



Continuous monitoring of marine metazoan diversity using sediment trap eDNA metabarcoding in the Ulleung Basin, East Sea, off the Korean Peninsula

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Abstract

Sediment trap environmental DNA (ST-eDNA) metabarcoding provides long-term, fine-scale monitoring of marine biodiversity, ideal for open-ocean regions where repeated sampling is challenging. By continuously collecting sinking particulate matter, ST-eDNA detects both persistent and transient species over time. Here, we used ST-eDNA metabarcoding to investigate fine-scale temporal changes in marine metazoan diversity in the Ulleung Basin, a pelagic region of the East Sea off the Korean Peninsula. Weekly sediment trap samples were collected at depths of 300 and 500 m between March and September 2019, leading to the identification of 178 species across 10 phyla and 23 classes. Arthropoda, Chordata, Mollusca, and Cnidaria were the dominant phyla. The mean number of species detected per week ranged from 10 to 71, with arthropods, chordates, and cnidarians showing peak occurrences in May. Species were categorized into (i) resident species, detected in ≥ 13 weekly samples, indicating persistent presence, and (ii) seasonal species, detected in 4–9 weekly samples, suggesting periodic occurrence. Approximately 50% of the species detected using ST-eDNA overlapped with those detected in Bulk-DNA (net-collected) and eDNA (seawater-filtered) surveys, while others were unique to ST-eDNA. These findings underscore the complementary role of ST-eDNA in capturing hidden and dynamic patterns of marine biodiversity.

Keywords continuous monitoring, sediment trap, environmental DNA (eDNA), marine metazoan diversity, DNA metabarcoding

Introduction

Marine biodiversity fluctuates in response to environmental changes and biological interactions (Butchart et al. 2010, Urban 2015), serving as a key indicator of ecosystem resilience, productivity, and stability (Butchart et al. 2010, Isbell et al. 2015). However, sustained biodiversity monitoring in oceanic regions remains logistically challenging due to harsh weather conditions and high operational costs (Benway et al. 2019, Suter et al. 2021). The Ulleung Basin, located in the East Sea off the Korean Peninsula, is oceanographically dynamic and ecologically important. Between 2006 and 2015, zooplankton surveys in this region were conducted at irregular intervals (1–3 times per year), providing preliminary insights into seasonal patterns (Kang et al. 2016). However, the low sampling frequency, combined with a reliance on morphology-based identifications, limited both temporal resolution and taxonomic breadth, hindering comprehensive biodiversity assessments. These challenges underscore the need for more sensitive and continuous monitoring approaches, par-

ticularly in biologically complex and physically dynamic ocean regions.

The mesopelagic zone (200–1000 m), where sunlight is insufficient for photosynthesis but still allows visual predation, represents a vast marine habitat encompassing ~31% of the global ocean volume (Sutton 2013, Reygondeau et al. 2018). This zone is considered a major reservoir of harvestable marine resources (Irigoien et al. 2014, Jennings and Collingridge 2015, Anderson et al. 2019) and hosts diverse zooplankton and midwater organisms that play a central role in the biological carbon pump (Robinson et al. 2010, Giering et al. 2014). Many of these organisms engage in diel vertical migration, ascending to the surface at night to feed and descending during the day to avoid visual predators, thereby contributing to the downward transport of organic carbon and energy (Hays 2003, Klevjer et al. 2016). Despite their ecological importance, mesopelagic communities remain poorly understood due to technological limitations and the predominance of sampling efforts focused on shallower layers (<200 m) (McIntyre 2010, Sutton et al. 2017). To enhance biodiversity assessments in

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this zone, there is a growing need for continuous and non-invasive monitoring approaches.

To address these limitations, sediment traps have garnered increasing attention as tools for biological monitoring. These instruments continuously collect sinking marine snow and organic particles, enabling the acquisition of time-series biological samples that reflect seasonal variation (Danovaro et al. 2017). Sediment traps are also well-suited for deployment in difficult-to-access oceanic and polar regions (Atherden et al. 2024). In addition to sinking particles, they often capture actively swimming organisms such as zooplankton and fish (often referred to as “swimmers”). These swimmer assemblages have been used to analyze zooplankton community structure in various regions, including the Northwest Pacific (Yokoi et al. 2018), the Mediterranean Sea (Danovaro et al. 2017), the Beaufort Sea, and the Franklin Bay, Canadian Arctic (Makabe et al. 2010, Makabe et al. 2016). However, conventional analyses based solely on swimmers often exclude the broader organic particle assemblages present in sediment trap samples, thus limiting biodiversity assessments. Moreover, morphological identification of swimmers can be hampered by damage to diagnostic traits and mixed debris that obscures key features.

To overcome the limitations of morphology-based species identification in mixed samples, DNA metabarcoding has gained traction as a powerful approach. This method amplifies DNA barcode regions—genetic loci that exhibit inter- and intraspecific variation—through high-throughput amplicon sequencing and identifies species by comparing sequences to a curated taxonomic reference library (Schloss et al. 2009, Bolyen et al. 2019). An alternative approach involves the whole-genome amplification of mixed-sample DNA, followed by the selective analysis of barcode regions to infer species-level diversity and quantify biomass (Kimmerling et al. 2018). DNA metabarcoding, which enables the simultaneous analysis of complex samples containing multiple species, has emerged as a key tool to overcome the limitations of single-organism barcoding (Deiner et al. 2017). It has been successfully applied to mixed zooplankton (Yang and Zhang 2020, Choi et al. 2024) and phytoplankton samples (Andersson et al. 2023) and the identification of contaminated single larva specimens (Park et al. 2024), as well as to the detection of fish species from environmental DNA (eDNA) without requiring physical specimens (McClenaghan et al. 2020). Additionally, this approach facilitates phylogenetic exploration of organisms that are difficult to distinguish morphologically, such as microeukaryotes and epi-endophytes (Bjorbaekmo et al. 2023). It is particularly useful for identifying cryptic and sibling species with subtle or indistinct phenotypes, thereby uncovering hidden biodiversity (Lindeque et al. 2013, Bucklin et al. 2021).

Applying eDNA metabarcoding to sediment trap samples, which include both swimmers and diverse organic particles, allows for species identification independent of morphological characteristics. eDNA metabarcoding utilizes DNA shed from biological materials such as excreta, cells, and tissue fragments to identify species present in an environment (Smart et al. 2015). By targeting taxonomically informative gene regions, this technique permits precise species identification even in samples where morphological characteristics are degraded (Deiner et al. 2017). Owing to its robustness and broad applicability, eDNA metabarcoding has been increasingly used to assess biodiversity in oceanic, deep-

sea, and polar environments (McClenaghan et al. 2020, Yang and Zhang 2020, Choi et al. 2024).

The East Sea, including the Ulleung Basin, is a semi-enclosed marginal sea situated between the East Asian continent and the Japanese Archipelago. It is a biologically dynamic region characterized by pronounced seasonal variation in the physical and chemical properties of seawater. In particular, the southwestern East Sea maintains high primary productivity due to the influence of the Tsushima Warm Current, coastal upwelling, and mesoscale physical processes such as eddies (Onitsuka et al. 2007, Hyun et al. 2009, Yoo and Park 2009). These hydrographic dynamics can strongly influence the spatiotemporal distribution of mesopelagic communities, including metazoans. Over the past 50–60 years, significant oceanographic changes have been observed in this region, including a 0.1°C–0.5°C increase in temperature within the upper 1000 m of the water column and the intensification of the oxygen minimum layer (Kim and Kim 1996, Kang et al. 2003). Such environmental shifts may alter the physiology, behavior, and community structure of metazoan organisms, potentially impacting the broader marine food web (Doney et al. 2012). These patterns underscore the importance of monitoring metazoan communities as indicators of long-term marine ecosystem change. Despite this, previous biodiversity assessments in the Ulleung Basin have relied primarily on net-based sampling, which is limited by low taxonomic resolution and inconsistent temporal coverage (Park and Choi 1997, Park et al. 1998, Kang et al. 2016). Moreover, the region's physical complexity—including eddies, seasonal fronts, and localized upwelling—poses challenges for tracking biological changes using conventional approaches (Park and Choi 1997, Park et al. 1998).

To address these gaps, this study applied sediment trap-based environmental DNA (ST-eDNA) metabarcoding in the Ulleung Basin. Therefore, in this study, we aimed to (i) characterize the high-resolution spatiotemporal dynamics of mesopelagic metazoan communities using sediment trap-derived eDNA (ST-eDNA) metabarcoding, and (ii) evaluate the feasibility of ST-eDNA as a long-term, complementary monitoring tool alongside conventional net-based (Bulk-DNA) and filtered seawater (eDNA) methods.

Materials and methods

Sample collection, processing, and preservation

To collect ST-eDNA time-series samples, sediment traps (NGK SMD-26S type) were deployed at two stations in the Ulleung Basin, East Sea off the Korean Peninsula: ST-I (37°00.00'N, 131°00.00'E; water depth 2371 m; trap depth 300 m) and ST-II (37°38.00'N, 131°21.50'E; water depth 2198 m; trap depth 500 m) (Fig. 1). Sediment traps were deployed and retrieved using the R/V Onnuri. A total of 26 samples per depth were planned through weekly collections from 25 March to 23 September 2019. Initially, sampling was designed at three depths (300, 1000, and 2000 m at ST-I; 500, 1000, and 2000 m at ST-II), but only the 300 and 500 m traps were successfully recovered due to environmental and operational limitations. The 500 m depth at ST-II was also selected to minimize potential disturbance from intense fishing activities in that region. In

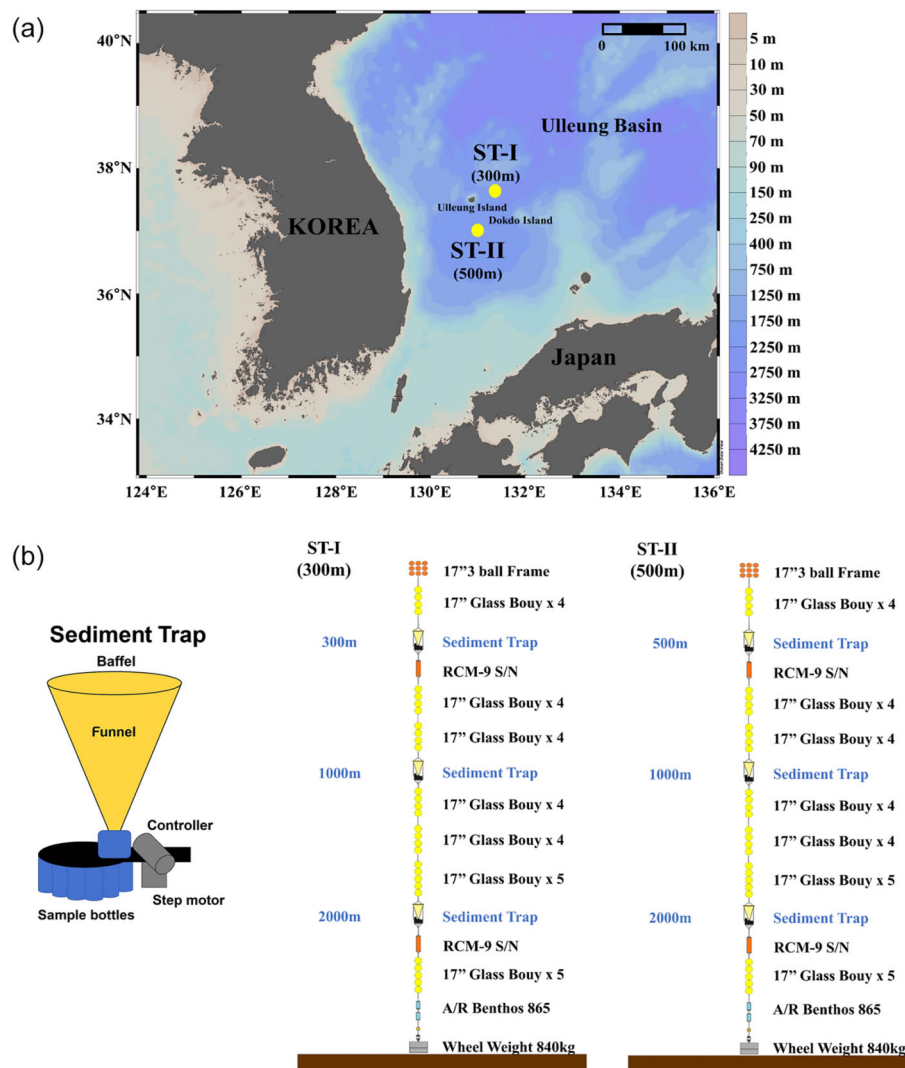


Figure 1 Overview of sampling locations, sediment trap configuration, and deployment setup for ST-eDNA collection in the Ulleung Basin. (a) Map showing the locations of sediment trap stations ST-I (300 m) and ST-II (500 m) in the Ulleung Basin, East Sea. The distance between the two stations is ~77 km. (b) Schematic representation of the sediment trap (NGK SMD-26S type) structure and its deployment configurations at ST-I and ST-II stations for ST-eDNA collection.

total, 23 samples were successfully recovered from ST-I (88% yield) and 19 from ST-II (73%) (Supplementary Table S1).

To preserve the sinking particle samples *in situ*, the trap bottles were pre-filled with a mixture of artificial seawater and 4% neutral buffered formalin prior to deployment. This preservation strategy follows widely adopted sediment trap protocols for long-term deployment and biological sample integrity (Knap et al. 1996). The total volume of the preservation solution was 500 ml per bottle, comprising 480 ml (96%) of artificial seawater with a salinity of 37.5 PSU and 20 ml (4%) of 4% neutral buffered formalin.

The final salinity of the mixed solution was adjusted to 36 PSU, slightly higher than the average surface salinity of the Ulleung Basin (~34 PSU), in order to create a density gradient that minimizes particle resuspension and promotes stable settling within the trap. Based on the known densities of the solution components—~1.030 g/ml for artificial seawater (37.5 PSU) and 1.08 g/ml for neutral formalin—the resulting density of the mixture was calculated to be ~1.0301 g/ml. This is higher than the ambi-

ent seawater density (1.025 g/ml at 34 PSU), providing a favorable physical condition that helps prevent overflow and reduces the risk of sample loss during deployment and recovery.

Genomic DNA extraction

To extract genomic DNA (gDNA), the formalin preservative was removed from each sample, after which a 10-ml aliquot of each ST-eDNA sample was transferred to a 50-ml centrifuge tube, and 30 ml of phosphate-buffered saline was added. The mixture was gently agitated for 2 min and centrifuged at $2000 \times g$ for 10 min. The supernatant was discarded, and this washing step was repeated twice. The resulting pellet (~100 μ l) was divided into two 2-ml microtubes, each containing a 5.0 mm stainless steel bead. Thereafter, the samples were homogenized using a TissueLyser II (Qiagen, Hilden, Germany) at 30 Hz for 3 min. gDNA was then extracted using a TIANamp Marine Animals DNA Kit (Tiangen Biotech, Beijing, China) according to the manufacturer's instructions. DNA was

eluted in 100 μ l of autoclaved, nuclease-free distilled water and stored at -20°C until further analysis.

PCR amplification and sequencing

To assess metazoan composition, extracted gDNA was subjected to metabarcoding targeting the mitochondrial cytochrome c oxidase subunit I (COI) gene. Libraries were constructed using a two-step polymerase chain reaction (PCR) approach. In the first PCR, a ~ 313 bp COI barcode fragment was amplified using the primers mICO1intF and jgHCO2198 (Leray et al. 2013). The 20- μ l first-round PCR reaction contained 2 μ l gDNA template, 10 μ l 2 $\times$ DNA Free-Multiplex Master Mix (CellSafe, Yongin-si, Korea), 0.4 μ l of each primer (10 pM), and 7.2 μ l nuclease-free water. Thermal cycling conditions for the first PCR were as follows: initial denaturation at 95°C for 5 min; 35 cycles of denaturation at 95°C for 30 s, annealing at 46°C for 30 s, and extension at 72°C for 1 min; and a final extension at 72°C for 10 min. A second, indexing PCR (to attach sample-specific indices) was performed with identical cycling conditions except for the annealing step, which was conducted at 55°C for 8 cycles (Amplicon et al. 2013). Final PCR products were verified on an agarose gel, purified using a QIAquick PCR Purification Kit (Qiagen), and quantified using a NanoDrop 1000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). Equimolar amplicon pools were further purified using AMPure XP beads (Beckman Coulter, Brea, CA, USA) and sequenced on an Illumina MiSeq platform (Illumina, San Diego, CA, USA).

Data processing and statistical analysis

All raw amplicon reads (42 samples in total) generated on the Illumina MiSeq were processed using QIIME 2 software (version 2023.5; Bolyen et al. 2019). Amplicon sequence variants (ASVs) were inferred from merged paired-end reads. We constructed an MZG COI reference library (MetaZooGene database, MZG) of 221 194 high-quality metazoan sequences by filtering a total of 602 592 sequences downloaded from MetaZooGene DB (Mode-C, release MZGdb-v2023-10) following the approach of Choi et al. (2024). ASVs matching this COI reference library at $\geq 99\%$ identity were retained; others were excluded as likely non-metazoan in origin (e.g. bacterial or fungal sequences). ASVs with fewer than 10 reads were removed to minimize cross-contamination and false positives (Suter et al. 2021, Choi et al. 2024, Zhang et al. 2024). Taxonomic assignments for ASVs followed the World Register of Marine Species (WoRMS) database (<http://www.marinespecies.org>). Duplicate ASVs identified as the same species were merged. Biogeographic and depth distribution data for species were obtained from FishBase, the Catalog of Fishes, and the Marine Biodiversity Institute of Korea (Fricke 2021, Froese and Pauly 2025, MABIK 2025). For downstream analyses, read counts were log-transformed [$\log(x + 1)$]. Temporal trends in metazoan diversity and the dominant phyla (Arthropoda, Chordata, Cnidaria, and Mollusca) at each depth (ST-I and ST-II) were visualized using weekly bar graphs and associated standard deviations. Presence-absence patterns were illustrated using heatmaps. Based on weekly occurrence data, we categorized representative taxa as either resident or seasonal species. Resident species were defined as those appearing in ≥ 13 weekly samples, including at least one instance of 4–9 consecutive weeks of detection. Seasonal species were defined as those recorded in ≤ 9 samples, with at least one

continuous detection period of 4–8 weeks. To compare metazoan taxonomic composition between depths, we analyzed 18 time-matched sample pairs (one from 300 m and one from 500 m in the same week; see [Supplementary Table S2](#)). Venn diagrams were used to illustrate shared and unique taxa between depths (Oliveros 2007). To evaluate the reliability of ST-eDNA results, we compared the ST-eDNA taxonomic profiles with those from Bulk-DNA (200 μ m mesh) and eDNA (seawater filtered, 0.45- μ m pore size) collected from the Ulleung Basin during summer 2019 (Choi et al. 2024). The comparison dataset comprised 79 samples in total, including 10 Bulk-DNA samples from 10 stations (collected from depths of 0–600 m), 44 eDNA samples from the same 10 stations (0–2100 m), and 25 ST-eDNA samples (13 from 300 m and 12 from 500 m depths) ([Supplementary Fig. S1](#)). Bray–Curtis dissimilarity matrixes were used for non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM). NMDS was run with 123 iterations, and ANOSIM was performed with 999 permutations to test for differences between groups (Clarke 1993). Taxonomic differences among sample types were assessed using Wilcoxon rank-sum tests (Wilcoxon 1992), with Benjamini–Hochberg correction applied to account for multiple comparisons (Benjamini and Hochberg 1995).

Results

Metazoan ASV identification

In total, 15 832 522 paired-end reads were generated from the ST-eDNA samples (ranging from 308 784 to 514 092 reads per sample; average $376\,965 \pm 46\,736$; [Supplementary Table S1](#)). After quality filtering, 633 965 reads matched the MZG COI reference library. ASVs with fewer than 10 reads were excluded. The final dataset contained 675 metazoan ASVs, with 5–139 ASVs per sample (average 31 ± 21 ; [Supplementary Table S3](#)).

A total of 178 metazoan taxa were identified from the 42 ST-eDNA time-series samples, based on 623 746 high-quality reads that matched the MZG COI reference library at $\geq 99\%$ identity. These taxa comprised 158 identified to species level, 18 to genus, and one each to family and order, spanning 10 phyla, 23 classes, 47 orders, 106 families, and 148 genera. The dominant phyla were Arthropoda (75 taxa; 42.1% of total), Chordata (42; 23.6%), Mollusca (24; 13.5%), and Cnidaria (16; 9.0%), while the remaining 6 phyla together accounted for 21 taxa (11.8%) ([Table 1](#)).

Temporal dynamics of major phyla

Time-series metabarcoding analysis of ST-eDNA collected from 300- and 500-m depths revealed distinct temporal shifts in metazoan diversity from March to September 2019 ([Fig. 2a](#)). The number of species detected per week ranged from 11 to 71, with a monthly mean of 23 ± 13 species.

During the early sampling period (late March, weeks 17–19), the number of detected species remained relatively low (11–17 species). This was followed by a sharp increase, peaking at 71 species in week 23 (early May). After this peak, species richness declined rapidly, reaching a low in week 28 (mid-June). From week 29 onward (late June through September), the number of species stabilized and fluctuated moderately between approximately 16 and 25 species per week.

Table 1 Metazoan diversity profile based on ST-eDNA metabarcoding at 300 and 500 m depths in the Ulleung Basin, East Sea (March–September 2019).

Phylum	Class	Order	Family	Genus	Species	%
Arthropoda	Thecostraca	1	4	6	6	3.4
	Ostracoda	1	1	2	2	1.1
	Malacostraca	3	8	12	14	7.9
	Copepoda	3	20	33	49	27.5
	Branchiopoda	2	2	3	4	2.2
Chordata	Thaliacea	1	1	1	1	0.6
	Asciacea	1	1	1	1	0.6
	Actinopterygii	6	25	37	40	22.5
Mollusca	Gastropoda	5	8	8	12	6.7
	Cephalopoda	1	2	3	3	1.7
	Bivalvia	3	6	8	9	5.1
Cnidaria	Scyphozoa	2	2	2	2	1.1
	Hydrozoa	4	10	12	12	6.7
	Anthozoa	2	1	1	2	1.1
Other 6 Phylum	9 Class	12	15	19	21	11.8
Total	23	47	106	148	178	100

Values represent the number of taxa identified at each taxonomic rank, with percentages indicating their proportion relative to the total.

Temporal patterns varied among the four dominant phyla (Fig. 2b–e). Arthropoda maintained a relatively consistent number of species throughout the study period, except for a pronounced spike in week 23 when the number of arthropod species was 2–3-fold higher than that on other dates. Chordata showed a rapid increase starting in April, peaking in week 23, and remained high until week 27 before declining. Cnidaria and Mollusca generally exhibited stable species numbers, although Cnidaria displayed a distinct spike in week 23. These results suggest that early May (around week 23) represents a key ecological transition period in the pelagic ecosystem of the Ulleung Basin.

Metazoan species richness at 300 m sharply increased from March to a peak of 71 species in early May, then stabilized with moderate fluctuations (mean: 18.1 ± 8 , June–September) (Supplementary Fig. S2a). Arthropoda, Chordata, and Cnidaria dominated during spring, particularly in early May (May_1, week 23) (Supplementary Fig. S2b–d), while Mollusca exhibited relatively higher richness in September (Supplementary Fig. S2e). At 500 m, metazoan species richness gradually increased to a peak of 27 species in mid-August and remained stable (mean: 21.3 ± 4.4 , August–September) (Supplementary Fig. S3a). Arthropoda and Chordata remained relatively stable throughout the study period (Supplementary Fig. S3b–c), whereas Cnidaria and Mollusca showed a slight increasing trend from August to September (Supplementary Fig. S3d–e).

Temporal occurrence patterns and species classification

Time-series analyses of species presence/absence across the four dominant phyla revealed diverse and structured weekly occurrence patterns (Supplementary Fig. 4–7). Detected species fell into three broad categories: (i) taxa with high frequency and extended occurrence over the sampling period, (ii) taxa with lower frequency but continuous presence over shorter durations, and

(iii) sporadically detected taxa without clear temporal continuity. Based on both detection frequency and consecutive occurrence duration, we identified 26 metazoan taxa that appeared in ≥ 4 consecutive weekly samples.

Among these, 9 species were classified as resident species, as they were detected in 13 or more of the 24 successfully collected weekly samples out of the planned 26 weeks, and typically persisted throughout most of the monitoring period (from early March to early September). For example, *Euphausia pacifica*, *Paracalanus parvus*, *Discoconchoecia pseudodiscophora*, *Paraecheta* sp. (Supplementary Fig. 4), and *Agalma elegans* (Supplementary Fig. 6) were consistently observed across nearly the entire time series, indicating high site fidelity in the Ulleung Basin.

In contrast, 17 species were classified as seasonal, appearing in 4–9 weekly samples, each with at least one continuous occurrence period of 4 or more weeks. *Nemopilema nomurai* (Supplementary Fig. 6), along with *Atlanta californiensis* and *Todarodes pacificus* (Supplementary Fig. 7), were primarily detected during summer or late-season weeks, indicating seasonal influxes or migratory behavior (see Supplementary Table S4 for detailed occurrence periods).

Depth-based comparison of metazoan communities

From 18 paired ST-eDNA samples collected simultaneously at 300 and 500 m, a total of 138 metazoan species were identified (Supplementary Table S2). Among these, 108 species were detected at 300 m and 93 at 500 m, with 63 species (45.7%) shared between the two depths (Fig. 3a). Depth-exclusive species included 45 taxa (32.6%) unique to 300 m and 30 (21.7%) unique to 500 m. Commonly detected taxa at both depths included Copepoda (24 species), Actinopterygii (7), Malacostraca (7), Gastropoda (4), and Bivalvia (5), indicating substantial overlap in the major taxonomic groups (Fig. 3b).

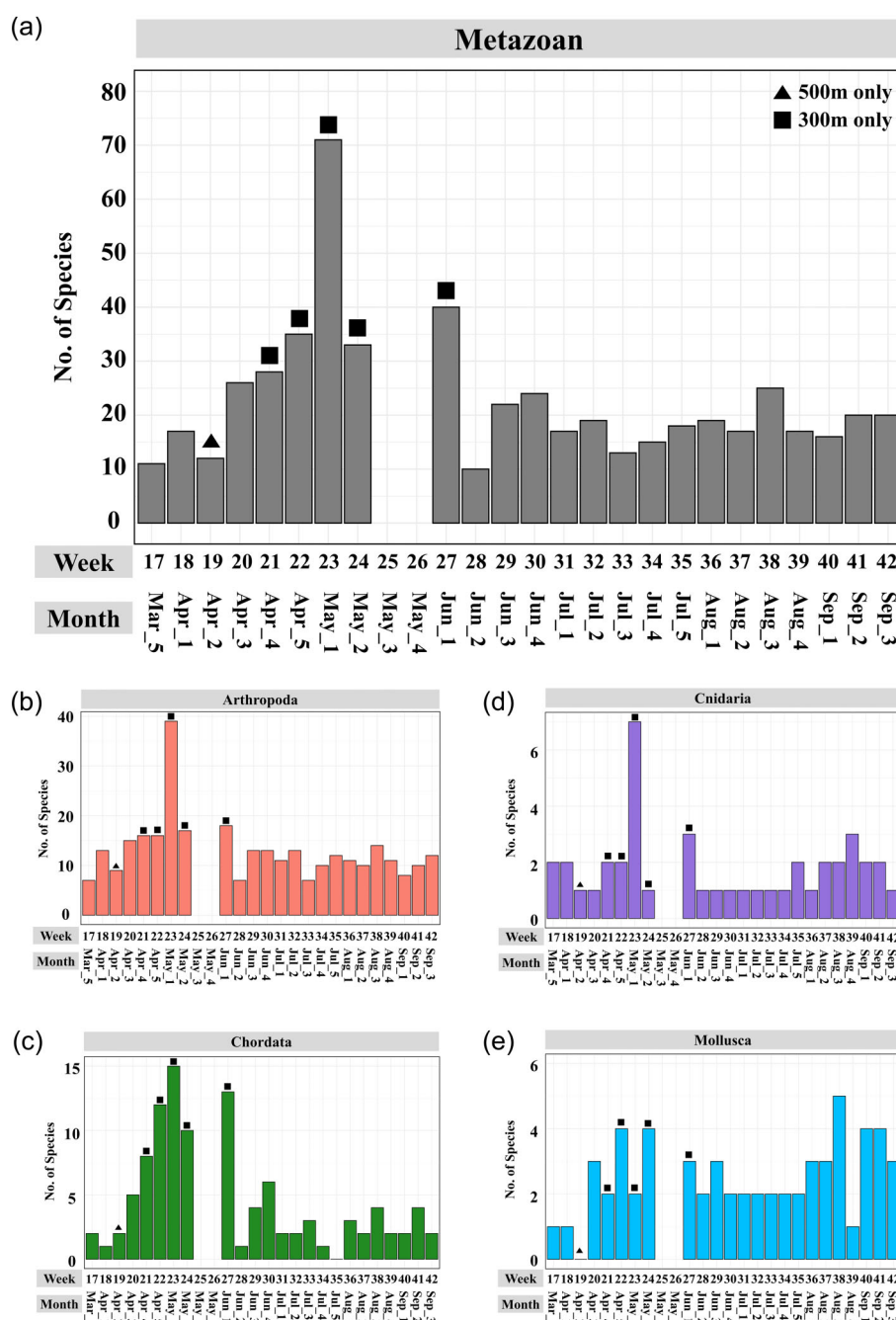


Figure 2 Seasonal variation in the average number of metazoan species and dominant phyla detected using ST-eDNA at 300- and 500-m depths in the Ulleung Basin (March–September 2019). ▲ indicates species detected only at 500 m; ■ indicates species detected only at 300 m. (a) Metazoan; (b) Arthropoda; (c) Chordata; (d) Cnidaria; and (e) Mollusca.

At 300 m, the dominant classes were Actinopterygii (25 species), Copepoda (35), Gastropoda (8), Malacostraca (10), and Bivalvia (6). Of the 45 exclusive species at 300 m, Actinopterygii accounted for the largest proportion (40%), followed by Copepoda (24.4%) and Gastropoda (8.9%). These 300-m-exclusive actinopterygians included epipelagic fish such as *Thryssa kammalensis*, *Paracentropogon rubripinnis*, and *Tarphops elegans* (Supplementary Table S5). Gastropods were also frequently detected at 300 m, whereas most copepod species at this depth showed sporadic occurrences (Supplementary Table S6).

At 500 m, the dominant classes included Copepoda (31 species), Actinopterygii (11), Malacostraca (8), Bivalvia (8), Gastropoda (7), and Hydrozoa (5). Among the 30 species exclusive to 500 m, Copepoda (23.3% of 500 m-exclusive taxa) and Actinopterygii (13.3%) were the most abundant groups, while other groups (e.g. Bivalvia, Polychaeta, and Hydrozoa) each contributed roughly 10%. Notably, deep-sea actinopterygians such as *Aptocyclus ventricosus* and *Careproctus rastrinus* were detected at low frequencies at 500 m alongside pelagic species such as *Trachurus japonicus*. Hydrozoan *Agalma elegans* and scyphozoan

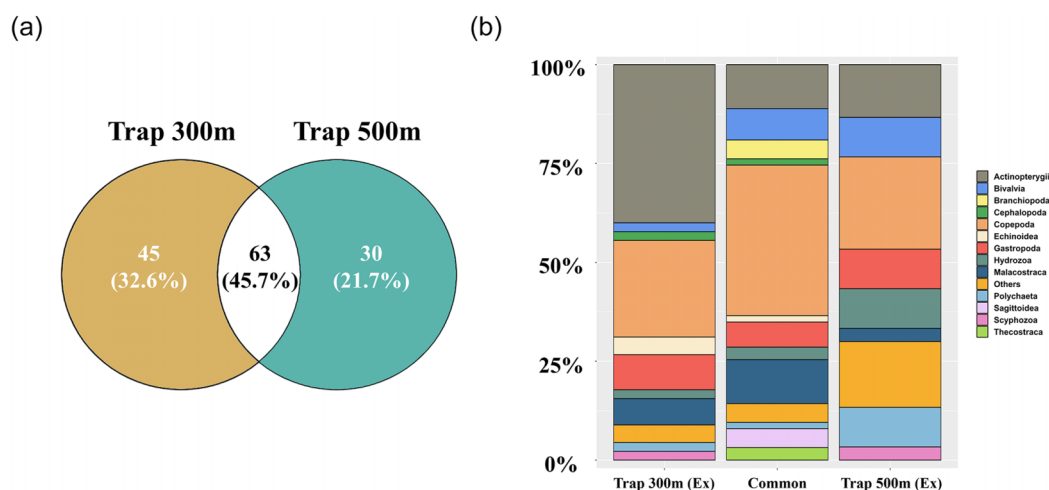


Figure 3 Comparison of metazoan species composition between 300- and 500-m depths in the Ulleung Basin (March–September 2019). (a) Venn diagram showing shared and unique species. (b) Stacked bar plot showing species composition by depth: “Common” (shared species), “Trap 300 m (Ex)” (exclusive to 300 m), and “Trap 500 m (Ex)” (exclusive to 500 m).

N. nomurai (jellyfish) were frequently observed at 500 m from July to September (Supplementary Table S7).

Comparison of ST-eDNA with net-collected DNA (Bulk-DNA) and sea water-filtered eDNA (eDNA)

To assess the reproducibility and complementary detection capability of sediment trap eDNA, we compared the metazoan species composition revealed by ST-eDNA with those from Bulk-DNA and eDNA collected in the Ulleung Basin during overlapping summer periods (June–August between 2019 and 2021). ST-eDNA time-series sampling (25 samples) detected 121 metazoan species, while Bulk-DNA (10 samples) and eDNA (44 samples) identified 175 and 140 species, respectively (Supplementary Table S8). Approximately half of the species detected by ST-eDNA overlapped with those found in Bulk-DNA or eDNA (Figs 4 and 5), supporting its consistency with conventional methods.

In addition, ST-eDNA uniquely identified 67 species (32.4%) not detected in eDNA, and 60 species (25.5%) not found in Bulk-DNA (Figs 4 and 5). These differences were further reflected in the community structure, as visualized by NMDS ordination based on Bray–Curtis dissimilarity (Fig. 6). Statistical tests confirmed significant differences in taxonomic composition ($P < 0.05$, Wilcoxon rank-sum tests with Benjamini–Hochberg correction), particularly for Copepoda, Gastropoda, Bivalvia, Hydrozoa, and Sagittoida (arrow worms), which exhibited distinct detection patterns (Supplementary Table S9).

Discussion

eDNA metabarcoding has emerged as a powerful tool for assessing marine biodiversity, primarily using filtered seawater samples to detect a broad range of metazoan taxa (Easson et al. 2020, Feng et al. 2022, Mo et al. 2024). In the present study, we applied eDNA metabarcoding to a novel substrate—ST-eDNA—marking the first time-series application of this method in a deep-sea pelagic envi-

ronment (Fig. 1). Weekly sampling over a 7-month period from two depths (300 and 500 m) in the Ulleung Basin yielded 178 metazoan taxa spanning 10 phyla and 106 families (Fig. 2, Table 1).

Formalin, which was used as a preservative in this study, is known to induce DNA cross-linking, fragmentation, and base modifications such as C-to-T deamination (Guo et al. 2022), and its damaging effects on DNA have been reported to be temperature-dependent (Berrino et al. 2020). These effects may act as potential sources of quality degradation in eDNA-based analyses. Nevertheless, the ST-eDNA samples analyzed in this study were collected at depths of 300 and 500 m, where seawater temperature remains stable at $\sim 0^{\circ}\text{C}$ – 1°C throughout the year (KORDI 2008). Under such cold and stable thermal conditions, temperature-dependent DNA degradation associated with formalin fixation is likely to have been limited. Consistent with this interpretation, the proportion of metazoan-derived valid sequences recovered from ST-eDNA samples averaged $\sim 3.9\%$, which is comparable to values reported in previous seawater-based eDNA studies conducted in the same region ($\sim 5.4\%$) (Choi et al. 2024). These results indicate that, despite the potential for formalin-induced DNA damage, the ST-eDNA data obtained in this study fall within the range of eDNA signals commonly observed in marine environments. Nearly half of the species identified using ST-eDNA were also detected in Bulk-DNA and eDNA samples collected during similar times and locations (Figs 4 and 5), further supporting the reproducibility and ecological validity of this approach. In addition, ST-eDNA recovered many unique taxa, particularly fast-swimming or migratory species such as Actinopterygii and Cephalopoda, which are often underrepresented in conventional plankton surveys. However, further validation is needed to assess detection efficiency relative to targeted methods (e.g. trawls and acoustics). These findings highlight ST-eDNA’s potential as a complementary, temporally resolved method to enhance the sensitivity and taxonomic breadth of marine biodiversity monitoring.

One of the key advantages of ST-eDNA is its high temporal resolution, which enables the detection of transient and seasonally dynamic taxa often missed by infrequent “snapshot” surveys. In our study, the weekly time-series from March to September revealed a clear seasonal turnover in metazoan communities, with

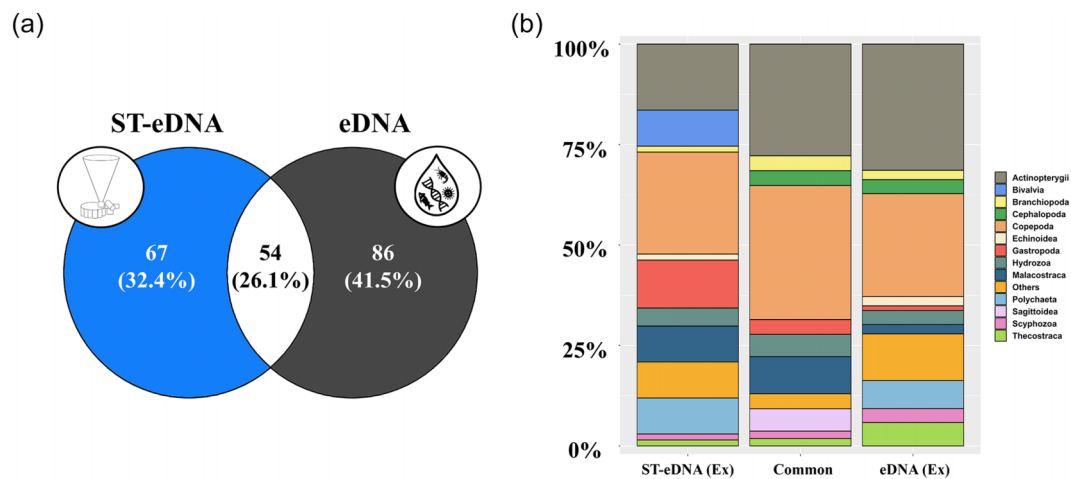


Figure 4 Comparison of metazoan species composition between ST-eDNA and eDNA in the Ulleung Basin (June–August). (a) Venn diagram showing shared and unique species. (b) Stacked bar plot showing the composition of common and exclusive species: “Common” (shared), “ST-eDNA (Ex)” (exclusive to ST-eDNA), and “eDNA (Ex)” (exclusive to eDNA).

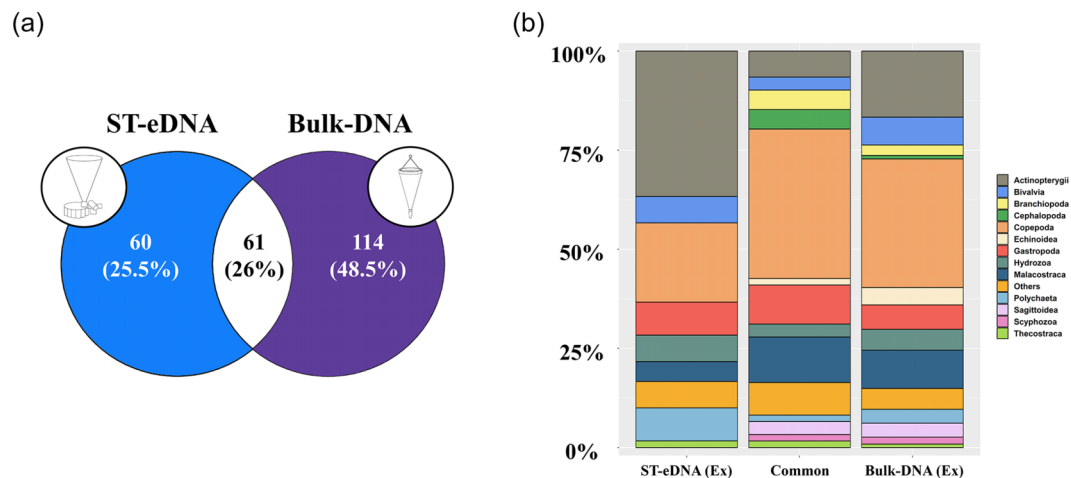


Figure 5 Comparison of metazoan species composition between ST-eDNA and Bulk-DNA in the Ulleung Basin (June–August). (a) Venn diagram showing shared and unique species. (b) Stacked bar plot showing the composition of common and exclusive species: “Common” (shared), “ST-eDNA (Ex)” (exclusive to ST-eDNA), and “Bulk-DNA (Ex)” (exclusive to Bulk-DNA).

total species richness peaking sharply in early May and then stabilizing through the summer (Fig. 2). This pattern aligns with long-term plankton survey data from the East Sea showing that biodiversity increases sharply in spring (Kang et al. 2016), though our weekly sampling provided a much more detailed view of this transition.

Based on occurrence frequency and continuity, we identified 9 resident species that persisted throughout the monitoring period and 17 seasonal species with localized detection peaks (Supplementary Figs 4–7; Supplementary Table S4). The resident species included widespread copepods (e.g. *Paracalanus parvus*, *Acartia omorii*), pelagic ostracods (e.g. *D. pseudodiscophora*), and other ecologically important crustaceans (e.g. *E. pacifica*, *Themisto japonica*). Among these, species such as *E. pacifica* (Chavtur and Bashmanov 2015, Lee et al. 2021), *D. pseudodiscophora* (Chavtur and Bashmanov 2015), and *P. parvus* (Park et al. 1998, Kang et al. 2016) have been previously reported as resident species in the East Sea. This suggests that time-series eDNA metabarcoding of

sediment trap samples is particularly effective for detecting resident species in open-ocean environments. The summer warming seasons may have triggered an influx of warm-water pelagic taxa into the Ulleung Basin, including *A. californiensis*, *N. nomurai*, and *T. pacificus*. Similarly, the late-summer appearance of *T. pacificus* (August–September) aligns with its known autumn-spawning migration into the East Sea from southern spawning grounds (Kim 1995, Moon et al. 2018). Together, these results demonstrate that ST-eDNA not only reflects local biodiversity but can also capture seasonal migrations and community responses to oceanographic variability.

Despite differences in sample type and collection strategy, our results show substantial overlap between ST-eDNA and conventional approaches (Bulk-DNA and eDNA). Approximately half of the species detected in ST-eDNA were also recovered by at least one of the other methods (Figs 4 and 5), indicating a strong level of reproducibility and taxonomic concordance. The dominance of Copepoda and Actinopterygii across all approaches

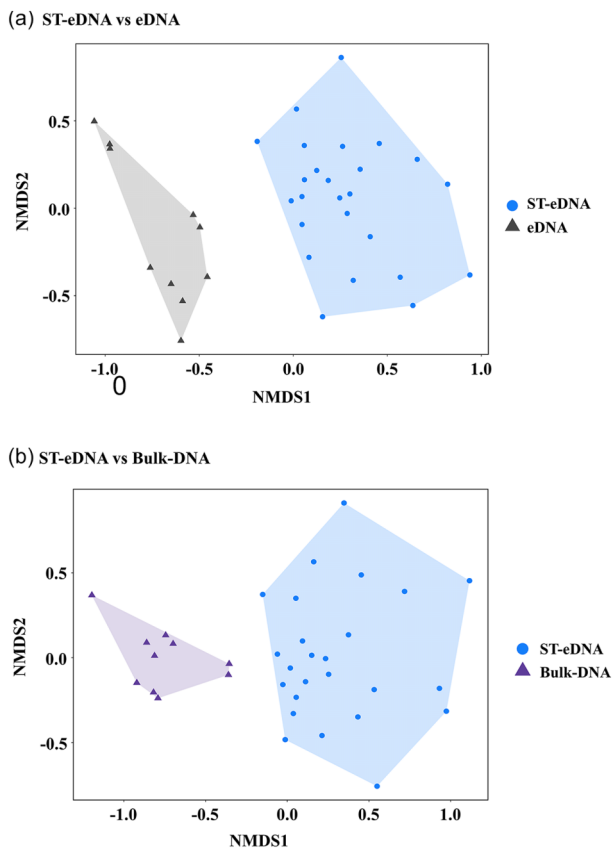


Figure 6 NMDS plots based on Bray–Curtis dissimilarities illustrating metazoan community differences by sampling method in the Ulleung Basin (June–August 2019). ANOSIM was used to evaluate statistical significance. (a) Comparison between ST-eDNA and eDNA samples, showing distinct clustering (stress = 0.21; global $R = 0.752$; $P < 0.01$). (b) Comparison between ST-eDNA and Bulk-DNA samples, also revealing clear community separation (stress = 0.19; global $R = 0.6313$; $P < 0.01$).

further supports the consistency of the core pelagic community structure.

At the same time, ST-eDNA revealed unique taxa not observed in the Bulk-DNA or eDNA datasets, including certain nektonic and benthic species such as *T. elegans*, *C. rastrinus*, and *A. elegans* (Figs 4 and 5). These differences likely reflect the methodological biases of the respective collection methods. For example, the coarse mesh size (200 μm) of nets used for Bulk-DNA may underestimate small or fragile organisms, while eDNA captures only free-floating particles at a single time point (Choi et al. 2024). In contrast, ST-eDNA passively accumulates sinking biological material over time, integrating signals from a broader spatiotemporal window. Moreover, the longer residence time of organic matter in sediment trap collectors likely enhances the detection of low-abundance or infrequently occurring species. Interestingly, the sharp rise in species richness in early May coincided with an anomalously high ($+3^{\circ}\text{C}$) sea-surface temperature, likely driven by an intensification of the Tsushima and East Korea Warm Currents (NIFS 2019).

Notably, despite the initial design to include sediment traps at mesopelagic and bathypelagic depths (1000 and 2000 m), successful sample recovery was limited to shallower traps (300 m at ST-I and 500 m at ST-II). This outcome likely reflects the challenging hydrographic conditions of the Ulleung Basin, where strong deep

currents, steep bathymetry, and mesoscale features such as eddies and internal waves hinder stable trap deployment and retrieval at greater depths. These physical constraints underscore the logistical challenges of long-term biological sampling in deep-ocean settings. Nevertheless, the high recovery yield at intermediate depths (73%–88%) demonstrates the practical feasibility of ST-eDNA application in mesopelagic zones under suitable conditions.

The applicability of the ST-eDNA approach should be evaluated in relation to its relative cost and logistical complexity compared with other eDNA sampling strategies. Seawater-based eDNA sampling typically requires repeated field access, large-volume water collection, filtration equipment, and substantial personnel effort, which can impose considerable operational burdens in offshore and deep-sea environments. In contrast, sediment traps enable the passive accumulation of particle-associated biological signals over extended periods following a single deployment, offering the potential to reduce the frequency of field visits and associated labor requirements in long-term monitoring programs.

However, these advantages are contingent upon stable trap operation and successful sample recovery. Under conditions of elevated particle flux or strong physical disturbance, the risk of sample loss may increase, emphasizing the need for carefully designed operational strategies that account for preservative composition, artificial seawater salinity, and physical conditions at the deployment depth. In this study, stable recovery rates were achieved at depths of 300–500 m, which should be interpreted not as an upper limit for ST-eDNA application, but rather as the depth range in which operational stability has been empirically demonstrated at present. With further optimization of trap design, preservative formulation, and site-specific deployment strategies, the application of ST-eDNA approaches may be extended progressively to greater depths in future studies.

Overall, our findings emphasize that ST-eDNA is not a replacement for traditional snapshot sampling approaches, but rather a valuable complement. When used in combination, these methods can provide a more holistic view of marine biodiversity, encompassing both persistent components and transient, episodic contributions to the metazoan community. The broader implications of our findings lie in the potential application of ST-eDNA for long-term biodiversity monitoring in offshore or deep-sea environments where conventional sampling is logistically difficult or cost-prohibitive. The ability of ST-eDNA to passively collect and preserve biological material over extended periods allows for retrospective and continuous monitoring of marine ecosystems, even in the absence of frequent field visits.

Conclusion

This study demonstrates the feasibility and effectiveness of ST-eDNA for high-resolution, time-series monitoring of marine metazoan biodiversity. Through weekly sampling over a 7-month period at 300- and 500-m depths in the Ulleung Basin, we identified 178 metazoan taxa, including both resident and seasonal species across the major phyla. Comparisons with conventional approaches (Bulk-DNA and eDNA) revealed that ST-eDNA is not only consistent with traditional methods in detecting dominant taxa such as Copepoda and Actinopterygii but also complements them by detecting additional species that previously went

undetected. The passive, continuous nature of ST-eDNA sampling enables the detection of ecologically significant patterns, including seasonal community shifts and responses to hydrographic anomalies. Our results underscore the value of ST-eDNA as a sensitive and integrative tool for biodiversity monitoring in offshore and deep-sea environments. Combined with existing eDNA methods, ST-eDNA offers a scalable and complementary approach for comprehensive marine ecosystem assessment under changing environmental conditions.

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Author contributions

Jae Ho Choi (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Methodology [lead], Software [lead], Writing – original draft [lead], Writing – review & editing [lead]), Young Il Kim (Investigation [equal], Funding acquisition [equal], Project administration [equal]), Sung Kim (Conceptualization [equal], Data curation [equal], Funding acquisition [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Writing – review & editing [equal]), Choong-gon Kim (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal]).

Supplementary material

Supplementary material is available at *ICES Journal of Marine Science* online.

Conflicts of interest

The authors declare no competing interests.

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Data availability

The raw sequence datasets generated and analyzed in this study are available in the NCBI Sequence Read Archive (SRA) under accession number PRJNA1221646.

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