

ARTICLE

Coastal and Marine Ecology

Monitoring dolphinfish catches and diel assemblage fluctuations using eDNA at fish-aggregating devices

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Abstract

Fish-aggregating devices (FADs) are man-made objects designed to attract fish, with the aim of facilitating spatially heterogeneous aggregations of marine species. These objects influence the structure of pelagic fisheries, consequently affecting fish distributions and interactions. One of the most iconic epipelagic species targeted using FADs is dolphinfish (*Coryphaena hippurus*), which has high commercial value in the Mediterranean Sea. However, the interactions between dolphinfish and FADs are still poorly understood, and the composition of fish assemblages attracted to these devices remains poorly characterized. Environmental DNA (eDNA) metabarcoding has emerged as a powerful tool for fisheries management. Here, we employed passive eDNA samplers (i.e., *metaprobes*) to collect information on the fish assemblages around five FADs in Maltese waters during a dolphinfish fishing day in January 2023. Samples were gathered during different diel phases: Three stations were sampled in the diurnal phase, while two were sampled during the crepuscular-evening phase. Through the amplification of the mitochondrial 12S gene region (Elas02 primers), we explored the relationship between *C. hippurus*-caught biomass and transformed read counts and investigated the composition of fish assemblages associated with FADs. A positive relationship was found between eDNA-transformed read counts of dolphinfish and their biomass (linear regression model, $R^2 = 0.62$, $p < 0.05$). Fish assemblages attracted by FADs were found to significantly change between diurnal and crepuscular-evening phases. Moreover, the indicator species analysis identified four species as being indicative of the crepuscular-evening phase (*Diaphus rafinesquii*, *Hygophum benoiti*, *Hygophum hygomii*, and *Lampanyctus pusillus*). The similarity percentage (SIMPER) test identified seven species as the main contributors to variations in dolphinfish-caught biomass. Of these, four species (*Sardina pilchardus*, *Trachurus trachurus*, *Engraulis encrasicolus*, and *Chelon labrosus*) showed a significant relationship between their transformed read

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counts and dolphinfish-caught biomass. Despite the small number of samples, this study highlighted the potential of low-cost passive eDNA collection to assess the composition of pelagic fish assemblages around FADs. This improves our understanding of the ecological dynamics around these fishing gears and helps to optimize fishing efficiency, thereby promoting sustainable fisheries management strategies.

KEYWORDS

Central Mediterranean Sea, *Coryphaena hippurus*, diel phases, eDNA metabarcoding, fish assemblages, fish-aggregating devices

INTRODUCTION

The aggregation behavior of fish has evolved to reduce the risk of individual predation, improve foraging, and/or increase mating success (Hamilton, 1971; Pitcher & Parrish, 1993; Stephens & Krebs, 1987). In pelagic marine environments, this natural aggregation behavior can be influenced by physical objects that attract pelagic species. This phenomenon has been exploited by small-scale fisheries through the introduction of fish-aggregating devices (FADs), which are designed to facilitate spatial aggregation in nutrient-poor, oligotrophic waters (Castro et al., 2002; Sinopoli et al., 2015). In the Mediterranean Sea, the Maltese, Tunisian, Sicilian, and Balearic fleets operate around FADs, mainly targeting juvenile stages (age 0 specimens) of dolphinfish (*Coryphaena hippurus*) (Moltó et al., 2022; Morales-Nin et al., 2000). This species plays a crucial economic role in both commercial small-scale and recreational fisheries, being regarded as a valuable commercial species worldwide due to its demand as a high-quality seafood product (Collette, 1986; Laspina & Said, 2022; Moltó et al., 2022).

The dolphinfish is a thermophilic, migratory, epipelagic species with a widespread distribution in tropical and subtropical regions. Its rapid growth rate and relatively short life span (about 4 years) make dolphinfish a resilient species to fishing pressure (Massutí et al., 1999; Moltó et al., 2022). These traits support the sustainability of fisheries, provided that effective management measures are implemented. Dolphinfish exhibit an attraction to floating objects, with previous studies indicating that they spend approximately 95% of their time within the first 10 m of the water column when such objects are present (Castriota et al., 2007; Oxenford & Hunte, 1999; Rose & Hassler, 1974; Whitney et al., 2016). In such circumstances, fish are captured by surrounding the fish school with nets, similarly to purse seining but without purse rings (Galea, 1961). Castriota et al. (2007) suggested that Mediterranean dolphinfish have no trophic relationship with fish assemblages associated with FADs,

questioning the interaction between *C. hippurus* and FAD-associated fishes. The ecological drivers determining the aggregation of individuals of this species around FADs remain largely misunderstood and deserve deeper investigation. However, FAD-related fisheries are very selective, limiting the possibility of collecting information on other species co-occurring in the fishing area through traditional taxonomic identification of fishing catches.

The advent of environmental DNA (eDNA) metabarcoding has recently revolutionized biodiversity surveying (Taberlet et al., 2018). This molecular approach, which allows the simultaneous identification of multiple taxa through high-throughput sequencing (HTS), has gained popularity as a time-efficient and cost-effective alternative to traditional sampling methods (McElroy et al., 2020; Thomsen et al., 2012). In marine environments, eDNA has been successfully employed to assess fish community status and complement trawl-based surveys (Salter et al., 2019; Thomsen et al., 2016; Zou et al., 2020), including applications in fisheries management (Maiello et al., 2022, 2024; Russo et al., 2021; Stoeckle et al., 2021). The collection of eDNA from marine ecosystems typically involves the filtration of large water volumes through a membrane (Tsuji et al., 2019; Turner et al., 2014), a process that can be time-consuming and challenging, especially when filters clog with particulates (Bessey, 2021; Mächler et al., 2016). Recently, passive eDNA collection methods have emerged as simpler and faster alternatives to active water filtration (Bessey et al., 2020; Kirtane et al., 2020; Verdier et al., 2022). The passive eDNA collection relies on the adsorption of DNA molecules onto samplers that are submerged for minutes, hours, or weeks (Cananzi et al., 2025). This has led to the development of a versatile, ready-to-use 3D-printed sampler, the *metaprobe*, which passively collects eDNA through sterile gauze and has been successfully deployed on commercial trawlers (Maiello et al., 2022). Despite the advantages of metabarcoding, its role in providing quantitative measurements remains limited; however, an increasing number of studies are addressing this topic

(Ficetola & Taberlet, 2023; Kelly et al., 2019; Lamb et al., 2019; Shelton et al., 2022). A key challenge lies in primer selection, as primer bias can lead to preferential amplification of some taxa over others (Ficetola & Taberlet, 2023). Also, drawbacks can occur at various workflow stages, including suboptimal field sampling, DNA extraction methods, and bioinformatics analyses (Ruppert et al., 2019). Incomplete or inaccurate reference databases and sequencing errors can further exacerbate these issues (Ruppert et al., 2019). A combination of data transformation, mock community calibration, and modeling offers avenues towards a more reliable use of quantitative sequencing data (Ershova et al., 2021; Marinchel et al., 2023; Shelton et al., 2022). In addition, recent results indicate that opportunistic eDNA collection during fishing activities could provide valuable data for assessing the abundance of target species together with the structure of the ecological communities in the areas where fishing activities occur (Maiello et al., 2024).

In this study, we employed metaprobes to passively collect eDNA from five sites during a fishing expedition targeting dolphinfish (*C. hippurus*) in Maltese waters. Based on comparative analyses by Maiello et al. (2024), which showed that Tele02 and Elas02 12S primers (Taberlet et al., 2018) yield comparable portrayals of fish assemblages, we chose to use the Elas02 primer pair for the metabarcoding analysis, maximizing the chance of detecting pelagic elasmobranchs associated with the study habitat. This pilot study specifically aimed at (1) using metaprobes for the first time in a pelagic marine environment to detect fish assemblages at FADs during two different diel phases (diurnal vs. crepuscular-evening) and (2) assessing the relationship between transformed read counts and caught biomass of *C. hippurus*.

Understanding the dynamics of fish assemblages at FADs is essential for effective fisheries management, ecological research, and assessing the broader influence of these structures on marine ecosystems and their associated communities.

MATERIALS AND METHODS

Sample collection

Samples were collected in January 2023 from five sites in the western Ionian Sea (Geographical Sub Area 15, Central Mediterranean Sea; Figure 1; Appendix S1: Table S1), on board the fishing vessel Simson (MFA-0214), specifically targeting *C. hippurus*. The net used during the dolphinfish FAD fishery was a surrounding net without a drawstring. This only surrounds the fish and needs to be pulled in very quickly before the fish dive down towards

the open bottom. The average bathymetry of the sampling sites was approximately 521 m (min depth 480 m, max depth 564 m; Appendix S1: Table S1). At three sites (D_M1, D_M2, and D_M3), samples were collected during the diurnal phase, while at the remaining two sites (C_M4 and C_M5) sampling took place in the crepuscular-evening phase. The sampling time for each site can be found in Appendix S1: Table S1. The shortest distance between stations was 0.94 km, observed between D_M1 and C_M5, while the maximum distance of 11.12 km occurred between D_M3 and C_M5.

eDNA was passively collected through the metaprobes: 3D-printed, hollow-perforated polylactide spherical probes (radius 8 cm) containing sterile gauzes for eDNA adsorption (Maiello et al., 2022, project available at: <https://github.com/GiuliaMaiello/Metaprobe-2.0>). In order to ensure rapid fishing operation, each metaprobe was attached to two expanded polystyrene floats using a 1.4 m length of nylon monofilament line. Each metaprobe was then thrown into the net at the start of the encircling operation and collected after the net was hauled aboard. Each metaprobe contained two sterile gauze rolls, which were treated as field replicates for each sampling site. The soaking time of each metaprobe (i.e., the time spent in water) ranged from 7 to 11 min depending on the duration of fishing operations (Appendix S1: Table S1). All the metaprobes operated at a depth of approximately 1.4 m. Once the net was recovered, the metaprobe was immediately retrieved and opened. The two gauzes were placed in separate sterile Falcon tubes (50 mL) filled with 99% ethanol for DNA preservation. Samples were stored cold on board and then, once the facilities were reached, conserved at -20°C until molecular analysis. A problem occurred at the D_M3 station when one of the two gauzes contained in the metaprobe unrolled and leaked out of it. The leaking part was cut off and removed. We decided not to proceed with the processing of this sample, as we presumed contamination that could not be adequately managed.

Information on the number of specimens and caught biomass (in kilograms) of the targeted species (*C. hippurus*) was recorded at each sampling site.

Molecular analysis

Samples were processed in specialized facilities for DNA extraction, separating pre- and post-polymerase chain reaction (PCR) procedures to minimize potential contamination. Before DNA extraction, each roll of gauze was divided into subsamples measuring approximately 2×2 cm. A sterilized ruler was used to measure each sample, and each subsample was cut into small pieces.

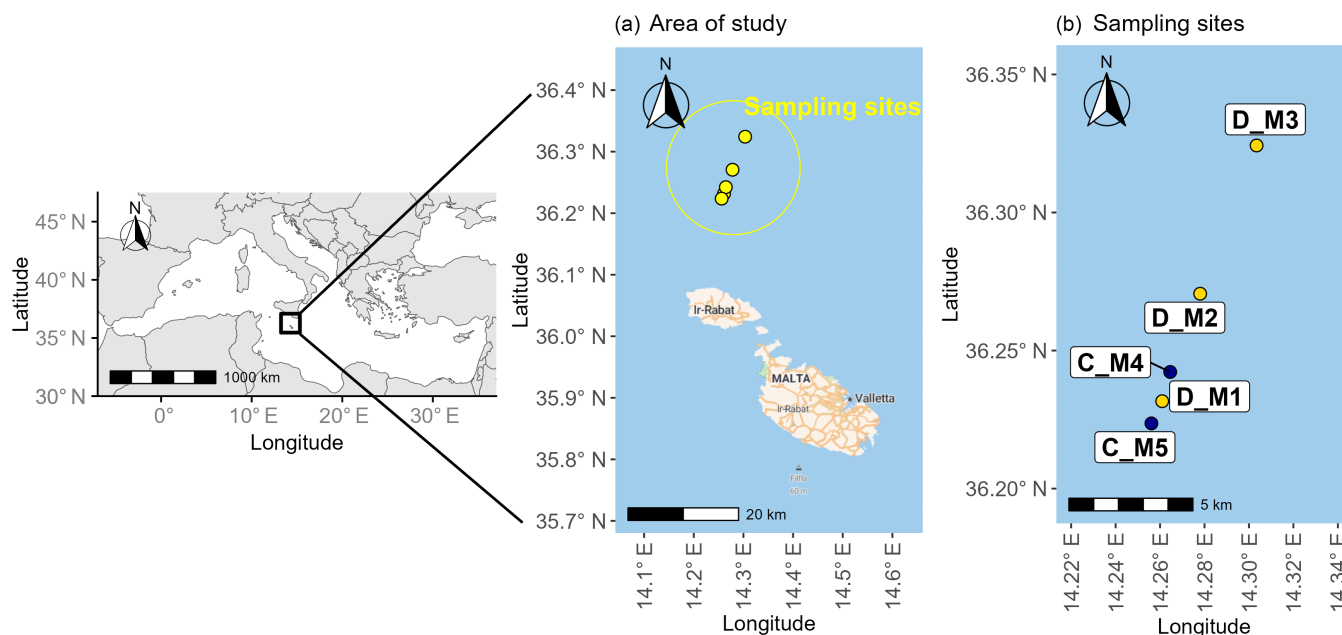


FIGURE 1 (a) Map of the study area in the Maltese waters in the Central Mediterranean Sea (GSA15), with (b) a focus on the sampling sites. Stations are color-coded and labeled according to the diel phase during which sampling took place: yellow and “D” for the diurnal phase, blue and “C” for the crepuscular-evening phase.

The pieces were then dried to avoid PCR inhibition caused by preservation in ethanol. The pieces were incubated in a solution of 1 mL EDTA (0.5 M, pH 8) and 0.25 mg/mL proteinase K at 55°C for approximately 12 h. After lysis, samples were centrifuged, and DNA was extracted with Roche Assembly Tubes silica columns (Dabney & Meyer, 2019). Samples were then amplified using the Elaso2 primers (forward: 5'-GTTGGT HAATCTCGTGCCAGC-3'; reverse: 5'-CATAGTAGG GTATCTAATCCTAGTTTG-3'), which target an approximately 171 bp amplicon of the 12S mitochondrial gene (Taberlet et al., 2018). The amplification of the targeted region was performed by an external service (Macrogen Europe) under the following thermocycling conditions: polymerase activation at 94°C for 15 min, followed by 40 cycles of 94°C for 1 min, 54°C for 1 min, 72°C for 1 min, and a final elongation of 72°C for 5 min. Each sample was amplified in triplicate, pooled, and purified. An extraction negative control and a PCR blank control were included to monitor potential contamination linked with procedures and reagents. Amplicons were finally sequenced at Macrogen Europe using a MiSeq sequencing platform (Illumina, San Diego, CA) with a 2 × 300 bp paired-end.

Bioinformatics analysis

The obtained demultiplexed fastq files were trimmed using Cutadapt version 3.5 (Martin, 2011), removing

primer sequences and their reverse complements in both directions, with the default maximum error rate of 0.1. Trimmed reads were then imported into QIIME2 (Bolyen et al., 2019) for quality filtering, denoising, merging, and classification. Quality filtering was performed with a minimum quality threshold of 38 per base. Denoising was performed with DADA2 (Callahan et al., 2016) using the q2-dada2 plugin with the following parameters: `-p-trunc-len-f 170` and `-p-trunc-len-r 169`. The obtained amplicon sequence variants (ASVs) were length filtered, retaining the sequences with a length between 140 and 200 (mean sequence length = 174.72 bp; Taberlet et al., 2018). Sequences were then classified using the VSEARCH algorithm (Rognes et al., 2016) against a custom reference database of Mediterranean fish species. This database was created by downloading 3709 sequences of the 12S ribosomal gene from NCBI, after obtaining the list of fish species from FishBase (Collins et al., 2021). The sequences were then compared with those in the database, and those showing an identity percentage of 97% or higher were assigned to the corresponding taxon. The metabarcoding dataset was exported from QIIME2 and then imported in R (ver. 4.4.1; R Core Team, 2022) for the post-sequencing removal of contaminant reads, which was performed using MICRODECON ver. 1.0.2 (McKnight et al., 2019), a specific R package developed for the identification and removal of contaminant reads found in negative controls. Through an iterative process, a constant (i.e., ASV fully emerged as a contaminant) is found and

used for sample decontamination. Specifically, the *decon* function was run using the default parameters, except for the “thresh” parameter, which was set to 1 to prevent the removal of rare taxa. The decontaminated metabarcoding dataset was then imported again in QIIME2 and collapsed to the lowest taxonomic level reached (i.e., genus or species). Sequences that remained unassigned were removed.

Statistical analysis

Statistical analyses were performed using R (ver. 4.4.1). Accumulation curves were calculated to assess the relationship between sampling effort and the number of ASVs. The *specaccum* function of the vegan R package (Oksanen et al., 2025) was employed for this purpose. Rarefaction curves were calculated and plotted to contrast the number of ASVs against sequencing depth, using *iNEXT* and *ggiNEXT* functions of the *iNEXT* R package (Hsieh et al., 2016; ver. 3.0.1). The number of reads was transformed using the fourth-root with the *tran* function of the analogue R package (ver. 0.17-6) to adjust for the exponential characteristics of PCR in the sequencing data (Ershova et al., 2021). The transformed read number was then corrected by normalizing each sample by the corresponding soaking time (hereafter we will refer to this transformation using transformed read counts). All the statistical analyses were conducted using the transformed read counts (as described). Species richness (α diversity) for each sample was calculated using the *specnumber* function in the vegan R package (Oksanen et al., 2025). The mean richness was computed for each site between replicas. Given the normal distribution of the data, a *t* test was performed to determine whether there were any significant differences in α diversity values between diel phases (diurnal vs. crepuscular evening). This was done using the R function *t.test*. The correlation between transformed read counts and caught biomass of *C. hippurus* (in kilograms) was calculated using the *cor.test* function of the stats R package (ver. 4.4.1), setting Spearman's method to account for the non-normality of the data. A linear regression model was then calculated using the *lm* function on the same data.

Other molecularly detected species were classified as potential prey or non-prey of the dolphinfish (Appendix S1: Table S2). The screening was conducted based on the bathymetric distribution, retaining pelagic finfish species and those undergoing daily vertical migration as potential prey species (source: <https://fishbase.mnhn.fr/search.php>). Non-prey species were identified as those exclusively associated with the seafloor and elasmobranchs.

The composition of fish assemblages was then analyzed through non-metric multidimensional scaling

(nMDS) based on Bray–Curtis distance, using the *metaMDS* function of the vegan R package. A linear regression model was then used to test whether the axes were explained by our variables (e.g., diel phase, depth, distance from the coast). Multivariate differences between sample groups (i.e., diel phase) were analyzed through the analysis of similarity (ANOSIM) to check for significant differences between the two diel phases and fish assemblages. The one-way ANOSIM test was performed using the *anosim* function of the vegan R package with 999 permutations and Bray–Curtis distance. To identify species associated with diurnal or crepuscular-evening phase, we used indicator species analysis with the *multipatt* function of the *indicspecies* R package and default parameters.

The similarity percentage (SIMPER) test was performed using the Bray–Curtis distance with the function *simper* of the vegan R package setting 999 permutations to assess which metabarcoding-detected species contributed the most to the differences in the caught biomass of *C. hippurus* among sites. The transformed read counts for species contributing more than 5% to the overall dissimilarities between stations were used to create a radar chart with the function *ggradar* of the *ggradar* R package (ver. 0.2). To evaluate the potential relationship between the eDNA signal of the species responsible for the dissimilarities in the caught biomass of dolphinfish, linear regression models were applied. The transformed read counts for each species were used as predictor variables, while the caught biomass of *C. hippurus* was used as the response variable. Separate univariate linear regression models were constructed for each species to determine whether variation in read counts was significantly associated with the caught biomass of *C. hippurus*. These models were implemented using the *lm* function.

All the figures were created using the ggplot2 R package (Wickham, 2016; ver. 3.5.1).

RESULTS

Fishing results of *C. hippurus*

The mean number of dolphinfish individuals recorded per station was 24.4 while the average biomass caught per station amounted to 37.96 kg. Specifically, the highest number of individuals (54) and biomass (80.4 kg) were caught at D_M1, the first station sampled in the diurnal phase of the fishing day (Table 1). This station is located between C_M4 and C_M5, which were sampled at a distance of 36 min apart during the crepuscular-evening phase. The number of dolphinfish caught at these two stations was 18 (C_M4) and 9 (C_M5), with a biomass of 27.4 and 15.3 kg, respectively. The farthest station from

TABLE 1 Results of fishing of *Coryphaena hippurus*: The number of specimens (N) and the caught biomass (in kilograms) are reported.

Station	No. specimens	Caught biomass (kg)
D_M1	54	80.4
D_M2	9	13.7
D_M3	32	53
C_M4	18	27.4
C_M5	9	15.3

the coast (D_M3) had the second highest number of individuals (32) and biomass (53 kg), while the second farthest station from the coast (D_M2) had the lowest number of individuals (9, together with C_M5) and biomass (13.7 kg).

Sequencing results

Sequencing yielded 3,805,026 raw reads. After trimming and bioinformatics analysis, a total of 52,783 merged reads were obtained from Illumina amplicon sequencing, representing 115 ASVs. The ASV accumulation curve (Figure 2a) indicates that the sampling was effective and approaching completion. Thus, the current sampling has relatively well captured the fish diversity (ASV richness). The rarefaction curves (Figure 2b) for all samples reached asymptotes, indicating that there was sufficient sequencing depth to capture most of the ASV diversity within each sample.

After the decontamination process, we retained 51,874 reads. Of these, 5064 reads remained unassigned, while the remaining 46,810 reads were taxonomically assigned and collapsed into 31 unique taxa (Appendix S1: Figure S1). Although the sequencing depth was reached for each sample, the amount of reads varied across samples, with some samples (i.e., D_M2) having lower values than others. The replicate with the highest number of reads was D_M1.2 (14,071), while D_M2.1 was the one with the lowest number of reads (575). *Trachurus trachurus* showed the highest transformed read counts (13,323), while *Mullus barbatus* showed the lowest (2). At the order level, Carangiformes and Clupeiformes exhibited the greatest relative abundance in the diurnal stations (D_M1 and D_M2). The orders showing the highest relative abundance in the crepuscular stations were Eupercaria/misc. at C_M4 and Carangiformes and Eupercaria/misc. at C_M5 (Appendix S1: Figure S2).

A total of 2410.54 transformed read counts were obtained after fourth-rooting and soaking time

normalization (Figure 3). The transformed read count per sample was 301.32 ± 142.85 (mean $\pm$ SD).

Spearman's correlation revealed a strong positive association between the transformed read count and the caught biomass (in kilograms) of *C. hippurus* ($r_s = 0.975$, $p < 0.01$). The linear regression model further highlighted the positive and significant relationship between the transformed read counts and the caught biomass (in kilograms) of *C. hippurus* ($R^2 = 0.62$, $p < 0.05$; Figure 4). In this specific case study, the reads transformed using the fourth-root transformation and accounting for the soaking time were able to estimate *C. hippurus* biomass.

The α diversity (species richness) ranged between 8 and 28 (Appendix S1: Table S3). The highest α diversity (28) was recorded in the first station sampled during the crepuscular-evening phase (C_M4.1 sample). The lowest α diversity (8) was recorded in the farthest station from the coast and was sampled during the diurnal phase (D_M2.1 sample). The mean species richness per site differed between diel phases, with crepuscular-evening sites showing higher richness (14–23 species) than diurnal sites (9–11 species). The null hypothesis (no significant differences) was rejected by the t test ($p > 0.05$).

nMDS revealed a pattern influenced by diel phases (diurnal vs. crepuscular-evening; Figure 5) with the first ordination axis showing a positive correlation with the diel phase (linear regression model, $R^2 = 0.77$, $p < 0.01$). Samples collected during the diurnal and crepuscular-evening periods formed two clusters, each surrounded by confidence ellipses (Appendix S1: Figure S3). Diurnal sites were positioned towards negative MDS1 values, while crepuscular-evening sites were distributed across the positive MDS1 range. This separation suggests consistent differences in community structure between the two diel phases. The ordination plot also highlighted distinct FAD-attracted fish assemblages (in terms of taxon composition) in response to the ecological daily pattern. Some species were present in both assemblages, while others appeared exclusively in one. Additionally, some taxa were amplified in a single replicate of a station (e.g., D_M4.1), clustering together in the right section of the ordination.

The one-way ANOSIM test performed between the assemblages of the four stations and the diel phases suggested a significant influence of the ecological daily pattern on the assemblages attracted by FADs ($R = 0.46$, $p < 0.05$).

The indicator species analysis identified 4 of the 31 taxa (i.e., *Diaphus rafinesquii*, *Hygophum benoitii*, *Hygophum hygomii*, and *Lampanyctus pusillus*) as significant indicators ($p < 0.05$) of the crepuscular-evening phase, as they were almost exclusively recorded during

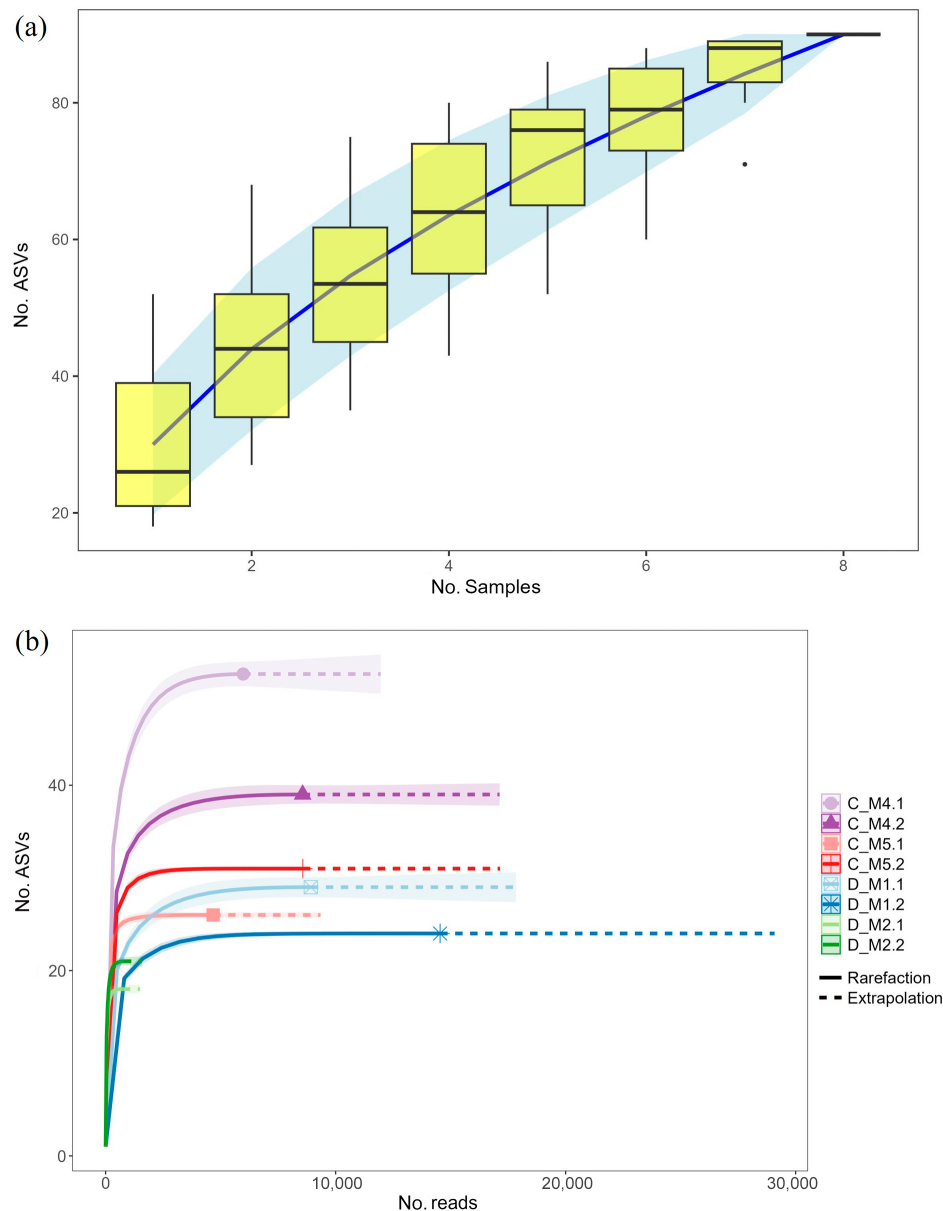


FIGURE 2 (a) Amplicon sequence variant (ASV) accumulation curves showing the number of sampled sites and the number of ASVs obtained. The blue line reports the mean accumulation trend, while yellow boxplots represent the variability across permutations. The midline in the boxplot represents the median number of ASVs per sample. The box limits represent the upper and lower quartiles, the whiskers represent the upper and lower extremes per sample, and the data point represents the outliers. (b) Rarefaction curves showing the relationship between sequencing depth (number of reads) and number of ASVs for each sampled station.

this diel phase (Table 2). Of these species, *L. pusillus* was the only one also recorded during the diurnal phase in D_M2.1. No species resulted as significant indicators for the diurnal diel phase.

The highest average Bray–Curtis dissimilarity recorded by SIMPER analysis across the four stations was 66.03, between D_M2 and C_M4 stations, while the lowest (34.54) was recorded between the stations sampled during sunset (i.e., C_M4 and C_M5) (Appendix S1: Table S4).

The species that mostly contributed to the dissimilarities among the four stations (i.e., contribution >5%) are

shown in Figure 6a. The highest transformed read counts of *T. trachurus*, *Sardina pilchardus*, *Chelon labrosus*, and *Engraulis encrasicolus* were recorded in the D_M1 site (highest caught biomass of *C. hippurus*). The highest transformed read counts of *Diaphus raphinesquii*, *Macroramphosus scolopax*, *Pagellus acarne*, and *H. hygomii* were found at C_M4 (second largest catch). D_M2 station (lowest caught biomass of *C. hippurus*) reported the lowest average transformed read counts per station for most of the seven species that majorly contributed to the dissimilarities between the fish assemblages,

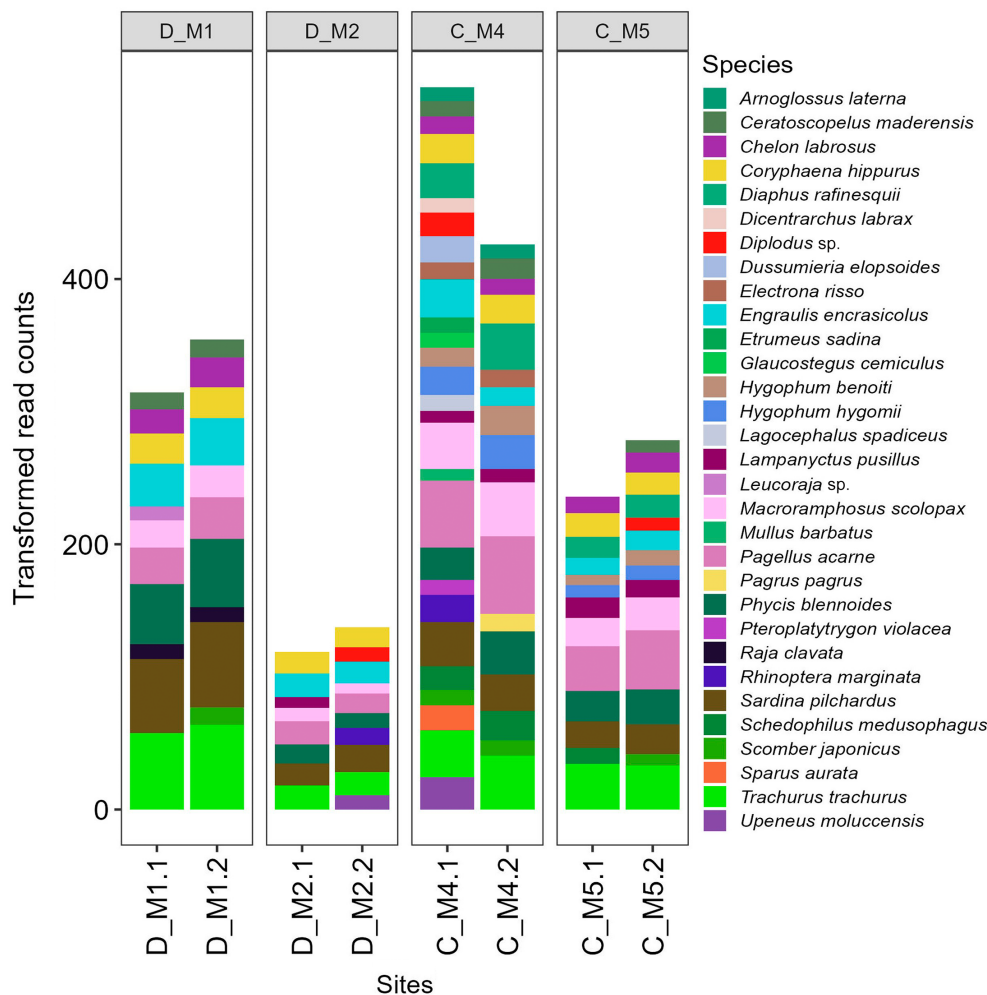


FIGURE 3 Bar plot of the fourth-root transformed number of reads of the amplified species corrected by soaking time (i.e., transformed read counts) for both replicas of each station. C, the crepuscular-evening phase; D, the diurnal phase.

except for *E. encrasicolus*. Linear regression models revealed positive and significant relationships between the caught biomass of *C. hippurus* and the transformed read counts of four species: *T. trachurus*, *S. pilchardus*, *E. encrasicolus*, and *C. labrosus* (Figure 6b). On the contrary, the transformed read counts of *D. rafinesquii*, *H. hygomi*, and *M. scolopax* were not significantly associated with the caught biomass of dolphinfish (Appendix S1: Figure S4).

DISCUSSION

The present study represents the first application of the metaprobe sampling approach in the pelagic domain, specifically during the fishing of *C. hippurus* associated with FADs in Maltese waters. Despite the low number of sampled stations, ASV richness approached completion and sufficient sequencing depth was achieved. However, variation in total transformed read counts among samples suggests potential biases introduced during the DNA

extraction or amplification steps, which may reflect differences in sample quality, DNA concentration, or PCR efficiency (Ruppert et al., 2019). For these reasons, we recognize the need to validate these initial findings by increasing the number of samples and the level of replication and by expanding the sampling activity both spatially and across different diel phases.

The results revealed a positive correlation between the transformed read counts and the caught biomass (in kilograms) of *C. hippurus*. However, due to the small number of sampling sites which can lead to uncertainty and potentially misleading relationships, these results cannot be generalized. Nevertheless, the fourth-root transformation of read numbers and soaking time may offer a useful framework for investigating the quantitative potential of passive eDNA metabarcoding. Finally, passive eDNA sampling has already been identified as a viable alternative to active eDNA filtration. By circumventing many of the technical limitations enforced by large water volume filtration, passive eDNA collectors

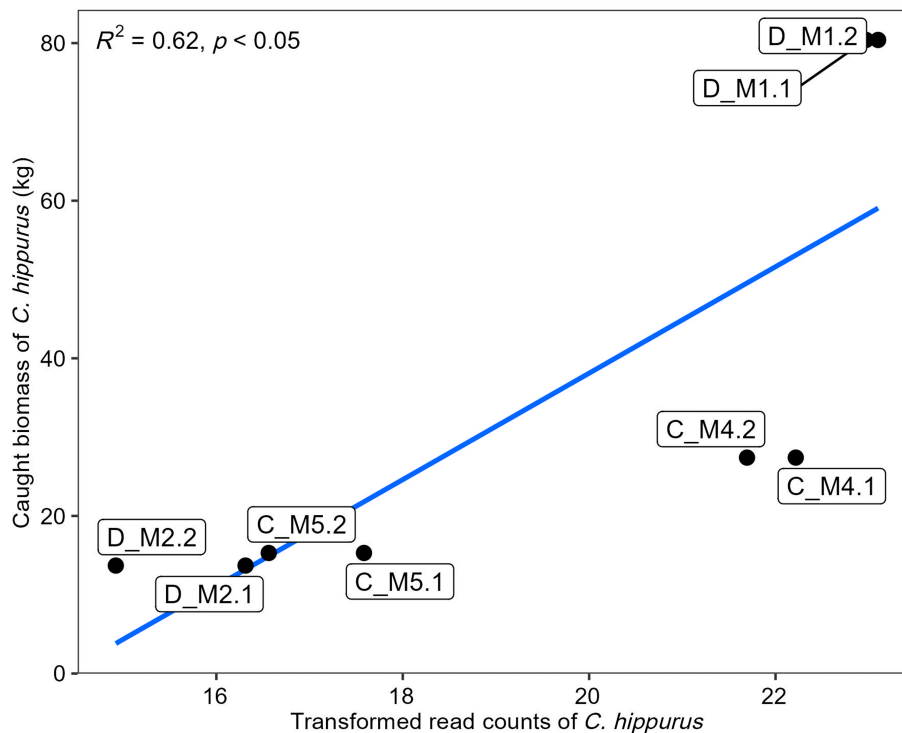


FIGURE 4 Linear model estimation of transformed read counts and biomass of *Coryphaena hippurus* caught.

enable an increase of biological and technical replicates, enhancing estimates of α and β diversity (Bessey, 2021; Lanzén et al., 2017). Although the optimal soaking time for efficient passive eDNA sampling remains unclear (Bessey et al., 2022), previous studies have investigated the impact of soaking time (Bessey et al., 2022; Zhang et al., 2024). Results indicate that effective sampling can be achieved in as little as 5 min of soaking (Bessey et al., 2022). Our study incorporates read number adjustment based on soaking time, as this can affect eDNA adsorption during short immersion periods. While our findings are preliminary, they suggest that slight variations in soaking time could affect the quantitative results.

The species identified by molecular analysis were all Mediterranean species known to occur in Maltese waters. However, some uncertainty arises regarding the detection of *Scomber japonicus*, a species primarily found in the Pacific and Asian coastal regions. While *S. japonicus* has previously been recorded as bycatch in Maltese waters (Moltó et al., 2020), *Scomber colias* is the species that typically inhabits the Mediterranean and Black seas (Collette & Nauen, 1983). Both species are present in the Mediterranean Sea, but the taxonomic status of *Scomber* spp. remains controversial (Catanese et al., 2010). Sanger sequencing and phylogenetic analysis can distinguish between the two species (Infante et al., 2007). Several detected species, such as *Arnoglossus laterna*, *C. labrosus*, *Dicentrarchus labrax*, *Glaucostegus cemiculus*, *H. benoitii*,

H. hygomii, *M. barbatus*, *Raja clavata*, and *Sparus aurata*, are typically demersal, but with wide depth ranges and species occurrences recorded up to the first 10 m of water column (source: <https://fishbase.mnhn.fr/search.php>, accessed 27/11/2024). The presence of such demersal species could be related to vertical migrations and/or to the occurrence of larvae or juveniles with a pelagic life stage. Eggs and/or juveniles of *C. labrosus* and *Lagocephalus spadiceus*, for instance, can occur in shallow waters and juveniles of *M. scolopax* have been identified in the gut content of Maltese *C. hippurus* (Boglione et al., 2006; Castriota et al., 2007; Xu et al., 2024). Although the dynamics of eDNA transport can be complex, especially offshore, due to the effects of currents, upwelling, stratification, and other oceanographic features (Barnes et al., 2014; Pilliod et al., 2014; Strickler et al., 2014), experimental studies show that the majority of detectable eDNA abounds within tens of meters from its source (Andruszkiewicz Allan et al., 2021; Murakami et al., 2019) and degrades below detectability within 48 h (Collins et al., 2018; Murakami et al., 2019). It is therefore reasonable to expect that the species detected by metabarcoding in our study likely occurred in spatial and temporal proximity to the sampling activity.

Furthermore, the diel phase (diurnal vs. crepuscular-evening) was found to influence the composition of fish assemblages attracted to FADs. Four species were identified as indicators of the crepuscular-evening phase.

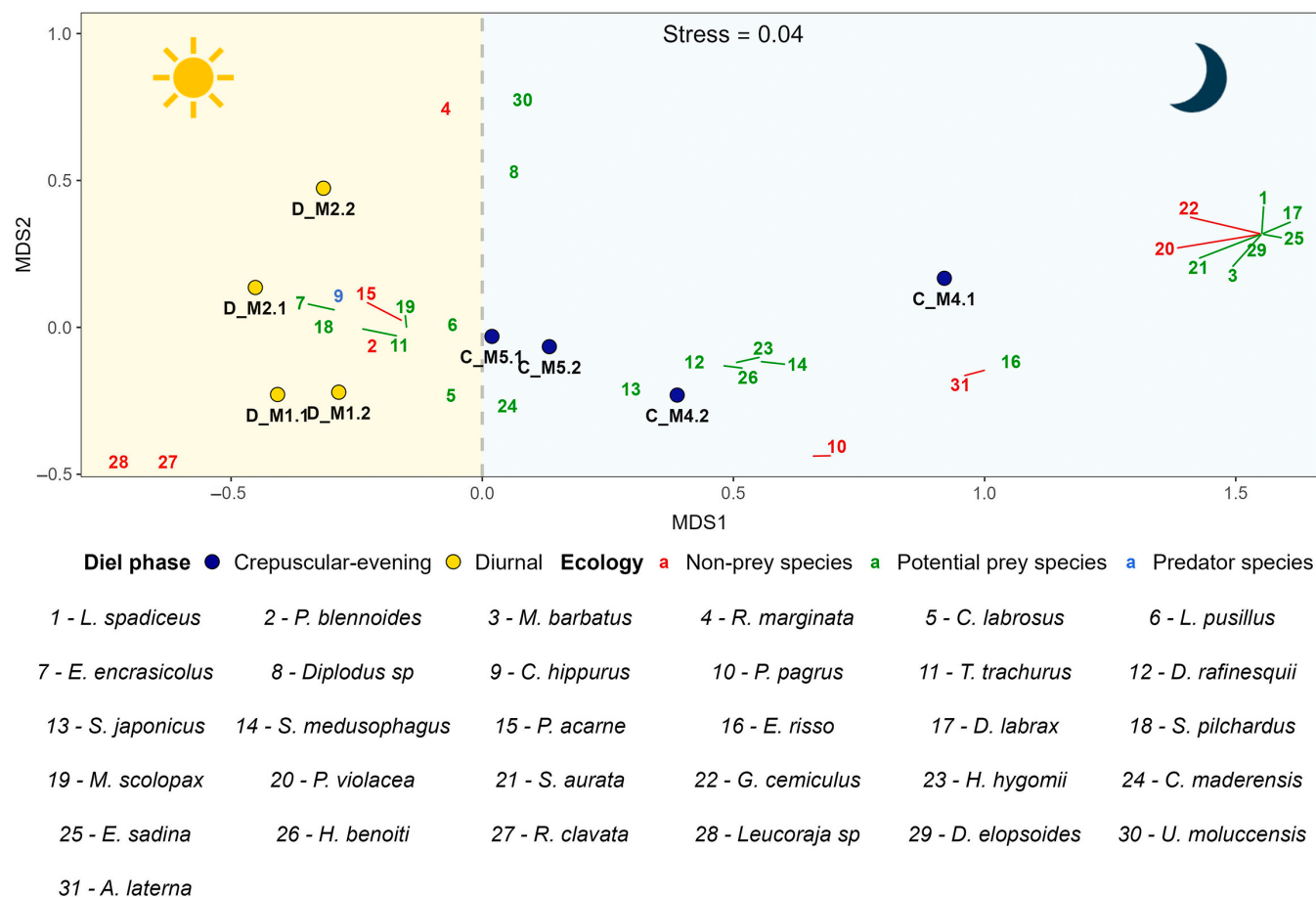


FIGURE 5 Non-metric multidimensional scaling (nMDS) ordination performed on fish assemblages. The ecology of the species was reported by highlighting potential prey species of the target species (*Coryphaena hippurus*) in green and non-prey species in red. Sampling stations are reported as dots and are highlighted in yellow for samples collected during the diurnal phase and in blue for samples collected during the crepuscular-evening phase.

TABLE 2 The diel phase, IndVal percentage, and *p* value for each significant species resulting from the indicator species analysis.

Species	Diel phase	IndVal (%)	<i>p</i>
<i>Diaphus rafinesquii</i>	Crepuscular-evening	100	0.02
<i>Hygophum hygomii</i>	Crepuscular-evening	100	0.02
<i>Hygophum benoitii</i>	Crepuscular-evening	100	0.02
<i>Lampanyctus pusillus</i>	Crepuscular-evening	92.3	0.02

Ideally, for a more robust comparison, the study would have sampled at each FAD during both diel phases. However, this study was conducted in collaboration with fishermen along their routine activity, and it was thus necessary to adapt our sampling to their rhythms and fishing locations. FADs were also placed along a transect with reduced distances, supporting the suitability of this

analysis. Moreover, our results align with those of previous studies by Capello et al. (2012) and Lopez et al. (2017), which reported diel phase-dependent fluctuations in fish assemblages using acoustic sampling. However, these differences may not be solely responsible for the observed behavioral variability, as the associative behavior of fish is the result of an unknown combination of factors (Leroy et al., 2015). Abiotic components of the environment, such as oceanographic variables and FAD densities, and biotic components such as the presence of predators, may also influence the associative behavior of fish (Lopez et al., 2017).

Seven species were identified as major contributors of dissimilarities in dolphinfish-caught biomass among stations, with a positive linear relationship between the transformed read counts of four of these species and *C. hippurus*-caught biomass. Massutí et al. (1998) suggested that *C. hippurus* exhibits diurnal feeding activity, thus identifying this species as a visual predator. However, our results only partially support this

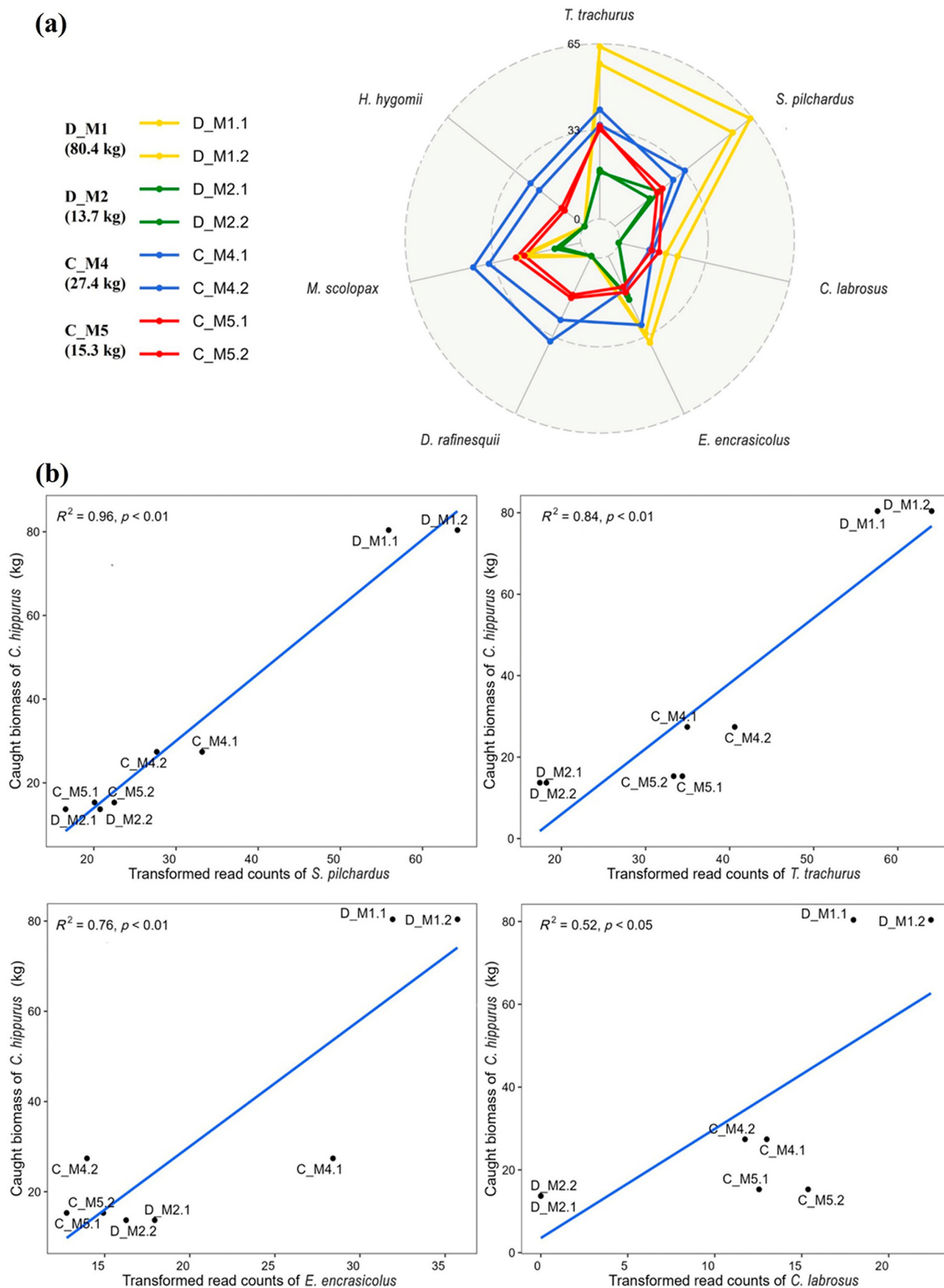


FIGURE 6 (a) Radar chart displaying the transformed read counts for each station replicate, focusing on species that contributed more than 5% to the dissimilarities in biomass caught of *Coryphaena hippurus* between stations, as identified by the similarity percentage (SIMPER) test. Different colors represent different stations, while replicates of the same station share the same color. Lines connect the points of each replicate. (b) Linear regression model of the transformed read counts of the species that contributed more than 5% to the dissimilarities in biomass caught of *C. hippurus* between stations and the biomass of *C. hippurus* caught. C, the crepuscular-evening phase; D, the diurnal phase.

conclusion. In fact, the highest biomass was recorded in the morning at D_M1 (09:09 a.m.), followed by the two crepuscular-evening sampled stations, that is, C_M4 and C_M5 (sampled at 16:56 and 17:32, respectively). The lowest biomass caught was recorded at D_M2 (10:18). The SIMPER analysis showed that some species (i.e., *T. trachurus*, *S. pilchardus*, *C. labrosus*, and *E. encrasicolus*) were qualitatively and quantitatively associated with higher dolphinfish biomass. These species have previously been identified as prey items of Majorcan and Maltese dolphinfish through the analysis of stomach contents (Bannister, 1976; Lozano-Cabo, 1961). The species that contributed more than 5% to the variation in dolphinfish biomass, but were not positively associated with the caught biomass of dolphinfish (i.e., *D. rafinesquii*, *H. hygomii*, and *M. scolopax*), can be related to the fish-dependent associative behavior, whereby pelagic fish species maintain contact with other species for reasons other than feeding on them (Capello et al., 2011; Soria et al., 2009). This kind of behavior is typically observed near floating objects (Fr  on & Dagorn, 2000). Furthermore, the availability of prey has been reported to significantly impact the daily distribution of large pelagic species (Pitcher & Parrish, 1993). These findings support the view of *C. hippurus* as an opportunistic feeder and visual predator, occurring in areas with abundant finfish prey (Massut   et al., 1998; Nunes et al., 2015; Varela et al., 2017; Varghese et al., 2013), rather than strictly to the diel phase.

Recent research started to emphasize environmental and economic challenges posed by FADs, particularly concerning the materials used and their ecological impact. This has prompted a shift towards using sustainable materials, such as balsa wood, sisal ropes, and cotton sheets for shading (Moreno et al., 2018), and a reduction in the number of FADs deployed (Sinopoli et al., 2020). Ecological impacts are mainly driven by the bycatch of nontarget species and by the alteration in the natural behavior of fish (Lopez et al., 2017). Additionally, earlier studies highlighted a lack of relationship between *C. hippurus* and species associated with FADs, suggesting that disadvantages of FADs may outweigh their benefits (Castriota et al., 2007; Sinopoli et al., 2015, 2019). For these reasons, studies focusing on the dynamics of assemblages at FADs are necessary to move towards a better management of these devices.

Passive eDNA appears to be a reliable tool for assisting with fisheries management. Further efforts should be made to consolidate and validate this quantitative relationship for more species. This could be useful for stock assessment, although the method cannot yet replace traditional methods, as it cannot provide direct information on the age, size, weight, life stage, or fecundity of the stock (Hansen et al., 2018).

CONCLUSIONS

This work represents a preliminary exploration of the potential application of metaprobes in the pelagic marine environment. It yielded encouraging results regarding the efficiency and reliability of passive eDNA metabarcoding sampling in pelagic waters, providing a promising approach for investigating the biomass of *C. hippurus*, assessing fish assemblages at FADs, and detecting diel assemblages fluctuations. The positive relationship between transformed read count and *C. hippurus* biomass highlights the potential of eDNA metabarcoding as a quantitative tool when soaking time is considered; however, further research is required to validate this relationship.

Despite the small sample size and the focus on a single species, this study emphasizes the potential of using passive eDNA collection to study the dynamics of fish assemblages at FADs, with the aim of optimizing fishing efficiency and promoting sustainable fisheries management. To validate these initial findings, future research should expand sampling efforts (e.g., multiyear and large-scale sampling) and broaden the scope of the investigation to include biomass information of multiple species.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw sequence data for the DNA metabarcoding experiment are available from the NCBI Sequence Read Archive under Bioproject accession PRJNA1225499. An R markdown code used for the statistical analysis and the associated input files (Marinchel, 2026) are available from Mendeley Data: <https://data.mendeley.com/datasets/52km8kd4n2/1>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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