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ORIGINAL PAPER

Jellyfish (Scyphozoa and Hydrozoa) as natural environmental DNA samplers: a case study in the Northern Adriatic sea

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Abstract

Conservation management, aimed at mitigating the ongoing biodiversity loss, critically relies on ecosystem monitoring to enable accurate estimates of species distributions and population sizes. Environmental DNA (eDNA) analysis has become increasingly popular for non-invasive and high-throughput species assessment, including fish species diversity. Beyond the established sample collection protocols, natural samplers of eDNA (nsDNA) – organisms that trap environmental genetic material in their tissues – show considerable promise, with recent work especially demonstrating the remarkable effectiveness of sea sponges. Here, the potential of jellyfish (phylum Cnidaria) to serve as motile, marine, pelagic natural samplers of eDNA was investigated through DNA metabarcoding using fish specific primers. Jellyfish are opportunistic marine predators known to consume fish eggs and larvae and their presence has been associated with certain fish species, making them potentially useful for open water fish assessment. Four species, the many-ribbed jellyfish (*Aequorea forskalea*, Class Hydrozoa), the moon jelly (*Aurelia solida*, Class Scyphozoa, Order Semaeostomeae), the barrel jellyfish (*Rhizostoma pulmo* Class Scyphozoa, Order Rhizostomeae) and the fried-egg jellyfish *Cotylorhiza tuberculata* (Class Scyphozoa, Order Rhizostomeae) were collected from the Italian waters of the Gulf of Trieste (northern Adriatic Sea) and nsDNA isolated, sequenced and analysed. Across all species, 28 fish Molecular Operational Taxonomic Units (MOTUs) were detected including pelagic species, benthic species likely spawning at the time of sampling, and species known to associate with the presence of jellyfish. We highlight the potential of jellyfish as tools for enhancing biodiversity monitoring, particularly in remote and inaccessible areas where conventional surveys may be difficult to employ.

Keywords Metabarcoding · Plankton · Fish · Mediterranean sea · Biodiversity monitoring

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Introduction

In recent decades, genetic monitoring has increasingly supported environmental management and policy decision-making by providing accurate estimates of biodiversity and species distribution (Rees et al. 2014). However, accurate biodiversity assessments in the marine environment are particularly challenging due to costs associated with covering both vast and remote areas (Ramírez et al. 2022). Whilst observational methods such as underwater visual surveys using SCUBA (Lindfield et al. 2014) or baited remote underwater videos (Jessop et al. 2022), and capture-based methods such as netting and trapping (Jovanovic et al. 2007) can provide important information about near-shore and shallow-water habitats, they are limited in utility for offshore and deep-sea species.

Analysis of environmental DNA (eDNA, DNA extracted from environmental samples such as water, soil, air) is becoming widely adopted (Rees et al. 2014; Shum and Palumbi 2021), and is particularly well-suited for aquatic environments, where DNA released by organisms is well mixed and diffused in the water column. Various studies have pointed out the universality (across the tree of life) (Stat et al. 2017) and low environmental impact (Bohmann et al. 2014) of eDNA analysis, demonstrating also its generally greater power in capturing both taxonomic and functional diversity, compared to traditional methods such as visual surveys, baited underwater videos and capture approaches (Aglieri et al. 2021).

Marine eDNA is traditionally obtained through seawater filtration using artificial membranes with different pore sizes (McQuillan and Robidart 2017). However, these methods can be cumbersome, requiring manual filtering that increases the risk for contamination (Alexander et al. 2023), entail a significant amount of single-use plastic, and can be affected by turbidity (Kumar et al. 2022). For offshore assessment, significant investment in advanced technologies such as automated real-time eDNA sampling systems (Hansen et al. 2020) and deep-sea robotic samplers (McQuillan and Robidart 2017) has been proposed.

Passive eDNA sampling methods, in which filter membranes or adsorbent-filled sachets are suspended in the water column (Kirtane et al. 2020; Bessey et al. 2021) offer an alternative to mechanical filtration systems but rely on the natural flow of water to bring eDNA into contact with the capture media, resulting in variable and unpredictable levels of eDNA capture, influenced by factors such as water currents and depth. Other low-cost eDNA samplers such as ‘metaprobes’ (perforated 3D-printed spheres containing sterile cotton that trap eDNA from the surrounding water) can be attached to fishing gear (Maiello et al. 2022), or deployed with SCUBA divers (Neave et al. 2025); However, these approaches still require long soaking times to accumulate sufficient material, which may not be feasible during short surveys, limited sea time, or in areas such as Marine Protected Areas (MPAs) where fishing activities are restricted.

A technique gaining increasing traction, inspired by diet metabarcoding (Siegenthaler et al. 2019; Shum et al. 2023), involves harnessing the eDNA accumulated by organisms, defined as natural samplers (Mariani et al. 2019), which trap eDNA in their tissues even beyond the spectrum of their target prey (Gallego et al. 2024). Natural sampling of eDNA can reduce plastic waste, simplify sample collection, and be a cost-efficient alternative, potentially overcoming the limitations of conventional sampling methods. To date, fish diversity in coastal ecosystems has been assessed through sampling crustaceans (Siegenthaler et al. 2019; Shum et al. 2023), sponges (Neave et al. 2023) and sea anemones (Cunnington et al. 2024) as natural samplers, with evidence showing that demersal sponges can also capture information on offshore biodiversity (Cai et al. 2024). However, all these sampled organisms are benthic, so they may not be suitable for properly monitoring biodiversity in pelagic waters.

Jellyfish are abundant pelagic organisms found throughout the world’s oceans (Barnes 1982). The subphylum Medusozoa includes the classes Scyphozoa (true jellyfish), Hydrozoa, Cubozoa (box jellyfish) and Staurozoa. Although jellyfish are often considered as passive zooplankton (Richardson et al. 2009) there is considerable evidence that they are not completely at the mercy of currents but can affect their position through both swimming against the flow (Malul et al. 2024) and vertical migration in order to utilise currents at depth (Honda et al. 2009). Thus, a notable advantage of using jellyfish as eDNA samplers is their ability to cover extensive areas as they move through seawater masses, both horizontally and vertically (Gershwin 2016). This attribute proves advantageous in studying vast areas where traditional eDNA sampling methods may be challenging or time-consuming. Furthermore, given the diversity of jellyfish in feeding strategies and prey (from mesozooplankton up to fish eggs and larvae (Titelman and Hansson 2006; Purcell 2018), tissue structures and ecological interactions (fish can both feed on jellyfish and establish symbiotic associations with them (Purcell and Arai 2001; Karplus 2014; Tilves et al. 2018)), different species and even different tissues may harbour distinct eDNA fragments.

Here, we examined the utility of four jellyfish species as natural samplers of eDNA at the border of the Marine Protected Area of Miramare (Trieste, Italy). Metabarcoding has previously been used to study dietary composition of *Aurelia coerulea* von Lendenfeld, 1884 (Sun et al. 2021), however, we are not aware of any studies applying DNA metabarcoding with a specific focus on fish species (hence not necessarily DNA originating from feeding processes).

Methods

Sample collection

Samples were collected at the Long-Term Ecological Research (LTER) site of the Gulf of Trieste (45.700831 N, 13.71000 E; https://deims.org/96969205-cfdf-41d8-979f-ff881ea8dc8b) situated at the edge of the Miramare Marine Protected Area, ~200 m offshore, with a bottom depth of ~17 m (Fig. 1).

Specimens belonging to four species (Fig. 2) were caught with a hand net from the boat: *Aequorea forskalea* Péron & Lesueur, 1810, *Aurelia solida* Browne, 1905, and *Rhizostoma pulmo* (Macri 1778) in May 2022 and *Cotylorhiza tuberculata* (Macri 1778) in July 2022. Species were selected based on both accessibility for sampling and their different feeding behaviours. The semaeostome *Aurelia* (class Scyphozoa), utilises tentacles to capture prey, subsequently transporting this to the mouth via the oral arms for digestion (Costello and Colin 1994; Gershwin 2016). In addition, *Aurelia* may be able to capture prey in mucus on the surface of the umbrella from which transfer to the oral arms can occur (Orton 1922). Rhizostomean jellyfish such as *Rhizostoma pulmo* and *Cotylorhiza tuberculata* (class Scyphozoa) lack marginal tentacles, and they rely mainly on water filtration through the manubrium (oral arms and scapulets). Prey, captured by the production of mucus and the presence of nematocysts and subsequently paralysed, is then taken up and transported to the stomach trough the multiple oral openings and canals on the oral-arms (Avian et al. 2022; Nagata et al. 2024; Motta et al. 2025). The Hydrozoan *Aequorea* (Purcell 2018) lacks oral arms, capturing prey in its long nematocyst-laden tentacles which transfer it to a highly contractile mouth.

Immediately following collection, jellyfish were transferred to the laboratory of the National Institute of Oceanography and Applied Geophysics (OGS) and dissected (transfer time < 30 min). *R. pulmo* and *A. solida* gut contents, oral arms, and umbrellas were isolated as distinct body parts. *A. forskalea* was separated only into a core section containing the gut and mouth area, and the umbrella. *C. tuberculata* specimens were processed whole without

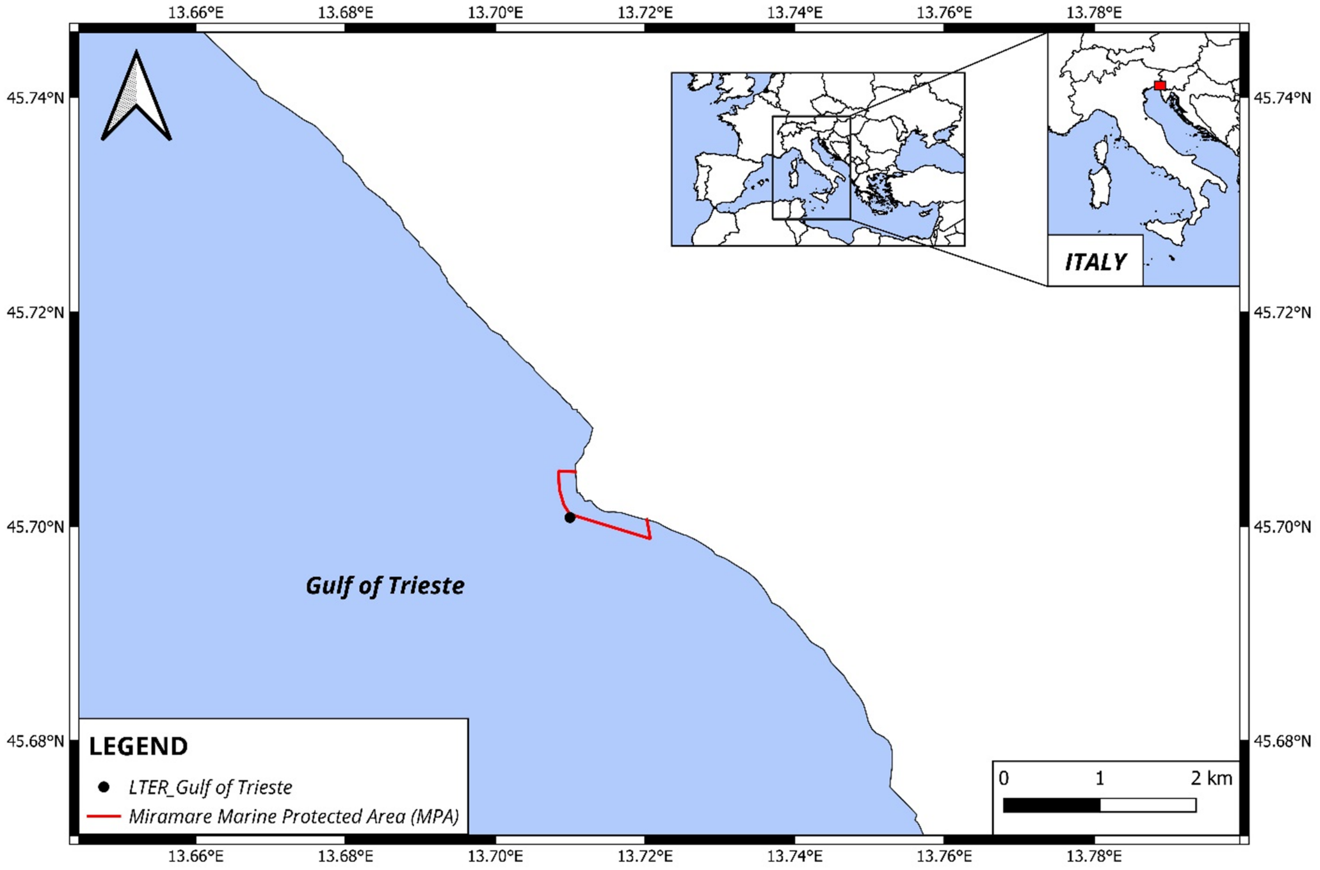

Fig. 1 Location of sampling at the Long-Term Ecological Research (LTER) site of the Gulf of Trieste. The boundaries of the Miramare Marine Protected Area are indicated

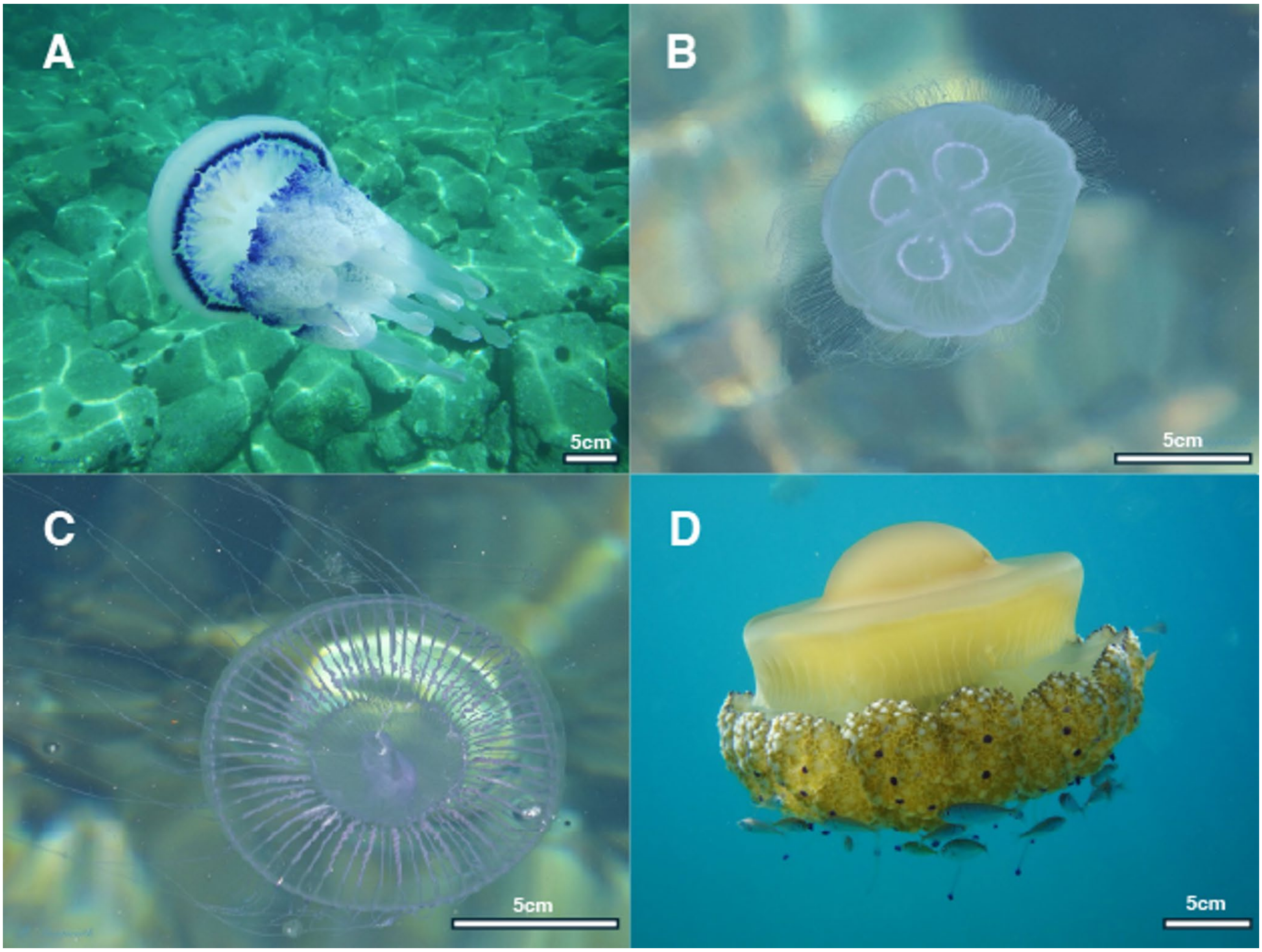

Fig. 2 Jellyfish species sampled: (**a**) *Rhizostoma pulmo*; (**b**) *Aurelia solida*; (**c**) *Aequorea forskalea* and (**d**) *Cotylorhiza tuberculata*. Photos courtesy of Riccardo Iungwirth

separation. Samples were preserved in 96% ethanol and stored at 4 °C then transported to Liverpool John Moores University (UK).

DNA extraction

DNA extraction was conducted in a dedicated eDNA lab in which standard eDNA laboratory protocols were followed to minimise the risk of contamination.

Samples were blotted dry then tissues were cut into smaller pieces prior to extraction. For guts, a partial drying step was performed in a Petri dish before extracting DNA from the remaining material. DNA was extracted using the modular mu-DNA protocol for tissue (Sellers et al. 2018). For full procedures see Supplementary material.

DNA amplification, library preparation, and sequencing

PCR amplifications were performed in triplicate using the Tele02 primers (Taberlet et al. 2018) which amplify a ~ 169 bp fragment of the mitochondrial 12 S rRNA gene. 20 µl PCR reactions contained 10 µl of 2× MyFi Mix (Meridian Bioscience), 1 µl each primer (10µmol), 0.16 µl BSA (Bovine Serum Albumin Solution, ThermoFisher Scientific), and 2 µl of DNA template with cycling conditions of 95 °C for 10 min, then 40 cycles of 95 °C for 30 s, 60 °C for 45 s, 72 °C for 30 s, with a final step of 72 °C for 5 min. Positive and no-template PCR controls were included in each PCR run. The positive PCR controls contained DNA extract (0.05 ng/µl) from the iridescent shark catfish, *Pangasianodon hypophthalmus*, which does not inhabit the sampling region. After PCR amplification, triplicate PCR products were pooled, then purified using Mag-Bind Total Pure NGS magnetic beads (Omega BioTek) with a 1:1 ratio of magnetic beads to PCR product and quantified using the Qubit dsDNA High Sensitivity Assay kit (ThermoFisher Scientific). Two libraries were created, one for *A. solida*, *R. pulmo* and *A. forskalea* ($N=24$) and the other for *C. tuberculata* ($N=3$, analysed alongside samples from a different project). Libraries were normalised and pooled in equimolar amounts then subjected to a further round of purification using magnetic beads, followed by library preparation using the NEXTFLEX Rapid DNA-Seq Kit for Illumina (Revvity), following the manufacturer's instructions. Libraries were quantified using qPCR and pooled at equimolar concentrations before sequencing on an Illumina iSeq100 instrument at Liverpool John Moores University.

Bioinformatic analysis

Bioinformatic analysis of the sequencing data followed the OBITools v1.2.11 metabarcoding pipeline (Boyer et al. 2016) with taxonomy assignment performed against a custom 12 S vertebrate reference database, constructed in silico from the EMBL database (Release version r143) using ecoPCR. MOTUs were retained only if they exhibited a sequence identity of at least 97%. Taxonomic assignments were further validated by manual BLAST searches to remove ambiguous MOTUs, while non-target reads (non-teleosts) were excluded from downstream analysis. More details on the bioinformatic process can be found in the Supplementary Material.

Statistical analysis

All analyses were conducted using R v4.2.3 (Oksanen et al. 2019). Bubble plots were generated to display proportional read counts per species (a proxy of relative abundance), calculated as the number of sequenced reads of each species divided by the total reads, using custom R-scripts. To assess the statistical significance of differences in MOTU detection among species and body parts, PERMANOVA analyses (1000 permutations) were performed based on Jaccard distances calculated from a binary presence-absence dataset that included all fish taxa. Non-metric multidimensional scaling (nMDS) based on Bray–Curtis dissimilarities was used to visualise patterns, through the adonis function from the vegan package in R (Oksanen et al. 2019).

Results

A total of 24 samples from May (sequenced as Run 1) generated 1,560,266 reads, and 3 samples from July sequenced as Run 2 generated 31,683 reads (see Supp Table 1 for full breakdown). Following quality filtering to remove non-teleost MOTUs and sequences with low percentage identity, 186,584 teleost reads from Run 1 and 30,321 reads from Run 2 remained for further analysis. No contaminating fish sequences were found in the controls.

Whilst total reads per sampled species were comparable, reads remaining following quality filtering varied substantially (Table 1; Suppl. Fig S1).

The taxon accumulation curve (Fig. 3) showed that number of MOTUs identified began to plateau at approximately 50,000 reads.

Variation in MOTU composition across jellyfish species and body parts was also visualised using a non-metric multidimensional scaling (nMDS) plot (Fig. 4) providing a visual representation of the relationships and groupings among the samples based on their dissimilarities. Distinct separation is evident in *C. tuberculata* samples (sampled in July), and to some extent *R. pulmo*. MOTU composition differed significantly between species (PERMANOVA pseudo $F=2.349$, df=3, $p<0.001$) and between tissues within species (PERMANOVA pseudo $F=2.139$, df=3, $p<0.001$) consistent with the nMDS analysis.

Body parts were then combined to summarise species detections in each jellyfish species.

Across all samples, 28 MOTUs were identified, four from *A. forskalea*, nine from *A. solida*, 16 from *R. pulmo* and 10 from *C. tuberculata* (Fig. 5). Of these 28 MOTUs, 20 were classified to species level, two to genus, two to subfamily (Gobiinae, Macrourinae), and four to family (Serranidae,

Table 1 The number of reads by major taxonomic group and number of fish motus identified from each species of jellyfish

	A. forskalea	*A. solida*	*R. pulmo*	*C. tuberculata*
Number of samples sequenced	6 (3)	9 (5)	9 (6)	3 (3)
Number teleost MOTUs	4	9	17	10
Fish reads	447	693	186,229	30,331
Mammal reads	0	897	4,631	0
Bird reads	618	18,808	18,011	1
Human reads*	260,964	514,805	554,078	1,328
Total reads	262,029	535,203	763,034	31,683
% fish reads	0.17	0.13	24.40	95.73

Number of samples sequenced is provided as total number of samples processed and sequenced (total number of samples containing teleost sequences)

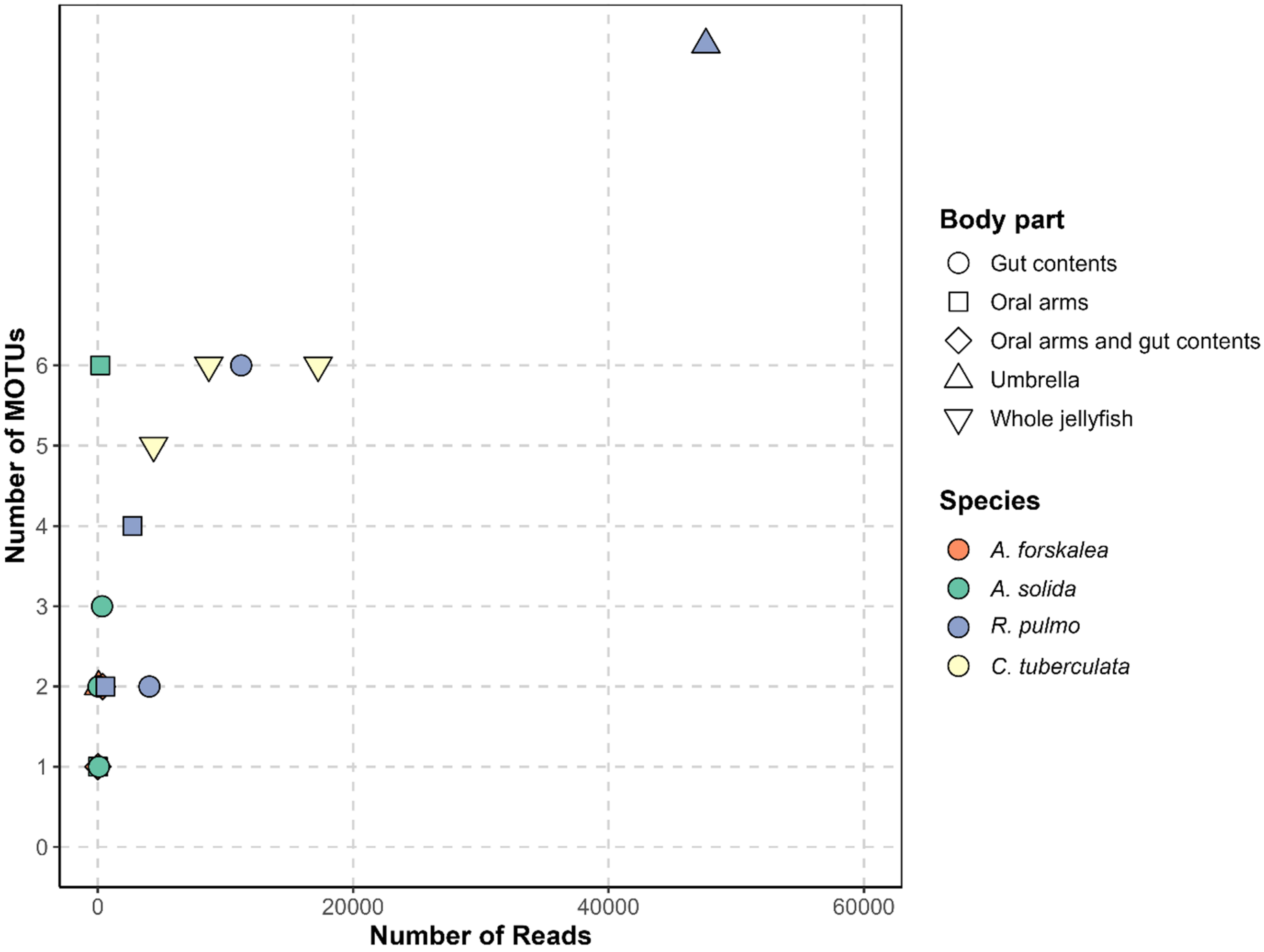

Fig. 3 Taxon accumulation curve. Number of reads and MOTUs identified are shown for different body parts (represented by shape) and species (represented by fill colour)

Callionymidae, Scophthalmidae, Blennidae). Reads from *A. forskalea* were dominated by grenadiers (Macrourinae), those from *A. solida* by shanny (*Lipophrys*) and turbot (Scopthalmidae), those from *R. pulmo* by dragonets (Callionymidea), gobies (Gobiidae) and serranids, and those from *C. tuberculata* by horse mackerel (*Trachurus mediterraneus*) and also gobies.

Discussion

Overall, we have shown that jellyfish can serve as natural samplers of teleost biodiversity, with the detection of 28 fish MOTUs across four jellyfish species (3 samples per species). However, we also show that the biodiversity recovered varies considerably among species, which indicates that the choice of jellyfish species is critical for the success of the approach, with *R. pulmo* and *C. tuberculata* generating substantially more DNA reads, with more MOTUs identified, than *A. forskalea* and *A. solida*. We show also that the use of specific body parts introduces stochasticity, leading to variation in the composition of eDNA in the samples and a potential loss of MOTUs unless the entire jellyfish specimen is sampled for eDNA analysis.

Differences in species detection among jellyfish may arise from variation in their phenology, morphology, feeding behaviour, and habitat preferences. In the northern Adriatic Sea, jellyfish are present year-round, but the pelagic sexual stage (medusae) of different species exhibits distinct seasonality. Of the jellyfish studied, *R. pulmo* is the only species present year-round, *A. solida* is more common from January to July, *A. forskalea* from February to May and *C. tubercolata* from May to September-October (Pierson et al. 2020).

R. pulmo and *C. tuberculata* lack true tentacles and instead they feed by continuous filtering of seawater on the large and complex surface area of their oral arms, where prey is captured and transported to the oral-arm opening for

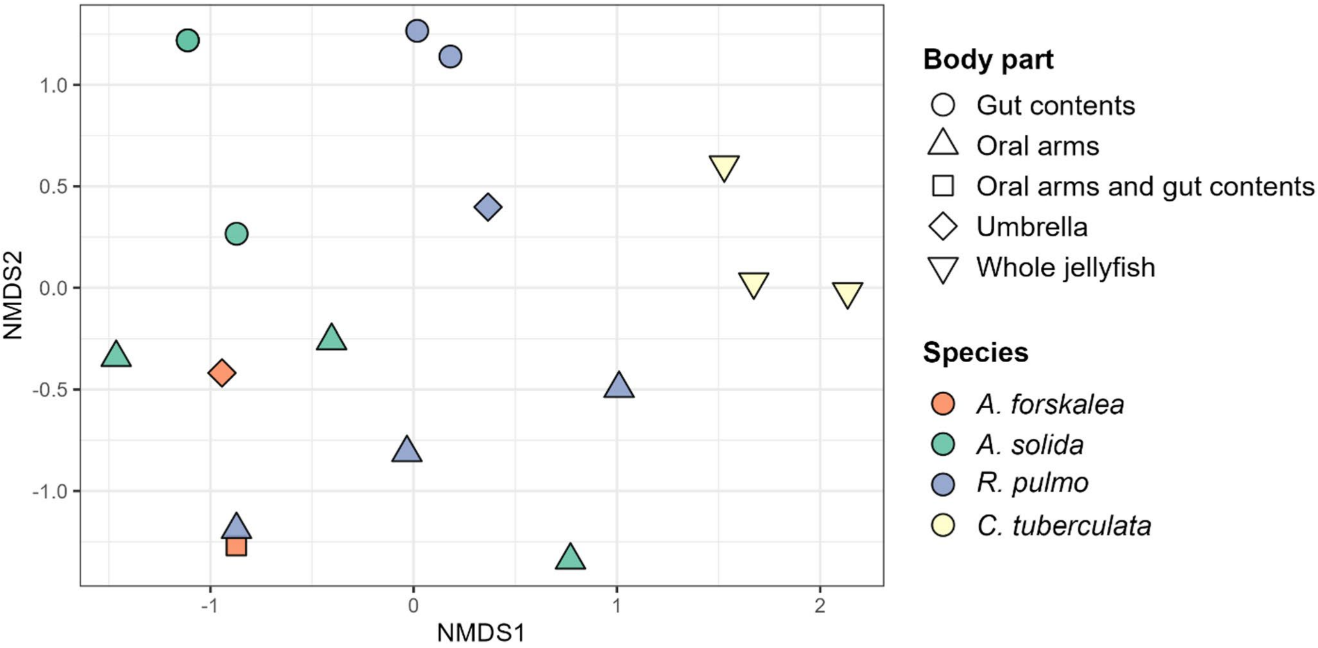

Fig. 4 Nonmetric multidimensional scaling plot (nMDS) plot with a stress value of 9.48×10^{-5} illustrating dissimilarity between samples based on Bray–Curtis dissimilarity. Colours denote different species while shapes indicate different body parts

ingestion (Nagata and Morandini 2018; Avian et al. 2022). In contrast, *A. solida* and *A. forskalea* use their tentacles to capture small planktonic organisms from the water, thus relying more on the passive capture of prey. Additionally, *C. tuberculata* hosts symbiotic zooxanthellae that contribute substantially to its metabolic demands (Djeghri et al. 2019; Enrique-Navarro et al. 2022) and typically inhabits the upper water column (0–2 m) (Kikinger 1992), likely to maintain optimal light conditions for its photosynthetic partners. Such ecological and feeding differences among jellyfish species may, in turn, influence MOTU composition. The two rhizostomean jellyfish are larger and possess more complex anatomy, which may allow them to encounter and trap a wider range of particles. Thus, the sheer mass and morphology of the organism arguably play a key role in determining the effectiveness of jellyfish as natural environmental DNA samplers.

It should be noted that, following quality filtering, the total reads remaining for the *A. solida* and *A. forskalea* samples was far below the number needed to capture the surrounding diversity, as shown by the accumulation curve. This was driven largely by a notable quantity of human and other non-teleost DNA reads in these samples. Whilst our lab workflows are designed to limit contamination with human DNA, sterile techniques were not followed in the field which could explain the high read counts. Future work should consider adoption of blocking primers in the PCR mix, a technique proven to selectively inhibit non-target DNA sequences (Boessenkool et al. 2012).

We also revealed significant differences in MOTUs detected between body parts. This may be due either to biological characteristics, with, for example, oral arms having a significant role in feeding, but may also be due to stochasticity. Combining reads across all body parts certainly reflects more accurately the detectable species diversity, but future work should examine this further, generating increased read counts for each tissue.

We successfully detected reads from pelagic species, benthic species, and species from deeper marine habitats in our data, demonstrating the potential of jellyfish as natural samplers of a wide range of teleost environments. Encouragingly, common pelagic Mediterranean species such as bluefish (*Pomatomus saltatrix* (Linnaeus, 1766)), scad (*Trachurus mediterraneus* (Steindachner, 1868)), anchovy (*Engraulis encrasicolus* (Linnaeus, 1758)) and European sprat (*Sprattus sprattus* (Linnaeus, 1758)) were detected.

Fish eggs and yolk-sac larvae, the so called ichthyoplankton, can form a large part of the diet of scyphomedusae (Arai 1997) and both *Aequeora* and *Aurelia* are known predators of fish eggs and larvae (Möller 1984; Purcell 1989). This could be a likely source of the eDNA detected from benthic species, such as flatfishes (Scopthalmidae), gobies (Gobiinae), blennies (Blenniidae), and dragonets (Callionymidae) or deeper water species such as hake (*Merluccius merluccius* (Linnaeus, 1758). The majority of Mediterranean marine fishes spawn between April and August (Tsikliras et al. 2010), when our sampling was conducted, and, during this period, numerous fish species engage in

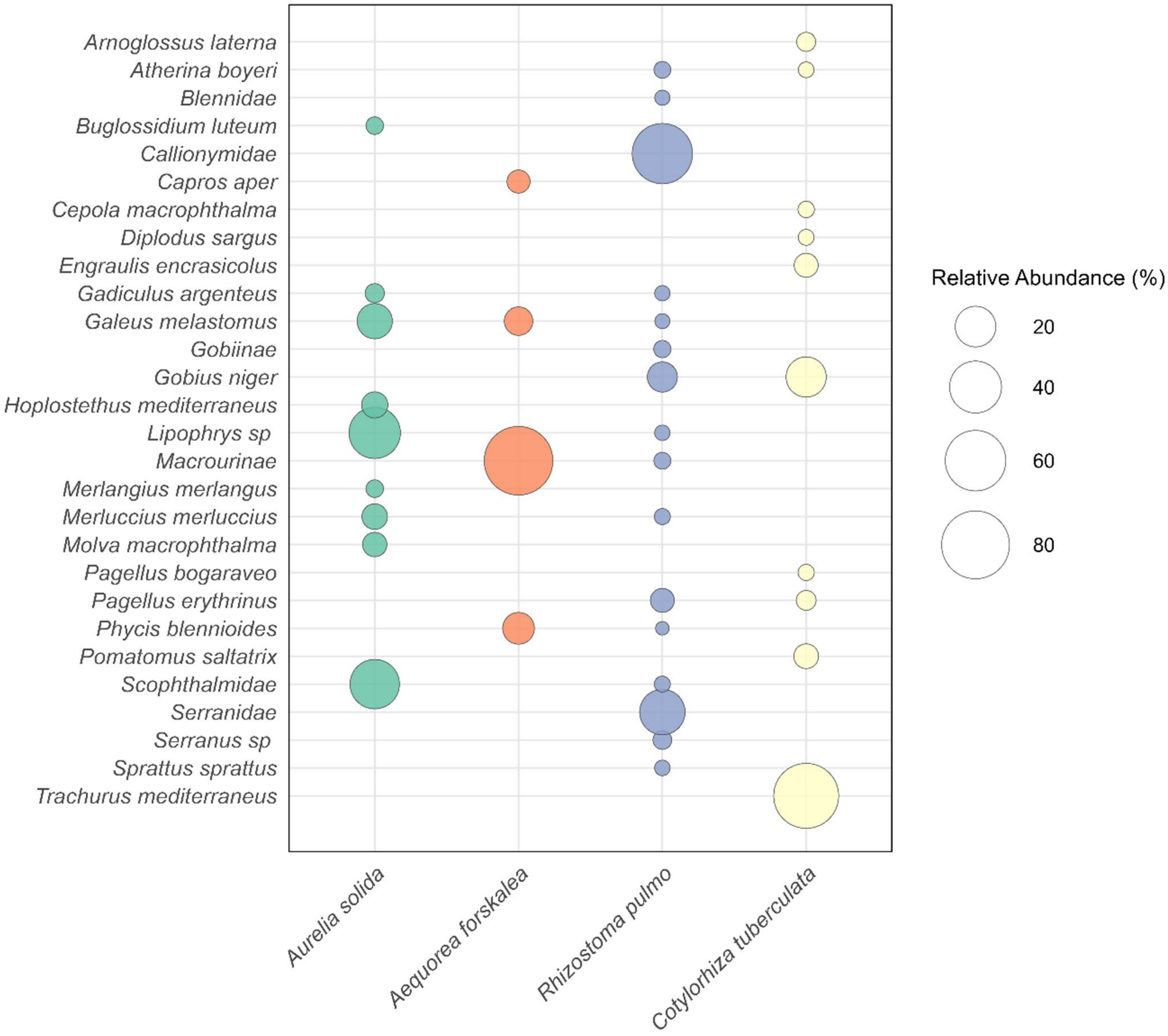

Fig. 5 Bubble plot showing the proportions of MOTUs for each of the four species of jellyfish

spawning activities on the Adriatic shelf, taking advantage of favourable conditions such as increased food availability and optimal temperatures (Jørgensen et al. 2008; Tsikliras et al. 2010). Even for species that undertake demersal spawning, larvae may then have pelagic stages, e.g. gobies have pelagic larval durations of 20–30 days (Beldade et al. 2007). Deeper-water species such as hake (*Merluccius merluccius*), which spawn year-round and occur also in the shallow Gulf of Trieste during the colder season, were not detected in our July sample, likely due to seasonal absence.

One of the MOTUs with the highest read counts belonged to the dragonet family (Callionymidae). Research on this family in the Mediterranean is limited (Dimarchopoulou et al. 2017), and little is known about their spawning behaviour or timing. In the Gulf of Trieste, between December 1986 and October 1988, eggs of *Callionymus maculatus* Rafinesque, 1810, *C. pusillus* Delaroche, 1809, and *C. risso* Lesueur, 1814 were recorded in February, June–November, and March–May, respectively (Mucchiut 1990). After four decades, spawning periods have likely shifted due to climatic variation; however, the peak in read counts observed in May suggests that Callionymidae in the Adriatic may currently spawn in spring.

The highest proportion of reads in the July samples of *C. tuberculata* came from the Mediterranean horse mackerel *(Trachurus mediterraneus*). The juvenile stage of this species is known to form associations with both *R. pulmo* and *C. tuberculata*, where the jellyfish act as passive hosts, providing protection from predators and serving as a potential food source through direct consumption or utilisation of captured plankton (Tilves et al. 2018; Mir-Arguimbau et al. 2019). It is intriguing that *T. mediterraneus* was detected only in the July samples, despite known associations with *R. pulmo*, and this may potentially, open interesting research avenues around the possible host choice for the juvenile stages of this species.

Conclusions

The detection of pelagic species common to the Northern Adriatic Sea, such as European sprat, hake, and Mediterranean horse mackerel, along with benthic species like dragonets, gobies and blennies, demonstrates the efficacy of jellyfish as eDNA samplers. However, the variance and stochasticity in the data set calls for a judicious choice of natural sampler species, and a collection of larger sample sizes. It is also of note that we did not develop a bespoke, optimised protocol for the retrieval of eDNA from jellyfish tissues and rather relied on previous protocols developed for other organisms (Harper et al. 2023). This may have contributed to inconsistent DNA yields, potentially leading to incomplete or biased representation of species in the metabarcoding dataset, and the observed high variance in MOTU detection among *A. solida*, *R. pulmo and A. forskalea* and *C. tuberculata* samples. Future studies should conduct periodic collections of jellyfish and surrounding water to explore seasonal patterns and possible trophic relationships, and undertake an evaluation of different extraction approaches. Nonetheless, with the implementation of more robust and efficient sampling and laboratory procedures, the use of jellyfish as natural samplers seem like a promising avenue for pelagic monitoring, especially in opportunistic contexts, in MPAs where invasive monitoring techniques are not applicable. and/or when other more established eDNA sampling procedures are too costly or logistically challenging.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-025-04784-4.

Author Contribution All authors contributed to the study conception and design. CM, VT, MA and GM organised sampling and/or sampled the jellyfish. Laboratory experiments, data collection and data analysis were conducted by CM, AVC, PS, SM and CSW. All authors interpreted the results. CM and CSW led the writing of the manuscript. VT and SM significantly contributed to editing the manuscript and critical review. All authors read and approved the final manuscript.

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Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information with reads mapped to species provided in Supplementary Table 1.

Declarations

Conflict of interest The authors have no competing interests to disclose.

Ethics approval This work had no ethical implications and no approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

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