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Underwater soundscape analysis reveals fish assemblage contrasts between protected and exploited areas in an African mangrove delta

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ABSTRACT

Mangrove estuaries are keystone habitats for many marine species, but their contribution to the tropical coastal fisheries is threatened by increasing anthropogenic pressures, including overfishing. Thus, the implementation of marine protected areas in mangroves is motivated by the need to ensure the fishing community's food security and economic livelihood, but there is a lack of affordable methods to monitor the effect of this management on fish. Here, we explored how passive acoustic monitoring (PAM) could be utilized in a case study of the Sine-Saloum estuary, Senegal. We compared biodiversity indices based on PAM and scientific fishing in two contrasted areas, one being heavily fished and the other protected. We computed fish sound abundance, richness, and diversity indices from underwater recordings in both areas in 2020 and 2024, and compared them to those obtained from conventional fish sampling methods. Acoustic-based indices were in accordance with fishing-based indices and showed anticipated differences between protected vs. exploited areas. This first PAM assessment in underwater mangrove suggests it might be a useful tool for MPA monitoring in this type of habitats, and open the way to continuous, fishery-independent, non-intrusive fish assemblage monitoring system. Such monitoring system would contribute to the establishment and acceptance of protected areas in mangroves ecosystems.

1. Introduction

In the context of increasing pressure on worldwide marine ecosystems, there is an urgent need to enhance monitoring of marine life for conservation and fisheries management (Estes et al., 2021; Golden et al., 2017). While traditional observer-based methods remain the most reliable approach, passive acoustic monitoring (PAM) has emerged as a new way to obtain ecosystem health indices in both terrestrial and marine environments through soundscape analysis. PAM now ranks among the main technology-based tools for biodiversity monitoring, complementing satellite-based remote sensing, camera systems, and eDNA methods (Sugai et al., 2019; Sueur et al., 2014; Ulloa et al., 2018; Van Hoeck et al., 2021; Stephenson, 2020). In coastal and estuarine ecosystems, a variety of conservation and fishery management plans, including marine protected areas (MPAs) and artificial reefs, have been implemented in response to overfishing and other anthropogenic disturbances such as agriculture, industry, tourism, infrastructure development and climate change that may impact fish habitat (Brochier et al., 2021). However, the success of these measures strongly rely on societal recognition of their effects, which necessitates an efficient monitoring

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system (Brochier et al., 2021; Pitcher and Seaman Jr, 2000; Quintana et al., 2021). The interaction of ecological, economic and social processes in mangroves makes them a particularly complex socio-ecological system for which co-management of protected areas is a promising strategy (Hagger et al., 2022). Mangroves host biodiversity hotspots, serve as key areas for the life cycle of many fish species, and provide critical resources to local populations, making their protection challenging and crucial for the resilience of coastal marine ecosystems (Gnansounou et al., 2022; Nanjo, 2022). Mangroves are also important for terrestrial biodiversity, with birdlife being particularly well-suited to Passive Acoustic Monitoring (PAM), as demonstrated in one mangrove and other wetlands (Branoff and Campos-Cerqueira, 2021; Mosikidi et al., 2023). However, little attention has been given to terrestrial PAM in these ecosystems, and no underwater PAM studies in mangroves have been published to date. Underwater sound recordings have proven to be an effective means of mobilizing fishers' local ecological knowledge (LEK) which can serve as basis for artisanal fisheries co-management (Brochier and Puig, 2023; Mbaye et al., 2021). Standard diversity and abundance indices are also needed to assess the effect of management decisions, and to initiate positive management feedback (Quintana et al., 2021). PAM could also provide these indices, as it has been shown to offer relevant fish assemblages indices in coral reef and rocky coastal oceanic environments (Desiderà et al., 2019; Carriço et al., 2020a) as well as in turbid estuarine environments (Souza Jr et al., 2023; Rowell et al., 2017). The purpose of our work was to assess the applicability of underwater PAM in mangrove ecosystems, as this approach had, to our knowledge, not yet explored.

The Saloum delta is an inverse, hyperhaline estuary in a Sahelian climate located in Senegal, West-Africa (Diouf, 1996; Simier et al., 2004). The salinity varies from 35 psu at the river mouth to >130 psu in the uppermost river areas. Nevertheless, some intermediate areas have salinities below 35 during the rainy season (from July to October) (Ecoutin et al., 2014). The delta is composed of a complex network of waterways that extend over ~250 km^2 including ~60,000 Ha of mangrove (Lombard and Andrieu, 2021). Mangroves cover almost the whole delta, but in its northern part the environment is much drier, and mangrove trees are smaller, with their overall extent reduced. Fish assemblages in the delta are exposed to hypersaline conditions and subject to increasing fishing pressure leading to over-exploitation (Ecoutin et al., 2010). In 2003, the first MPA was implemented in its southern part, covering a 15-km-long secondary water branch called the Bamboung bolong. Secondary waterway branches are locally called "bolongs". As Senegal's first demonstrative MPA, the Bamboung bolong was managed as a no-take area, and scientific fishing monitoring was performed seasonally (Ecoutin et al., 2014). From 2008 to 2012, this monitoring was performed simultaneously in the Bamboung bolong and in a similar but unprotected area, the Sangako bolong, demonstrating the effect of the no-take area by contrasting the fish assemblage in both areas (Sadio et al., 2015).

During the last decade, given the recognized success of the Bamboung MPA in rebuilding local fish stocks, several MPAs were created at the initiative of local communities. These "Community MPAs" rely on a participatory approach to co-management. However, governance issues were observed, due to the lack of scientific monitoring, which is essential for reaching consensus on establishing usage rules, as well as the lack of control due insufficient funding (Dahou, 2010). In this context, the combination of species inventories and the creation of a sound library of vocal fishes present in these areas could help estimate the diversity and composition of the local fish assemblages, making PAM a cheaper and a more effective monitoring tool for fish communities. In addition, pirogue engines can also be detected by PAM (Kammegne et al., 2023), which could help monitor fishers' compliance with the proposed rules.

The purpose of the present study was to contribute to the development of PAM as a non-intrusive method for monitoring mangrove fish assemblages by comparing acoustic-based indices with those derived from experimental fishing. We worked with data collected in the Bamboung and Sangako bolongs where fish assemblages had been previously well described using scientific fishing methods (Sadio et al., 2015), and under contrasting fishing pressures (no-take vs. open access). Thus, the question addressed here was whether the known differences in fish assemblages between the two sites could be measured through PAM, with the aim of providing a simpler alternative for monitoring fish in mangroves and enhancing conservation efforts in these important ecosystems.

2. Materials and methods

2.1. Hydrophones deployment

Three surveys were performed in the Sine-Saloum Estuary in Senegal in 2020, 2023 and 2024, (Fig. 1). In 2020, two "Snap" hydrophones (Loggerhead Instruments, Sarasota, FL, USA, using HTI-min-96 hydrophones, HighTech Inc., Long Beach, MS, USA) were deployed. The hydrophones were set to record continuously at 44.1 kHz (13.98 dB gain), producing a series of 4-minute consecutive audio files. The instruments were installed at the entrance of two secondary waterways ramifications (locally called "bolongs"), about 2 km from the main channel, the Diomboss river, and approximately 10 km from each other. The precise location of the hydrophones matched historical monitoring stations in Bamboung (13°49.920′ N; 16°32.415′ W) and Sangako (13°51.390′ N; 16°28.302′ W) bolongs, hereafter referred to BBG and SGK stations. The hydrophones were placed inside a protective cage, positioning the hydrophone itself ~50 cm above the riverbed, and tied to the mangrove with a rope approximately 5 m from the shore, at ~2–3 m and ~4–5 m depths respectively in BBG and SGK depending on the tide. In 2020, the instruments were deployed on 12/01/2020 at 19:14 (BBG) and 17:36 (SGK) to the 12/01/2020 at 10:06 (BBG) and 10:10 (SGK). During the 2020 sampling, the sun rose at 7:16 and set at 18:38. The operation was repeated in 2023 but the data logger deployed in the fishing area was not recovered, thus the 2023 acoustic data, collected only in BBG, were not

Fig. 1. Map of the working area, showing the location of the two sampled stations (BBG and SGK) and the villages were the social survey was performed.

used in this study. In 2024 the operation was repeated with only one "Snap" data logger and one handheld hydrophone (H2d Aquarian audio hydrophone connected to a Zoom F3 recorder). The Snap was deployed at the BBG station, following the same protocol as in 2020, from 01/05/2024 at 12:30 to 01/07/2024 at 6:00. Meanwhile, manual recordings were performed with the handheld hydrophone at SGK, from a canoe, during four trips: (1) the 01/05/2024 from 12:20 to 14:15 and (2) from 21:00 to 23:55, (3) the 01/06/2024 from 10:00 to 10:30 and (4) the 01/07/2024 from 5:20 to 5:45. During the 2024 sampling, the sun rose at 7:32 and set at 18:52.

2.2. Acoustic data analysis

For data labeling, we subsampled 30-second sequences at the beginning of each hour, for 24 h starting from 00:00 the 12/02/2020 in BBG and SGK and from 00:00 the 01/06/2024 in BBG. In SGK for 2024, due to the logistical constraints inherent to manual recording the time interval between records was longer, with each recording lasting 15 min, from which we randomly subsampled 1-minute sequences on 01/05/2024 at 13 h53, 21 h27 and 23:49; on 01/6/2024 at 10:06 and on 07/06/2024 at 5:37. Thus, in total 42 min of records were labeled (Table 1). Fish sounds were temporally labeled based on simultaneously listening to and visualizing the spectrogram of the raw recording (44.1 kHz) using Audacity (V. 3.5.1, www.audacityteam.org). The FFT window length was adapted to the duration of the annotated sounds, generally, 4096 points but reduced to 1024 for short pulsations to allow more precisely annotate the sound. The manual labeling was performed in two steps. First, identified sequences were assigned a specific arbitrary name corresponding to a given "sound type". For each labeled sound record, a corresponding annotation file was exported from audacity, including the start and end times of each labeled sound sequence and the corresponding sound type label. Second, after annotating the whole dataset, sound types were compared and those sharing very similar spectral characteristics, which were estimated as potential variations of the same species, were grouped into "sound categories". The process was repeated independently by two annotators, to control for potential observer bias.

The effects of sampling hour, station, and year on the variability in fish call rate (calls per minute) were examined using a generalized linear model (GLM, $n = 77$) with a Poisson distribution and a log-link function.

Acoustic abundance, richness, and the Shannon diversity index were computed based on the sound category labels. As in (Carriço et al., 2020a), acoustic abundance per sound category represented the mean number of sounds per minute, averaged over a 24-hour cycle, and acoustic richness was the number of sound categories detected during the same 24-hour cycle. These indices were compared with those computed from fish sampling data collected between 2008 and 2012 at the same locations in BBG and SGK (Sadio et al., 2015), using traditional and standardized fishing methods.

Finally, based on the exhaustive list of fish species reported from historical experimental fishing in the Bamboung MPA (Ecoutin et al., 2013), a literature study was performed to seek which species reported in the area belong to a family known to produce sounds.

Table 1
Summary of records subsamples labeling in Bamboung (BBG, protected area) and Sangako (SGK, fished area) in December 2020 and January 2024.

	Bamboung (BBG)		Sangako (SGK)	
Campaign	2020	2024	2020	2024
Subsample duration	12′ (24 * 30″)	12′ (24 * 30″)	12′ (24 * 30″)	6′ (6 * 60″)
Number of sounds labeled	521	577	82	35
Average Sounds per minutes	43.4	48	6.8	5.8
Sounds types	19	43	11	6
Sounds Category	10	11	4	5
Shannon index	1.4	1.7	1.2	0.7

2.3. Fish sampling and social survey

The description of fish assemblages in BBG and SGK recording stations was obtained from historical fish sampling, dedicated fish sampling, and a social survey of local fishers' perceptions. Experimental fish sampling, as well as artisanal fishing, occurs in open waters adjacent to the shore, which is covered by mangroves.

Historical (2008–2012) fish sampling was performed using a purse seine net (length 250 m, height 20 m, 14 mm side mesh), operated with the same boat and the same fishers' team in all samplings. Immediately after fishing, fish were identified, weighted, measured, and sex and maturity stage determined. Sampling was performed three times per year, corresponding to the three contrasted hydroclimatic seasons in the region (Wet-warm, Dry-Cold, Dry-warm, (Simier et al., 2004)). From this database, we extracted fish sampling data from stations "BBG 10" and "SGK 1" which precisely corresponded to the places of acoustic monitoring (see Section 2.1). As usual in experimental fishing, species abundance corresponded to the number of individuals collected for each species, and species richness was the number of species collected (Simier et al., 2004). The contribution of sampling station, year and season on the fish abundance variability was explored by fitting a generalized linear model (observation number = 29) with a Poisson distribution and a log link function.

A subsampling of the historical dataset corresponding to dry-cold season was used to compare abundance richness and diversity index with the acoustic-derived index as PAM occurred between these periods. One of the abundance values was excluded from this analysis, because it corresponded to a particular event of a fish school entering the net (*E. fimbriata and S. maderensis*), causing an outlier value (This occured in the BBG sampling site in 201119127 individuals were collected).

To complement historical fish sampling and check for their consistency with current observations, supplementary fishing operations were performed March 30, 2023, at SGK and BBG and repeated on April 2, 2023, at BBG. These operations were performed with a 200-meter-long and 8-meter-deep encircling gillnet, which was deployed from the beach with a pirogue. Because of the different protocol, which has been the new protocol for fish assemblage monitoring in the MPA since 2014, the data collected could not be comparable to the historical ones, but these operations could be used to confirm the stability of the fish assemblage differences historically observed between the two sites.

Finally, a social survey was designed to assess local fishers' perceptions of fish assemblage contrasts between SGK and BBG study sites. Although fishing was prohibited in BBG, the study area was located just near the MPA boundary, and many fishers did fish in this area. In the questionnaire (provided as supplementary data), information about fishers' experience and practice was collected, followed by questions about the perception of fish quantity and species in both sites, and their explanations for these differences. The survey was performed by a local sociology student from the community. Twelve experienced fishers who knew the exact location were included in the survey, which took place on January 5 and 6, 2024, in the five main fishing villages of the area (Fig. 1).

3. Results

3.1. Fish sounds labeling

A total of 1215 sound sequences were labeled, most of them (1098) in the BBG records (Table 1). The subsampling strategy (30 s per hour, for 24 h) allowed us to detect the expected contrast between the two studied areas, and similar results could be obtained using only the nighttime records (Fig. S1). The larger time intervals between records in the 2024 campaign for SGK still allowed us to detect the expected contrast between SGK and BBG (Fig. S2). Fish calls per minute, averaged over a 24-hour cycle, were stable between the two periods, and highly contrasted with approximately 7 times more sounds in the protected area (45.7 calls per minute in BBG vs 6.2 in SGK). In both years, all sound types detected in SGK were also found in BBG. The initially detected sound types shared common characteristics and thus were further grouped into twelve categories based on frequencies and sequences (Table 2), as in (Desiderà et al., 2019). Twelve sound categories occurred in BBG and four in SGK. 55 % of the samples occurred at night, and night records contained 64 % of all annotated sound sequences. However, the number and percentage of nighttime occurrences varied significantly among sound categories (Table 2). In 2020 and 2024, different sound categories dominated the soundscape in the two areas (Table 3). In 2020 the most abundant sound categories were “A” (252 calls), “alpha” (190 calls) and “S1” (54 calls); they occurred only in BBG. In 2024, the most abundant sound categories were “zebu” (224 calls) and “alpha” (200 calls). In BBG (2020 and 2024) and SGK (2024), acoustic abundance and richness were approximately 30 to 60 % higher at night. However, in SGK (2020) acoustic abundance was only about 20 % higher at night compared to daytime, while richness remained the same (Fig. S1).

3.2. *Comparison of acoustics vs historical experimental fishing indices*

Acoustic abundance was more strongly contrasted between BBG and SGK than fish abundance from experimental fishing, although both indices clearly differ between the two stations (Fig. 3). The results of the GLM applied to the historical fishing monitoring data indicate that fish abundance varied across years, stations, and seasons, although none of the coefficients were statistically significant at the 0.05 level, except for the intercept ($p = 0.0014$). The effect of station SGK01 appears negative ($\beta = -1.7469$) and was the only factor that appeared (marginally) significant ($p = 0.065$), suggesting a trend toward lower abundance at this location (Table 4). The results of the GLM applied to PAM data showed that both station and year significantly impact the number of calls per minute. The negative coefficient for station SGK ($\beta = -1.8756$, $p < 0.005$) suggested a substantially lower call rate at this station, while the positive and significant effect of year 2024 ($\beta = 0.0953$, $p < 0.05$) indicates a slight increase in call frequency compared to the baseline year (Table 5).

A strong consistency was found in the differences in Abundance, Richness, and Diversity between BBG and SGK when using fishing monitoring or acoustic monitoring (Fig. 4). In BBG, the mean acoustic richness (8.2) exceeded fish species richness (5.1). In SGK, acoustic and fish species richness were similar (~3-4), but fish species richness was also more variable in historical experimental fishing. In both cases the Shannon diversity index was approximately 55 % higher in BBG than in SGK (Fig. 4). Specifically, the average Shannon diversity index was 1.6 times higher in BBG than in SGK while in experimental fishing, it was 1.5 times higher in BBG than in SGK.

The literature review (Looby et al., 2023) revealed that among the 86 fish species listed in the area, 73 are known to vocalize or belong to a family known to vocalize elsewhere and 13 were observed as mature individuals, thus potentially emitting reproduction-related sounds at the time of recording (Table 6).

3.3. *Dedicated experimental fishing and fishermen’s perception*

The dedicated fish sampling and social survey showed that the differences in fish assemblages observed in the past between BBG and SGK have remained similar since the establishment of the protected area.

Dedicated experimental fishing conducted in March and April 2023 showed contrasting results between BBG and SGK but also suggested low replicability (Table S3). In March 2, only four individuals were caught, belonging to four species (Shannon diversity index = 1.39), while in BBG 12 individuals from five species were caught (Shannon diversity index =1.23). In April 2, the fishing operation was repeated in BBG, where 26 individuals from eight species were caught (Shannon diversity index =1.82). In March 2, at SGK, fishermen said they had seen traces of recent fishing operation in SGK, and they mentioned a particularly strong current at BBG. These two factors may have caused the low catch that day.

All the fishermen who participated in the social survey said that the same species could be caught in BBG and SGK, but in much higher numbers in BBG. Fishermen explained this contrast by citing the very high exploitation level of SGK and acknowledged the role of protection measures in BBG. Three fishermen also mentioned that BBG had already sheltered more fish than SGK before the MPA closure (in 2003) due to its remoteness and proximity to the ocean (see discussion in Section 4.1). The robustness and consistency of the differences between the two sites were also confirmed by the MPA manager, who leads the local fisheries co-management with fishermen and regularly samples the MPA with local fishermen and has done so since 2012.

4. Discussion

To our knowledge, the present study is the first passive acoustic monitoring study conducted in an African mangrove. Our results further reinforce and extend to mangroves previous findings in oceanic and estuarine environments, showing that contrasts in fish assemblages observed through traditional fish surveys were also reflected in PAM (Carriço et al., 2020a; Souza Jr et al., 2023; Rowell et al., 2017), thus contributing to establish confidence in its use as a fish monitoring tool. Despite missing information about sounds identification and acoustic fish behavior, our results showed that PAM was able to differentiate protected from unprotected areas. While direct listening and average spectrogram analyses allowed us to detect qualitative differences, individual sound sequence labeling allowed us to compute quantitative

Table 2

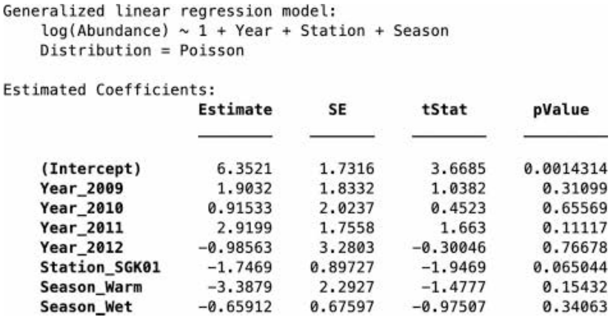
Characteristics on the main sound categories annotated recorded in BBG and SGK in December 2020 and January 2024.

Sound category	Nb sound types included	Frequency modulation (FM) or pulses (P)	Min Freq. or fundamental (Hz)	Max Freq. or highest harmonic (Hz)	Mean duration (seconds)	Nb pulses	Chorus	Nb sounds detected (% at night)
A	2	FM	270	1200	1	–	Yes	282 (72 %)
ET	1	FM	220	1000	0.5	–	No	17 (100 %)
Lambda	1	FM	200	1000	0.9	–	No	1 (100 %)
S1	1	P with FM	500	1400	1	50 (2 × 25)	yes	55 (100 %)
B	1	P	100	800	1	>20	No	32 (62.5 %)
alpha	4	FM and P	100	1000	0.2–0.5	1–3	No	390 (63 %)
Beta	1	P	500	7000	0.2–0.5	12–25	No	18 (100 %)
Gama	4	P	100	1500	0.2–0.7	2–4	No	39 (59 %)
tho	2	P	100	2000	0.1	1	No	52 (67 %)
zeta	2	P	100	500	0.65	3	No	101 (64 %)
DiamTeri	1	P	600	7000	0.2	10	No	21 (29 %)
Zebu	1	FM	50	1000	1.6	–	Yes	224 (49 %)

Table 3
Number, percentage of annotated sound categories and number of subsamples in which these were found in Bamboung, the protected area (BBG) and Sangako, the fished area (SGK) in 2020 and 2024, computed from annotated subsamples (Table 1).

Sound category	Bamboung (BBG)						Sangako (SGK)					
	2020			2024			2020			2024		
	Nb sounds	%	Nb subsamples	Nb	%	Nb subsamples	Nb sounds	%	Nb subsamples	Nb sounds	%	Nb subsamples
A	252	48.1	20	30	5.2	10	0	0	0	0	0	0
B	1	0.2	1	31	5.4	13	0	0	0	0	0	0
ET	10	1.9	1	7	1.2	4	0	0	0	0	0	0
S1	54	10.3	4	1	0.2	1	0	0	0	0	0	0
alpha	147	28.1	22	166	28.8	23	43	52.4	22	34	69.4	5
beta	13	2.5	2	3	0.5	1	0	0	0	2	4.1	1
gamma	16	3.1	11	21	3.6	10	2	2.4	2	0	0	0
lambda	1	0.2	1	0	0	0	0	0	0	0	0	0
tho	2	0.4	2	35	6.1	13	8	9.8	6	7	14.3	3
zeta	28	5.3	9	41	7.1	16	29	35.4	17	3	6.1	1
Zebu	0	0	0	221	38.3	23	0	0	0	3	6.1	1
DiamTeri	0	0	0	21	3.6	5	0	0	0	0	0	0

Table 4
Result of the GLM analysis on historical experimental fishing monitoring.

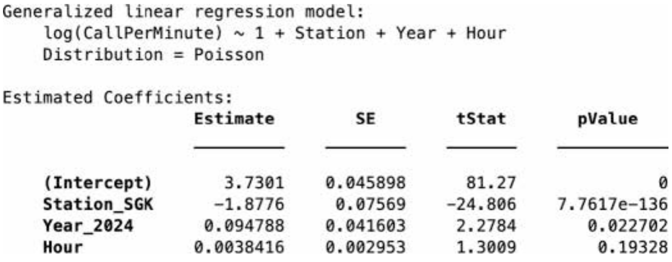


```
Generalized linear regression model:
    log(Abundance) ~ 1 + Year + Station + Season
    Distribution = Poisson

Estimated Coefficients:
                    Estimate       SE        tStat       pValue
                    ________    _______    ________    _________

    (Intercept)       6.3521     1.7316      3.6685    0.0014314
    Year_2009         1.9032     1.8332      1.0382      0.31099
    Year_2010        0.91533     2.0237      0.4523      0.65569
    Year_2011         2.9199     1.7558       1.663      0.11117
    Year_2012       -0.98563     3.2803    -0.30046      0.76678
    Station_SGK01    -1.7469    0.89727     -1.9469     0.065044
    Season_Warm      -3.3879     2.2927     -1.4777      0.15432
    Season_Wet      -0.65912    0.67597    -0.97507      0.34063
```

Table 5
Result of the GLM analysis on fish call per minutes.



```
Generalized linear regression model:
    log(CallPerMinute) ~ 1 + Station + Year + Hour
    Distribution = Poisson

Estimated Coefficients:
                   Estimate         SE        tStat        pValue
                   _________    ________    _______    ___________

    (Intercept)       3.7301    0.045898      81.27              0
    Station_SGK      -1.8776     0.07569    -24.806    7.7617e-136
    Year_2024       0.094788    0.041603     2.2784       0.022702
    Hour           0.0038416    0.002953     1.3009        0.19328
```

indices that aligned with the established knowledge of fish assemblages based on experimental fishing and visual census (Fig. 4).

4.1. Contrasted fish assemblage and soundscape between BBG and SGK

The 2023 fish sampling and the 2024 fishers' social survey confirmed the stability of the differences in fish assemblages between BBG and SGK as previously documented, with significantly higher fish abundance in the MPA. The higher abundance of target species in BBG, described by fishermen in the social survey, aligns with experimental fishing which also showed a more diverse fish assemblage in BBG compared to SGK (Sadio et al., 2015). Historical experimental fishing data from the PAM recording stations reinforced these differences in fish assemblage parameters at these specific stations (Sadio et al., 2015, Figs. 3 and 4). These differences were attributed to the no-take vs open access fishing regulations rather than intrinsic site characteristics, given the similarity of environmental parameters between the two sites and the fact that experimental fishing monitoring had already shown contrasts in fish assemblages before and after the fishing closure in BBG (Ecoutin et al., 2014, 2013; Sadio et al., 2015). Indeed, since the establishment of the Bamboung MPA in 2003, a rapid shift in the trophic structure of the fish assemblage was observed, with a notable increase in larger marine predatory fish species in BBG, while SGK remained dominated by smaller estuarine detritivores fish species (Colléter et al., 2012; Brochier et al., 2013). The species sampled in SGK were also found in BBG (Sadio et al., 2015), which corresponds with the overlapping sound sequences categories recorded at both sites (Table 3). Since many of the fish species reported in the area belong to a family that is known to vocalize in other regions (Table 6), a greater fish abundance in BBG would be expected to be reflected in the PAM data, which is indeed the case (Table 3, Figs. 3 and 4). However, this relationship could vary depending on the vocal behavior of the species producing the sounds. Future studies should investigate these behaviors to further refine and better quantify the relationship between soundscape patterns and fish assemblages observed in this study. For instance, the sound pressure level of a chorus linked to a specific fish spawning aggregation could serve as an indicator of that species' abundance; as documented in other estuarine ecosystems (Souza Jr et al., 2023).

The PAM indices in BBG and SGK were more contrasted and less variable than those from experimental fishing (Figs. 3 and 4). The high variability in experimental fishing indices may be partly due to intrinsic variability of fishing gear efficiency (Charles-Dominique, 1989; Wessel and Winner, 2003). Furthermore, in experimental fishing the catch strongly depends on specific environmental conditions at the time of the fishing operation. In particular, the effect of tide was illustrated by the contrasting results of the two consecutive fishing operations in BBG in 2023. In contrast, the PAM-derived index proposed in this study provided a more stable representation of fish assemblage parameters. On the other hand, anthropogenic acoustic disturbance from pirogue motor noise was absent in BBG but was present in some subsamples in SGK. Although it did not interfere with the sound labeling process, it may have caused stress to vocal species, potentially biasing the acoustic index toward lower values in SGK and thereby increasing the contrast with BBG.

4.2. Sound abundance and richness

Sound sequence labeling was conducted manually after several unsuccessful attempts to employ unsupervised methods, mainly due to the highly noisy soundscape dominated by "cliks" (Ulloa et al., 2018). However, the obtained dataset will be valuable beyond the present study for training deep learning algorithms, which have demonstrated their

Table 6
Fish species caught during Bamboung marine protected area monitoring between 2003 and 2011 (from “Inventaire faunistique de l’aire marine protégée de Bamboung: guildes fonctionnelles (écologique et trophique)”). In bold, species that belong to a genus known to include vocal species (according to Looby et al. 2024). *: species identified as vocal. In grey, species that were particularly abundant at the site of the passive acoustic monitoring. ♥: species spawning at the time of the survey. Some genus or species have changed name, previous names are in parenthesis.

Family	Species name	Cross-referencing with recorded sounds
Acanthuridae	***Acanthurus monroviae***	
Albulidae	***Albula vulpes*** *	Tho / Zeta = Thump (Fish & Mowbray 1970)
Ariidae	***Carlarius (Arius) heudelotti***	
	Carlarius (Arius) latiscutatus ♥	Beta = Stridulation in *A. seemani* (Heyd & Pfeiffer 2000)
	Carlarius (Arius) parkii	Beta = Stridulation in *A. seemani* (Heyd & Pfeiffer 2000)
Batrachoididae	***Batrachoides liberiensis*** *	A / Zebu = Swoop (Staaterman 2017, Staaterman et al., 2018), Boatwhistle (Amorim & Vasconcelos 2008, Amorim et al., 2008, 2010) + personal recordings
Belonidae	***Ablennes hians***	
	Strongylura senegalensis	
	Tylosurus crocodilus	
Blenniidae	***Hypleurochilus langi***	
Carangidae	***Scyris (Alectis) alexandrinus***	
	Caranx hippos *	
	Caranx rhonchus	
	Caranx senegallus	
	Chloroscombrus chrysurus *	
	Hemicaranx bicolor	
	Lichia amia	
	Trachinotus ovatus *	Zeta = Knock (Zhang et al., 2021, Liu et al., 2023)
	Trachinotus teraia ♥	
Carcharhinidae	*Carcharhinus leucas*	
Chaetodontidae	***Chaetodon hoefleri***	
Cichlidae	***Sarotherodon melanotheron*** *	Gamma = Rolling sound (Akian et al. 2020)
	Coptodon (Tilapia) guineensis ♥	
Clupeidae	***Ethmalosa fimbriata*** * ♥	
	Sardinella aurita *	
	Sardinella maderensis *	
Cynoglossidae	*Cynoglossus monodi*	
	Cynoglossus senegalensis ♥	
Dasyatidae	***Fontitrygon (Dasyatis) margarita***	
	Fontitrygon (Dasyatis) margaritella	
Drepaneidae	*Drepane africana*	
Echeneidae	***Echeneis naucrates*** *	
	Remora remora *	
Elopidae	*Elops lacerta*	
	Elops senegalensis	
Ephippidae	***Chaetodipterus lippei***	Zeta = Knock in *C. faber* (Fish & Mowbray 1970)
	Ephippus goreensis	
Epinephelidae	***Epinephelus aeneus***	B = Chorus (Mann et al., 2010) and RH sounds (Zayas Santiago et al., 2020) in *E. guttatus*, Chorus in *E. striatus* (Schärer et al., 2012)
Exocoetidae	*Fodiator acutus*	
Gerreidae	***Eucinostomus melanopterus***	Zeta = Knock in *E. gula* and *E. havana* (Fish & Mowbray 1970)
	Gerres nigri ♥	Zeta = Knock in *G. cinereus* (Fish & Mowbray 1970)
Gobiidae	***Awaous lateristriga***	
Haemulidae	***Brachydeuterus auritus***	
	Plectorhinchus macrolepis	
	Pomadasys incisus	
	Pomadasys jubelini	
	Pomadasys perotaei ♥	
Hemiramphidae	***Hemiramphus brasiliensis*** ♥	
Lutjanidae	***Lutjanus dentatus***	
	Lutjanus goreensis	Zeta = Knock / Boom in *L. synagris*, *L. analis*, *L. apodus*, *L. griseus*, *L. jocu* (Fish & Mowbray 1970, Kannan et al., 2020)
Monodactylidae	*Monodactylus sebae* ♥	
Moronidae	***Dicentrarchus punctatus***	Zeta = Thump in *Morone saxatilis* (Fish & Mowbray 1970)
Mugilidae	***Chelon (Liza) dumerili***	
	Neochelon (Liza) falcipinnis	
	Parachelon (Liza) grandisquamis	
	Mugil bananensis	
	Mugil cephalus *	
	Mugil curema *	
Myliobatidae	***Aetomylaeus (Pteromylaeus) bovinus***	
	Rhinoptera marginata	
Paralichthyidae	*Citharichthys stampflii*	
Polynemidae	***Galeoides decadactylus***	
	Polydactylus quadrifilis	Zeta = Knock in *P. virginicus* (Fish & Mowbray 1970)
Pristigasteridae	***Ilisha africana*** ♥	
Scaridae	***Scarus hoefleri***	
Sciaenidae	***Argyrosomus regius*** *	Lambda = Adult social sound (Perieira et al 2020) ; S1 = Grunt (Vieira et al. 2019)
	Pseudotolithus elongatus	
	Pseudotolithus senegalensis *	S1 = personnal observation
	Pseudotolithus senegallus	
	Pseudotolithus typus	
Scombridae	***Orcynopsis unicolor***	
	Scomberomorus tritor	
Serranidae	***Serranus cabrilla***	Tho = Thump in *S. tigrinus* (Fish & Mowbray 1970)
Soleidae	***Dagetichtys lusitanicus (Synaptura lusitanica)***	
Sparidae	***Diplodus bellottii***	Zeta = Thump in *D. argenteus* (Fish & Mowbray 1970)
Sphyyraenidae	***Sphyraena afra***	
	Sphyraena guachancho *	Zeta = Knock in *S. barracuda* (Fish & Mowbray 1970)
Syngnathidae	***Hippocampus algiricus***	
	Syngnathus typhe (pelagicus)	
Synodontidae	*Trachinocephalus myops*	
Tetraodontidae	***Ephippion guttifer*** ♥	
	Lagocephalus laevigatus *	
	Sphoeroides spengleri *	Beta = Scrapes in *S. maculatus* (Fish & Mowbray 1970)
Torpedinidae	*Torpedo sp.*	
Trichiuridae	*Trichiurus lepturus*	

(*continued on next page*)

efficiency in detection the most frequent sound sequences (Waddell et al., 2021; Kammegne et al., 2023).

The acoustic richness observed in BBG (12 categories) was in the lower range of previous observations in other ecosystems, which range from 9 categories in the Azores seamounts, 22 in coral reefs, to 37 in South African canyons (Carriço et al., 2020a; Ruppé et al., 2015; Putland et al., 2017; Bertucci et al., 2020), although the recording duration considered in these studies was much longer (years). Thus, the acoustic richness in SGK (4 categories) was exceptionally low, likely due to the particularly high fishing pressure. “A”, “S1” and “zebu” sounds, recorded only in BBG, occurred either as isolated calls or in ‘choruses’, i.e. vocalizations produced “en masse” (Parsons et al., 2016), partly simultaneously but with distinct frequencies (Fig. 2). Choruses typically shape to local soundscapes. For example, 7 types of choruses were recorded along the Australian coast over a year and a half, predominantly on different days, but sometimes choruses also occurred simultaneously (Parsons et al., 2017). The 24-hour average acoustic abundance found in BBG (~46 calls per minute, Table 1) was particularly high compared to observations in other ecosystems. For example, based on the data reported in the literature we calculated that in the Azores seamounts, it was 0.7 sounds per minute, while in the gulf of Mexico it peaked at 2 sounds per minute (Carriço et al., 2020a; Boyd et al., 2021). This aligns with previous observations showing that fish sounds were more abundant at night (Carriço et al., 2020a).

4.3. From acoustic to fish assemblage indices

Although the fish sounds detected were not yet be attributed to exact fish species, many potential species were identified (Table 6). Some fish species produce a sound when manipulated by humans in the air which might be a distress call (Ladich et al., 2021); it was the case of *Pomadasys perotaei, Batrachoides liberensis* and *Ephippion guttifer*, but there was no evidence that the same species were responsible for the recorded calls.

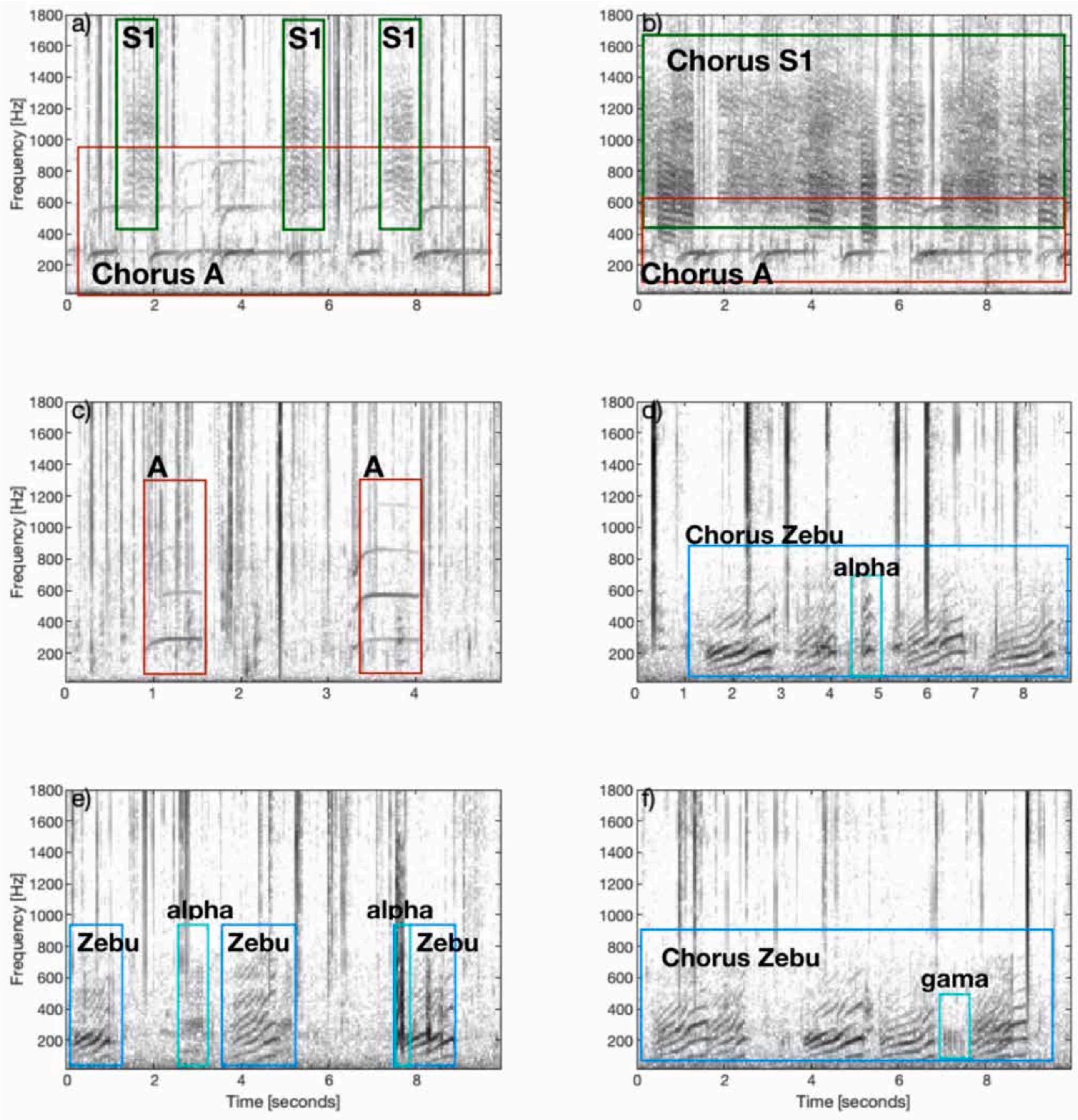


Fig. 2. Spectrograms showing examples of sounds categories ‘A’, ‘S1’ and ‘zebu’. The short-term Fourier transform used a 4096-hamming window with 50 % overlap. a) ‘A’ chorus with isolated ‘S1’; b) simultaneous A and S1 chorus; c) isolated ‘A’, d) and e) ‘zebu’ chorus with ‘alpha’ in between, f) chorus of superposed zebu sounds with a ‘gamma’ sound in between.

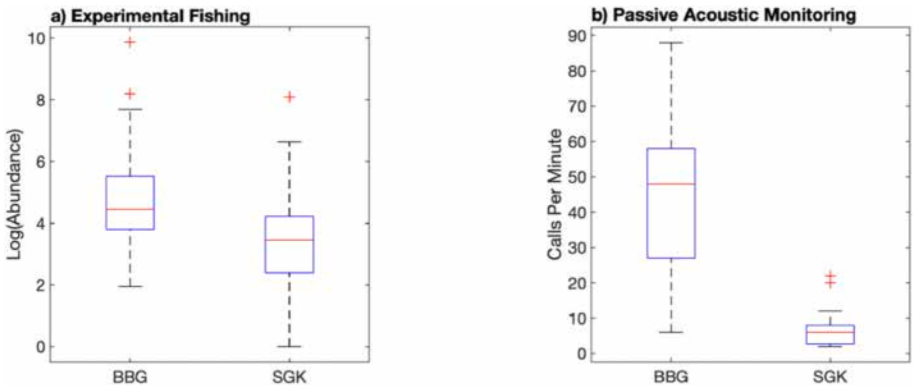


Fig. 3. Box plots showing the contrast between the protected (BBG) and unprotected (SGK) sites based on fish abundance in historical experimental fishing (a, *p* value = 0.12) and fish calls per minutes in passive acoustic monitoring (b; p value <0.001). Abundance (a) needed to be log-transformed to respect the normality test. See details of the glm in Tables S1 and S2.

Spearfishermen from Dakar identified *Batrachoides liberensis* to be responsible for different kinds of sounds which may include the “S1” sound category (Brochier and Puig, 2023), but direct evidence is missing. On the other hand, in a nearby area we recorded a “S1” sound simultaneously with catching a *Pseudotolithus senegalensis*, suggesting this species emitted the sound, which would be in line with the kind of sounds emitted by this family of fish (Table 6), particularly by *Argyrosomus regius* to which the “*Lambda*” sound could also be attributed based on (Vieira et al., 2019). Two catfish species (*Arius latiscutatis* and *Arius parkii*) observed in the fish samples may be responsible for our “beta” stridulatory sound category, frequently observed in other catfish species (Heyd and Pfeiffer, 2000). We cannot exclude that this sound type could also be produced by a member of the family Tetraodontidae as it may sound like “*scrapes*” described in *Sphoeroides maculatus* (Fish and Mowbray, 1970). The “gamma” category could be attributed to *Sarotherodon melanotheron* as it resembles the rolling sound described in the same species (Akian et al., 2020). Our “alpha” category includes several short sounds sequences which sounds similar to the “\kwa” sound described for *Scorpaena* spp. (Bolgan et al., 2019), but this species was not observed in this area. The “zeta” category resembles “Knock” sounds described in many different vocal species (Fish and Mowbray, 1970) and would deserve further investigation to be attributed to a particular candidate. Some sounds were not taken into account in the labeling process such as the higher frequency dolphins calls, as we focused on the lower <3 kHz, and the omnipresent “clicks” that constantly cover the whole spectrum several times per seconds in both sites; these are usually attributed to snapping shrimps (Johnson et al., 1947), although this species was not described in this area. We

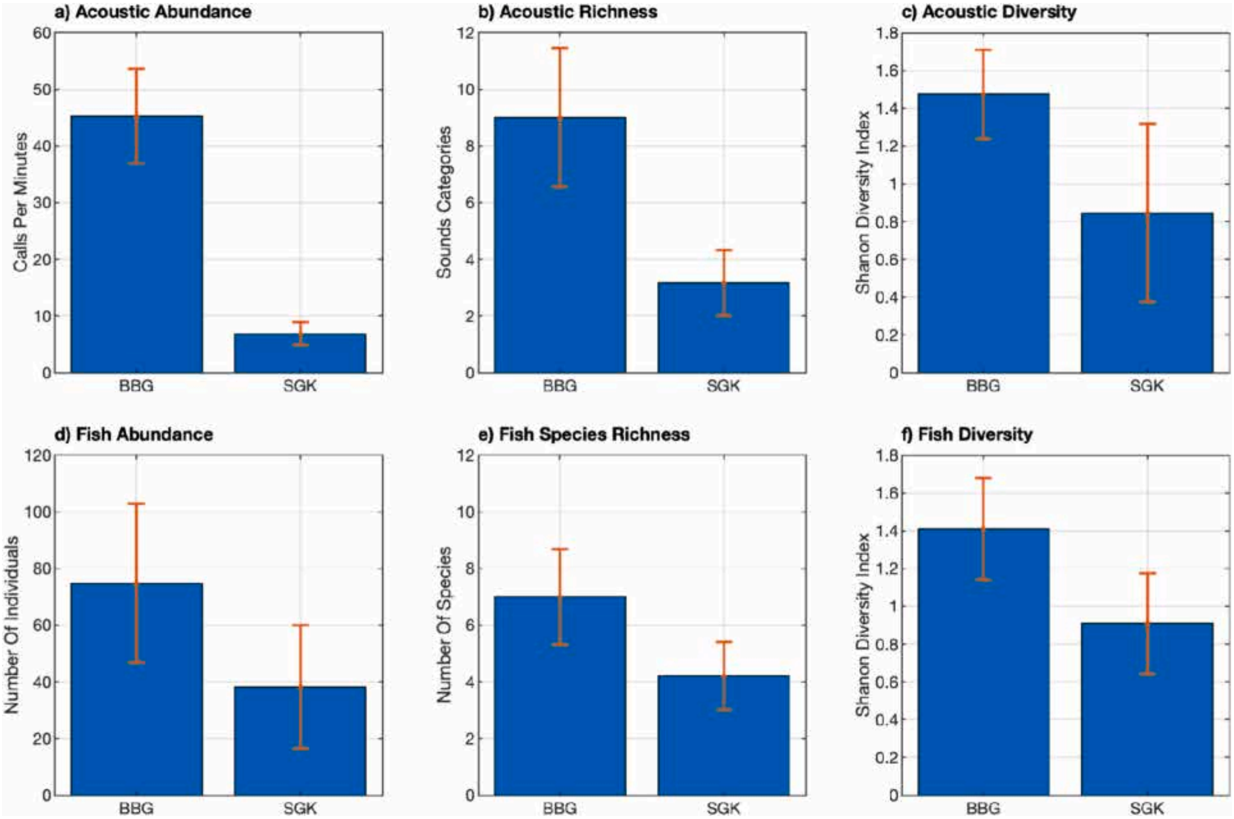


Fig. 4. Comparison of passive acoustics monitoring (a,b,c) Vs historical experimental fishing (d,e,f), indices in protected area (BBG) and fished area (SGK). Standard deviation was computed from interannual variability as well as diel variability for PAM.

hypothesized that mangrove oysters, which were observed near both recording sites, could be responsible for these sounds.

It cannot be excluded that non-identified sounds could be emitted by other organisms than fish, such as crabs for example (Boon et al., 2009). However, as terrestrial ecological studies have shown that higher-taxon richness predict wholesale species richness (Williams and Gaston, 1994; Mazaris et al., 2010), one could expect that the diversity in sounds may reflect species richness, even if all the sounds were not emitted by species from the same family or order. In underwater marine acoustics, it was previously observed that non-identified sound types diversity index matches the fish taxa diversity index, e.g. (Desiderà et al., 2019), and it is also the result we obtained (Fig. 4). The link between fish and sounds abundance is also intuitive, as more individuals might produce more sound sequences but comparing the acoustic abundance to abundance obtained from fish sampling techniques would require knowledge of sound sequences attenuation (Carriço et al., 2020b) as well as differences in fish acoustic behavior among species and environmental conditions (Ladich, 2019). In our case, the contrast in abundance between the protected and fished area was more marked in sounds than in fish sampling (Figs. 3 and 4). The approach should be replicated on different sites to strengthen the results. Indeed, preliminary results following the present study suggested that the fine-scale spatial variability of fish sounds needs to further studied, especially in highly heterogeneous environment such as mangrove estuaries comprising water streams of variable size, depth and different levels of connectivity with the sea, and mangrove covering. This natural spatial heterogeneity needs to be understood before PAM can be used to map fish assemblages in mangrove estuaries.

Combining the acoustic abundance and richness using the Shannon diversity index produced similar diversity indices to the average Shannon diversity index computed from fish sampling (Fig. 4). Whether the diversity index derived from PAM is higher or lower than the one obtained by fish sampling depends on the number and the behavior of soniferous species in the fish assemblage, which could be described for any fish assemblage. For example in Azores, the Shannon diversity index derived from PAM was lower than the one calculated from fish sampling (Carriço et al., 2020a). Our results suggest that the few soniferous species recorded were representative of the full fish assemblages, thus even if the soniferous species were not target species for fisheries, they might be associated with species usually captured in fish sampling (Picciulin et al., 2013).

4.4. Conclusion and perspective

PAM provided relevant information allowing to contrast fish assemblage abundance, richness and diversity in the mangrove ecosystem study case, between protected and exploited areas. Thus, the multiplication of PAM stations at the scale of the estuary could provide information on the heterogeneity of fish assemblage distribution to inform decision-making in MPA design. Also, the repetition of PAM at the same stations may allow for the observation of fish assemblage evolution based on the protection status. In particular, the fishing community - including children and non-fishers - can observe the effects of the MPA. Underwater records needed to estimate these parameters could be collected relatively easily, even by the fishers themselves, opening the possibility of a participative monitoring system. For this, automated data analysis systems would be required to rapidly perform the analysis which was done manually here from new records. However, to date, given the state of the knowledge in this area PAM cannot provide information about species in presence, intra-specific sex-ratios, size spectra and maturity, which are also important parameters for management. Thus, PAM would not replace fish sampling but could allow to fill monitoring holes and to ensure comparable, objective data along time series, and support co-management decisions (Brochier et al., 2021). In the future, the identification of local fish sounds will make it possible to improve acoustic fish descriptors, by designing specific experiments (Mouy et al., 2023) and/or by integrating fishers' ecological knowledge of soniferous fish species (Brochier and Puig, 2023), and the data collected meanwhile will make possible retrospective analysis. With specific knowledge of fish sound characteristics and spawning aggregation behavior, some commercial vocal species' biomass can be estimated with PAM (Rowell et al., 2017; Stratoudakis et al., 2024). Combining such single species indicators with ecosystem indicators would to provide ecosystem-based management (Howell et al., 2021).

Other non-intrusive methods for marine biodiversity monitoring are generally more complex to deploy. In the study area, active acoustic monitoring, or sonar, was used simultaneously with the historical fish sampling, but failed to detect the differences in fish assemblages between the protected and unprotected areas observed in experimental fishing (Béhagle et al., 2018). The authors explained this result by the numerous constraints and limitations inherent to sonar deployment in such shallow environments - constraints also experienced in other estuaries, although single-species biomass could be estimated in the particular case of fish spawning aggregations (Rowell et al., 2017). The nearly constant water turbidity also prevents the use of optical based systems, such as BRUVS (Baited Remote Underwater Video) or direct visual censuses. Environmental DNA is a promising method, but still not sure it can assess abundance, and it continues to be a costly technique.

Compared to other non-intrusive methods PAM could be a reliable and sustainable solution for mangrove MPA monitoring, in particular in areas where monitoring programs rely on unstable or short-term funding and where constant fish sampling protocols cannot be maintained. The recent development of open source low-cost hydrophones and recorders that can be locally assembled and repaired (Caldas-Morgan et al., 2015; Lamont et al., 2022) opens the way to citizen science and the onset of participative acoustic monitoring (Abrahams et al., 2021; Norden et al., 2021) as part of artisanal fisheries monitoring. For this purpose, at the local scale, bioacoustics research may now focus on understanding the soundscape spatial-temporal dynamics, i.e. describing the underwater heterogeneity of fish assemblages in the mangroves. Fish species sound identification is rapidly growing (Looby et al., 2023; Vieira et al., 2024), and these databases combined with artificial intelligence may allow automatic detection of many species, although local training datasets may still take time to grow. Also, fish acoustic behavior may be specific to local context, as for example linked to the spatio-temporal dynamics of fish spawning aggregations and migration patterns (Mooney et al., 2020). Aerial PAM has been shown to very effective for bird monitoring in mangroves and other wetlands (Branoff and Campos-Cerqueira, 2021; Mosikidi et al., 2023); it may bring indirect information on fish distribution through the monitoring of fish predator birds. Thus, coupled passive acoustic monitoring above and below water might bring interesting insights. Finally, combining participative PAM with local ecological knowledge and artificial intelligence should bring a virtuous circle for the artisanal fisheries co-management (Brochier et al., 2021; Quintana et al., 2021).

CRediT authorship contribution statement

Timothée Brochier: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Field work. **Oumar Sadio:** Methodology, Formal analysis, Data curation, Field work. **Mamadou Diop:** Project administration, Data curation, Field work. **Frédéric Bertucci:** Writing – review & editing, Investigation, Field work. **Caouis Kammegne:** Data curation, Field work. **Théophile Bayet:** Data curation, Field work. **Balbine Olive Mboua Etoga:** Data curation, Field work. **Hoover Esteban Pantoja Sanchez:** Writing – review & editing, Data curation, Field work. **Alassane Bah:** Funding acquisition. **Yann Tremblay:** Writing – review & editing, Investigation, Conceptualization, Data curation, Resources, Field work.

Declaration of competing interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111051.

Data availability

Data will be made available on request.

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