidal flats ecosystem driven by local benthic primary production (Carlier et al., 2015). The latter ecosystem was exclusively sampled in our study, with a particular focus on the shallow subtidal flat regions, which have not been investigated in the past. These areas are within the National Park of the Banc d’Arguin and the main primary producers are seagrass.

The broad aim of this study is to compare the fish assemblage of vegetated (seagrass) and unvegetated (soft bottom) habitats in the Banc d’Arguin, which contains the most significant seagrass meadows of the Atlantic coast of Africa. yet poorly understood as fish habitat. For this goal, we aim specifically to assess effects of habitat type (vegetated/unvegetated), season (winter/spring) as minimum and maximum seagrass growth periods, and site (local variability) on fish abundance, diversity, and eveness, while assessing also influential species.

2. Methodology

2.1. Study region

The Banc d’Arguin, located along the coast of Mauritania, is a shallow coastal wetland, of over 10,000 km^2 (Wolff and Smit, 1990). It extends from Cap Blanc (20°460 N 17°020 W) in the north, to Cap Timiris (19°230 N 17°020 W) in the south (Araujo and Campredon, 2016; Schaffmeister et al., 2006). The coast is shallow and presents mudflats, channels, sand banks, and islands of variable sizes, and large subtidal and intertidal seagrass beds, experiencing a semi-diurnal tide with a typical range of 1.5–2.5 m (Araujo and Campredon, 2016). Because of its location, the Banc d’Arguin is influenced by the Canary upwelling system in the north, one of the biggest in the world (Arístegui et al., 2009), and is also exposed to iron-rich desert dust winds, making it a hypertrophic system with high primary production. This in turn supports large stocks of fish, shrimp, and other species relying on high levels of primary and secondary production (Carlier et al., 2015; Araujo and Campredon, 2016). The Banc d’Arguin also represents a winter refuge for millions of migrating shorebirds every year (Altenburg et al., 1983; Araujo and Campredon, 2016). In 1976, the PNBA, one of the biggest MPAs in Africa, and registered in the UNESCO World Heritage List (Araujo and Campredon, 2016; Trégarot et al., 2020) was created with an area of more than 12,000 km^2. It was designated a Ramsar Site, Wetland of International Importance at International level in 1982.

The large seagrass beds of the Banc d’Arguin are composed of three species: *Zostera noltii*, *Cymodocea nodosa*, both temperate species that are near the southern limit in Mauritania, and *Halodule wrightii* a tropical species that reaches Mauritania as its northern limit in the east Atlantic (Green and Short, 2003; Chefaoui et al., 2021). *Z. noltii* forms intertidal meadows with very high densities, but can also occur in upper subtidal areas. The average leaf width and length (maximum length 19.6 ± 2.5 cm) are higher than *Halodule wrightii* but smaller than *Cymodocea nodosa* (Chefaoui et al., 2021). *Cymodocea nodosa* creates the major subtidal habitats due to its very large leaf sizes. Although shoot density is often lower than the two other species, the long (maximal leaf length 38.4 ± 7.9 cm) and wide leaves create very suitable shelter habitat as subtidal vegetation areas (Chefaoui et al., 2021). *Halodule wrightii* is found mixed with *C. nodosa* in the top centimeters of depth of the subtidal zone or alone reaching deeper areas, and has short thin leaves (maximum length (14.7 ± 1.8 cm) and low shoot densities, creating a smaller habitat structure (Chefaoui et al., 2021). All three seagrass species can be found along the Banc d’Arguin (Cunha and Araújo, 2009) but the tropical one is rarer in the north (Chefaoui et al., 2021) and in some sites they appear intermingled together at the upper subtidal levels.

2.2. Study sites

This study was carried out in the east to south-eastern part of the Banc d’Arguin between Iwik and Mamghar (Fig. 1). These areas have large seagrass beds and tidal flats. Sampling was conducted in areas having both zones with vegetated habitat (V) and without seagrass beds (unvegetated (UV)) within the same geographic area. Within each site, two sampling locations were selected, with one presenting a bare sand bottom without any vegetation, and one with seagrass beds covering the whole sampling area. All sites needed to have a low slope allowing the deployment of a beach seine at an average depth of 0.7–1 m at low tide. Regarding the vegetated habitats, the seagrass coverage area needed to be large enough to sample 3 times in the same site. *C. nodosa* was dominant at all sites, while *H. wrightii* and *Z. noltii* were observed intermingled with *C. nodosa* at some sites.

The three study sites (Fig. 1) were located in Mamghar, Iwik and the islands and channels West of Iwik.

In **Mamghar (A)** the unvegetated habitat consists of bare sand near Cap Timiris (19°22′16″ N 16°31′52″ W). The vegetated location situated on the eastern part of Mamghar in the Baie de Saint-Jean, has large seagrass beds extending along the entire coastline of the bay (19°25′09″ N 16°22′23″ W).

Iwik (B) has large seagrass beds to the north of Iwik (19°53′00″ N 16°17′34″ W) as well as large shallow sand banks near the Iwik station of the National Park (19°54′18″ N 16°18′35″ W).

The **islands and channels west of Iwik (C)** are mostly covered by seagrass meadows. This site allowed sampling off the coast, in order to see if the species compositions were different in these Channel Islands. The vegetated habitat was found close to Kiji, a large island of 13.5 km^2 with very dense, tall and extended subtidal seagrass beds all around the area (19°43′19″ N 16°30′05″ W). The unvegetated area was found close to the small island of Nair (19°52′07″ N 16°23′29″ W), situated North-East from Kiji.

A lanche, a traditional wooden sailing boat of the Imraguen fishermen, was used to reach sites located on the islands.

2.3. Sampling design

The sampling for this study was carried out in December 2021

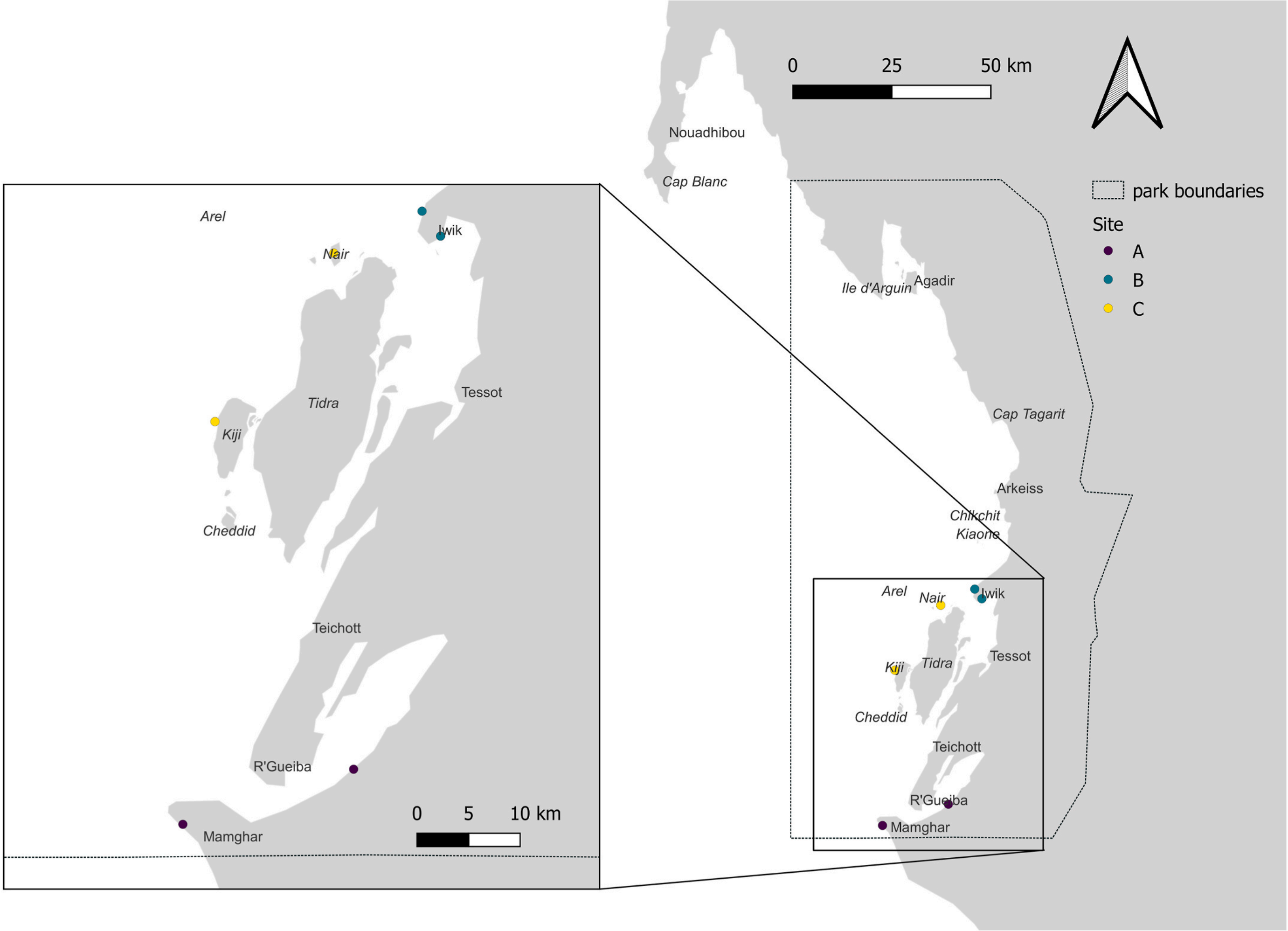

Fig. 1. Map of the Banc d'Arguin with PNBA boundaries and a detailed view of the study area. Season and seagrass: drivers of fish assemblage structure in the Banc d'Arguin, Mauritania.

(winter) and April 2022 (spring). These two months represent contrasting extremes; seagrass died off (lost many leaves) during the winter due to burial and turbidity caused mainly by storms, and maximal growth during spring, before the summer heat also starts to cause stress. Marine macrofauna were collected using a 17 m, 9 mm mesh size beach seine net. The net was dragged perpendicular to the shore with an equal open area (10–12 m) between replicates. Standardized tows were carried out around low tide. The net was deployed perpendicular to the shore around 30 m from the shore at a depth between 70 cm and 1 m, and then towed for 50 m along the beach, a distance which delivers better results than greater beach seine towing distances (Lombardi et al., 2014). After this, two researchers slowly closed the net as they headed to the shore, ensuring that the bottom of the net (footrope) was in contact with the bottom all the time. The area sampled with each tow ranged from 800 to 1000 m^2. Three replicate tows were performed and considered at each location. In a few times the net rolled on itself on the bottom leaving space for the fish to escape and resulting in an almost empty tow: in such cases a fourth tow was conducted.

All individuals caught were identified, measured (total length (TL) in mm), and weighed (g). For large individuals, such as rays, this was done in the field in order to release the specimens alive. Photographs were taken for later identification of specimens that could not be identified before being released. Smaller individuals were transported in labelled plastic bags in coolers and processed fresh in the laboratory.

2.4. *Species identification*

In order to identify the species, identification keys and literature based on the fishes known to be found in Mauritania were used (Bonnet, 1969; Seret and Opic, 1981; Vakily et al., 2002). The expertise of IMROP (Mauritanian Institute of Fisheries) researchers and fisheries observers was very important; as the local observers at each site helped in identifications. Websites such as "www.fishbase.org", where an extensive list of all the fish species recorded in Mauritania can be found were also used. Fresh fish were sorted and identified in the laboratory based on the external morphological characteristics such as body shape, pattern of colors, scale size and number, position and shape of the fins, and number of rays on the fins, following Strauss and Bond (1990).

Six invertebrate taxa (*Sepia officinalis*, *Hippolyte inermis*, *Palaemon elegans*, *Penaeus* spp., *Sicyonia carinata*, *Callinectes* sp.) were caught and identified, but were not considered in the analysis given that the focus of the study was on the juvenile fish community. *Callinectes marginatus* was extremely abundant and caught in all sites and habitats and in both seasons. With the exception of *Penaeus* spp. where 4 out of 68 individuals were caught at unvegetated habitats (site A), all other invertebrates were caught exclusively in vegetated habitat, and mostly in site B (5 out of 6 taxa).

2.5. *Data analysis*

In order to infer about the nursery effect of the sampled habitats, the size of each species compiled allowed us to calculate the density of juveniles based on the length at first maturity (L50) for each species (Veiga et al., 2006) using length information available through “Fishbase” (Froese and Pauly, 2023). The total weight of each species was calculated as well as the proportion of juveniles found.

To assess general differences in the fish assemblages, three diversity indices, species richness (N), Shannon Wiener diversity (H′) and evenness (Hill’s ratio = H’/N) were determined through the diversity function of the vegan package in R (Oksanen et al., 2020). All indices were tested for normality (Shapiro Wilk’s test) and homogeneity of variance (Levene’s test) and according to these results ($\alpha = 0.05$) site specific differences between the seasons were assessed using Analysis of Variances (ANOVA).

Differences in the community composition were assessed after square root transformation of abundance data in order to reduce the relative influence of the most frequent species (Clarke and Green, 1988). Then, a non-metric multi-dimensional scaling (NMDS) was performed using the Bray-Curtis index. To determine species that significantly contributed to differences between habitats or seasons, a SIMPER analysis was performed. A redundancy analysis (RDA) with habitat, season and site as explanatory variables was performed. The effect of both habitat and season on community composition was assessed through a PERMANOVA.

All analyses were performed in R environment version 4.3.2 (R Core Team, 2023).

3. Results

The majority (94 %) of individuals caught were fish, with a high proportion of juveniles (98.7 %). Considered in the study were a total of 3615 individuals and at least 42 fish species belonging to 24 families were identified (Appendix Table A.1). Blennies (Blennidae), Gobies (Gobiidae), and Pipefish (genus *Syngnathus*) were not identified to the species level.

Fourteen taxa (*Atherina boyeri*, *Eucinotomus melanopterus*, *Mugil capurrii*, *Chelon dumerili*, *Diplodus sargus*, *Pomadasys incisus*, *Dicentrarchus punctatus*, *Sphoeroides spengleri*, *Stephanolepis hispida*, *Solea senegalensis*, *Halobatrachus didactylus*, Gobiidae n. i., Blennidae n. i., and *Epiphion guttifer* in declining order) accounted for 95 % of the total abundance.

17 species were only found in spring, whereas five species were only found in winter, and 20 species were found in both seasons. Simultaneously, a higher number of individuals were caught in spring (n = 2242) than winter (n = 1373). A total of 2452 individuals (68 %) were found in vegetated habitats, while 1163 individuals were recorded in unvegetated habitat. The same tendency is also observed with the species number; as 21 species were only found in vegetated habitats, five only in unvegetated and 16 in both.

Overall, 45 % of all individuals were caught in site B (n = 1621), 36 % in site A (n = 1287) and a 19 % in site C (n = 707). A total of 16 species were only found in site A, three only in site C, while ten species were found in at least two of the sites and 13 taxa occurred at all sites (*H. didactylus*, Blennidae n. i., *E. melanopterus*, *S. hispida*, *D. punctatus*, *C. dumerili*, *M. capurrii*, *P. incisus*, *S. senegalensis*, *D. sargus*, *E. guttifer*, *S. spengleri,* and *Synaptura lusitanica)*.

Abundance, species richness and diversity were higher in vegetated habitats, whereas evenness was lower (Fig. 2). Species richness was higher with a mean of 13.7 species in vegetated habitats compared to 6.2 in unvegetated habitats. However, the difference is non-significant ($p = 0.09$), and there were no significant differences between habitats for the other indices (two-way ANOVA, Appendix Table A.2). A marginally non-significant difference ($p = 0.056$) was detected for the interaction of habitat and season for evenness, with the lowest evenness observed in vegetated habitats in spring (evenness = 0.056) while all other season-habitat combinations are approximately twice as high (Winter UV = 0.108; Winter V = 0.149; Spring UV = 0.169). No significant differences

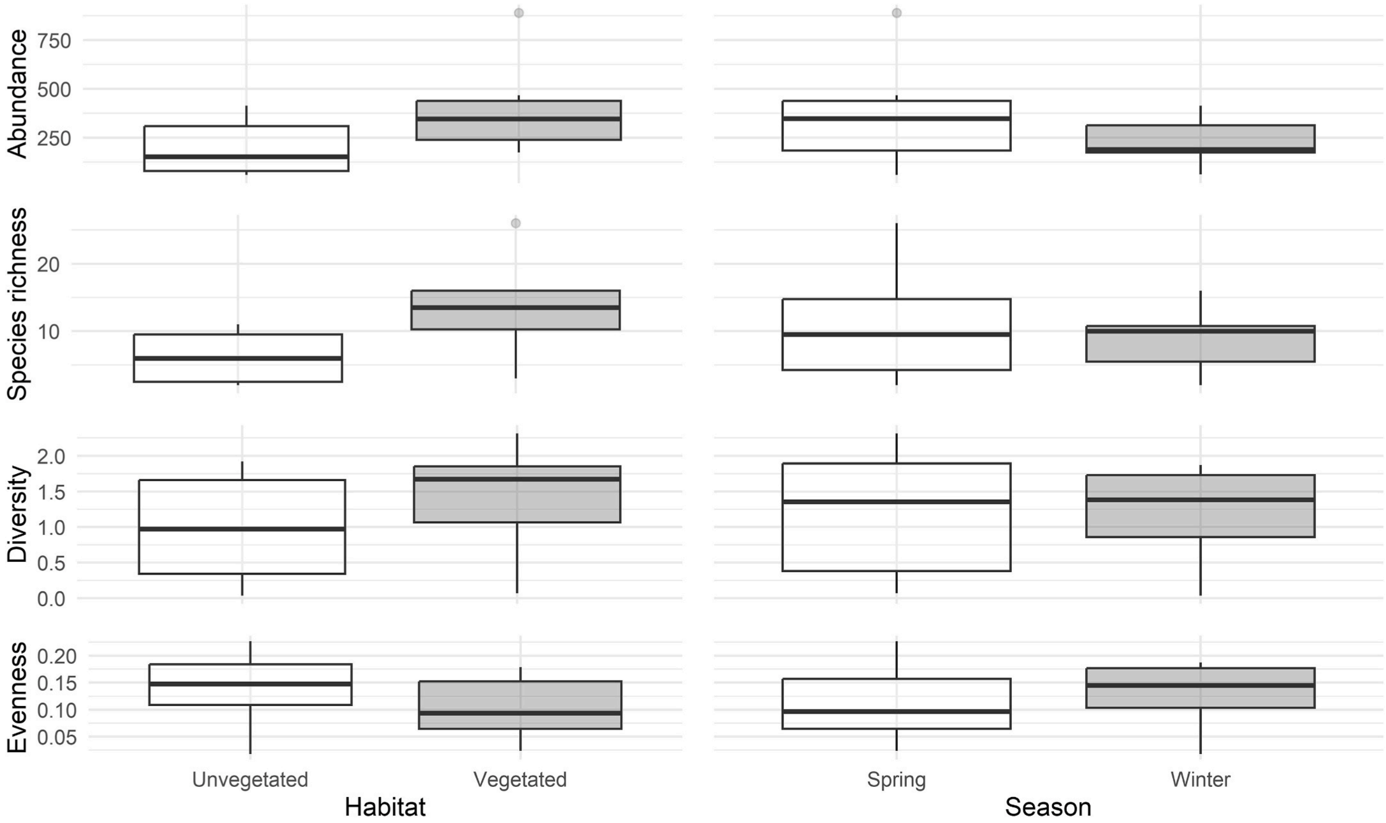

Fig. 2. Abundance, species richness, Shannon-Wiener diversity index, and evenness by habitat (vegetated vs unvegetated) and season (spring vs. winter).

in any of the four indices were found between seasons (two-way ANOVA, Appendix Table A.1).

Out of the three sites, site A had the highest abundances, species richness and diversity, site B was characterized by the overall lowest species richness, diversity but also the lowest evenness and site C, while having the lowest abundance, supported a high diversity with the greatest evenness out of the sites sampled (Fig. 3, Appendix Figure A.1).

Multivariate analyses show that variation in the assemblage is strongly influenced by season, with a gradient from winter to spring along the NMDS1 axis (Fig. 3, stress = 0.099). Habitat is less influential, although the V and UV winter sites form distinct groups, followed to a lesser extent by the V spring sites, with the spring UV sites showing the least similarity. In habitat-specific comparisons, vegetated habitats displayed less variation between sites than unvegetated habitats, both for winter and spring.

Four species (*A. boyeri*, *E. melanopterus*, *M. capurrii*, and *C. dumerili*) contributed to 53.7 % and 49.2 % of dissimilarity in assemblages of different seasons and habitats, respectively (Appendix Table A.3). *A. boyeri* only occurred in spring samples and was absent at site C (Appendix Table A.1). This species displayed notably high abundances at site B (1035 individuals, U and UV combined) and was more abundant in vegetated than unvegetated habitats. *E. melanopterus* was highly abundant in winter samples but only one individual was found in spring. No distinct pattern in habitat preference could be detected, except for site B where this species was more abundant in unvegetated habitats. Although found in both seasons, *M. capurrii* was more abundant in spring and in site-specific comparisons the abundance decreased in unvegetated habitats. While also occurring in spring samples C. *dumerlii* had higher abundances in winter samples and was more abundant in unvegetated habitats of every site-specific pairing.

The Redundancy Analysis (RDA) highlights associations of these four species to certain explanatory variables (Fig. 4). The explanatory variables explained 60.1 % of the variation in the assemblage composition, while 39.9 % of the variation was explained by unconstrained factors. Habitat was related to the RDA2 axis while season was associated with the RDA1 axis. Winter and unvegetated habitats with the previously identified indicator *C. dumerlii* (CD) were plotted in the second quadrant while spring and vegetated habitats associated with *M. capurrii* (MC) were situated in the fourth quadrant. A pattern in sites was apparent, distinguishing site B (first quadrant) from site A and C (third quadrant). *A. boyeri* (AB) was located between site B and spring, underlining the strong association to site B and the role of this species in the distinction of the site. *E. melanopterus* (EM) was strongly correlated with the negative RDA1 axis, demonstrating strong association with the winter season but a weak relation to the habitat factor. Other notable species were *D. sargus* (DS), plotted in the fourth quadrant, thus associated with spring and vegetated habitats, and three species that show weak associations with habitats: *S. senegalensis* (SSe) with unvegetated habitats and *S. spengleri* (SSp) and *S. hispida* (SH) with vegetated habitats, while also being situated near the site A and C centroids.

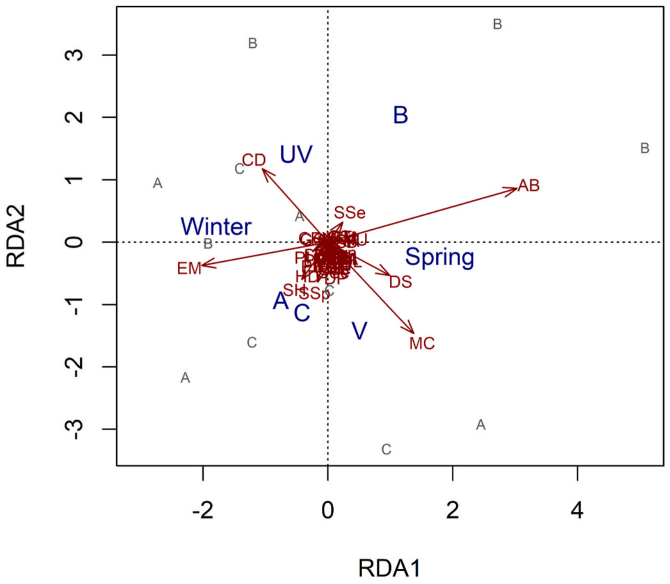

Fig. 4. Redundancy Analysis (RDA) on dominant species abundances. Factors (in blue) are season (winter, spring), habitat. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The PERMANOVA showed that all factors (season, habitat type, and site) considered were significant, as well as the interaction of habitat and season while the interaction of site and season was marginally non-significant ($R^2 = 14.67$ %; $p = 0.052$) (Appendix Table A.4). The factor explaining the most variation was season (25.1 %), followed by site (17.7 %) and the interaction of the two (14,7 %). Habitat accounted for 13.8 % of variation in the assemblage, another 11.1 and 10.1 % of variation are explained by interactions of habitat with site and season, respectively, while 7.6 % of variation could not be explained by factors considered in the analysis.

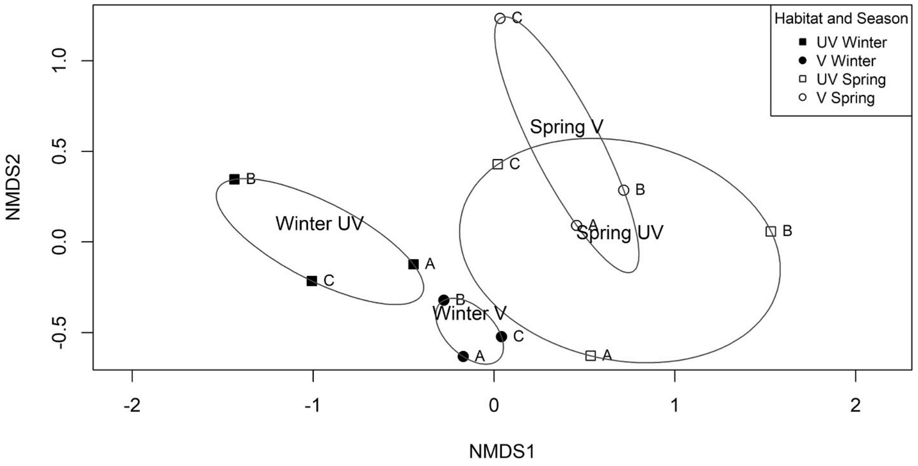

Fig. 3. NMDS on abundance square root transformed data. Stress = 0.099. The factors season and habitat are displayed by colour and shape, respectively: winter (black), summer (white), unvegetated (UV) habitat (square), and vegetated (V) habitat (circle).

4. Discussion

Our data show species richness in vegetated areas reaching double that of unvegetated habitats, with increased abundance and diversity but lower evenness. Notably, four times as many species were found exclusively in vegetated habitats compared to bare sand, highlighting the importance of seagrass for species that depend on this habitat at least at one stage of their life cycle. No studies have assessed the effect of habitat on community assemblages in the Banc d'Arguin. In other habitats worldwide with characteristics similar to those of the Banc d'Arguin, such as coastal nearshore waters and shallow water lagoons and estuaries (Connolly, 1994; Gray et al., 1996; Travers and Potter, 2002; Erzini et al., 2022, 2024) the species richness, diversity and total abundance of fishes were generally higher in seagrass than unvegetated habitats. Seagrass habitats are structurally complex ecosystems that offer shelter, protection from predators, and a greater abundance of food resources compared to sandy environments, serving as nurseries for juveniles of commercially important species (Heck et al., 1997; Nakamura et al., 2012). The beneficial impact of vegetated habitats on species richness, abundance, biomass, and diversity is well-documented in the literature (Gray et al., 1996; Bell and Pollard, 1989; Guidetti, 2000). This trend was also observed in our study, with higher values for these parameters in vegetated habitats, however the differences were not statistically significant due to high variance. In winter, slightly higher evenness and lower abundance were observed, though these differences were also not statistically significant. However, the limitations of univariate indices in detecting changes in fish assemblages, particularly in seagrass habitats, have been previously noted (Soykan and Lewison, 2015; Guidetti and Bussotti, 2002).

Multivariate analyses (NMDS, PERMANOVA) suggest that season is a stronger explanatory factor in fish assemblage variation than habitat. The effect of habitat may have been reduced by patchy seagrass coverage in vegetated treatments. Although efforts were made to maintain uniform seagrass density across replicates, the inclusion of sandy bottom areas within vegetated treatments cannot be ruled out, potentially biasing the results. Additionally, the study design did not account for the proximity of unvegetated sites to seagrass meadows, which may have influenced assemblage similarity, as closer proximity could result in greater resemblance between the habitats (Ferrell and Bell, 1991). However, other studies using beach seines observed high similarity of bare sandy habitats and *Zostera* meadows (e.g. Jenkins et al., 1997).

Seasonal variation within habitats could further mask the effect of habitat on the assemblage, attributing changes to season when they could be due to the interaction of both factors. Distinct seasonal changes in assemblage structure have previously been linked to fluctuations in environmental variables and habitat complexity especially in *C. nodosa* and *Z. noltii* meadows (Guidetti and Bussotti, 2000), which are highly susceptible to seasonal dynamics (Marbà et al., 1996).

Season is an important factor influencing species assemblages, especially reflecting the recruitment of juveniles of dominant species (Ribeiro et al., 2006; Schaffmeister et al., 2006; Embarek et al., 2017). Fish assemblages of a lagoon and estuary in Portugal varied seasonally due to recruitment of marine migrant species in spring whereas lagoon resident species accounted for seasonal differences in unvegetated habitats (Veiga et al., 2006; Ribeiro et al., 2006, 2012). Indeed, the species assemblage fluctuates between seasons due to speciec-specific spawning events and migration to and from the open ocean (Hyndes et al., 1999; Thiel and Potter, 2001). In our study, the mugilid *C. dumerili* was dominant in unvegetated habitats while *Mugil capurii* was more frequently associated with vegetated habitat. This only partially aligns with previous findings that resident species and juveniles of larger species such as sparids generally dominate seagrass, while schooling species like mugilids are typical of unvegetated areas (Bell and Pollard, 1989; Gray et al., 1996; Verdiell-Cubedo et al., 2007).

The NMDS revealed less seasonal variation in fish assemblages within vegetated habitats, a pattern consistent with previous findings showing greater similarity in complex habitats like seagrass meadows and rocky reefs compared to unvegetated sand (Guidetti, 2000). This has been linked to the higher presence of resident species in seagrass and more transient species in unvegetated areas (Travers and Potter, 2002). In our study, estuarine-dependent species (i.e. *E. melanopterus*, *M. capurrii*, *C. dumerili*) are responsible for dissimilarities in assemblages between seasons and habitats. Their juveniles, with limited dispersal, are strong indicators of recruitment variability, as their abundance is influenced by fecundity and early-stage mortality rates, and they settle in shallow vegetated habitats like seagrasses, where food and shelter promote growth (Heck et al., 1997; Hannan and Williams, 1998; Nakamura et al., 2012). However, certain species, particularly lagoon residents, may shift to unvegetated habitats at specific life stages due to changes in food preferences and predator avoidance strategies (Hannan and Williams, 1998; Nakamura et al., 2012). As juveniles mature, they migrate to deeper waters, typically preferring coral or rocky reefs, which alters species composition between seasons (Nakamura et al., 2012).

In this study, four species (*A. boyeri*; *E. melanopterus*, *M. capurrii*, *C. dumerili*) substantially contribute (49.2–53.7 %) to differences between habitat and season, respectively. Five more species (*P.incisus*, *S. spengerli*, *S. hispida*, *S. solea*) as secondary drivers of assemblage structure, cumulatively explain an additional 15–18 % of variation.

- The sandsmelt ***A. boyeri*** was found exclusively in spring samples, with higher abundances in vegetated habitats, though absent at some study sites (site C). As a planktivorous fish, *A. boyeri* does not dependent on specific habitat but atherinids dominate seagrass meadows of *Z. noltii* and *C. nodosa* in Mediterranean and Atlantic lagoons (i.e. Guidetti and Bussotti, 2002; Pombo et al., 2005; Gürkan, 2013; Embarek et al., 2017). This resident species is strongly associated to nearshore coastal waters and is highly adapted to variable inshore environments, tolerating wide ranges of environmental conditions (Henderson and Bamber, 1987). Its absence from offshore sites could be due to different environmental conditions not assessed in this study, although patchy distribution is common among planktivores (Guidetti, 2000; Freitas et al., 2019). As a consequence of genetic divergence between populations (Henderson and Bamber, 1987), tolerance ranges may vary locally. In Spain, *A. boyeri* spawns from March to June, peaking in April (Fernández-Delgado et al., 1988), with other studies extending the period to September (Gençoğlu and Ekmekçi, 2016 and references therein). Assuming similar patterns in the Banc d'Arguin, the high abundance of juveniles in April suggests a recent spawning peak.
- ***E. melanopterus*** was highly abundant in winter samples and virtually absent in spring. Juveniles of the estuarine-dependent Flagfin mojarra inhabit estuaries, coastal rivers, lagoons, and sandy habitats (Albaret and Desfossez, 1988; Chaves and Otto, 1999; Reis-Filho et al., 2019; Solari et al., 2010). In this study, no distinct habitat preference was detected, except for site B where this species was more abundant in unvegetated habitats. *E. melanopterus* juveniles exhibit ontogenetic habitat shifts and dietary changes depending on habitat and salinity gradients (Reis-Filho et al., 2019; Gning et al., 2010; Ramos et al., 2016). Its absence in spring may result from migration to deeper waters after a winter period of recruitment and maturation (Albaret and Desfossez, 1988). While Mauritania is the northern limit of *E. melanopterus* distribution, range expansions of this species in the western Atlantic have been documented (Solari et al., 2010), suggesting potential changes in occurrence and abundance due to climate change.
- The Leaping African mullet ***M. capurrii*** was present in both seasons but more common in spring, with lower abundances in unvegetated habitats. As an estuarine-dependent species, seasonal abundance patterns in the Banc d'Arguin may be linked to its reproductive cycle, which begins around December–January and concludes by June in Senegal, (Ndour, 2014).

- The grooved mullet ***C. dumerili*** was more abundant in winter, consistently favoring unvegetated habitats. Adult catches in the Banc d'Arguin peaked in August (Gushchin and Fall 2012), potentially relating to a peak in spawning in late summer as observed in South Africa (van der Horst and Erasmus, 1981) and explaining high juvenile abundances of this estuarine-dependent species in winter. *C. dumerili* appears to favor unvegetated areas, closely related species were previously found to prefer sandy habitats for schooling (Ribeiro et al., 2012; Gray et al., 1996).

The Banc d'Arguin serves as an important nursery for resident and marine migrant species with differing spawning periods, reflected in seasonal patterns of fish assemblages. In an earlier study, juvenile abundance peaked in February and August, with the latter also showing the highest species richness, although this was influenced by rare species and species-specific seasonal fluctuations (Gushchin and Fall 2012).

Distribution patterns of juveniles vary between ocean spawners and residents, with increased species richness and higher concentrations of newly recruited juveniles, especially from ocean-spawned larvae, in suitable habitats near lagoon entrances (Hannan and Williams, 1998). A similar decline in richness along deep channels from the open coast towards the coastline has been observed in the Banc d'Arguin (Gushchin and Fall 2012).

In our study, the highest number of species and 16 species exclusively occurred in Mamghar (site A) at the southern boundary of the park; species encountered here comprised both residents and ocean-spawners/marine migrants. Notably, residents are primarily temperate species, and their presence at the southern limit of the study area can be attributed to a north-south current in the Banc. In contrast, the ocean spawners found in Mamghar are only tropical species, highlighting the significance of the Banc for the early life stages of these species. The distribution of ocean-spawned larvae may be further constrained by the region's numerous islands, sandbanks, and shallows, which disrupt water circulation. Future research is needed to determine whether climate change is driving the increased frequency of tropical species in the Banc d'Arguin or if deeper waters near Mamghar support a higher diversity of species.

Differences in assemblages between sites may reflect local environmental characteristics rather than variation in seagrass species composition, which was consistent across vegetated sites. Site A (Mamghar), located near the southern boundary and lagoon entrance, exhibited the highest species richness, abundance, and diversity. This may be due to its transitional position between coastal and lagoonal systems, which likely enhances the overlap of estuarine residents and ocean-spawned juveniles. In contrast, Site B, situated on an important bird breeding island (Veen et al., 2018) showed the highest overall abundance but lowest species richness, diversity, and evenness. Nutrient input from seabird excrement may contribute to this pattern. Seabird-derived nutrients can enrich sediments and boost primary productivity, in turn increasing algal or invertebrate biomass and species richness which was the highest at site B. Potentially a few opportunistic species are favored while overall assemblage diversity is reduced (Kolb et al., 2010). Site C, located closest to the coast and in proximity to Iwik -one of eight villages within the Banc d'Arguin-supports the lowest total abundance and exhibited high diversity and evenness. Water arriving at this site passes through an extensive network of channels, islands, and mudflats, potentially reducing larval input or altering habitat characteristics through sedimentation or hydrodynamic filtering. These site-level differences suggest that proximity to the open ocean, spatial positioning, and nutrient dynamics influence fish assemblages across the Banc d'Arguin.

While this study provides valuable insights into the fish assemblages of vegetated and unvegetated habitats in the Banc d'Arguin, several limitations should be acknowledged. Our sampling was restricted to the southern area of the Parc National du Banc d'Arguin (PNBA), a region characterized by a complex mosaic of islands, mudflats, and tidal channels. This spatial limitation directly affects the generalization of our findings, as the northern PNBA is less sheltered and influenced by different physical drivers, potentially supporting distinct fish assemblages. However, the northern part of the park also has less seagrass habitat and is therefore less relevant for the research question addressed in this study. The composition of seagrass species was not directly assessed, but our findings were derived from *C. nodosa* dominated meadows and seagrass meadows dominated by smaller growing species may support different fish assemblages. Additionally, sampling was carried out only in December and April, selected to represent contrasting seasonal extremes. During winter, seagrass meadows experience partial die-off due to burial and increased turbidity caused mainly by dust and wind storms, while spring represents a period of maximal growth before the onset of summer-induced stress. However, the exclusion of other months limits our ability to capture the full annual cycle of fish assemblage dynamics and habitat conditions. Fish assemblage data were based on pooled samples per site and habitat. Nevertheless, each individual haul covered a substantial area of approximately 800–1000 m^2. Given this relatively large sampling area, variation is unlikely to have significantly affected species richness or diversity estimates. Finally, the absence of concurrent environmental measurements (e.g., turbidity, salinity, or nutrient levels) limits our ability to identify the physical drivers underlying observed differences in fish assemblages.

Our study indicates that seagrass habitats play an important role in supporting higher species richness, abundance, biomass, and diversity, although these differences were not statistically significant. Seagrass meadows of the PNBA serve as important nurseries for juvenile fish, particularly commercially important species, as demonstrated by the significantly higher number of species found exclusively in vegetated habitats compared to unvegetated areas. Seasonal variation, particularly in winter, was linked to changes in species assemblages, with slight increases in evenness and decreases in abundance, although these changes were also not statistically significant.

Although this study did not quantify the monetary value of the fish provisioning services of seagrass, the importance of seagrass habitats for fisheries has been demonstrated in a number of studies worldwide. A meta-analysis based on 11 studies across southern Australia based on sampling of juvenile fish in vegetated and unvegetated habitats with beach seines showed that total annual seagrass enhancement was 980 g m^{-2}, corresponding to 9.8 t per hectare for the commercial fisheries, worth approximately 19,840 € ha^{-1} y^{-1} (Blandon and zu Ermgassen, 2014a,b). Jänes et al. (2020) compared the average enhancement in annual fish biomass production from seagrass, mangrove and tidal marsh habitats in Australia and estimated that seagrass habitats were 2.9 and 32 times more productive than mangrove and tidal marsh habitats. Jackson et al. (2015) estimated that seagrass habitat fish provisioning services accounted for 4 % and 6 % respectively of the Mediterranean commercial and recreational fisheries landings, and Tuya et al. (2014) estimated that the value of seagrass to Gran Canaria Island inshore fisheries was 606,239 € y^{-1}. In countries near to Mauritania, Erzini et al. (2023) estimated that the approximately 67 km^2 of seagrass habitat in Senegal contributed 2,600,000 € and 8,100,000 € in 2018 and 2019 to local commercial fisheries, and the lifetime economic value of 10 commercial species from 1.14 km^2 of seagrass habitat in Guinea-Bissau, was estimated to be 94,000 €. The production of juveniles of the 12 most important commercial within seagrass habitat of the Ria Formosa lagoon in southern Portugal was approximately double that of unvegetated habitat with lifetime economic values for vegetated habitat ranging from 10,700 € ha^{-1} to 22,028 € ha^{-1} (Erzini et al., 2022). The calculated potential yield of single cohorts of seven of the most important commercial species if fished at the optimal fishing mortality rate ($F_{0.1}$) ranged from 457,227 € to 643,842 € (Erzini et al., 2024).

While univariate metrices (abundance, species richness, diversity, and evenness) come short in assessing differences in assemblages between habitats and seasons, multivariate analyses showed that season is a stronger driver of assemblage structure than habitat. This underscores the value of multivariate approaches in capturing the complexity of ecological communities, where univariate indices may fail to detect subtle but ecologically meaningful patterns. The assemblage of juvenile fishes is strongly influenced by seasonal patterns in the Banc d'Arguin, due to species-specific reproductive periods and recruitment to inshore habitats. Despite this study covering only two seasons, seasonal peaks in abundance were observed for the most common species. While habitat played a less significant role than season in shaping assemblage composition, it remains critical for several species. The biology of the most influential species shows that associations with habitat and season are reflecting ontogenetic shifts, recruitment patterns, and reproductive cycles.

4.1. Future research directions

With the predicted changes in seagrass distributions and associated fish communities due to climate change and given the importance of the Banc d'Arguin as a nursery, a standardized, large-scale, long-term monitoring program should be implemented, based on a stratified sampling design covering the whole Banc d'Arguin. The number of sampling sites should be greatly increased, and sampling should take place over all seasons, not just winter and spring as in this study. Regular mapping of seagrasses should also be carried out. Long-term monitoring can provide valuable information on recruitment variability of key commercial species as well as changes in species assemblages and allow calculation of production and fish provisioning services of vegetated and unvegetated habitat. In addition to standardized beach seine surveys at shallow depths, beam trawl surveys should also be carried out in the deeper channels and areas where beach seines cannot be used. Commercial fishing activity (fishing effort, catches, catch per unit effort, size distributions) should also be monitored in order to evaluate the effect of fishing on changes in abundance of juveniles in the nurseries and on the fish assemblage structure. Such information is essential for fisheries management and conservation.

CRediT authorship contribution statement

Nicolas Compain: Writing – original draft, Formal analysis, Investigation, Data curation, Conceptualization. **Antonia I.M. Mallmann:** Writing – original draft, Visualization, Validation, Data curation, Formal analysis. **Ebaye Sidina:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Mohammed Bourweiss:** Writing – review & editing, Investigation. **Mamadou Abdoul Ba:** Writing – review & editing, Investigation. **Ismaila Samba Talla:** Writing – review & editing, Investigation. **Alioune Niang:** Writing – review & editing, Investigation. **Karim Erzini:** Writing – review & editing, Validation, Supervision, Methodology, Data curation, Formal analysis, Conceptualization. **Ester A. Serrão:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109451.

Data availability

The data is shared in Table A1 of the Supplementary Material

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