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ORIGINAL ARTICLE

Structure of the zooplankton community and trophic interactions in a pelagic system influenced by internal island-trapped waves

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Abstract: Zooplankton plays a crucial role in marine ecosystems, serving as an important link between primary producers and higher trophic levels. This study investigates zooplankton community structure and distribution in the area influenced by physical phenomena of internal island-trapped waves (ITWs) in the southern Adriatic. To assess the responses of the different zooplankton groups to ITWs, high-frequency sampling was carried out in July 2022. The results revealed pronounced shifts in zooplankton community composition, with taxa such as *Evadne spinifera*, *Oithona* spp., and *Paracalanus parvus parvus* exhibiting the most dynamic responses to nanophytoplankton availability. *Centropages typicus* and *Temora stylifera* showed depth-specific distribution patterns, reflecting their feeding preferences for microphytoplankton and adaptability in food sources. Organisms such as tintinnids, copepod nauplii, and radiolarians responded strongly to ITWs, while *Oikopleura longicauda* responded with a time lag, suggesting complex trophic interactions influenced by both biological and physical factors. These findings highlight the response of zooplankton community structure to specific physical dynamics, which likely influence trophic interactions and may affect the efficiency of energy transfer in the pelagic food web. The study emphasises the importance of high frequency sampling for capturing the fine-scale ecological processes that determine zooplankton dynamics in physically dynamic environments.

***Keywords*:** pelagic ecosystem; microzooplankton; mesozooplankton; high-resolution sampling; Adriatic Sea

Sažetak: STRUKTURA ZOOPLAKTONSKE ZAJEDNICE I TROFIČKE INTERAKCIJE U PELAGIJSKOM SUSTAVU POD UTJECAJEM UNUTARNJIH VALOVA VEZANIH UZ OTOK. Zooplankton ima ključnu ulogu u morskim ekosustavima jer djeluje kao važna poveznica između primarnih proizvođača i viših trofičkih razina. Ovo istraživanje proučava strukturu i raspodjelu zooplanktonske zajednice na području pod utjecajem fizikalnog fenomena unutarnjih valova vezanih uz otok (engl. Internal Island-Trapped Waves, ITWs) u južnom Jadranu. Radi procjene odgovora različitih skupina zooplanktona na ITWs, provedeno je učestalo uzorkovanje tijekom srpnja 2022. godine. Dobiveni rezultati ukazuju na izražene promjene u sastavu zooplanktonske zajednice, pri čemu su taksoni poput *Evadne spinifera*, *Oithona* spp. i *Paracalanus parvus parvus* pokazali najizraženije reakcije na dostupnost nanofitoplanktona. *Centropages typicus* i *Temora stylifera* pokazali su specifične obrasce vertikalne raspodjele, što odražava njihove prehrambene preferencije prema mikrofitoplanktonu i sposobnost prilagodbe različitim izvorima hrane. Organizmi poput tintinida, kopepodnih nauplija i radiolarija snažno su reagirali na prisutnost ITWs dok je *Oikopleura longicauda* pokazala vremenski odgođen odgovor, što upućuje na složene trofičke interakcije pod utjecajem kombinacije bioloških i fizikalnih čimbenika. Ovi nalazi ističu osjetljivost sastava zooplanktonske zajednice na lokalnu fizikalnu dinamiku, koja vjerojatno modulira trofičke odnose te može utjecati na učinkovitost prijenosa energije unutar pelagičke hranidbene mreže. Studija naglašava važnost visoke vremenske rezolucije uzorkovanja za razumijevanje fine dinamike ekoloških procesa koji oblikuju ponašanje zooplanktona u fizički promjenjivim morskim okolišima.

***Ključne riječi*:** pelagijski ekosustav; mikrozooplankton; mezozooplankton; uzorkovanje visoke rezolucije; Jadransko more

INTRODUCTION

As a key regulator in marine ecosystems, zooplankton link primary producers to organisms at higher trophic levels, significantly influencing ecosystem functioning. Their distribution, community structure, and feeding behaviour are shaped by environmental factors, including physical oceanographic processes (Zhao *et al.*, 2022). In oligotrophic environments such as the southern Adriatic Sea, where nutrient availability is limited, understanding the drivers of zooplankton dynamics is essential for assessing ecosystem productivity and health.

Planktonic consumers are operationally divided into two main groups based on size: microzooplankton (<200 µm), which includes protists such as ciliates and dinoflagellates and juvenile metazoans, and mesozooplankton (>200 µm), which primarily consists of metazoans such as copepods and cladocerans (Stoecker *et al.*, 1996; Paffenhöfer, 1998; Quevedo and Anadón, 2000). Considering the feeding behaviour of zooplankton, the

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community can generally be described as omnivorous, with specific herbivorous, carnivorous, or detritivorous constituents. These feeding strategies are reflected in the dominant taxonomic groups, such as copepods, cladocerans, chaetognaths, pteropods, planktonic tunicates, and gelatinous zooplankton, including siphonophores and hydrozoan medusae.

Preferences for the prey further complicate the feeding limitations to size classes generally divided into pico-feeding, nano-feeding, micro-feeding, and grazing (Hunt *et al.*, 2017). For example, an omnivorous calanoid copepod like *Centropages typicus* feeds actively on nano-size algae or yolk-sac fish larvae (Calbet *et al.*, 2007), and an omnivorous unselective cyclopoid copepod *Oithona similis* feeds on copepod nauplii, marine snow aggregates, or faecal pellets discarded by larger copepods such as *Acartia* or *Calanus* (Maar *et al.*, 2006). Herbivorous *Evadne* spp. has been reported to feed on microphytoplankton (Nival and Ravera, 1979), ciliates (Cruz *et al.*, 2020) and nanophytoplankton (Broglio *et al.*, 2004). Similarly, appendicularians filter-feed on pico-sized phytoplankton (Nakamura *et al.*, 1997; Lučić, 1998). Special attention should be attributed to the family Oncaeidae feeding on particulate organic matter if in excess (Lučić *et al.*, 2019).

Tintinnids and radiolarians show considerable trophic flexibility, feeding on a wide range of prey. While both can ingest picoplankton, tintinnids mainly consume nano-sized phytoplankton such as small flagellates (Dolan, 2010). Radiolarians have an even broader diet, including bacteria, diatoms, dinoflagellates, ciliates, and occasionally metazoans like copepod nauplii (Swanberg and Caron, 1991; Eskinazi-Sant'Anna, 2006; Coots *et al.*, 2025). The size structure of phytoplankton plays a crucial role in zooplankton nutrition. In some cases, picophytoplankton, contrary to expectations, contribute significantly to the diet of certain zooplankton taxa (25–65%), whereas microphytoplankton may account for less than 20% (Hunt *et al.*, 2017). Similarly, Fonda Umani *et al.* (2005) found autotrophic picoplankton contributing the most to the biomass of natural assemblages in the Gulf of Trieste, the Adriatic Sea, during the stratified summer period. They also reported a clear dominance of calanoid copepods in terms of both composition and abundance. These findings highlight the presence of highly efficient trophic pathways that channel energy from the smallest phytoplankton fractions to the higher trophic levels (Hunt *et al.*, 2017).

The Island Mass Effect (IME), characterized by increased biological productivity around small islands, is attributed to localized upwelling and enhanced mixing (Doty and Oguri, 1956; Gove *et al.*, 2016). Internal island-trapped waves (ITWs), observed around various islands globally, including Lastovo Island in the Adriatic Sea (Orlić *et al.*, 2011; Mihanović *et al.*, 2014), facilitate nutrient fluxes and may amplify IME, further enhancing zooplankton productivity and shaping community composition (Ljubešić *et al.*, 2024). The most prominent response to ITWs around Lastovo Island has been reported in picophytoplankton and bacterioplankton, specifically in terms of their ecological functions (Ljubešić *et al.*, 2024; Mucko *et al.*, 2025). Metabarcoding of microbial and plankton communities during the same study, showed enhanced diversity and network complexity during ITWs events, indicating short-term restructuring of microbial food webs (Mucko *et al.,* 2025). Furthermore, time-lagged responses of phytoplankton to internal waves were observed, with smaller fractions such as picophytoplankton reacting more rapidly than microphytoplankton (Wang *et al.*, 2007; Ma *et al.*, 2021). Zooplankton, being highly responsive to changes in food availability and environmental conditions, are well-suited for investigating the effects of ITWs on smaller phytoplankton fractions, which constitute their primary prey (Pernica *et al.*, 2013).While previous studies have demonstrated that such physical processes enhance net primary production (NPP) (Ljubešić *et al.*, 2024), their impact on short-term zooplankton composition, vertical distribution and trophic responses remains poorly understood.

This study aims to understand the community-compositional and behavioural fine scale responses of zooplankton to small scale physical processes such as temperature gradients and daily thermocline oscillations in the highly stratified water column system. High-resolution sampling allows detailed monitoring of variations in food availability, while taxonomic research provides the foundation for investigating the feeding preferences of dominant species. This integrative approach enables a comprehensive exploration of the ecological and functional aspects of zooplankton communities.

MATERIAL AND METHODS

Study site and sampling design

Lastovo Island, located in the southern Adriatic Sea (42°45'00" N, 16°52'00" E), Croatia, measures 10 kilometers in length and 5.8 kilometers in width. The topography between Lastovo and the South Adriatic Pit features a gentle slope between the 100 and 200-meter isobaths, followed by a steeper incline beyond that point.

The research was conducted, from 13 to 22 July 2022, at station S1 (Fig. 1). Time and frequency of sampling were based on forecasts from operational meteorological and oceanographic models, which were provided five days in advance, to predict an optimal well-developed ITW episodes (Ljubešić *et al.*, 2024). The field experiment began on 13 July during an intense ITW event that lasted from 10 to 15 July, while the second pronounced episode occurred from 17 to 21 July (Ljubešić *et al.*, 2024). Sampling continued until 22 July (Table 1). Phytoplankton was sampled (total of 98 samples analysed) with 5 L Niskin bottles at discrete depths selected according to *in situ* thermohaline profile based on the position of the thermocline (Table 1). Sampling depths

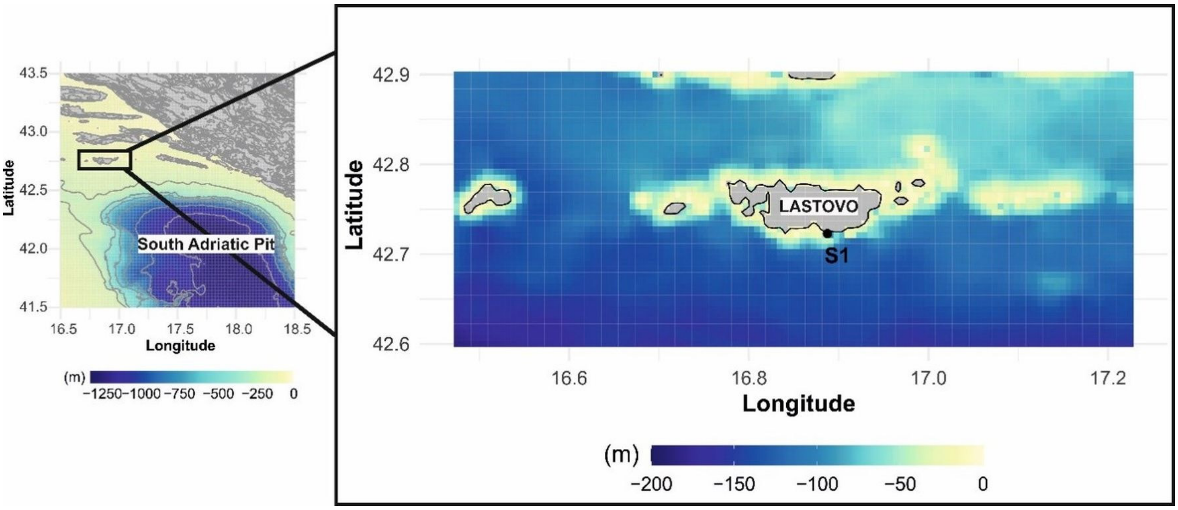

Fig. 1. Study area (Lastovo Island, South Adriatic) with sampling station S1 (Cape Struga) during the investigation period in July 2022.

corresponded to the zooplankton net layers (Table 1). Samples (250 mL) were preserved with 2% neutralized formaldehyde, and phytoplankton was identified and counted under an inverted Zeiss Axiovert microscope following the Utermöhl (1958) method. For picophytoplankton, 1.5 mL of sample was fixed with 100 µL of glutaraldehyde (36%), deep frozen in liquid nitrogen, and stored at −80 °C until analysis. Abundances were determined on a BD FACSVerse flow cytometer (BD Biosciences, Franklin Lake, NJ, USA) equipped with a standard filter setup and with 488 nm laser excitation, as described in Babić *et al*. (2018).

Table 1. Dates and times of sampling at station S1. The symbol x indicates time points when micro- and mesozooplankton were sampled in two layers. Numerical values indicate the depths (m) at which phytoplankton was sampled, both at times with x and at times when only phytoplankton was collected. Values shown in bold correspond to sampling during ITWc events.

UTC+2	06:00	12:00	18:00	24:00
13/07/2022	**x** **0, 30, 65, 75**	**x** **0, 20, 30,75**		
14/07/2022	**x** **0, 30, 75**	**x** **0, 30, 75**	**x** **0, 30, 65**	**x** **0, 30, 65**
15/07/2022	**x** **0, 30, 65**		x 0, 12, 65	
16/07/2022	x 0, 65		x 0, 29, 65	
17/07/2022	**x** **0, 29, 65**	**0, 29, 65**	**x** **0, 29, 65**	**x** **0, 12, 29, 65**
18/07/2022	**x** **0, 29, 65**	**2, 29, 65**	**x** **0, 29, 65**	**x** **0, 29, 65**
19/07/2022	**x** **0, 29, 65**	**0, 29, 65**	**x** **0, 29, 65**	**0, 29, 65**
20/07/2022	**x** **0, 29, 65**	**0, 29, 65**	x 0, 29, 65	
21/07/2022	x 0, 12, 29, 65		0, 12, 20, 29, 65	
22/07/2022	x 0, 20, 65		0, 12, 29, 65	

Zooplankton was collected with two modified Nansen opening–closing nets (mesh sizes 53 µm and 200 µm; 57 cm mouth diameter) equipped with a messenger-operated closing mechanism and towed at ~1 m s^{-1}. Sampling was performed in two layers: the lower layer, from 2.5 m above the seafloor to the thermocline, and the upper layer, from the thermocline to the surface. Samples were preserved with 4% buffered formaldehyde. Both microzooplankton and mesozooplankton were divided into subsamples using a Folsom splitter; representative fractions (1/8 and 1/16 for microzooplankton, 1/32 for mesozooplankton) were analyzed, while the entire samples were also examined to account for rare species. Microzooplankton were analyzed under an Olympus IMT-2 inverted microscope at 100× and 400× magnification, while mesozooplankton were counted using a Nikon SMZ800 stereomicroscope according to Harris *et al*. (2000).

Data analysis and visualization

To compare abundances between phytoplankton and zooplankton communities, phytoplankton abundances were averaged across the surface and thermocline depths to correspond with the zooplankton counts in the upper layer, while daily abundance values from the deep layer were compared to the zooplankton abundances in the lower layer.

Statistical analysis was conducted on zooplankton community samples. Specifically, differences in zooplankton group abundances among distinct layers were further evaluated using the Mann-Whitney U test (Zar, 1974), a non-parametric method used to assess whether two independent groups significantly differ in their distributions. Similarity Percentages Analysis (SIMPER) (Clarke, 1993) was used to estimate the contribution of dominant zooplankton species to the average dissimilarity between the upper and lower layers in the mesozooplankton fraction.

Redundancy analysis (RDA), a constrained ordination method, was applied to examine the co-occurrences between dominant zooplankton species/groups and phytoplankton groups, and to assess how community variability relates to water column stratification and the presence of ITWs. The explanatory variables included the presence of ITWs and water column layers (upper and bottom) defined by temperature values, while the response variables were the abundances of zooplankton species/groups (ind. m^{-3}), picophytoplankton (cells mL^{-1}) and nano-, and microphytoplankton (cells L^{-1}). Prior to RDA, plankton abundances were log-transformed using *decostand* function. Four RDA models (response variables ~ explanatory variables) were run, combining different sets of plankton: 1) zooplankton groups, micro-, and nanophytoplankton; 2) zooplankton groups and picophytoplankton; 3) dominant zooplankton species, micro-, and nanophytoplankton; and 4) dominant zooplankton species and picophytoplankton. Permutation ANOVA (analysis of variance) was applied to each model to test its significance. The analysis was conducted in RStudio using *ggvegan* package (Simpson and Oksanen, 2025).

Data visualization was performed in RStudio with *ggplot2* package (Wickham, 2016), Grapher^{TM} software from Golden Software, LLC and Microsoft Excel, and statistical analysis was done in Primer 6 (Clarke and Gorley, 2006).

RESULTS

Zooplankton community composition and abundance dynamics

The microzooplankton showed a high overall abundance, with a high proportion of tintinnids and juvenile individuals (nauplii, copepodites and larvae). The maximum abundance in the upper layer was recorded on 13 July 2022 with a value of 12066 ind. m^{-3}, after which a slight decrease was observed until 17 July 2022 (Fig. 2A). This was followed by a moderate increase that peaked on 20 July before decreasing again by 22 July. Below the thermocline, the trend was similar to the upper layer, but with less fluctuation. The lowest value of 2006 ind. m^{-3} was measured on 22 July (Fig. 2A).

The microzooplankton community composition was relatively uniform in both layers, largely due to the consistent presence of a few dominant taxa. According to the Mann-Whitney test, significant dissimilarity was found between the upper and lower strata for most taxa, with Cladocera, copepod nauplii and Harpacticoida showing the strongest significance (Table 2), followed by Protista, Calanoida copepodites and Pteropoda. The average percentage contributions of all major groups are shown in Fig. 2C and Table 2. Overall, copepod nauplii were recognised as predominant in both strata (45.0% and 41.7% in the upper and lower strata, respectively; Fig. 2C). Calanoid copepodites were in second place, followed by smaller cyclopoids (Fig. 2C). The average abundance of copepod nauplii was 2215 ± 1323 ind. m^{-3} and ranged from a minimum of 968 ind. m^{-3} to a maximum of 7446 ind. m^{-3}. Furthermore, within the Protista, the radiolarians were most abundant in the upper layer and the tintinnid *Codonellopsis schabi* and the mussel larvae in the lower layer (Fig. 2C). Throughout the entire research period, mesozooplankton abundances remained generally consistent, and they exhibited less pronounced separation between upper and lower layers compared to microzooplankton (Fig. 2A).

The mesozooplankton community in the investigated area comprised 11 major taxonomic groups, with a total of 77 identified taxa (Table S1). Copepoda were the most abundant and diverse group, followed by gelatinous zooplankton (siphonophores and hydrozoan medusae), Cladocera, Ostracoda, Appendicularia, Pteropoda, Chaetognatha, Thaliacea, Misidacea and various meroplanktonic larvae. Copepods contributed between 45%

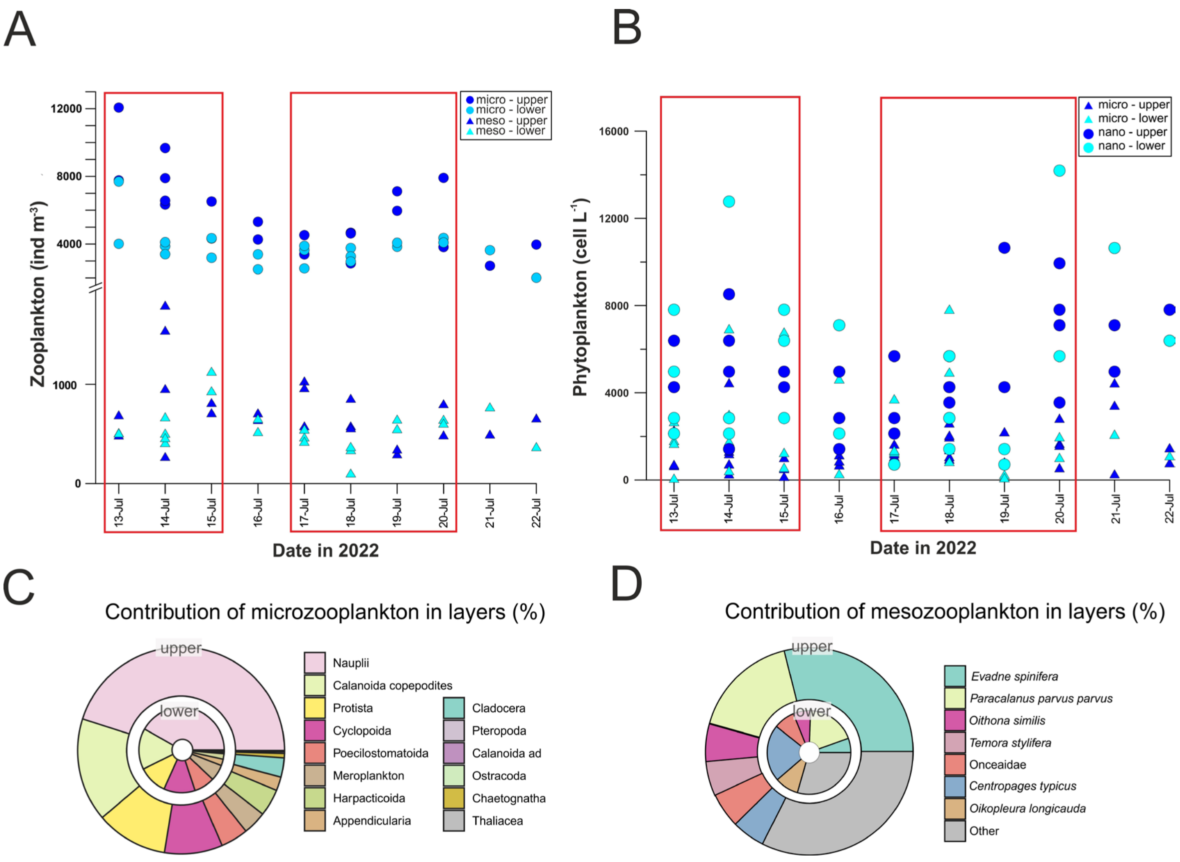

Fig. 2. Temporal variability of the abundance of total microzooplankton and mesozooplankton in layers above and below the thermocline at the S1 station in July 2022 **(A)**; temporal variability of the phytoplankton abundance in layers above and below the thermocline, divided into microphytoplankton and nanophytoplankton **(B)**; microzooplankton contribution over layers **(C)**; mesozooplankton dissimilarity contribution over layers according to SIMPER analysis **(D)**. Red rectangles on A and B plots highlight dates during ITWs.

and 93% of the total mesozooplankton abundance, with the average contribution of 75%. Among copepods, Calanoida juveniles were the most abundant (196 ± 137.11 ind. m^{-3}), followed by Calanoida adults (167 ± 104.20 ind. m^{-3}) and Cyclopoida (adults and juveniles) (94 ± 54.81 ind. m^{-3}), while Harpacticoida and Poecilostomatoida were present in considerably lower numbers (2 ± 9.03 ind. m^{-3} and 28 ± 17.32 ind. m^{-3}, respectively). Cladocerans were the second most numerous group, comprising up to 45% of the total mesozooplankton, with an average contribution of 12% and a maximum abundance of 316 ind. m^{-3}. According to the Mann-Whitney test, significant dissimilarity between upper and lower layers for mesozooplankton was observed only for Cladocera ($p < 0.0001$) and Harpacticoida ($p < 0.05$).

Among copepods, *Oithona* spp., *Paracalanus parvus parvus*, and *Centropages typicus* were the most dominant taxa, while Appendicularia, particularly *Oikopleura (Coecaria) longicauda*, also contributed significantly to the overall community structure. The composition of dominant mesozooplankton taxa (≥ 5% dissimilarity contribution according to SIMPER analysis) varied between layers (Fig. 2D and Table S2). *Oithona similis* and Oncaeidae were equally present in both layers. *Evadne spinifera* and *Paracalanus parvus parvus* dominated the upper layer, while *Centropages typicus* and *Oikopleura longicauda* contributed the most to the lower layer. *Temora stylifera* showed variations across depths (Fig. 2D).

Variability in the zooplankton community in relation to phytoplankton

After the initial period of ITWs (13-15 July 2022), nanophytoplankton began to recover in abundance (Fig. 2B). Following the peak of the second ITW period (19 July), nanophytoplankton recovered, peaking on 20 and 21 July (Fig. 2B).

The most significant impact on the community structure was observed among taxa known to occasionally feed on nano-sized phytoplankton, primarily *Evadne spinifera*, *Oithona* spp., and *Paracalanus parvus parvus* (Figs. 3 and 4), as supported by RDA (Fig. 5C, D). *E. spinifera* was predominantly concentrated in the upper layer, particularly during ITWs (13-15 July and 17-19 July), with an abundance peak above the thermocline (Fig. 3). Given its high proportion in dissimilarity contribution (28.91%, Table S2), it may have contributed to

Table 2. Abundances of all major groups/taxa within total microzooplankton according to layers: mean contribution to the whole community is indicated with % (contr %).

	Upper layer				Lower layer				Mann Whitney test (p value)
	min	max	mean ±SD	contr %	min	max	mean ±SD	contr %	
Protista	166	1860	699±416.85	11.2	158	907	409±172.58	10.8	$p < 0.05$
Cladocera	10	853	194±198.88	3.0	0	57	17±19.21	0.4	$p < 0.0001$
Copepod nauplii	1200	7446	2790±1534.40	45.0	968	3452	1552±530.70	41.7	$p < 0.001$
Calanoida copepodites	256	2266	986±500.25	16.2	205	1770	605±321.88	15.8	$p < 0.01$
Calanoida adults	0	122	13±37.05	0.3	0	116	8±26.12	0.2	NS
Cyclopoida	187	1403	547±287.88	9.1	270	617	434±112.69	12.1	NS
Harpacticoida	0	781	247±149.76	4.2	9	366	86±78.56	2.2	$p < 0.001$
Poecilostomatoida	59	580	234±125.54	4.3	112	531	286±87.84	8.0	NS
Ostracoda	0	41	4±9.96	0.1	0	23	6±7.93	0.2	NS
Pteropoda	0	176	45.43±53.55	0.7	0	67	11±16.93	0.3	$p < 0.005$
Appendicularia	20	353	122±89.42	2.1	3	160	76±43.35	2.1	NS
Chaetognatha	0	38	7±11.79	0.1	0	29	4±7.56	0.1	NS
Thaliacea	0	2	0.07±0.33	0.0	0	9	0.43±1.91	0.0	NS
Meroplankton	44	553	229±146.43	3.7	93	472	226±118.37	6.1	NS

*NS- not statistically significant

grazing pressure on nanophytoplankton, particularly on 20 July (Fig. 2B), which is also indicated by RDA (Fig. 5C). However, once ITWs weakened (e.g., 15 July, 18:00 and 20 July, 18:00), *Evadne* populations declined (Fig. 3). From 15 to 17 July, *Oithona* reached high abundance in the lower layer, comprising 18% of the total community (Table S1). This temporal overlap with low nanophytoplankton abundance on 17 July suggests a possible trophic interaction (Fig. 4), also indicated by RDA (Fig. 5C). Following this period, as *Oithona* spp. population declined, nanophytoplankton began to recover, indicating potential grazing pressure by small copepods. During the second ITW event (17 July onward), a peak in surface abundance was observed, possibly driven by upward thermocline oscillations. Conversely, after ITWs subsided (20-22 July), the presence of *Oithona* spp. in deeper layers slightly increased, suggesting a possible retention effect (Fig. 4), and its preference for lower layers was confirmed with RDA (Fig. 5C, D).

Paracalanus parvus parvus exhibited a preference for the upper layer (Figs. 4 and 5C, D), with consistently higher abundance throughout the sampling period and distinct peaks on 14 and 20 July (the final day of ITWs) (Fig. 4). A temporary increase in the lower layer on 15 July recorded during a no-ITW period, indicates a short-term shift in distribution likely driven by changes in prey availability. Overall, the species remained surface-dominated, responding dynamically to ITW-driven variability in nanophytoplankton (Fig. 4). As the *Evadne* population declined, *Oithona* and *Paracalanus* persisted, migrating to the lower layer reflecting their ability to adjust to changing environmental conditions (Figs. 2D and 4).

Centropages typicus displayed a higher dissimilarity contribution in the lower layer (22.20%) than in the upper layer (5.16%), with notable peaks on 14-16 July, particularly in the lower layer (Table S3, Fig. 5C, D). In contrast, *Temora stylifera* was more abundant in the upper layer (Figs. 4 and 5C, D), with peaks on 13 and 20 July (Fig. 4). However, due to its low dissimilarity contribution (5.16% in the upper layer and < 5% in the lower therefore unlisted, Table S3), its impact on the phytoplankton community was limited.

Tintinnids were the most abundant microzooplankton during ITWs, followed by copepod nauplii and radiolarians (Fig. 3). They may contribute to grazing pressure during the first ITWs, alongside copepod nauplii and radiolarians in the upper layer (Fig. 3), as confirmed with RDA (Fig. 5A, B). The appendicularian *Oikopleura longicauda* which is capable of retaining pico- as well as nano-sized particles showed a delayed peak in abundance, reaching the highest numbers on the last day of ITWs and the following day (Fig. 3). During periods without ITWs, *Oikopleura* dominated both layers, first appearing in the lower layer and later migrating to the upper layer during the second ITW event, where it likely

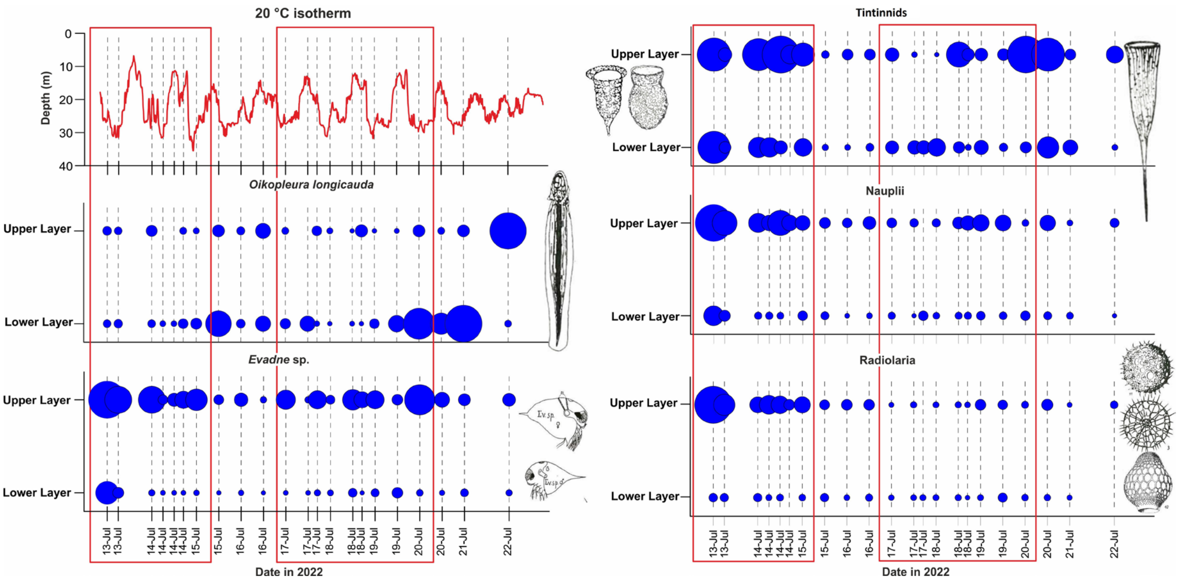

Fig. 3. Total abundances of *Oikopleura longicauda*, *Evadne* sp., tintinnids, copepod nauplii and Radiolaria are represented in bubble-plots in a daily manner; red rectangles highlighting dates during ITWs. Bubble radius scaled according to min and max values for each taxon (all data shown in Table S2). Abundances are shown with accompanying 20 °C isotherm depths representing thermocline oscillations. Drawings of taxa are modified from Trégouboff and Rose (1957).

continued feeding on the remaining pico-fraction. RDA confirmed its tendency for deep layers and cooccurrences with picophytoplankton (Fig. 5D).

Oncaeidae contributed 5.44% in the upper layer and 8.16% in the lower layer (Table S3), showing a similar distribution pattern to ITW events as the rest of the copepods (Fig. 4).

RDA confirmed observed cooccurrences in the upper and lower layers, elucidating that the highest variability among layers (RDA1 = 32.63%) is explained by zooplankton dominant species and micro- and nanophytoplankton (Fig. 5).

The RDA models (Fig. 5) were significant (Table S4), supporting the aforementioned findings. Water column layer accounted for more variability in community structure (RDA1) than ITWs presence (RDA2) (Fig. 5). Along the first axis (RDA1 = 32.63%), *E. spinifera*, *P. parvus parvus* and *T. stylifera* grouped with nanophytoplankton in the upper layer, whereas *C. typicus*, *Oithona* spp. and *O. longicauda* were associated with microphy-

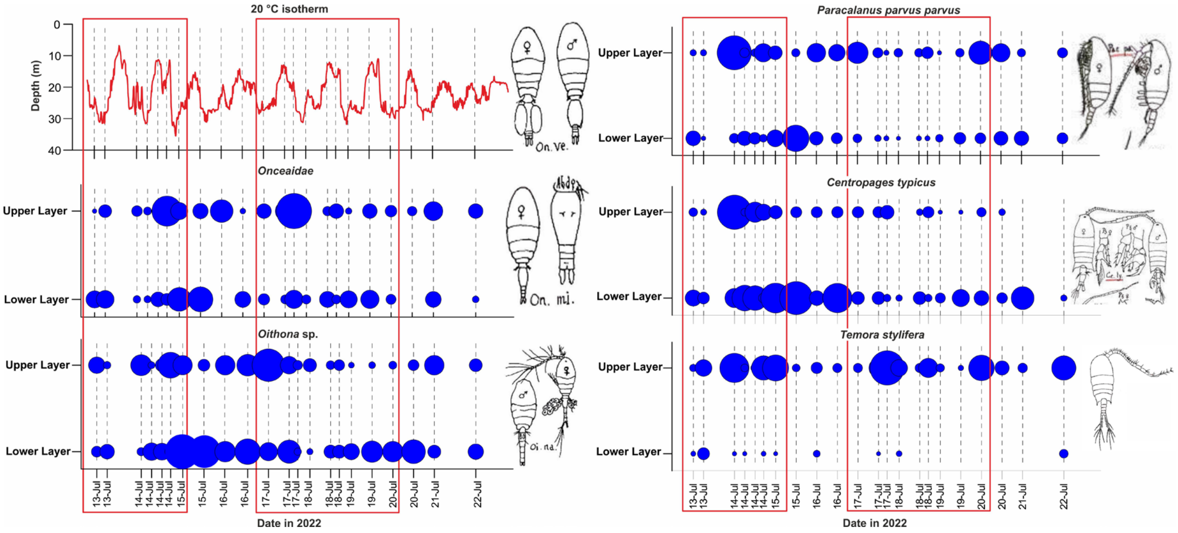

Fig. 4. Total abundances of dominant copepods: Oncaeidae, *Oithona* sp., *Paracalanus parvus parvus*, *Centropages typicus* and *Temora stylifera* represented in bubble-plots in a daily manner; red rectangles highlighting dates during ITWs. Bubble radius scaled according to min and max values for each taxon (all data shown in Table S2). Abundances are shown with accompanying 20 °C isotherm depths representing thermocline oscillations. Drawings of taxa are modified from Trégouboff and Rose (1957).

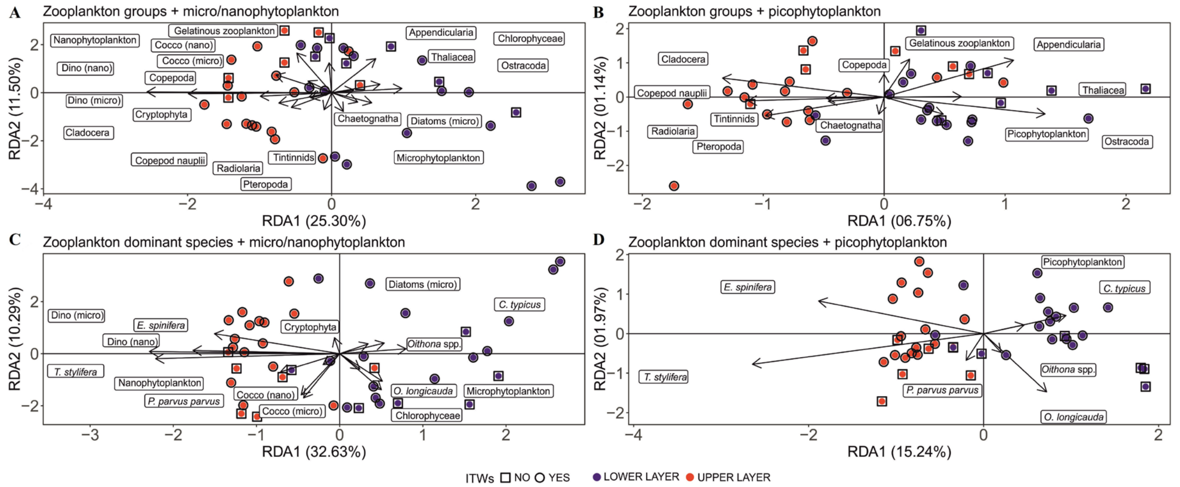

Fig. 5. Redundancy analysis (RDA) ordination plots showing the relationships between zooplankton groups or dominant species and phytoplankton size classes in relation to water column layers (color-coded) and the presence or absence of internal island-trapped waves (ITWs, indicated by symbols). From left to right and top to bottom: zooplankton groups with micro- and nanophytoplankton **(A)**; zooplankton groups with picophytoplankton **(B)**; dominant zooplankton species with micro- and nanophytoplankton **(C)**; and dominant zooplankton species with picophytoplankton **(D)**. Abbreviations: Dino (dinoflagellates), Cocco (coccolithophorids).

toplankton in the lower layer (Fig. 5C), and with picophytoplankton in the lower layer (RDA1 = 15.24%, Fig. 5D). Copepod nauplii, Copepoda, Cladocera, Pteropoda, Radiolaria and Tintinnida were more related to the upper layer and nanophytoplankton (RDA1 = 25.30%, Fig. 5A), while Appendicularia, Chaetognatha, Ostracoda and Thaliacea co-occurred in the lower layer with microphytoplankton (RDA1 = 25.30%, Fig. 5A) and picophytoplankton (RDA1 = 6.75%, Fig. 5B). The proportion of variance explained by water column layer and ITWs was the highest for dominant zooplankton species and picophytoplankton (41.33%, Table S4), followed by dominant zooplankton species and micro-, nanophytoplankton (16.01%, Table S4).

DISCUSSION

Zooplankton community structure

Investigating zooplankton dynamics is a challenge due to their spatial and temporal variability and the limitations of sampling methods. Discrepancies in mesh sizes (250 µm in many studies vs 200/53 µm here) can affect taxa composition, but both microzooplankton and mesozooplankton communities generally follow patterns defined by dominant taxonomic groups. Zooplankton diversity and abundance are similar to other zooplankton communities reported in studies conducted in coastal waters of the South Adriatic Sea (Vidjak *et al.*, 2012; Miloslavić *et al.*, 2015; Hure *et al.*, 2022). The dominance of copepods, particularly calanoids, is generally consistent with previous findings in other coastal areas of the Adriatic Sea (Vidjak *et al.*, 2006, 2007, 2012; Hure *et al.*, 2022), although some regional and seasonal deviations, such as increased cladoceran or cyclopoid abundance, have been reported (Miloslavić *et al.*, 2015).

The composition of the zooplankton community in the southern Adriatic shows a clear seasonal and vertical differentiation, with different taxa dominating the surface and deep layers (Kršinić, 1998; Miloslavić *et al.*, 2015; Hure *et al.*, 2022). In this study, calanoid copepods such as *Centropages typicus* dominate the lower layers grazing on diatoms, dinoflagellates and small animal larvae. This observation could be explained by short-term diel vertical migration - a behaviour controlled by ambient radiation that allows zooplankton to feed during the night in food-rich, shallow waters when the risk of visual (light-dependent) predation is minimal (Bandara *et al.*, 2021).

This result also agrees with that of Hure *et al.* (2022), who stated *C. typicus* is mainly influenced by temperature fluctuations and belongs to the strata at 50-100 m depth, while *P. parvus parvus* made a greater contribution to the community in mixed winter periods. This study also demonstrated that the nano- and pico-sized filter-feeder *Oikopleura longicauda* dominated the lower layers. Similarly, Hure *et al.* (2018) confirmed the dominance *of O. longicauda* within the first 100 m layer in the southern Adriatic. In contrast, the surface layers were dominated by herbivorous cladocerans such as *Evadne spinifera*, typically most abundant during summer stratification periods and in surface layers of the enclosed marine lake on Mljet Island (Miloslavić *et al.*, 2014). Additionally, omnivorous cyclopoid copepods of the genus *Oithona*, especially *O. similis*, *O. nana* and many cyclopoid copepods, have been reported to favour surface layers (Vidjak *et al.*, 2012; Miloslavić *et al.*, 2012, 2014).

Regarding the temporal distribution of microzooplankton and mesozooplankton, this study is characterised by high frequency sampling during one season, which was carried out based on specific hypotheses. Although there are no similar studies comparing daily changes in the community, Pestorić *et al.* (2016) showed dominance of cyclopoids Oncaeidae and Oithonidae, with predominantly estuarine species: *Oncaea* spp.*, Oithona nana, O. similis, Acartia clausi, Paracalanus parvus parvus, Euterpina accutifrons, Centropages kroyeri, Clausocalanus jobei, Temora stylifera* and *Coryaeus* spp., in weekly sampling at the innermost station in Boka Kotorska Bay. The high prevalence of Oncaeidae in weekly sampling in the study by Lučić *et al.* (2019) in the environmentally influenced sea lake Veliko Jezero on the island of Mljet is another comparable result to this study, indicating the zooplankton community in the coastal waters of Lastovo Island is more similar to the communities in coastal areas than open waters of the southern Adriatic.

Predator-prey dynamics in an ITW-forced environment

Prey size classes (pico-, nano- and micro-) have been at the centre of the description of food chains in numerous studies, where the definition of the components of these classes led to conclusions about the pathways formed by the dominant predator groups (e.g. the "copepod pathway") (Sommer *et al.,* 2002; Calbet and Landry, 2004; Calbet and Saiz, 2005). In addition, the size structure of phytoplankton communities has implications for the length of the food chain and the efficiency of bottom-up energy transfer when larger phytoplankton classes predominate (Hunt *et al.*, 2017), mesozooplankton have been shown to graze microzooplankton, mainly ciliates, which account for up to 10% of the permanent C uptake (Hunt *et al.*, 2017). Moreover, notable increases in copepods alongside phytoplankton (mainly Chrysophyceae and Dictyochophyceae) in micro fractions during the same experiment reported by Mucko *et al*., (2025) suggested a potential top-down control mechanism on prey during bloom senescence phases along with detritus recycling pathways following ITWs. Within this study, a possible response of the vertical and trophic structure of the zooplankton community to ITWs was recorded. The most pronounced response was observed among small zooplankton taxa, particularly *E. spinifera*, *Oithona* spp., and *P. parvus parvus*, which are known to feed on a range of prey, including nano-sized phytoplankton.

E. spinifera was predominantly concentrated in the upper layer, particularly during ITW events, during which an enhanced primary productivity in the thermocline layer was observed (Ljubešić *et al.*, 2024). After this event, a significant population decline was recorded. Similarly, Villate *et al.* (2014) found the highest abundances of *E. spinifera* grazing upon nanophytoplankton blooming in surface waters influenced by the Ebro plume (NW Mediterranean Sea) during June. RDA further supported these findings by grouping *E. spinifera, P. parvus parvus* and *T. stylifera* with the upper layer and nanophytoplankton, while associating *C. typicus* and *O. longicauda* with the micro-, and picophytoplankton in the lower layer. In addition, *Oithona* spp. was shown to prefer lower layers, which is in contrast to other research that observed its high abundances in the surface layers (Vidjak *et al*., 2012; Miloslavić *et al*., 2012, 2014). This suggests that the vertical distribution of *Oithona* spp. is more flexible than previously thought and can be strongly influenced by short-term variability, such as ITW-driven changes in prey availability. The ecological importance of *Oithona* is well documented: it exerts strong grazing pressure on nanophytoplankton (Vargas and González, 2004; Khanaychenko *et al*., 2018) and feeds on ciliates, heterotrophic dinoflagellates, nanoflagellates, and copepod nauplii (Lampitt and Gamble, 1982; Nakamura *et al*., 1997; Nakamura and Turner, 1997). With their low metabolic rates and broad food spectrum, *Oithona* spp. can maintain stable populations under fluctuating environmental conditions (Lampitt and Gamble, 1982), while ITW-induced nutrient fluxes may periodically boost their abundance, strengthening their role in microbial food webs and energy transfer toward higher trophic levels (Turner, 2004). On the other hand, *P. parvus parvus*, although grouped with the upper layer in this study, is a widespread calanoid copepod in coastal waters, known to feed both on phytoplankton and on heterotrophic protists (Suzuki *et al.*, 1999; Ding *et al.*, 2023), highlighting the trophic plasticity of dominant copepod taxa in the system.

It is estimated that ~50% of the autotrophic energy enters the "copepod pathway" in picophytoplankton-dominated systems, such as in the Lastovo Island's coastal waters (Ljubešić *et al.*, 2024), but those pico-sized cells are primarily grazed by microzooplankton (heterotrophic flagellates and ciliates), surging the energy further toward larger copepods (Sommer *et al.*, 2002). Among dominant copepod species, *T. stylifera* and *C. typicus* are omnivorous and opportunistic, consuming a wide range of prey, including diatoms, dinoflagellates, ciliates, and smaller zooplankton (Turner, 1984; Carlotti *et al.*, 2007). Top-down control of these taxons shown in this study can be extrapolated to previous conclusions drawn by Halsband-Lenk *et al.* (2001) in the Ligurian Sea, who noted these copepods grazing microzooplankton following the peak of microphytoplankton abundances, with diatoms dominating spring and autumn communities. Additionally, Carotenuto *et al.* (2006) reported that high occurrence of *T. stylifera* in the Catalan Sea during summer stratification was attributed to food availability rather than fecundity, whereas *C. typicus* was observed to have the greatest fecundity during spring (Saiz *et al.*, 2007), in correspondence to the highest Chl *a* concentration. The aforementioned gives us room to hypothesize that *T. stylifera* abundances favourably peaked due to food availability in both layers, while *C. typicus* did not show that pattern in the coastal waters of Lastovo Island. Within this study, *C. typicus* may have influenced microphytoplankton abundance in the lower layer during no-ITW periods, while *T. stylifera*, although relatively more abundant in the upper layer compared to the lower, had a limited overall impact due to its small total population size. Nevertheless, *T. stylifera* is recognized for its high feeding capacity (Gaudy, 1974), suggesting that even numerically modest populations may exert a functional influence, particularly in microphytoplankton-rich conditions.

The group of microzooplankton, including tintinnids, radiolarians and early developmental stages of zooplankton (copepod nauplii), responded strongly to ITWs, whereas *Oikopleura longicauda* showed a time-lagged peak with a preference for lower layers. This pattern coincided with nanophytoplankton dynamics, their main food source, suggesting that their presence reflects favourable feeding conditions rather than a direct top-down control mechanism. Unlike copepods, they use mucous filter-feeding structures to capture particles smaller than 5 µm, making them important grazers in pelagic food webs, especially in oligotrophic environments (Gorsky and Fenaux, 1998; Flood and Deibel, 1998) such as the Lastovo archipelago, where ITWs influence nutrient availability (Ljubešić *et al.*, 2024). However, they are also found in nutrient-rich coastal waters, due to their high filtration rates (Bochdansky *et al.*, 1998; Deibel, 1998; Lombard *et al.*, 2011). Their rapid growth, high turnover rates, and production of fast-sinking discarded houses play an active role in carbon export and vertical flux of organic matter (Lombard *et al.*, 2010; Durkin *et al.*, 2022).

Copepod nauplii represent one of the most abundant counterparts of microzooplankton and are a key part of the copepod life cycle, however, little is known about their feeding behaviour (Craig *et al.*, 2014). Assumptions in the calculation of conceptual food webs include copepod nauplii feeding alike to the adults, but Vogt *et al.* (2013) reported that the upper size limit of prey ingested by copepod nauplii is much smaller than that of their adult counterparts. Their high abundance likely results from small prey dominance, efficient mesh sizes (Garcia *et al.*, 2021), ITW-enhanced productivity (Ljubešić *et al.*, 2024), and the fact that the study period coincides with the reproductive season of copepods.

Tintinnids are heterotrophic filter feeders, capable of capturing prey on a variety of particles smaller than approximately 40% of the oral diameter of their lorica, including bacteria, cyanobacteria, and small flagellates (Dolan, 2010). Radiolarians, on the other hand, are considered opportunistic predators capable of consuming a wide range of planktonic organisms, from picoplankton to metazoans (Blackbourn, 1974; Swanberg and Caron, 1991; Coots *et al.*, 2025). Our findings suggest that tintinnids, together with radiolarians and copepod nauplii, may have contributed to the grazing pressure on picophytoplankton and bacterioplankton during the first ITW event. While tintinnids spanned throughout the entire water column, copepod nauplii and radiolarians accumulated mostly in the upper layer. However, towards the second ITW episode, the abundances of tintinnids, copepod nauplii and radiolarians dropped, allowing the pico size-class to recover (Ljubešić *et al.*, 2024). The post-ITW bloom of tintinnids may have been facilitated by grazing on microphytoplankton by copepods, which released degraded diatom material usable by tintinnids (Krawczyk *et al.*, 2015).

Finally, omnivores such as the most diverse copepod family, Oncaeidae, showed no clear response to ITWs, suggesting a more generalized role within the zooplankton community. Sparse changes in the Oncaeidae abundances with shifting thermocline could also reflect their negative correlation to temperature shown by Lučić *et al.* (2019). Additionally, it is well known from literature that Oncaeidae will feed upon a variety of prey sizes, from bacteria, diatoms, dinoflagellates, *Phaeocystis* colonies, radiolarians, silicoflagellates, nematocysts of cnidarians, fish larvae, chaetognaths, pieces of larger individuals such as calanoid copepods and appendicularians, all towards the sediment particles (Turner, 1986). Aforementioned Oncaeidae reported behaviour in marine coastal waters supports their wide ecological niche and opportunistic feeding preferences. Therefore, Oncaeidae proved to be an important counterpart in "copepod pathway" shaping overall carbon export in conditions of induced primary production in ITWs, influencing the coastal waters of Lastovo Island.

CONCLUSION

This study highlights the influence of ITWs on zooplankton community structure and their role in shaping trophic interactions in coastal waters. Our results suggest a potential response of zooplankton taxa such as *Evadne spinifera* and *Oithona* spp. to the nanophytoplankton bloom during ITW events, indicating that zooplankton may contribute to grazing pressure on nano- and microphytoplankton. The pico-feeding Appendicularia and omnivorous Oncaeidae also played an important role, reflecting the complexity of pelagic food webs.

Although our study focused on the short-term and vertical distribution patterns of zooplankton in response to ITWs, future research should also investigate feeding interactions between different zooplankton groups. Understanding these relationships, including possible trophic cascade effects, would provide a more complete picture of the dynamics within the zooplankton community.

Furthermore, this high-resolution study contributes to a better understanding of zooplankton dynamics in physically dynamic environments and emphasises the need for high-frequency sampling campaigns to capture the complexity of these interactions. Overall, our results point to the potential of ITWs as a physical driver of ecological change in the southern coastal Adriatic and support their integration into future ecosystem and biogeochemical modelling.

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REFERENCES

Babić, I., Mucko, M., Petrić, I., Bosak, S., Mihanović, H., Vilibić, I., Dupčić Radić, I., *et al.* 2018. Multilayer approach for characterization of bacterial diversity in a marginal sea: From surface to seabed. Journal of Marine Systems, 184, 15-27. https://doi.org/10.1016/j.jmarsys.2018.04.002

Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V., Eiane, K. 2021. Two hundred years of zooplankton vertical migration research. Biological Reviews, 96(4), 1547-1589. https://doi.org/10.1111/brv.12715

Blackbourn, D.J. 1974. The feeding biology of tintinnid protozoa and some other inshore microzooplankton. PhD thesis, University of British Columbia, 224 pp. https://doi.org/10.14288/1.0053248

Bochdansky, A.B., Deibel, D., Hatfield, E.A. 1998. Chlorophyll *a* conversion and gut passage time for the pelagic tunicate *Oikopleura vanhoeffeni* (Appendicularia). Journal of Plankton Research, 20(11), 2179-2197. https://doi.org/10.1093/plankt/20.11.2179

Broglio, E., Saiz, E., Calbet, A., Trepat, I., Alcaraz, M. 2004. Trophic impact and prey selection by crustacean zooplankton on the microbial communities of an oligotrophic coastal area (NW Mediterranean Sea). Aquatic Microbial Ecology, 35, 65-78. https://doi.org/10.3354/ame035065

Calbet, A., Landry, M.R. 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnology and Oceanography, 49(1), 51-57. https://doi.org/10.4319/lo.2004.49.1.0051

Calbet, A., Saiz, E. 2005. The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology, 38, 157-167. https://doi.org/10.3354/ame038157

Calbet, A., Carlotti, F., Gaudy, R. 2007. The feeding ecology of the copepod *Centropages typicus* (Kröyer). Progress in Oceanography, 72(2-3), 137-150. https://doi.org/10.1016/j.pocean.2007.01.003

Carlotti, F., Bonnet, D., Halsband-Lenk, C. 2007. Development and growth rates of *Centropages typicus*. Progress in Oceanography, 72(2-3), 164-194. https://doi.org/10.1016/j.pocean.2007.01.011

Carotenuto, Y., Ianora, A., Di Pinto, M., Sarno, D., Miralto, A. 2006. Annual cycle of early developmental stage survival and recruitment in the copepods *Temora stylifera* and *Centropages typicus*. Marine Ecology Progress Series, 314, 227-238. https://doi.org/10.3354/meps314227

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18(1), 117-143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K.R., Gorley, R.N. 2006. PRIMER v6: user manual/tutorial. PRIMER-E: Plymouth, 192 pp.

Coots, N.L., Blanco-Bercial, L., Gile, G.H. 2025. Polycystine radiolarians associate with diverse phytoplankton. Journal of Plankton Research, 47(3), fbaf010. https://doi.org/10.1093/plankt/fbaf010

Craig, C., Kimmerer, W.J., Cohen, C.S. 2014. A DNA-based method for investigating feeding by copepod nauplii. Journal of Plankton Research, 36(1), 271-275. https://doi.org/10.1093/plankt/fbt104

Cruz, J., Teodósio, M.A., Garrido, S., Ben-Hamadou, R., Chícharo, L., Ré, P., Santos, A.M.P. 2020. Plankton community and copepod production in a temperate coastal lagoon: What is changing in a short temporal scale? Journal of Sea Research, 157, 101858. https://doi.org/10.1016/j.seares.2020.101858

Deibel, D. 1998. Feeding and metabolism of Appendicularia. *In* The Biology of Pelagic Tunicates (ed. Q. Bone). Oxford University Press. pp. 139-150. https://doi.org/10.1093/oso/9780198540243.003.0008

Ding, Z., Sun, X., Qiao, Y., Liu, Y., Liu, J. 2023. Feeding behavior responses of the small copepod, *Paracalanus parvus*, to toxic algae at different concentrations. Animals, 13(19), 3116. https://doi.org/10.3390/ani13193116

Dolan, J.R. 2010. Morphology and ecology in tintinnid ciliates of the marine plankton: correlates of lorica dimensions. Acta Protozoologica, 49(3), 235-244.

Doty, M.S., Oguri, M. 1956. The island mass effect. ICES Journal of Marine Science, 22(1), 33-37. https://doi.org/10.1093/icesjms/22.1.33

Durkin, C.A., Cetinić, I., Estapa, M., Ljubešić, Z., Mucko, M., Neeley, A., Omand, M. 2022. Tracing the path of carbon export in the ocean though DNA sequencing of individual sinking particles. The ISME Journal, 16(8), 1896-1906. https://doi.org/10.1038/s41396-022-01239-2

Eskinazi-Sant'Anna, E.M. 2006. *Sticholonche zanclea* (Protozoa, Actinopoda) in fecal pellets of copepods and *Euphausia* sp. in Brazilian coastal waters. Brazilian Journal of Biology, 66(3), 839-847. https://doi.org/10.1590/S1519-69842006000500009

Flood, P.R., Deibel, D. 1998. The appendicularian house. *In* The Biology of Pelagic Tunicates (ed. Q. Bone). Oxford University Press. pp. 105-124. https://doi.org/10.1093/oso/9780198540243.003.0006

Fonda Umani, S., Tirelli, V., Beran, A., Guardiani, B. 2005. Relationships between microzooplankton and mesozooplankton: competition versus predation on natural assemblages of the Gulf of Trieste (northern Adriatic Sea). Journal of Plankton Research, 27(10), 973-986. https://doi.org/10.1093/plankt/fbi069

Gaudy, R. 1974. Feeding four species of pelagic copepods under experimental conditions. Marine Biology, 25(2), 125-141. https://doi.org/10.1007/BF00389261

Garcia, T.M., Santos, N.M.O., Campos, C.C., Costa, G.A.S., Belmonte, G., Rossi, S., Soares, M.O. 2021. Plankton net mesh size influences the resultant diversity and abundance estimates of copepods in tropical oligotrophic ecosystems. Estuarine, Coastal and Shelf Science, 249, 107083. https://doi.org/10.1016/j.ecss.2020.107083

Gorsky, G., Fenaux, R. 1998. The role of Appendicularia in marine food webs. *In* The Biology of Pelagic Tunicates (ed. Q. Bone). Oxford University Press. pp. 161-170. https://doi.org/10.1093/oso/9780198540243.003.0010

Gove, J.M., McManus, M.A., Neuheimer, A.B., Polovina, J.J., Drazen, J.C., Smith, C.R., Merrifield, M.A., *et al.* 2016. Near-island biological hotspots in barren ocean basins. Nature Communications, 7(1), 10581. https://doi.org/10.1038/ncomms10581

Halsband-Lenk, C., Nival, S., Carlotti, F., Hirche, H.-J. 2001. Seasonal cycles of egg production of two planktonic copepods, *Centropages typicus* and *Temora stylifera*, in the north-western Mediterranean Sea. Journal of Plankton Research, 23(6), 597-609. https://doi.org/10.1093/plankt/23.6.597

Harris, R., Wiebe, P., Lenz, J., Skjoldal, H.R., Huntley, M. (eds). 2000. ICES zooplankton methodology manual. Academic Press, 684 pp. https://doi.org/10.1016/B978-012327645-2/50000-1

Hunt, B.P.V., Carlotti, F., Donoso, K., Pagano, M., D'Ortenzio, F., Taillandier, V., Conan, P. 2017. Trophic pathways of phytoplankton size classes through the zooplankton food web over the spring transition period in the north-west Mediterranean Sea. Journal of Geophysical Research: Oceans, 122(8), 6309-6324. https://doi.org/10.1002/2016JC012658

Hure, M., Mihanović, H., Lučić, D., Ljubešić, Z., Kružić, P. 2018. Mesozooplankton spatial distribution and community structure in the South Adriatic Sea during two winters (2015, 2016). Marine Ecology, 39(1), e12488. https://doi.org/10.1111/maec.12488

Hure, M., Batistić, M., Garić, R. 2022. Copepod diel vertical distribution in the open southern Adriatic Sea (NE Mediterranean) under two different environmental conditions. Water, 14(12), 1901. https://doi.org/10.3390/w14121901

Khanaychenko, A., Mukhanov, V., Aganesova, L., Besiktepe, S., Gavrilova, N. 2018. Grazing and feeding selectivity of *Oithona davisae* in the Black Sea: Importance of cryptophytes. Turkish Journal of Fisheries and Aquatic Sciences, 18(8), 937-949. https://doi.org/10.4194/1303-2712-v18_8_02

Krawczyk, D.W., Witkowski, A., Juul-Pedersen, T., Arendt, K.E., Mortensen, J., Rysgaard, S. 2015. Microplankton succession in a SW Greenland tidewater glacial fjord influenced by coastal inflows and run-off from the Greenland ice sheet. Polar Biology, 38(9), 1515-1533. https://doi.org/10.1007/s00300-015-1715-y

Kršinić, F. 1998. Vertical distribution of protozoan and microcopepod communities in the South Adriatic Pit. Journal of Plankton Research, 20(6), 1033-1060. https://doi.org/10.1093/plankt/20.6.1033

Lampitt, R.S., Gamble, J.C. 1982. Diet and respiration of the small planktonic marine copepod *Oithona nana*. Marine Biology, 66(2), 185-190. https://doi.org/10.1007/BF00397192

Ljubešić, Z., Mihanović, H., Matek, A., Mucko, M., Achterberg, E.P., Omand, M., Pestorić, B., *et al.* 2024. Marine plankton community and net primary production responding to island-trapped waves in a stratified oligotrophic ecosystem. Heliyon, 10(18), e37788. https://doi.org/10.1016/j.heliyon.2024.e37788

Lombard, F., Eloire, D., Gobet, A., Stemmann, L., Dolan, J.R., Sciandra, A., Gorsky, G. 2010. Experimental and modeling evidence of appendicularian-ciliate interactions. Limnology and Oceanography, 55(1), 77-90. https://doi.org/10.4319/lo.2010.55.1.0077

Lombard, F., Selander, E., Kiørboe, T. 2011. Active prey rejection in the filter-feeding appendicularian *Oikopleura dioica*. Limnology and Oceanography, 56(4), 1504-1512. https://doi.org/10.4319/lo.2011.56.4.1504

Lučić, D. 1998. Annual variability in the population density distribution of appendicularians in coastal areas of the southern Adriatic. Monte Carlo: CIESM, 35(2), 464-465.

Lučić, D., Hure, M., Bobanović-Ćolić, S., Njire, J., Vidjak, O., Onofri, I., Gangai Zovko, B., *et al.* 2019. The effect of temperature change and oxygen reduction on zooplankton composition and vertical distribution in a semi-enclosed marine system. Marine Biology Research, 15(4-6), 325-342. https://doi.org/10.1080/17451000.2019.1655161

Ma, L., Xiao, W., Laws, E.A., Bai, X., Chiang, K.-P., Liu, X., Chen, J., *et al.* 2021. Responses of phytoplankton communities to the effect of internal wave-powered upwelling. Limnology and Oceanography, 66(4), 1083-1098. https://doi.org/10.1002/lno.11666

Maar, M., Visser, A.W., Nielsen, T.G., Stips, A., Saito, H. 2006. Turbulence and feeding behaviour affect the vertical distributions of *Oithona similis* and *Microsetella norvegica*. Marine Ecology Progress Series, 313, 157-172. https://doi.org/10.3354/meps313157

Mihanović, H., Beg Paklar, G., Orlić, M. 2014. Resonant excitation of island-trapped waves in a shallow, seasonally stratified sea. Continental Shelf Research, 77, 24-37. https://doi.org/10.1016/j.csr.2014.01.014

Miloslavić, M., Lučić, D., Njire, J., Gangai, B., Onofri, I., Garić, R., Žarić, M., *et al.* 2012. Zooplankton composition and distribution across coastal and offshore waters off Albania (Southern Adriatic) in late spring. Acta Adriatica, 53(2), 165-180.

Miloslavić, M., Lučić, D., Gangai, B., Onofri, I. 2014. Mesh size effects on mesozooplankton community structure in a semi-enclosed coastal area and surrounding sea (South Adriatic Sea). Marine Ecology, 35(4), 445-455. https://doi.org/10.1111/maec.12101

Miloslavić, M., Lučić, D., Žarić, M., Gangai, B., Onofri, I. 2015. The importance of vertical habitat gradients on zooplankton distribution in an enclosed marine environment (South Adriatic Sea). Marine Biology Research, 11(5), 462-474. https://doi.org/10.1080/17451000.2014.955802

Mucko, M., Russo, L., Matek, A., Grgurević, F., Pestorić, B., Achterberg, E.P., D'Alelio, D., *et al.* 2025. Influence of Internal Island-Trapped Waves on Plankton Structure and Trophic Networks in Stratified Oligotrophic Coastal Waters. Marine Environmental Research, 107578. https://doi.org/10.1016/j.marenvres.2025.107578

Nakamura, Y., Suzuki, K., Suzuki, S., Hiromi, J. 1997. Production of *Oikopleura dioica* (Appendicularia) following a picoplankton 'bloom' in a eutrophic coastal area. Journal of Plankton Research, 19(1), 113-124. https://doi.org/10.1093/plankt/19.1.113

Nakamura, Y., Turner, J.T. 1997. Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? Journal of Plankton Research, 19(9), 1275-1288. https://doi.org/10.1093/plankt/19.9.1275

Nival, S., Ravera, S. 1979. Morphological study of the appendages of the marine cladoceran *Evadne spinifera* Muller by means of the scanning electron microscope. Journal of Plankton Research, 1(3), 207-213. https://doi.org/10.1093/plankt/1.3.207

Orlić, M., Beg Paklar, G., Dadić, V., Leder, N., Mihanović, H., Pasarić, M., Pasarić, Z. 2011. Diurnal upwelling resonantly driven by sea breezes around an Adriatic island. Journal of Geophysical Research, 116(C9), C09025. https://doi.org/10.1029/2011JC006955

Paffenhöfer, G.-A. 1998. Heterotrophic protozoa and small metazoa: feeding rates and prey-consumer interactions. Journal of Plankton Research, 20(1), 121-133. https://doi.org/10.1093/plankt/20.1.121

Pernica, P., Wells, M.G., Sprules, W.G. 2013. Internal waves and mixing in the epilimnion of a lake affects spatial patterns of zooplankton in a body-size dependent manner. Limnology and Oceanography: Fluids and Environments, 3(1), 279-294. https://doi.org/10.1215/21573689-2409149

Pestorić, B., Drakulović, D., Hure, M., Gangai Zovko, B., Onofri, I., Lučić, P., Lučić, D. 2016. Zooplankton community in the Boka Kotorska Bay. *In* The Boka Kotorska Bay Environment (eds. A. Joksimović, M. Djurović, A.V. Semenov, I.S. Zonn, A.G. Kostianoy). Springer. pp. 231-270. https://doi.org/10.1007/698_2016_35

Quevedo, M., Anadón, R. 2000. Spring microzooplankton composition, biomass and potential grazing in the central Cantabrian coast (southern Bay of Biscay). Oceanologica Acta, 23(3), 297-310. https://doi.org/10.1016/S0399-1784(00)00128-6

Saiz, E., Calbet, A., Atienza, D., Alcaraz, M. 2007. Feeding and production of zooplankton in the Catalan Sea (NW Mediterranean). Progress in Oceanography, 74(2-3), 313-328. https://doi.org/10.1016/j.pocean.2007.04.004

Simpson, G., Oksanen, J. 2025. ggvegan: ‘ggplot2’ Plots for the ‘vegan’ Package. R package version 0.1.999.

Sommer, U., Stibor, H., Katechakis, A., Sommer, F., Hansen, T. 2002. Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. Hydrobiologia, 484(1), 11-20. https://doi.org/10.1023/A:1021340601986

Stoecker, D.K., Gustafson, D.E., Verity, P.G. 1996. Micro- and mesoprotozooplankton at 140*W in the equatorial Pacific: heterotrophs and mixotrophs. Aquatic Microbial Ecology, 10, 273-282. https://doi.org/10.3354/ame010273

Suzuki, K., Nakamura, Y., Hiromi, J. 1999. Feeding by the small calanoid copepod *Paracalanus* sp. on heterotrophic dinoflagellates and ciliates. Aquatic Microbial Ecology, 17, 99-103. https://doi.org/10.3354/ame017099

Swanberg, N.R., Caron, D.A. 1991. Patterns of sarcodine feeding in epipelagic oceanic plankton. Journal of Plankton Research, 13(2), 287-312. https://doi.org/10.1093/plankt/13.2.287

Trégouboff, G., Rose, M. 1957. Manuel De Planctonologie Méditerranéenne (Manual of Mediterranean planktonology). Centre National de la Recherche Scientifique, 218 pp.

Turner, J.T. 1984. Zooplankton feeding ecology: contents of fecal pellets of the copepods *Temora turbinata* and *T. stylifera* from continental shelf and slope waters near the mouth of the Mississippi River. Marine Biology, 82(1), 73-83. https://doi.org/10.1007/BF00392765

Turner, J.T. 1986. Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the northern Gulf of Mexico. Marine Ecology, 7(4), 289-302. https://doi.org/10.1111/j.1439-0485.1986.tb00165.x

Turner, J.T. 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zoological Studies, 43(2), 255-266.

Utermöhl, H. 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik (Methods of collecting plankton for various purposes are discussed). Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen, 9(1), 1-38. https://doi.org/10.1080/05384680.1958.11904091

Vargas, C.A., González, H.E. 2004. Plankton community structure and carbon cycling in a coastal upwelling system. I. Bacteria, microprotozoans and phytoplankton in the diet of copepods and appendicularians. Aquatic Microbial Ecology, 34, 151-164. https://doi.org/10.3354/ame034151

Vidjak, O., Bojanić, N., Kušpilić, G., Marasović, I., Ninčević Gladan, Ž., Brautović, I. 2006. Annual variability and trophic relations of the mesozooplankton community in the eutrophicated coastal area (Vranjic Basin, eastern Adriatic Sea). Journal of the Marine Biological Association of the United Kingdom, 86(1), 19-26. https://doi.org/10.1017/S0025315406012811

Vidjak, O., Bojanić, N., Kušpilić, G., Ninčević Gladan, Ž., Tičina, V. 2007. Zooplankton community and hydrographical properties of the Neretva Channel (eastern Adriatic Sea). Helgoland Marine Research, 61(4), 267-282. https://doi.org/10.1007/s10152-007-0074-7

Vidjak, O., Bojanić, N., Matijević, S., Kušpilić, G., Ninčević Gladan, Ž., Skejić, S., Grbec, B., *et al.* 2012. Environmental drivers of zooplankton variability in the coastal eastern Adriatic (Mediterranean Sea). Acta Adriatica, 53(2), 243-262.

Villate, F., Uriarte, I., Olivar, M.P., Maynou, F., Emelianov, M., Ameztoy, I. 2014. Mesoscale structure of microplankton and mesoplankton assemblages under contrasting oceanographic conditions in the Catalan Sea (NW Mediterranean). Journal of Marine Systems, 139, 9-26. https://doi.org/10.1016/j.jmarsys.2014.05.004

Vogt, R.A., Ignoffo, T.R., Sullivan, L.J., Herndon, J., Stillman, J.H., Kimmerer, W.J. 2013. Feeding capabilities and limitations in the nauplii of two pelagic estuarine copepods, *Pseudodiaptomus marinus* and *Oithona davisae*. Limnology and Oceanography, 58(6), 2145-2157. https://doi.org/10.4319/lo.2013.58.6.2145

Wang, Y.-H., Dai, C.-F., Chen, Y.-Y. 2007. Physical and ecological processes of internal waves on an isolated reef ecosystem in the South China Sea. Geophysical Research Letters, 34(18), L18609. https://doi.org/10.1029/2007gl030658

Wickham, H. 2016. Data Analysis. *In* ggplot2: elegant graphics for data analysis (ed. H. Wickham). Springer. pp. 189-201. https://doi.org/10.1007/978-3-319-24277-4_9

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, 620 pp.

Zhao, W., Dai, L., Chen, X., Wu, Y., Sun, Y., Zhu, L. 2022. Characteristics of zooplankton community structure and its relationship with environmental factors in the South Yellow Sea. Marine Pollution Bulletin, 176, 113471. https://doi.org/10.1016/j.marpolbul.2022.113471