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Black coral patches and reef fish diversity: An integrative multidisciplinary approach

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ABSTRACT

The black coral *Antipathes galapagensis* is a habitat engineer that may play critical roles for marine biodiversity but is still largely underexplored because typically found in the mesophotic zone. However, *A. galapagensis* occasionally colonizes shallow waters providing an excellent opportunity to assess its ecological role. Here, we compared the reef fish assemblages between rocky reefs with and without black coral in the Bay of La Paz (Mexico). To achieve a comprehensive understanding of the diversity in each habitat, we adopted an integrative approach that combined different methodologies tailored for specific groups, i.e., Underwater Visual Census for conspicuous, Passive Acoustic Monitoring for nocturnal soniferous, and environmental DNA for cryptobenthic species. Black coral habitats were found in isolated patches rather than extensive forests and demersal fish assemblages were largely similar between the habitats, except for Lutjanidae, with higher densities in the black coral habitat. However, small benthic fish species (5–20 cm) showed higher species richness, density, and distinct compositions in black coral. Historical fish surveys in reefs of the region confirmed these findings. Acoustic analyses revealed differences between the sites, although no relationship with black coral was detected. Although environmental DNA supported the role of black coral for Lutjanidae, it failed to capture the diversity of cryptobenthic fish, pointing to methodological challenges discussed in our study. Overall, our findings underscore the ecological significance of black coral for reef fishes, even in isolated patches, and highlight the need for further extensive studies on this underexplored and imperiled habitat.

1. Introduction

Structural complexity increases habitat heterogeneity by creating microhabitats that serve as shelters, foraging grounds, and breeding sites for numerous marine organisms, thereby promoting marine biodiversity (Graham and Nash, 2013; Darling et al., 2017). In tropical environments, the hermatypic corals mainly shape the structural complexity of shallow water reefs, with most of these corals depending on symbiotic zooxanthellae (Spalding et al., 2001). In mesophotic reefs, which extend from 30 to ca. 150 m in depth, light availability restricts the growth of zooxanthellate corals (Lesser et al., 2009), but other organisms, such as asymbiotic corals (hermatypic or ahermatypic) and sponges, may thrive and contribute to the formation of complex habitats (Kahng et al., 2017). However, due to logistic and technical challenges, little is known about the role of these organisms in structuring fish diversity in the mesophotic zone (Kahng et al., 2017). Given the pervasive impacts of global change on marine habitats across the entire depth gradient (Smith et al., 2009; Doney et al., 2012), it is imperative to elucidate these habitats' role in sustaining marine faunal diversity.

Among azooxanthellate corals, black corals (Antipatharia) are

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distributed across all oceans at depths ranging from 2 to 8,600 m in areas with hard substrates, low-light, and strong current (Pasternak, 1977; Davis and Cohen, 1968; Wagner et al., 2012). Black corals present a wide variety of morphologies, *i.e.,* unbranched, branched into a bush, fan, feather, or bottlebrush (Wagner et al., 2012). The branched morphotype can form dense aggregations, sometimes becoming ecologically dominant over large areas and thus creating underwater forest-like environments (Wagner et al., 2012). Although black coral biology and ecology remain poorly understood, mainly because over 75 % of the species live at depths greater than 50 m (Cairns, 2007), pioneering studies revealed black coral habitat can host a high marine fauna diversity, and serve as foraging and nurseries sites (Parrish et al., 2002; Boland and Parrish, 2005; Love et al., 2007; Cau et al., 2017).

In certain regions of the world, when optimal light and current conditions are present, black corals can establish colonies in relatively shallow waters, occurring at depths between 15 and 30 m (Grange, 1985; Bo et al., 2009; Terrana et al., 2020), providing excellent opportunities to study their ecology. In the Tropical Eastern Pacific, *Antipathes galapagensis* is distributed from the Gulf of California to Ecuador and can be found from shallow to mesophotic habitats, with records indicating its presence between approximately 5 and 200 m (Agarwal et al., 2024; Matamoros-Calderón et al., 2021; Bo et al., 2012; Lavorato et al., 2021). Within this region, the Gulf of California (GC) appears to be a particular hotspot for shallow-water black corals, with *A. galapagensis* recorded at multiple sites between 15 and 30 m from north to south (Munguia-Vega et al., 2018, 2020; Lavorato et al., 2021). *Antipathes galapagensis* is a branched morphotype that can create animal forests and may play essential roles in marine life, potentially offering shelters for a myriad of organisms thereby sustaining diversity. The GC is characterized by tropical to temperate environmental conditions (Lluch-Cota et al., 2010) where the northwards cold waters limit the symbiotic corals to its southern part, and rocky reefs are the dominant habitat in shallow waters (Reyes-Bonilla, 2003; Santander Monsalvo et al., 2018). The nutrient-rich waters of the GC, driven by complex topography, advection of deep waters, thermohaline circulation, and wind-driven upwelling in coastal shallows (Lavín and Marinone, 2003; Alvarez-Borrego, 2010), offer ideal conditions for the establishment of black coral (Lavorato et al., 2021).

The overexploitation of black corals, mainly for medicinal purposes and jewelry (Bruckner, 2016), has led to a global scale regulation by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Since 1981, all black coral species have been listed in CITES Appendix II (Convention on International Trade in Endangered Species of Wild Fauna and Flora, 2007), regulating their international trade through export permits. In Mexico, black coral exploitation began in the 1960s in the Mexican Caribbean and the GC, depleting black coral populations at depths accessible by diving (Padilla and Lara, 2003; Wills López, 2008). Since then, the black coral species in Mexican waters have been on the Mexican national protected species list, prohibiting their extraction (Secretaría de Medio Ambiente y Recursos Naturales NOM-059, 2010). As cold-water affinity species, black corals are also vulnerable to the tropicalization of the GC (Favoretto et al., 2022). Yet, despite the widespread distribution of the black coral in the GC and its vulnerability, the ecology of *A. galapagensis* is still poorly known.

The GC is both a biodiversity hotspot (Brusca, 2010) and a highly productive fishing region, accounting for 70 % of Mexico's total fisheries catch (Cisneros-Mata, 2010), with reef fishes serving as crucial resources for small-scale fisheries (Sala et al., 2004; Arreguín-Sánchez et al., 2017). Given the importance of the GC for both biodiversity and fisheries, it is essential to understand how each habitat in the region contributes to sustaining fish populations and maintaining the goods and services that the GC offers. The few studies investigating the relationship between black corals and fishes revealed how important this habitat can be as it serves as shelter or foraging sites for many species (Boland and Parrish, 2005; Gress et al., 2023 preprint), promotes specialization (Bosch et al., 2023), shapes fish assemblages composition, and boosts the abundance of various species (Aburto-Oropeza and Balart, 2001; Gress et al., 2023 preprint). In the GC, black coral is thought to serve as an important habitat for commercially valuable grouper species, although this hypothesis has not been tested yet (Sala et al., 2003; Aburto-Oropeza et al., 2008).

Reef fish monitoring is traditionally conducted by underwater visual census (UVC) performed by scuba divers or video recordings. However, UVC may overlook key components of fish communities, underestimating cryptobenthic and vagrant elusive species (Willis, 2001; Boussarie et al., 2018). Additionally, UVC are not that adequate in assessing nocturnal species, as surveys conducted at night require artificial lighting, which can alter fish behavior (Ryer et al., 2009). These limitations underscore the need for alternative approaches that can complement UVC method. Although several studies have employed multiple methodologies, their primary aim was to compare their efficacies (Honeyman et al., 2023; Cabrito et al., 2024), and few have leveraged the complementary strengths of these methods to target distinct components of fish assemblages. In this study, we aim to investigate the relationship between black coral habitat and reef fish assemblages in the southern part of the GC by integrating three distinct methods to obtain a more comprehensive monitoring of fish assemblages. In addition to UVC, we conducted Passive Acoustic Monitoring (PAM), and environmental DNA (eDNA) analyses to monitor conspicuous, nocturnal soniferous, and cryptobenthic species, respectively. We hypothesize that rocky reefs with black coral habitats, by representing a more complex habitat, will host a higher density of reef fish and potentially distinct fish assemblages than rocky reefs without antipatharians.

2. Material and methods

2.1. Sites selection and characterization

In the bay of La Paz, six sites were known to host the black coral *A. galapagensis* at a depth range of 15–30 m (Fig. 1). Two sites are located around islets close to the mainland coast, and four are along the coast of the Espiritu Santo Archipelago. These six sites are found in highly productive waters undergoing eutrophic conditions (annual average chlorophyll-a concentration higher than 1 mg m^{-3}; Antoine et al., 1996, Fig. 1). We extracted the chlorophyll-a concentrations for the bay from the NOAA online database with a spatial resolution of 2.5 km and a time resolution of 8 days for the year 2020 (https://coastwatch.pfeg.noaa.gov/data.html).

Of the six sites known to host black corals, four were deep rocky reefs (15–30 m), while the other two were a wreck and a mesophotic reef (~50–60 m; Fig. 1). The rocky reef Los Islotes, north of the Espiritu Santo Archipelago, hosted black coral 20–30 years ago (Aburto-Oropeza and Balart, 2001), but recent reports indicate their absence today. Therefore, we focused on the four deep rocky reefs with black coral in La Paz Bay, excluding the wreck (an artificial habitat) and the mesophotic rocky reef (>50 m depth) for reasons of logistical and diving limitations. This selection ensured consistent comparisons between natural rocky reef habitats with black coral and a control rocky reef at similar depths without black coral. Using a multidisciplinary approach (scuba-diving surveys, passive acoustic monitoring and eDNA), we were limited in the number of control sites by logistical and financial constraints. Consequently, we selected the most suitable available site. La Ballena is a rocky reef without antipatharians, ~20 m deep, and was the only deep (15–30 m) rocky reef near black coral sites. Fishing is permitted at La Ballena, as in most black coral sites, except for San Rafaelito (Fig. 1). It also supports fish diversity levels comparable to other rocky reefs at similar depth around Espiritu Santo (Maniquet, 2024). In addition to these five sites surveyed during the same campaign period, the study included other sites around the Espiritu Santo Archipelago with historical visual census data. We also incorporated two additional sites where acoustic recordings were obtained outside the main campaign. These

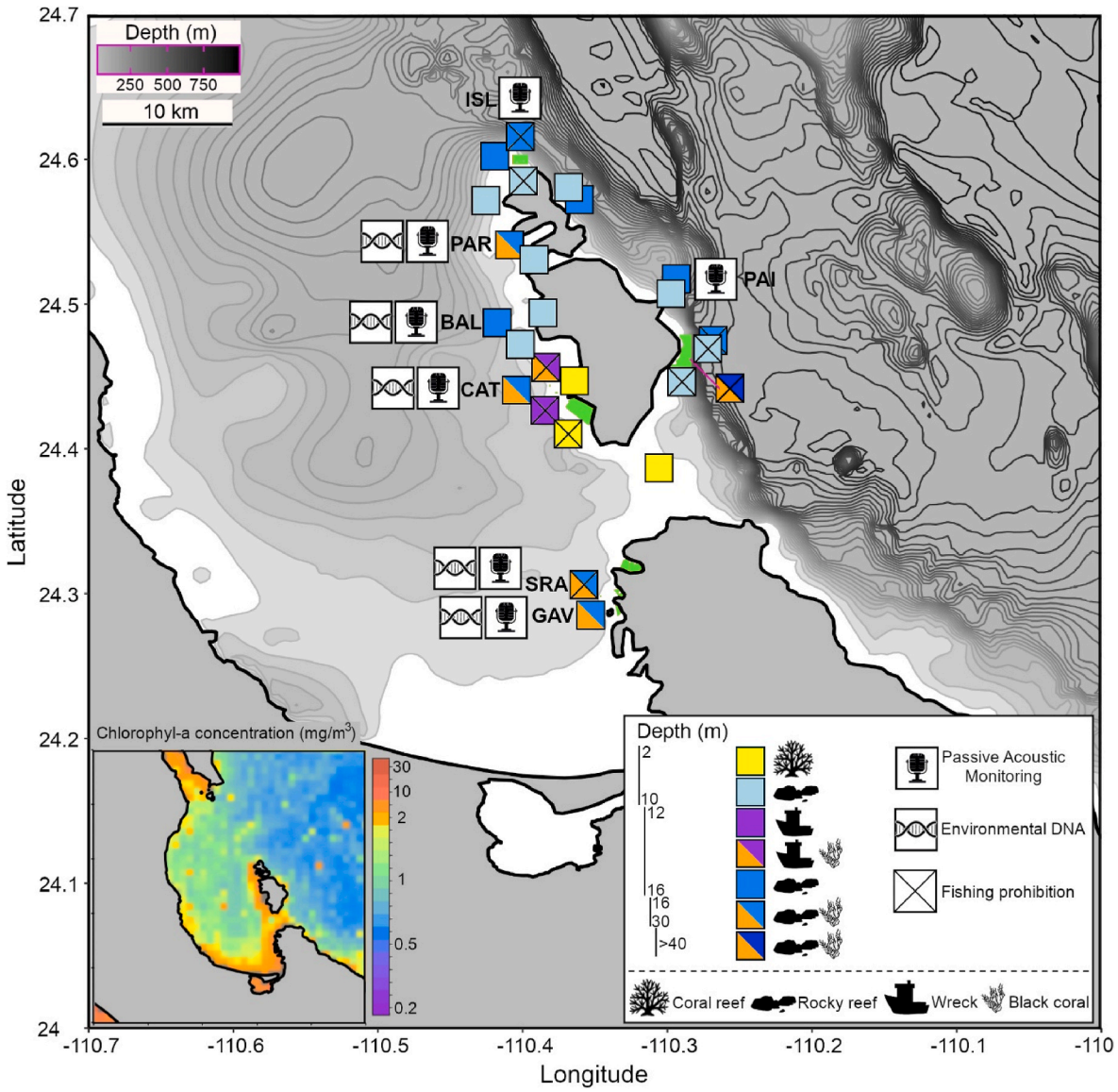

Fig. 1. Map of the Bay of La Paz showing the surveyed sites. The bathymetry of the bay is indicated with 30 m isobaths and the chlorophyll-a concentration is displayed in the inset map. The colored-squares indicate the different reef habitats in the area for which reef fish monitoring datasets were available, at least with scuba diving method. Green areas represent no-take zones. The hydrophone and DNA symbols indicate the sites where hydrophones were deployed, and DNA samples collected. Acronyms of the sites with at least two methods are indicated. The list of the sites with only scuba diving monitoring datasets can be found in supplementary material (Appendix C, Table C1). BAL: La Ballena; CAT: La Catedral; GAV: La Gaviota; ISL: Los Islotes; PAI: El Pailebote; PAR: La Partida; SRA: San Rafaelito. Additional information on sites ISL and PAI can be found in the 'Results Validation' section. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

additional datasets were used in the "Results confirmation" section to validate patterns identified in the main comparative analysis (Fig. 1).

We surveyed the five selected sites from July to September 2023. To ensure safe diving practices at a depth of 30 m, we characterized the sites by implementing a method tailored to the limited bottom time available for non-technical diving. We counted black coral colonies along six 30 × 2 m belt transects and measured the height of the tallest colony at each meter. Along the same belt-transect, we measured the depth every 2 m using a diving computer placed on the seafloor. The variance of the 90 depth measurements per site was then calculated to estimate the relief of the seafloor.

2.2. Reef fish assemblage surveys

We monitored different components of the reef fish assemblages by integrating three complementary methodologies: UVC for diurnal conspicuous fish larger than 5 cm, PAM for nocturnal soniferous fish, and eDNA for cryptobenthic reef fish families—i.e., families in which more than 10 % of species are smaller than 50 mm (Brandl et al., 2018).

2.2.1. Scuba diving transects

Two experienced divers conducted fish assessments along two 30 m-long belt transects in opposite directions. On the outward journey, divers surveyed within a width of 2 m demersal, conspicuous fish species, defined as species larger than 5 cm and moving within or between the reefs. On the return journey, and within a width of 1 m, divers cautiously looked for small (5–20 cm), benthic fish, closely associated with the seafloor, e.g., territorial species and individuals sheltering in their habitat such as black coral branches. Each diver performed one transect per dive to respect safety conditions. Species were identified and counted along the belt transects to estimate the species richness (number of species) and the density of fish (number of individuals per

100 m^2). Estimated total lengths of individual fishes were visually assessed and recorded in size classes of 10 cm (11–20 cm, 21–30 cm, etc.), except for the first class (5–10 cm), which had a smaller range. Each site was visited seven times, resulting in 14 transects per site.

2.2.2. Passive acoustic monitoring

To monitor nocturnal soniferous fish, we deployed on the seafloor of each site an autonomous underwater acoustic recorder (SNAP, Loggerhead Instruments; Sarasota, FL, USA) connected to a HTI-96-Min hydrophone (sensitivity of ca. −170 dB re 1 $V\mu Pa^{-1}$, with a flat frequency response from 2 Hz to 30 kHz). The SNAPs were left for 2 weeks at each site. Sounds were recorded for 1 min every 10 min at a sampling rate of 44.1 kHz with 16-bit resolution. We adopted a duty cycle of 1 min recording every 10 min to balance temporal resolution with storage and battery constraints, a compromise shown to preserve key acoustic metrics while reducing data volume (Thomisch et al., 2015), and because it is commonly used in reef soundscape monitoring (Raick et al., 2023a; Jarriel et al., 2024; McCammon et al., 2025). Due to the limited number of recorders, all the sites could not be monitored simultaneously. We aimed to survey the control site concurrently with the black coral sites whenever possible. A total of eight distinct nights of acoustic recordings were analyzed across the four black coral sites, with each site studied on three different nights. The control site was analyzed simultaneously on six of those nights. All recordings were carried out from 7:00 p.m. to 7:00 a.m., with at least three days between each night (Appendix A, Table A1). Nights were selected based on boat traffic, prioritizing those with minimal boat passages (qualitatively assessed) and we spaced the selected nights over the two-week recording period. Audio files were subsampled to 4 kHz, as most fish are known to produce sounds in the low-frequency range (0–2 kHz; Cato, 1978). Fish sound types were visually and aurally identified, and counted using the software Raven Pro 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology; Ithaca, NY, USA) with a fast Fourier transformation (FFT) size of 256, 90 % overlap, and Hanning window. Fish sounds were classified using a dichotomous key (Desiderà et al., 2019; Raick et al., 2023a, 2023b). This method was selected over acoustic indices, due to their low reliability in marine environments (Raick et al., 2023c, 2025). The sounds were classified in different 'sound types' based on the presence and type of frequency modulations, duration, peak frequency, and pulse period. The details of the sound identification key are provided in Appendix A (Fig. A1). After these steps, sound types with at least ten occurrences were retained for the analyses. Two sound types formed choruses, making impossible to count each sound individually. In this case, we divided the duration of the chorus by the average duration of the specific sound type to estimate its abundance. We quantified the fish sound type richness, i.e., the number of different sound types and their abundance per hour.

2.2.3. Environmental DNA

We visited each site twice within a two-week interval and collected two 2 L water samples per visit (i.e., 4 L per visit, for a total of 8L per site; Appendix B, Table B1). Water samples were collected using 1 L wide-mouth Nalgene bottles, positioned within 10 cm of black coral colonies or above the substrate at the control site. Samples were collected prior to the UVC surveys to minimize the presence of human DNA in the water. Water samples were kept in a cooler in the field, and each 2 L field replicate was filtered within 4 h on the same day in the laboratory using a sterile 0.45 μm Whatman mixed cellulose ester membrane filter. This was accomplished using a Nalgene reusable 45 mm bottle top filter unit connected to a vacuum pump. All collection and filtration equipment were cleaned with 10 % commercial bleach solution for 15 min and rinsed with tap water. Tap water samples were taken to the field and processed along with the other water samples to detect contamination during the collection and filtration steps (i.e., field controls). We extracted the DNA from the membrane filters using Qiagen DNeasy Blood and Tissue kits (Qiagen) with minor modifications (Valdivia-Carrillo et al., 2021). All eDNA extractions were conducted using equipment dedicated solely to eDNA, located in a low-density eDNA room and hood. The equipment was cleaned with 10 % bleach, followed by 70 % ethanol, and exposed to UV light for 15 min before each extraction. Negative controls were extracted simultaneously with the eDNA samples to monitor contamination. Preparation of PCR reactions took place in the low-density eDNA room and hood, targeting a ~65 bp fragment of the 12S rDNA gene region, specifically designed to target fish (Valentini et al., 2016). In order to control the effectiveness of our method to detect the cryptobenthic reef fish of the Gulf of California, we created a mock community composed of equimolar concentrations of tissue-derived genomic DNA of 33 cryptobenthic fish species and four small benthic reef fish species (Appendix B, Table B2). We treated the mock community exactly as the eDNA samples. Each of the 20 field replicates was amplified twice in a PCR1 and PCR2 reactions containing unique combinations of multiplex identifiers (Valdivia-Carrillo et al., 2021). We included negative controls during PCRs to monitor contamination. Detailed PCR conditions, clean-up, and DNA quantification methodologies are provided in the supplementary material (Appendix B). We pooled the four PCR2 replicates from each of the 10 site/date combinations, including the cryptobenthic fish mock community, and two replicates of the negative controls (field, DNA extraction and PCR steps) and sequenced them with Illumina NextSeq Mid-output (2 × 150 bp). We implemented bioinformatic analyses with the free version of usearch 11.0.667 (Edgar, 2010). We merged, trimmed, and filtered sequences using the functions fastq_mergepairs, fastq_truncate, and fastq_filter. Quality filtering parameters included a minimum length of 77 bp and a maximum expected error rate of 1. We removed singletons (sequences with an abundance of 1) using the function fastx_uniques. We removed chimeras and generated OTUs (Operational Taxonomic Units) with 97 % sequence identity using cluster_otus. For the taxonomic assignment of OTUs, we used the online BLAST tool to compare sequences against the NCBI-GenBank database and a custom reference database that included sequences of 60 fish species, 36 of which are cryptobenthic reef fish species from the Gulf of California (Mac Loughlin et al., 2025). The parameters applied were as follows: we selected the "somewhat similar sequence (blastn)" program, set the maximum number of target sequences to 100, and used an expected threshold of 0.05. Additionally, a word size of 11 was chosen, with a maximum match in a query range of 0. The match/mismatch scores were set to 2 and -3, respectively, while gap costs were assigned as 5 for presence and 2 for extension. We made the taxonomic assignments using the best 100 hits in MEGAN MEtaGenome Analyzer v6.25.10 (Huson et al., 2007); by applying the following LCA parameters: min score 90, max expected 1E-10 and top percent 2.0. Taxonomic assignments were performed with thresholds of percent identity tailored to each taxonomic rank: ≥88 % for class-level assignments, ≥91 % for family-level assignments, ≥94 % for genus-level assignments, and ≥97 % for species-level assignments, following a previous study in the area (Valdivia-Carrillo et al., 2021). If an OTU was detected in either of the two negative controls, it was excluded from the analysis of the field samples. When multiple taxonomic assignments were possible, priority was given to taxa known to occur in the study area based on previous surveys and distribution records.

2.2.4. Results validation

As we were only able to monitor a single control site, we complemented our dataset with the UVC from a monitoring program (conducted by Sociedad de Historia Natural Niparajá A.C.) surveying various reefs around the archipelago of Espiritu Santo since 2005, including deep (~15 m) and shallow (<10 m) rocky reefs, shallow hermatypic coral reefs, and wrecks (Fig. 1). Niparajá used the same methodology as our study, except that all the individuals were identified and counted on the outward journey. The divers in this program performed four to six 30 × 2 m transects per dive. Therefore, we selected the last three years (2019–2022; the program stopped in 2023) to create a balanced

sampling size per site with our dataset. Similarly, we confirmed the PAM analysis with two additional rocky reefs where we deployed hydrophones at depth around 20 m in March 2024 at the site El Pailebote and in July 2024 at the site Los Islotes (Fig. 1).

2.3. Statistics

2.3.1. Scuba diving transects

We ran linear models to compare reef fish richness and density between sites. For species richness, we used the raw data and the Ordinary Least Squares method (OLS) as the variance was homogenous. For the density, we log-transformed the values to meet the assumption of residuals normality and used the Weighted Least Squares (WLS) method to account for variance heterogeneity across sites. We did not detect severe autocorrelation within residuals (r = 0.23 and 0.24). We performed Principal Component Analyses (PCA) to explore variations in the composition of reef fish assemblages between the habitats. For the demersal reef fish, we applied a double Hellinger transformation to decrease the weight of the dominant species. For the small benthic fishes, we standardized the variables giving an equal weight of each species in the PCA (small number of species, see results). The PCA served only for an exploratory purpose, then, we ran species-specific models to identify species with higher densities in black coral sites. For the demersal fish, we selected species from families thought to use black corals as a habitat according to previous studies and personal observations (Aburto-Oropeza and Balart, 2001; Boland and Parrish, 2005; Gress et al., 2023 preprint). We selected two groupers (Epinephelidae): the large-size benthopelagic *Mycteroperca rosacea* and the medium-size benthic *Cephalopholis panamensis,* as black coral is hypothesized to be an important habitat for groupers (Aburto-Oropeza et al., 2008). As Lutjanidae have been reported to be found in higher density in black coral habitats (Gress et al., 2023 preprint), we selected the commonly seen species *Lutjanus argentiventris*. Angelfish (Pomacanthidae) and butterflyfish (Chaetodontidae) are known to prey on black coral (Boland and Parrish, 2005, personal observation). Thus, we selected the four species observed in our transects: the two angelfishes *Holacanthus passer* and *Pomacanthus zonipectus*, and the two butterflyfishes *Chaetodon humeralis* and *Johnrandallia nigrirostris*. We further analyzed *L. argentiventris* abundance by size classes (5–30 cm and 30–50 cm), defined based on reported mean maturity length (~32 cm; Piñón et al., 2009). We also ran species-specific models on each of the small-sized benthic species. For each species and size classes, we performed generalized linear models (GLM) with either a logarithmic or square-root link function and a Poisson or Negative Binomial distribution to fix the overdispersion of the residuals. Finally, we checked our results from UVC by considering a larger set of habitats using historical data. Heterogeneity of the variance was not detected, the dispersion of the residuals was close to 1, and only low to moderate correlations of the residuals were detected (r = 0.09–0.35).

2.3.2. Passive Acoustic Monitoring

We ran linear mixed-effects models to compare fish sound types richness and abundance across sites. Sites were the fixed variable, and several random variables were considered to avoid residual correlations: the date, the hour, and their interactions with the site. No parametric violations were detected, and the correlation of the residuals was low (r = 0.15–0.25). As for the scuba-diving transects, we performed a PCA to explore variations in the composition of fish sound types between the habitats. To do so, we considered the mean of sound count per site and hour (merging the nights). Separating the nights in the PCA gave the same results, but the display was less interpretable. As for small benthic species, we standardized the variables giving an equal weight to each sound. After exploring the abundance of each sound types per site, we noticed that only one sound type could show differences (in total abundance) between habitats (Appendix A, Fig. A2). As it turned out that this sound always occurred at dusk (from 8:00 to 10:00 p.m.), we ran a model considering only these hours to compare the different sites. Finally, we checked this result by considering additional control reefs. We used a Negative Binomial model to account for residual dispersion. No variance heterogeneity was noted, and a low correlation of the residuals was detected (r = 0.23 and 0.24).

2.3.3. Environmental DNA

First, we counted the number of families, genera, and species of Actinopterygii detected in our samples and the number of OTUs assigned per taxonomical level to determine the success of taxonomic assignments at the different level. We ran OTU accumulation curves in the function of the number of DNA sequences analyzed (sequence depth) to detect whether the number of sequences was enough to capture the diversity of OTU in our sites. We checked the species detection rate, sequence abundance per species, and sequence dissimilarity within our cryptobenthic mock community. These metrics were then compared to those of the conspicuous fish mock community from the Gulf of California, as reported by Valdivia-Carrillo et al. (2021), to assess the effectiveness of detecting cryptobenthic reef fish of our method. Sequence dissimilarities were calculated in MEGA11 (Tamura et al., 2021) using the 'No. of differences' method under the 'Model/Method' setting, with default parameters. Then, we used descriptive statistics for the eDNA analysis as the sample number was insufficient to run quantitative models. We visualized the number of OTUs detected per Actinopteri family per site. We used a Venn diagram to identify OTUs shared among black coral sites and absent in our control site. Then, we performed a PCA on the number of OTUs per family and per site, applying a double Hellinger transformation to explore the OTU assemblages' compositions between habitats. As the number of points (sample size) was relatively low to run the PCA, we artificially created variability with bootstrapping. Specifically, we generated 1,000 datasets by randomly selecting OTUs with replacements, which created different subsets containing approximately two-thirds of the OTUs (James et al., 2013). Finally, within each site, we compared the number of OTUs per cryptobenthic reef fish families encountered in the study (Gobiidae, Chaenopsidae, Labrisomidae, and Tripterygiidae) as well as for the families of species included in the species-specific model derived from the visual census section.

All analyses and figures were implemented in the R environment version 4.4.0 (R Core Team, 2024) with the following packages: cowplot (Wilke, 2024), dplyr (Wickham et al., 2023), ggplot2 (Wickham, 2016), glmmTMB (Magnusson et al., 2017), gridExtra (Auguie, 2017), lme4 (Bates et al., 2015), MASS (Venables and Ripley, 2013), nlme (Pinheiro and Bates, 2006), rcompanion (Mangiafico, 2024), vegan (Oksanen et al., 2022), and VennDiagram (Chen and Boutros, 2011).

3. Results

3.1. Site characterization

The relief of the seafloor (variance of the depth) was not higher in black coral sites than in the control reef of La Ballena (Fig. 2A). The density of *A. galapagensis* colonies was similar in three black coral sites (0.35–0.42 colonies m^{-2}) *but higher* in La Catedral (0.67 colonies m^{-2}, Fig. 2A). The height distribution of the colonies was similar between the sites, except for La Gaviota, where we observed taller colonies (Fig. 2B). Finally, we observed variations in the morphology of the colonies among the sites, with La Gaviota, San Rafaelito, and La Catedral dominated by bush-like morphology while La Partida presented a tree-like morphology dominance (Fig. 2C).

3.2. Reef fish assemblage surveys

3.2.1. Underwater visual census

We recorded a total of 6,564 fish (demersal and small benthic), comprising 56 species from 22 families. On average, each transect

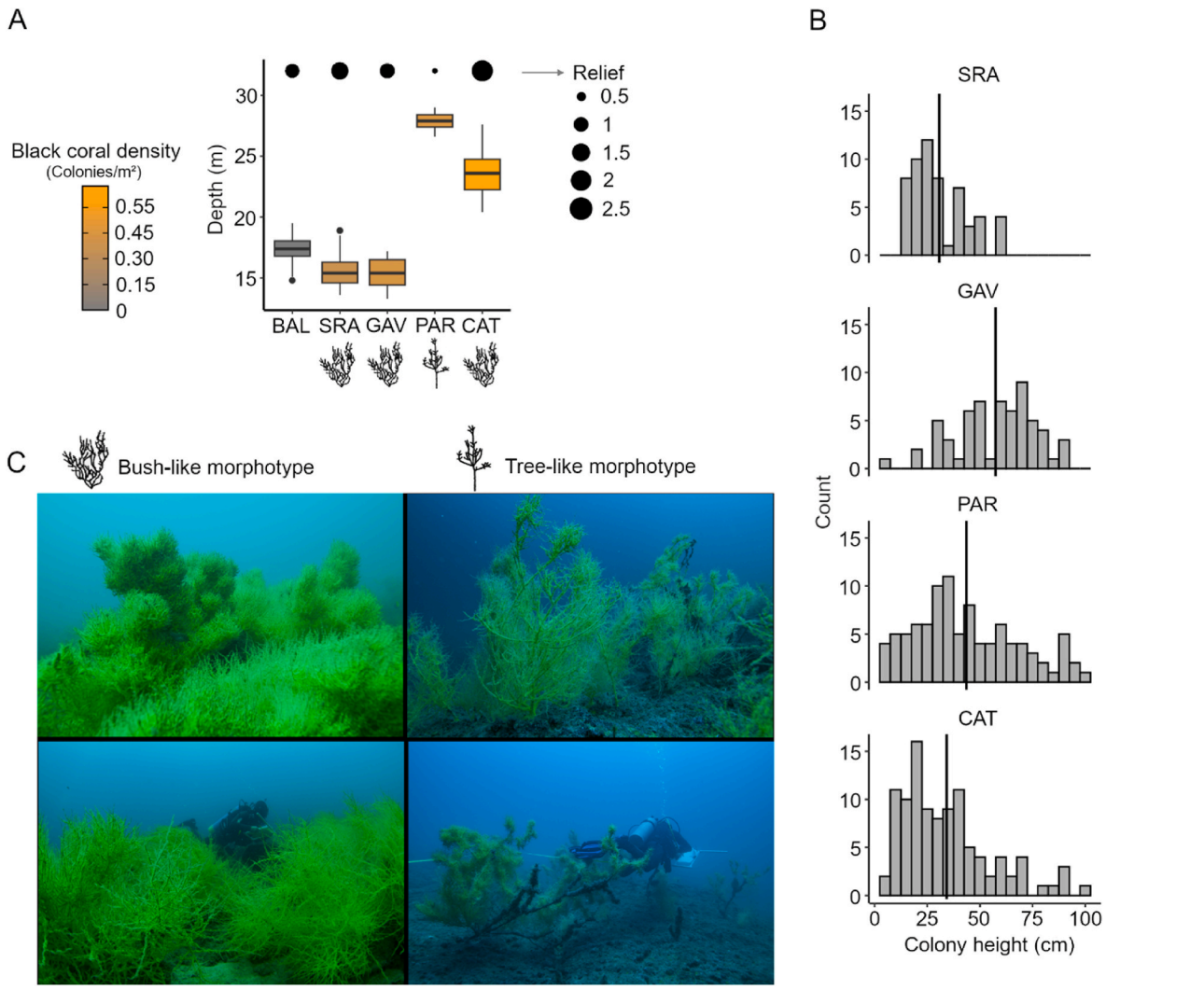

Fig. 2. A. Boxplot of the depth measured along the transects for each site, with the site's relief presented by the circle size, the black coral density in each site as a color gradient, and their dominant black coral morphology. B. The distribution of black coral height in each site, with the mean height represented by the black vertical line. C. In situ photos of the two types of black coral morphology. BAL: La Ballena; CAT: La Catedral; GAV: La Gaviota; PAR: La Partida; SRA: San Rafaelito. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

yielded 95 ± 55 fish, representing 15 ± 3 species (mean ± SD). Demersal fish species richness and density did not significantly differ (95 % confidence intervals (CI) crossing 0) between black coral sites and the control habitat (Fig. 3A; Appendix C, Table C2). Additionally, we did not observe differences in assemblage composition along the first two axes of the PCA according to the density of black coral colonies (Fig. 3B). None of the species-specific models for demersal reef fish detected higher fish density in all the black coral sites than in the control reef (Fig. 3C; Appendix C, Table C2). However, the snapper *Lutjanus argentiventris* was significantly more abundant (95 % CI not crossing 0) in three of the four black coral sites than in the control reef (Fig. 3C; Appendix C, Table C3).

To ensure robustness in species-level analyses, only small benthic fish species observed in at least 5 % of transects and present at a minimum of three sites were included. This threshold yielded six species: the grouper *Alphestes immaculatus*, the serranid *Serranus psittacinus*, the pufferfish *Canthigaster punctatissima*, the damselfishes *Chromis limbaughi* and *Stegastes rectifraenum*, and the hawkfish *Oxycirrhites typus*. We detected significant differences for small benthic fish, with higher species richness and abundance recorded at sites hosting black coral with a bush morphology dominance (Fig. 4A; Appendix C, Table C2). Additionally, the fish assemblage's composition seemed to vary along the black coral density according to the first two axes of the PCA (Fig. 4B). Finally, species-specific models revealed a significant higher abundance of three out of the six small benthic species, i.e. *A. immaculatus*, *C. punctatissima*, and *O. typus*, in the black coral habitat than in the control site (Fig. 4C; Appendix C, Table C3). Marginal differences (95 % Confidence Interval (CI) barely crossing zero) were also observed for a fourth species, *Serranus psittacinus* (Fig. 4C).

3.2.2. Passive Acoustic Monitoring

We analyzed a total of 1,192 1-min audio samples, classifying 34,187 nocturnal sounds into 15 distinct sound types (Appendix A, Fig. A3). The characteristics of these sound types are described in Appendix A. We observed lower fish sound type richness at sites with black coral and no evidence of higher fish sound abundance associated with black coral presence (Fig. 5A; Appendix A, Table A2). The composition of nocturnal reef fish sound assemblages varied between sites (Fig. 5B). The first axis of the PCA differentiated sites with black corals from the control reef, while the second axis separated the deeper sites La Catedral and, to a lesser extent, La Partida from the other reefs (Fig. 5B). The nocturnal pattern of fish sound production also differed between black coral sites and the control reef, with a distinct peak at dusk for the former (Fig. 5C). This peak was driven mainly by the sound type "highFPT-1", which was

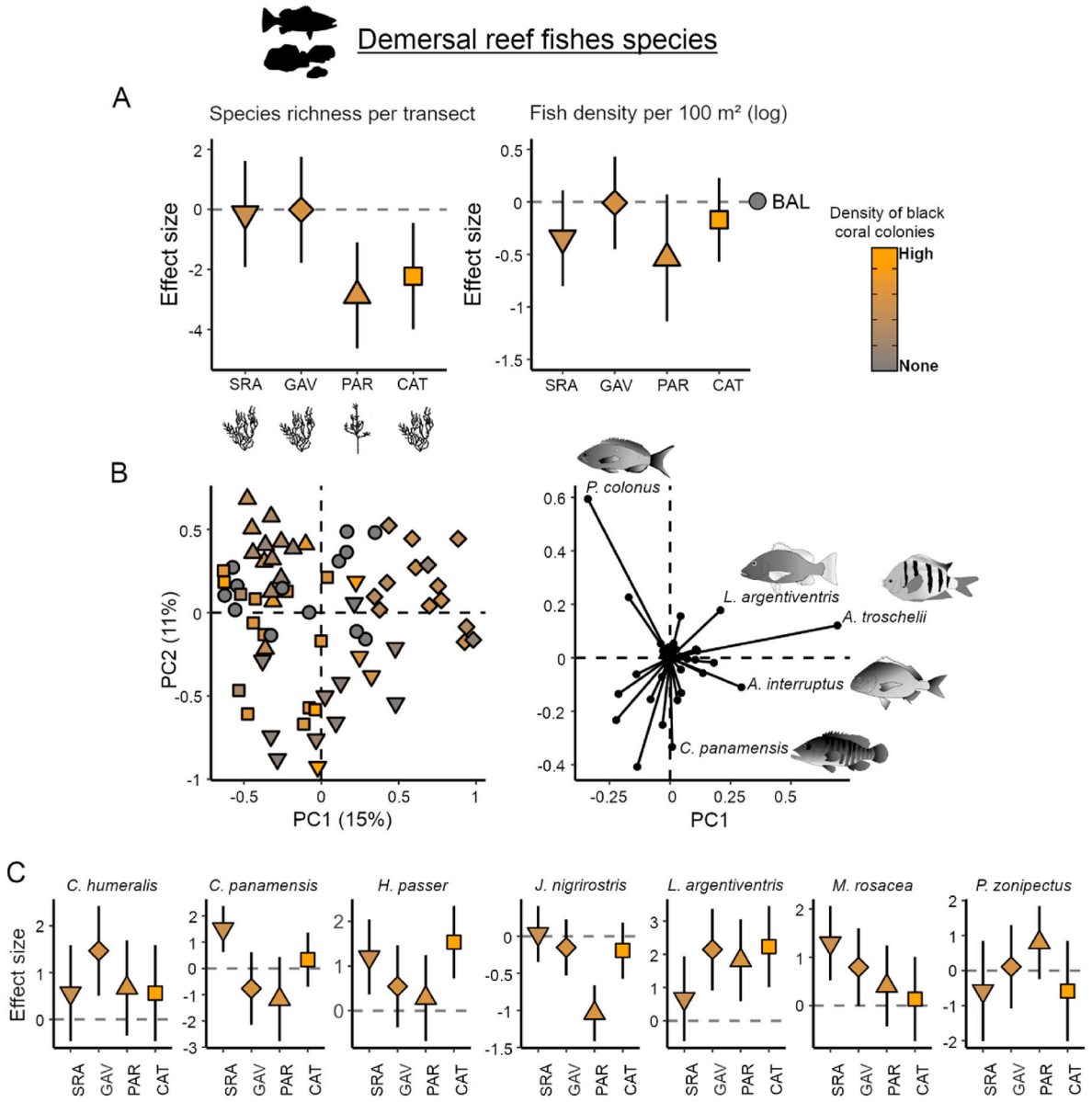

Fig. 3. A. Comparison of species richness and abundance of demersal reef fish between sites, estimates, and 95 % CIs from linear models are illustrated. The control site "BAL" is represented with a dashed horizontal line. B. Principal Component Analysis on fish assemblages and associated biplot. C. Comparison of the abundance of specific species between sites, estimates, and 95 % CIs from the generalized linear models are illustrated. The control site "BAL" is represented with a dashed horizontal line. 95 % CIs that do not cross the dashed horizontal line indicate a significant difference.

significantly more abundant in black coral sites (Fig. 5D; Appendix A, Table A3). HighFPT-1 was a high frequency fast pulse train characterized by peak frequency of about 819 ± 101 Hz, a duration of 264 ± 55 ms, a pulse period of around 34 ± 5 ms, and a pulse number of 7.8 ± 2.4 (mean ± SD).

3.2.3. *Environmental DNA*

Due to the low number of sequences of the first replicates of La Gaviota, we removed it from the analysis. From 4.4 M raw paired-end reads, 400k sequences that passed the quality filters were clustered into 582 Actinopterygii OTUs. From these, 83 % of the OTUs were taxonomically assigned to 29 families, 67 % to 44 genera, and only 15 % to 38 species. Few OTUs (24), representing 12 % of the total sequences assigned, were assigned to cryptobenthic reef fishes (CRFs) families (Fig. 6A). We focused our eDNA analyses at the family level due to the low success of taxonomic assignments at the genus and species levels. We did not observe a difference in OTU richness between the black coral site and the control reef (Fig. 6B). Only one OTU assigned to the Serranidae was detected in all the black coral sites, not the control site. Five OTUs were detected only in the three bush-like black coral sites and were assigned to the Gerreidae, Merlucciidae, and Pomacentridae (Fig. 6C). The PCA highlighted that the OTU composition differed between sites but also between replicates, illustrating high temporal variability (Fig. 6D). The PC1 separates five of the seven black coral samples from those of the control reef, primarily driven by the contribution of Lutjanidae (Fig. 6D). Contrary to our expectations (samples collected close to the substrate and incorporation of many CRFs species in the library), the eDNA failed to capture the CRFs diversity. Even in the mock, only 11 of the 33 CRFs species were detected while conspicuous species were well detected (Appendix B, Table B2). Given the limited number of CRFs OTUs detected, we did not observe higher richness for any CRFs families in the black coral habitat. The black coral sites showed higher OTU richness for the Lutjanidae, while the control reef had higher OTU richness for the Serranidae and Tetraodontidae (Fig. 6E).

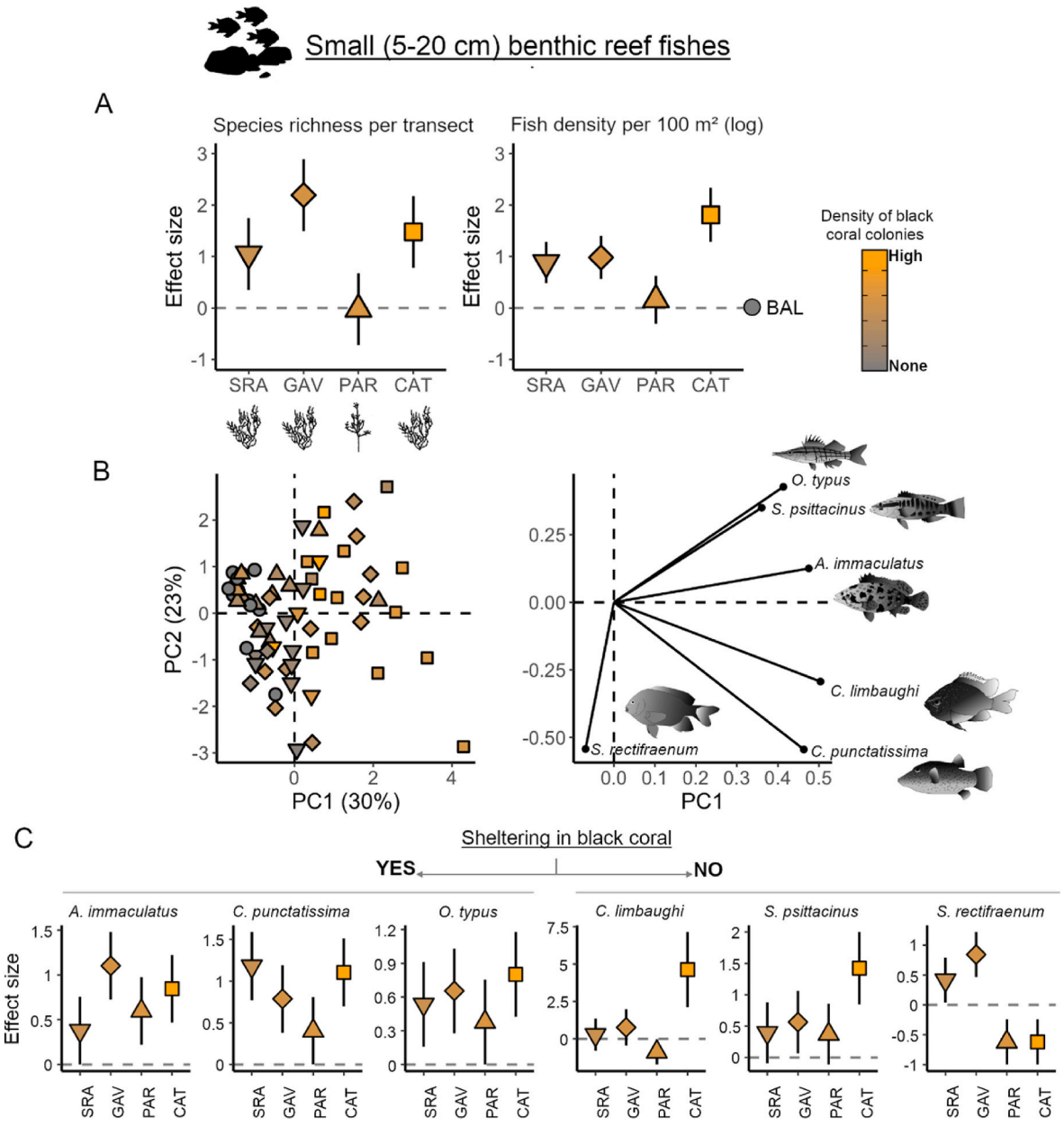

Fig. 4. A. Comparison of species richness and abundance of small benthic reef fish between sites, estimates and 95 % CIs from linear models are illustrated. The control site "BAL" is represented with a dashed horizontal line. B. Principal Component Analysis on fish assemblages and associated biplot. C. Comparison of the abundance of each species between sites, estimates, and 95 % CIs from the generalized linear models are illustrated. The control site "BAL" is represented with a dashed horizontal line. 95 % CIs that do not cross the dashed horizontal line indicate a significant difference.

3.2.4. Results validation

*The UVC results were largely confirmed when comparing to a larger panel of sites and habitat. For demersal fish, Lutjanus argentiventris had a higher abundance in black coral than the other habitats except the wreck (*Fig. 7A; Appendix C, Table C4). Analysis by size class showed higher juvenile (5–30 cm) densities in black coral habitats and shipwrecks compared to other habitats. For adults (30–50 cm), no clear difference among habitats was detected (Appendix C, Figure C1, Table C5). For the small benthic species, the four species detected in higher abundance in the black coral habitat in the first set of analyses, clearly showed higher density than in any other habitats in the region with *O. typus* totally absent in the other habitats. This second set of analyses also confirmed that the damselfishes *C. limbaughi* and *S. rectifraenum* were not more abundant in black coral habitat but were associated with deep and shallow waters, respectively *(*Fig. 7A; Appendix C, Table C4). However, the higher abundance of high-FPT1 was not confirmed with additional deep rocky reefs showing similar abundance of this sound type than in the black coral habitat (Fig. 7B; Appendix A, Table A3).

4. Discussion

The density of *Antipathes galapagensis* colonies was relatively low in the four black coral sites (0.5 ± 0.1 colonies m^{-2}), with isolated patches rather than continuous black coral forests. Such forests have been reported in other regions of the Eastern Tropical Pacific in both the mesophotic zone and shallow waters with colony densities two to five times higher than those observed in our study (Segovia, 2023; Agarwal et al., 2024). The Bay of La Paz is in the southern part of the GC, where the subtropical environmental conditions probably limit the presence of black coral forests in shallow waters. However, the black coral densities

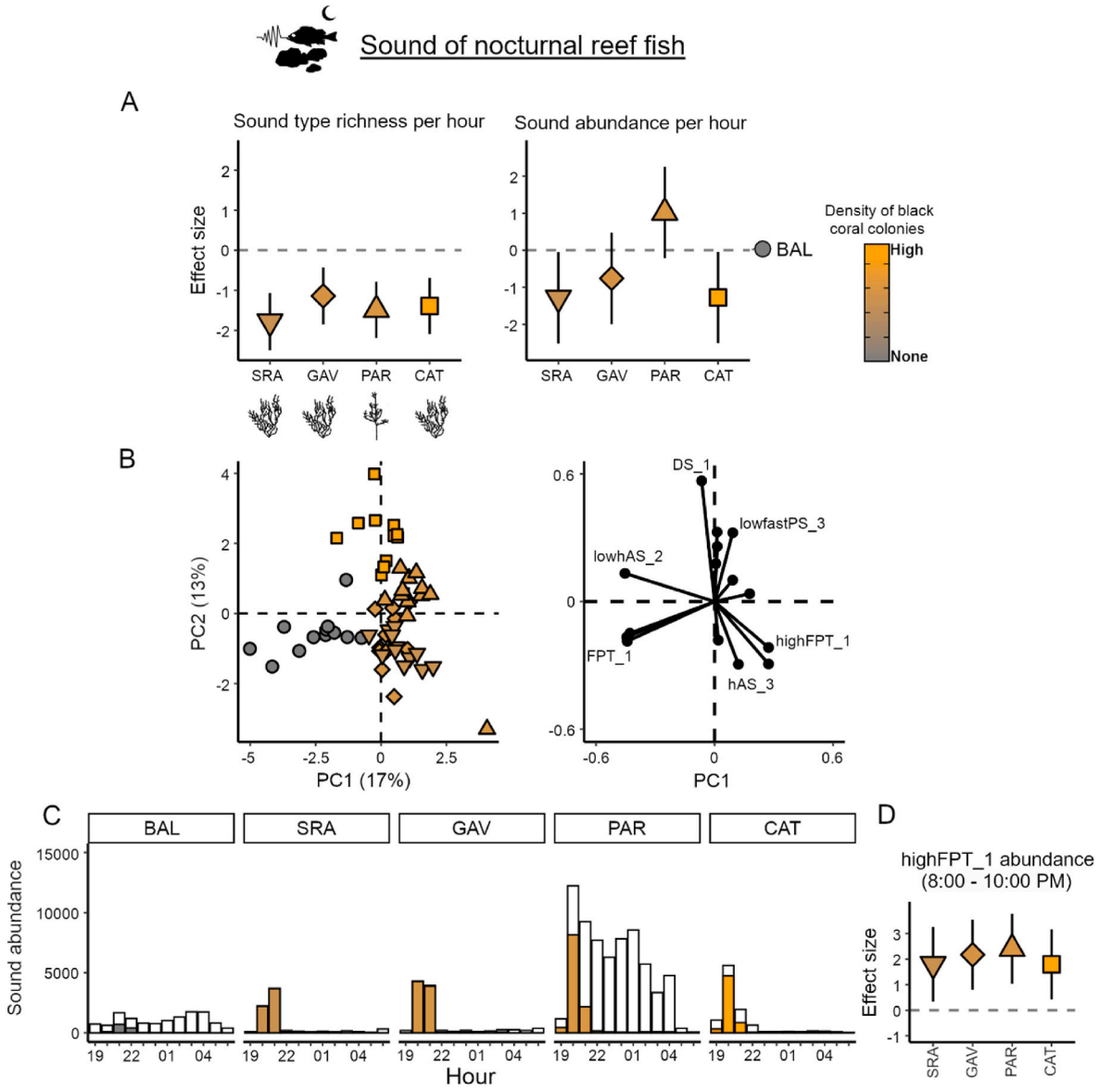

Fig. 5. A. Comparison of sound types richness and abundance between sites, estimates, and 95 % CI from linear mixed models are illustrated. The control site "BAL" is represented with a dashed horizontal line. B. Principal Component Analysis of reef fish sound types composition and associated biplot. C. Nocturnal sound distribution pattern illustrated by the mean count of sound per hour and site. The colored bars represent the contribution of the sound type highFPT-1. D. Comparison of the abundance of the sound type highFPT-1 between sites, estimates, and 95 % CI from the generalized linear mixed model are illustrated. The control site "BAL" is represented with a dashed horizontal line. 95 % CIs that do not cross the dashed horizontal line indicate a significant difference.

were similar to those reported 17 years ago in the Bay of La Paz, when the sites La Catedral and La Partida were monitored, although the size of the colonies seemed to be smaller nowadays (41 vs. 70 cm; Wills López, 2008).

In the context of patches of relatively small colonies, it was unlikely to detect a clear effect of black coral on demersal, highly mobile fish species in terms of richness, abundance, and assemblage composition. We only found that *Lutjanus argentiventris*, a commercially important species (González-Acosta et al., 2018), was more abundant in black coral than in most of the other habitats, only being equaled by the shipwrecks where fishing is prohibited. Shipwrecks provide a highly complex habitat known to host important population of large predators (Simon et al., 2011; Maniquet, 2024). We also examined *Lutjanus argentiventris* size classes (defined based on the reported mean maturity length of ~32 cm; Piñón et al., 2009) and found more juveniles (5–30 cm) in black coral habitats and shipwrecks than in other habitats. We found no significant difference in adult (30–50 cm) densities among habitats, suggesting that habitat associations may be stronger during juvenile stages. Although *Lutjanus argentiventris* is commercially targeted, three of the four black coral sites are open to fishing, with only San Rafaelito protected. Our broader historical dataset includes sites with varying fishing pressure, so abundance differences likely reflect habitat associations rather than fishing effects alone. Furthermore, our eDNA analysis also detected more OTUs associated with Lutjanidae in black coral sites than in our control site. The affinity of Lutjanidae with black coral was reported in other studies, where individuals used black coral colonies as shelter from currents or to ambush prey (Gress et al., 2023 preprint). We must note that our study was not designed to investigate specific behaviors such as feeding interactions with black coral and that future studies tailored on fish behavior could reveal undetected pattern here.

In contrast with demersal fishes, the complex microhabitat created by black coral patches seem to shape the diversity of small (5–20 cm) benthic reef fishes. In this group, four of the six species were observed in higher densities than in any other reef habitats in the Bay of La Paz.

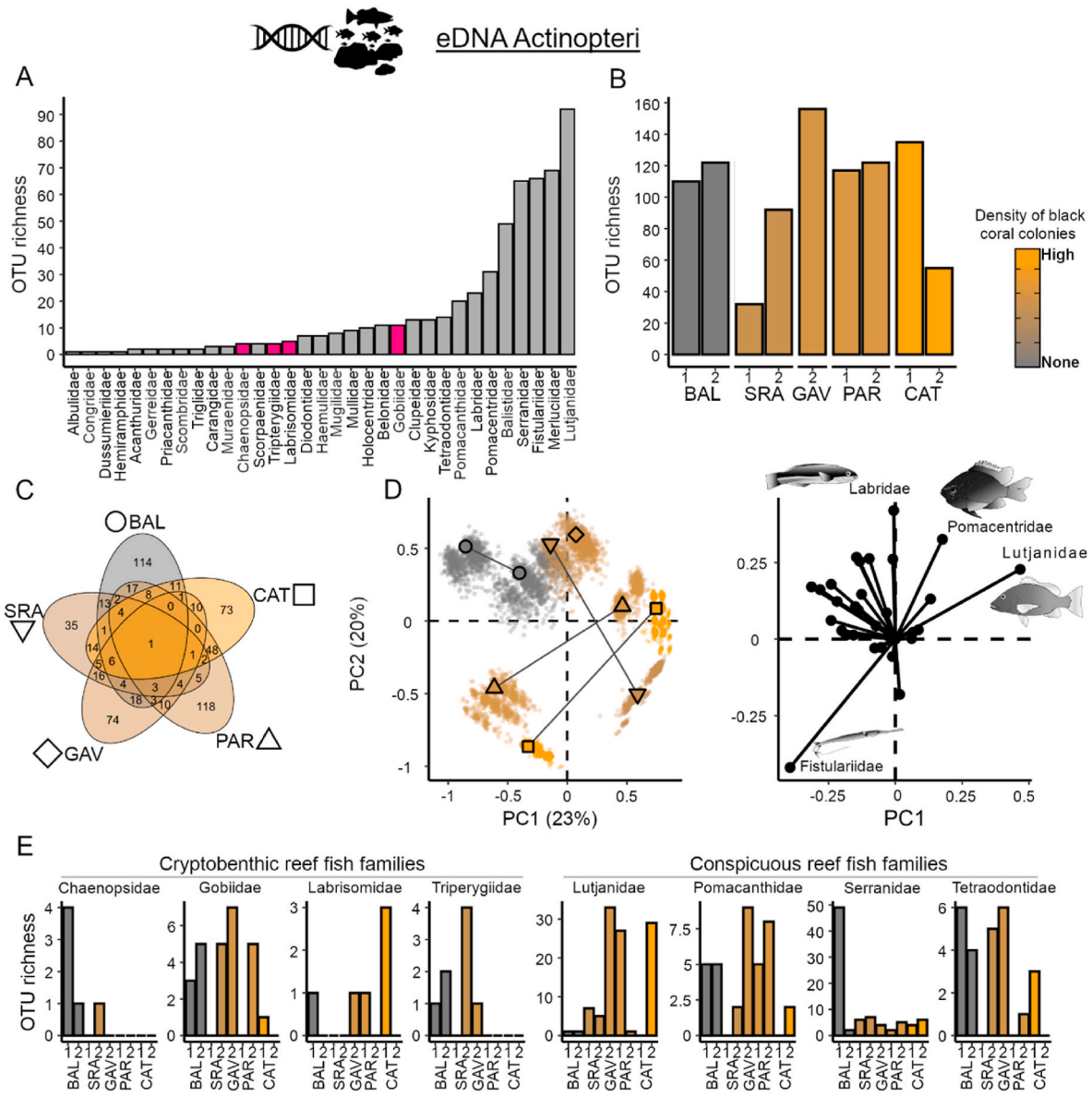

Fig. 6. A. OTU richness per fish families. Cryptobenthic reef fish families are highlighted in pink. B. OTU richness per replicates per site C. Venn diagram of OTU overlap between the sites. D. Principal Component Analysis (PCA) on the OTU richness per sample and fish families. The Biplot of the PCA is shown. E. OTU richness for cryptobenthic reef fish families and some demersal reef fish families per replicates per site. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Notably, the hawkfish *O. typus*, was exclusively found within black coral colonies, which was also noted in previous studies (Boland and Parrish, 2005; Matamoros-Calderón et al., 2021). The two last species are damselfishes that do not hide in the black coral. The territorial species, *S. rectifraenum*, which is typically found in shallow waters (either rocky or coral reefs) and the colonial species, *C. limbaughi*, which is found at higher depths, whatever the reef type. The black coral associated species represent diverse trophic groups and may benefit from black coral habitat for feeding interactions, sheltering or both (Appendix C, Figure C2). We observed the pufferfish *C. punctatissima* (omnivorous) to feed on black coral, finding in Antipatharians additional resources. The three other species are small carnivores that could use the black coral as shelter to ambush invertebrates or small fishes such as CRFs, to protect themselves from larger species, or to feed on specific preys found in black coral (the case of *O. typus* should be investigated). We also observed different behaviors between the two serranioid species *A. immaculatus* and *S. psittacinus*, the former sheltering within or below the black coral and the latter being observed outside the colonies. A similar observation was also reported for other *Serranus* species considered resident in black coral habitats (Bo et al., 2024). According to these observations, black coral could provide enhanced opportunities to capture prey in small carnivorous reef fishes. Black coral could be an important habitat for groupers (Aburto-Oropeza et al., 2008). Although we cannot support this hypothesis for large species with patches of colonies, we did highlight the importance of black coral for small benthic serranioids, and the role of black coral under the form of forest on larger species deserved future research, especially in the light of economic importance of this group. Although our primary comparison relied on a single control site (La Ballena), we also incorporated historical UVC data from multiple sites spanning varied habitats (without black coral) and depths to reduce site-specific bias and strengthen our analysis. Prior studies report comparable fish richness and biomass at La Ballena relative to other deep rocky reefs around the island (Maniquet, 2024), supporting its relevance as a control site. This broader context helps confirm our observed patterns and highlights consistent differences in fish assemblages associated with black coral habitats.

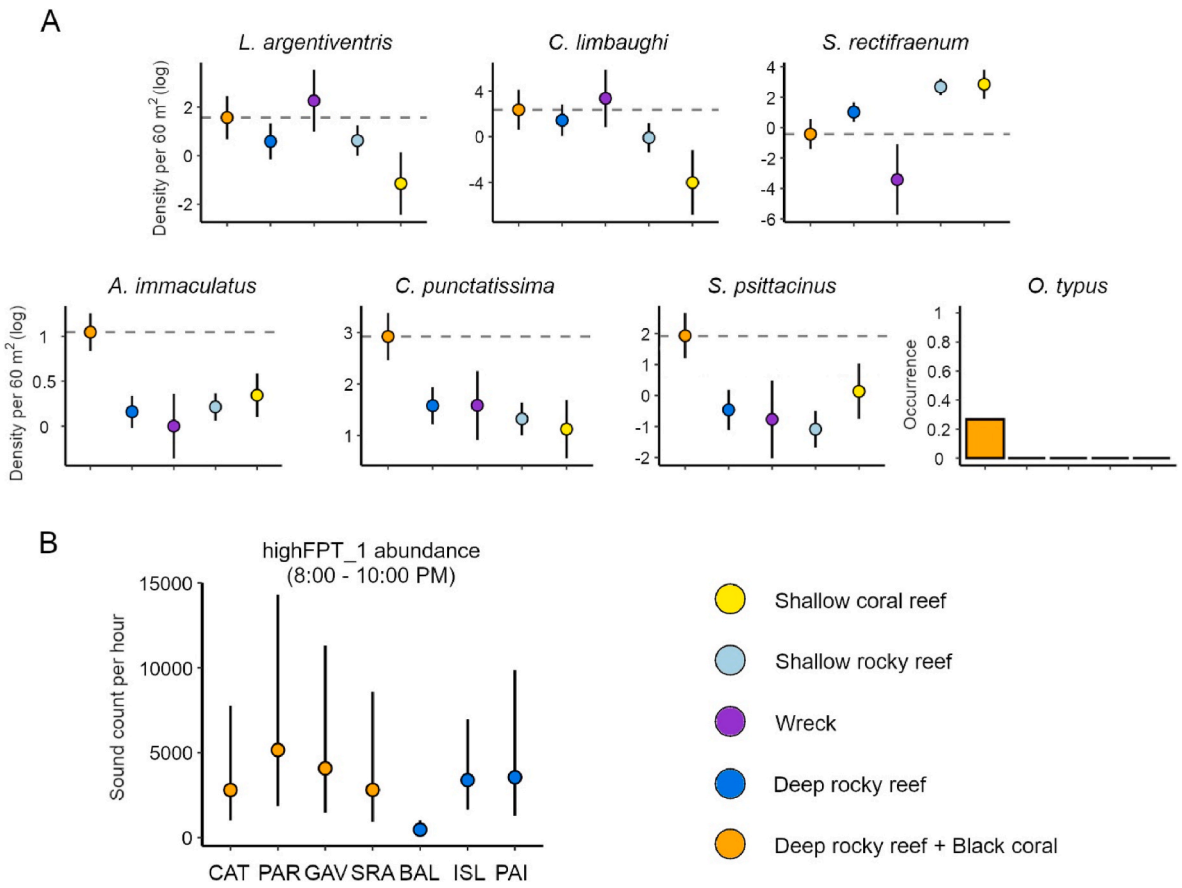

Fig. 7. A. Comparison of species density across habitats, with estimates and 95 % CIs derived from generalized linear mixed models (GLMMs). The dashed horizontal line represents the mean prediction for the black coral habitat. B. Comparison of the abundance of highFPT-1 sound type across sites, with estimates and 95 % CIs from GLMM.

Fish sounds recorded at night were likely produced by reef-resident species, since pelagic predators visiting reefs nocturnally are generally not soniferous, and little evidence exists of active vocalization among them (Rice et al., 2022; Looby et al., 2024). Moreover, the studied sites are not surrounded by deep waters (Fig. 1), which makes unlikely vertical migrations of fishes coming from the depths. Reef fish sounds can reflect ecological processes such as courtship, spawning, territorial defense, or feeding interactions (Amorim, 2006; Ladich, 2015). However, because our recordings were nocturnal and many sound types remain unidentified, assigning specific behaviors to all observed sounds is challenging. We therefore focused our analysis on detecting habitat-level differences between black coral and control reefs. While the nocturnal soniferous fish communities seem to vary between sites, we did not detect pattern in association with black coral. We found even lower sound richness in black coral than in the control site. The black coral habitat seemed to present choruses of the sound highFPT-1 at dusk, this latter being poorly represented in the control habitat. When comparing highFPT-1 features to the ones of sounds produced by *Cynoscion othonopterus* (Scianidae), an endemic species from the northern portion of the Gulf of California (Erisman and Rowell, 2017), we see that pulse period is highly similar between the two (35 vs 38 ms). On the other hand, the peak frequency differs (820 vs. 384 Hz). In our study sites, Sciaenidae were observed in different sites, sheltering in the caves and crevices of rocky reefs but not in the black coral, at least during the day making suspicious our finding of higher sciaenid's sounds at black coral habitat as a general pattern. Indeed, our additional data in two other rocky reefs confirmed that the low amount of highFPT-1 in the control site was characteristic of the site itself instead of a general pattern.

As black coral seems to boost diversity and abundance of small benthic reef fishes between 5 and 20 cm, we expected a similar result for the cryptobenthic reef fishes (CRFs) as the CRFs are closely associated to the substrate and sensitive to habitat complexity and modifications (Olivier et al., 2023; Jáquez-Domínguez et al., 2025). The CRFs are challenging to monitor except with specimen collection (Ackerman and Bellwood, 2000), and it is why we opted for the eDNA method to investigate their diversity. Based on the accumulation curves of the Actinopteri OTU detection related to the sequencing effort (Appendix B, Figure B1), we were close to reaching sequencing plateaus. This indicates that most fish diversity detectable with our method was captured, and that only a modest increase in sequencing effort would be needed to detect additional OTUs. We followed the same methods as a previous study, giving convincing results with conspicuous reef fish species in the GC (Valdivia-Carrillo et al., 2021). Our eDNA survey yielded a total of 582 OTUs across 5 sites within a ~15 km radius, with an average of 104 OTUs and 438,000 sequences per site. These values compare favorably with those reported by Valdivia-Carrillo et al. (2021), who detected 542 OTUs across 24 sites distributed over a much broader area of the GC (45 OTUs and 198,000 sequences per site on average). This comparison highlights the effectiveness of our sampling design and sequencing effort in capturing fish biodiversity. However, the eDNA analysis failed to capture the diversity of CRFs in our study, underscoring the limited capacity of this method to detect cryptobenthic fishes, as also reported at a broader scale across the Gulf of California by Mac Loughlin et al. (2025). That may be due to different reasons, such as the low amount of CRFs DNA sequences in the water, the water sample volume collected, the depth of sequencing, the primer choice, or the quality of the library. As in a recent study finding convincing results with

CRFs (Brodnicke et al., 2024), we collected water samples close to the substrate, and filtered a similar volume of water. That study nevertheless reported over 1.5 million sequences assigned to fish per site, reflecting a much greater sequencing depth. Additionally, we, added the sequences of 36 CRFs species of the GC to the NCBI-GenBank database to build our library (Mac Loughlin et al., 2025). However, each cryptobenthic fish species was represented by one individual, not necessarily collected in the Bay of La Paz (Appendix B, Figure B2). Therefore, inter-population variation and population structure for CRF within the Gulf of California could explain a lack of detection, as recently reported for *Elacatinus puncticulatus* (De Jesús-Bonilla et al., 2025). Interestingly, we met the same problem with the mock (artificial community), where DNA sequences of the same individuals as in the library were used, but we were only able to detect one-third of the CRFs species, while all or most of the conspicuous species were detected (this study; Valdivia-Carrillo et al., 2021). Therefore, the lack of detection cannot only be attributed to the field study or the quality of the library. Many CRFs species are endemic to the GC, with endemicity reaching 40 % (Galland, 2013). Their speciation may have occurred more recently than in conspicuous species, resulting in higher similarities in their DNA sequences and making sequence assignment more challenging for this group, highlighting the need to expand and improve reference sequencing of CRFs. Nonetheless, the dissimilarities between the specific-DNA sequences used in the mocks were similar between CRFs and conspicuous species (Appendix B, Figure B3). Additionally, we observed a strong disequilibrium in the assignment of DNA sequences between species, with some species having much more sequences than others, despite that the same DNA concentration was pooled for each species (Appendix B, Figure B3). Although this was observed in the mocks of conspicuous and CRFs, the trend was more pronounced for the CRF with one species accounting for one-third of the assigned DNA sequences, compared to 18 % for the conspicuous. As the number of sequences in the mocks was not that high (150,000), this unbalanced assignment could explain the limited species detection. None of the four CRFs families presented higher OTU richness in the black coral sites. However, because the eDNA method poorly performed for CRFs, we could not adequately test our hypothesis linking or not the CRFs diversity with the black corals. Improving the eDNA methods for CRFs or using other methods, such as individual collection, are required. Considering both conspicuous and CRFs species, the family-OTU assemblage compositions differed between sites. Consistent with the UVC data, the Lutjanidae separated the black coral sites from the control site and were the only family exhibiting higher OTU richness in black coral habitats. The observed site discrimination indicates that eDNA can distinguish geographically close sites (a few km). Nevertheless, temporal variability also appears to be a significant factor in eDNA analysis, as the difference between replicates is as strong or even more pronounced than within-site variability, and this parameter should be considered in future studies.

The previous studies using a multidisciplinary method to monitor fish assemblages revealed each method's pros and cons and their complementarity (Honeyman et al., 2023; Cabrito et al., 2024). Here, we did not aim to compare them but to integrate them, each focusing on a specific group of the fish community and giving a more holistic view of fish diversity. By using three different approaches, we highlighted the importance of black coral patches for small benthic reef fishes in comparison to other habitats such as rocky and coral reefs, the lack of effect of black coral on nocturnal soniferous reef fishes, and, although eDNA corroborated some results, methodological caveats of this last method for studying CRFs. The tropicalization of the southern GC (Favoretto et al., 2022) is a threat to black corals, and its ecological role must be investigated and quantified. By increasing habitat complexity, black coral seems indeed to boost diversity. However, the role of extensive black coral forests is still unknown in the region and poorly investigated worldwide. Testimonies based on photographs and videos show that black coral forests are present in the Central and Northern GC under temperate environmental conditions, some of which are famous tourist diving spots. Our study, one of the first to consider the association of black coral with marine fauna in the region, reveals that black coral forests deserve future robust and quantitative estimation of their host marine diversity.

CRediT authorship contribution statement

Florian Rabasco: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Adrian Munguia-Vega:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Xavier Raick:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Eric Parmentier:** Writing – review & editing, Resources, Funding acquisition. **Luis Hernández:** Writing – review & editing, Methodology, Conceptualization. **Leonardo Huato-Soberanis:** Writing – review & editing, Methodology, Conceptualization. **Héctor Reyes-Bonilla:** Writing – review & editing, Resources. **Carlos Sánchez-Ortiz:** Resources, Methodology, Conceptualization. **Damien Olivier:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing interest

The authors declare they have not any conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107401.

Data availability

All the files and R code necessary to reproduce the analyses of this study are available on Zenodo at https://doi.org/10.5281/zenodo.16540403. The data from the civil society organization Sociedad de Historia Natural Niparajá A.C. are available under request.

The Raw 12S sequences data for all samples were deposited in GenBank Bioproject PRJNA1260186. https://www.ncbi.nlm.nih.gov/sra/PRJNA1260186.

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