



Primary productivity impacts community structure of euphausiids in the low-latitude Indian and Pacific Oceans

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Abstract

Euphausiids are a vital component of global marine micronekton. To reveal the primary environmental factors influencing euphausiid distribution patterns in the previously overlooked low-latitude ecosystems, we investigated a large-scale community structure of euphausiids covering the North Pacific subtropical gyre (NPSG) and low-latitude eastern Indian (EI), and South Pacific Oceans (SP). A total of 41 euphausiid species from six genera were identified. Integrated primary production (PP) correlated significantly with the euphausiid abundance and species diversity and displayed the most critical influence on the variations in euphausiid community structure in low latitudes. Dissolved oxygen (DO) was the second significant environmental driver. Due to the distinct distribution patterns of euphausiid species in response to different PP and DO levels, the low-latitude euphausiid assemblages were mainly distinguished into subtropical and tropical communities. The subtropical euphausiid community associated with lower PP and higher DO demonstrated significantly lower euphausiid abundance but higher diversity than the tropical community. *Euphausia brevis*, *E. mutica*, and *Stylocheiron abbreviatum*, which characterize the subtropical community, appear to depend less on the phytoplanktonic prey. *Euphausia diomedea* and *Hansarsia gracilis*, typifying the tropical population, showed stronger hypoxia tolerance. Additionally, each community was further divided into three subgroups under the influence of surface PP (subtropical: marginal NPSG, central NPSG, and austral EI-SP subgroups; tropical: the Bay of Bengal, equatorial EI, and equatorial EI-SP subgroups). These results suggested that food resource is the most important in shaping euphausiids' community structure in an oligotrophic ecosystem with subtle hydrography gradients.

Keywords Community structure · Euphausiid · Low-latitude · Primary production · Species diversity

1 Introduction

Euphausiids (Order Euphausiacea) are shrimp-like crustaceans that inhabit oceanic basins worldwide. They are vital pelagic ecosystem components, contributing to approximately 5–10% of total zooplankton biomass (Everson 2008).

Through diel vertical migration, many euphausiid species accelerate the transport of organic matter produced by phytoplankton photosynthesis from the euphotic zone to the deeper sea (Bianchi et al. 2013). Euphausiids are also significant links between lower and higher trophic levels in marine ecosystems as they feed on marine snow, phytoplankton, and small zooplankton (Dilling et al. 1998; Park et al. 2011) and function as frequent prey for commercially important fishes, marine mammals, and birds (Roger 1994). Thus, ascertaining the community structure and biomass of euphausiids is important for determining the fate of primary production and flux of organic matter to the deep ocean through the food web (Steinberg et al. 2008).

The worldwide distribution of the present 86 nominal euphausiid species has been systematically reported by Brinton et al. (2000). Euphausiid assemblages exhibit an apparent affinity for water masses, since they quickly react to changing hydrographical conditions, leading to

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a different community structure (Brinton 1962; Gibbons et al. 1995). Seawater temperature has been well-documented as the most crucial environmental factor affecting the euphausiid community structure. A summary of euphausiid standing stocks is available for the Atlantic Ocean (Letessier et al. 2009; 2011b) as well as for the Pacific Ocean (Letessier et al. 2011a). These studies confirm that the abundance and species richness of euphausiids in the two oceans were most influenced by sea surface temperature, linking higher euphausiid species richness with warmer seawater based on the species-energy hypothesis (Rohde 1992). Rutherford et al. (1999) and Rombouts et al. (2009) reached a similar conclusion in the global biodiversity pattern across other marine taxa.

Notable in the aforementioned studies are observations of considerably weaker impacts of seawater temperature on zooplankton community variation above 25 °C. This implies that other environmental factors should appear more significant in determining euphausiids' community structure in low-latitude open-water ecosystems which are generally characterized by higher temperatures. For instance, it has been shown that food resource availability might influence euphausiid distribution in the southeastern Indian Ocean (9–32° S, 110° E; McWilliam 1977) and may also be responsible for the differences in euphausiid species composition between the eastern and western North Pacific subtropical gyre (Zhou et al. 2021). Low dissolved oxygen levels were shown to prevent the existence of some euphausiids without good hypoxia tolerance (Tremblay et al. 2010, 2020; Seibel et al. 2016; Sutton and Beckley 2017), whereas surface circulations could disperse euphausiids beyond their normal distribution limits (Sutton and Beckley 2016). A comprehensive survey of euphausiid communities across subtropical and tropical zones covering different open oceans is required to gain deeper insight into a factor controlling community structures of euphausiids in low-latitude ecosystems.

The Pacific Ocean is the oldest and largest ocean basin (Barkley 1968). It hosts 59 of the 86 species of euphausiids (Brinton 1962; Brinton et al. 2000), with the North Pacific subtropical gyre (NPSG) being one of the hotspots of euphausiid species diversity (Letessier et al. 2011a). However, investigations on euphausiid spatial displacements, particularly the species-specific responses caused by changing environments, have been largely focused on mid-high latitudes or productive systems (Brinton and Townsend 2003; Yoon et al. 2006; Ambriz-Arreola et al. 2012; Rivera-Gómez et al. 2019; Lilly and Ohman 2021). The Indian Ocean contains two-thirds of the world's euphausiid species (Brinton and Gopalakrishnan 1973). However, the Indian Ocean has received less attention than the Pacific and Atlantic Oceans due to its dynamic hydrography and limited accessibility. To fill this knowledge gap, there is a need to investigate the

distribution of euphausiid species in low-latitude regions of the Pacific and Indian Oceans.

In the present study, euphausiids were collected mainly from the subtropical/tropical regions in the Pacific and eastern Indian Oceans. We posited that primary production, as a proxy for food available in the environment, is a significant driver for structuring the distribution and association of euphausiid species in low latitudes. To test this hypothesis, we present (1) the euphausiid abundance, species diversity, and the representative euphausiid species; (2) the primary drivers of the euphausiid distribution variations; and (3) how the representative species of euphausiids associate with these drivers in the low-latitude Indian and Pacific Oceans.

2 Materials and methods

2.1 Field collection

Sampling was conducted onboard the *R/V Hakuho-Maru* at 25 stations during the KH17-4, KH18-6, and KH19-6 cruises (Fig. 1, Table 1). The study sites are located mainly in the subtropical and tropical areas of the Indian and Pacific Oceans (except NP3 located in the California Current [CC] and NP4 in the subarctic-subtropical transition zone of the eastern North Pacific [Rodén 1971]). At each station, zooplankton samples were collected at night from approximately 500 m depth to the surface using oblique tows of Matsuda-Oozeki-Hu Trawl (MOHT; Oozeki et al. 2007) at 3–4 knots of the ship speed. The MOHT in this study had a square mouth of 2 m² mouth area (1.43 × 1.43 m) and 1.95 mm mesh size. A flow meter was attached to the net to measure the filtered water volume. Samples were promptly split after landing of the net onboard, and one-eighth or one-fourth of the aliquots were fixed with 5% buffered formaldehyde for community structure analysis. Vertical profiles of water temperature, salinity, and dissolved oxygen (DO; mL O₂ L⁻¹) between 0 and 500 m at all stations were recorded using a conductivity-temperature-depth (CTD) system (SBE-911 plus; Sea-Bird Electronics) and dissolved oxygen sensor (SBE-43; Sea-Bird Electronics). Mixed layer depth (MLD) was determined using a $\Delta T = 0.2$ °C criterion relative to a 10-m reference level on individual profiles (de Boyer et al. 2004). For chlorophyll *a* (Chl-*a*) measurements, water samples were collected using Niskin bottles attached to the CTD system at 13 intervals from 0 to 250 m at each station. Chl-*a* was extracted with *N, N*-dimethylformamide, and its concentration was analyzed using a Turner fluorometer (Turner Designs). Additionally, nitrogen fixation rate and primary production were measured at depths corresponding to 100%, 10%, 1%, and 0.1% of surface light density

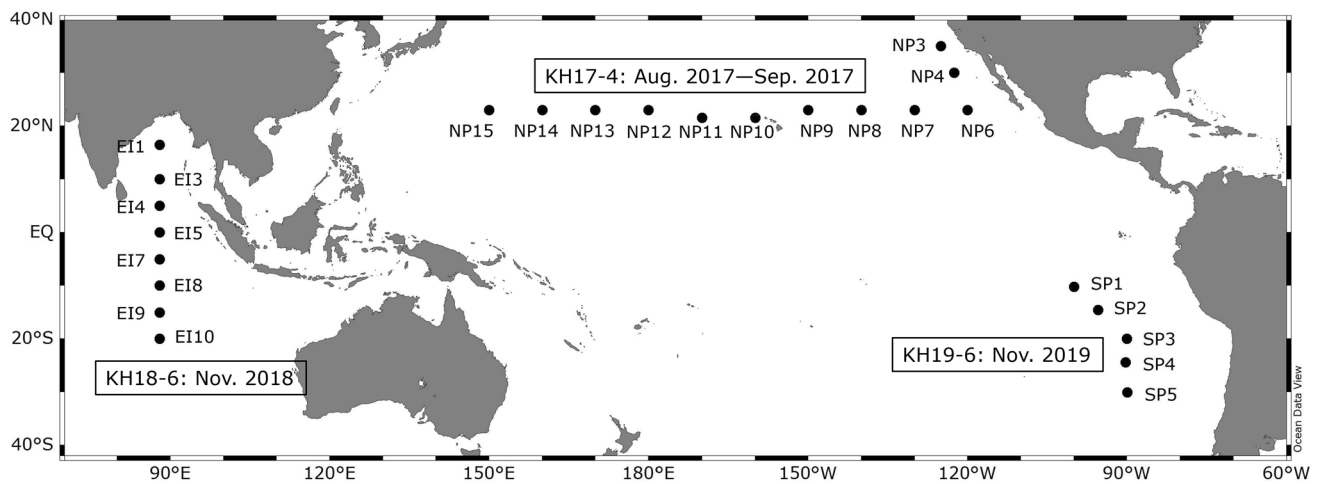


Fig. 1 Sampling locations of the present study. Samples were collected at 25 stations during three cruises (KH17-4, KH18-6, and KH19-6) across different ocean basins: The North Pacific Ocean (NP3–15), Eastern Indian Ocean (EI1–10), and South Pacific Ocean (SP1–5)

Table 1 Sampling information including cruise, date, location, sampling time, and depth of each station

Area	Station	Date	Sampling time	Latitude	Longitude	Depth (m)	
North Pacific Ocean (KH17-4)	NP3	17 Aug. 2017	2:37–4:10	35.00° N	125.00° W	394	
	NP4	19 Aug. 2017	1:12–2:50	30.00° N	122.50° W	509	
	NP6	21 Aug. 2017	21:15–22:46	23.00° N	120.00° W	489	
	NP7	24–25 Aug. 2017	23:40–1:25	23.00° N	130.00° W	504	
	NP8	27 Aug. 2017	0:40–2:23	23.00° N	140.00° W	499	
	NP9	31 Aug. 2017	1:40–3:32	23.00° N	150.00° W	495	
	NP10	3 Sep. 2017	21:27–22:50	21.50° N	160.00° W	481	
	NP11	14 Sep. 2017	1:05–2:40	21.50° N	170.00° W	488	
	NP12	17 Sep. 2017	0:35–2:17	23.00° N	180.00°	488	
	NP13	19 Sep. 2017	22:22–0:00	23.00° N	170.00° E	491	
	NP14	22–23 Sep. 2017	23:20–0:52	23.00° N	160.00° E	482	
	NP15	28 Sep. 2017	0:58–2:18	23.00° N	150.00° E	490	
	Eastern Indian Ocean (KH18-6)	EI1	9 Nov. 2018	4:18–5:59	16.50° N	88.01° E	479
		EI3	13 Nov. 2018	0:48–2:14	10.01° N	88.00° E	496
		EI4	15 Nov. 2018	0:43–2:20	5.00° N	88.00° E	496
EI5		18–19 Nov. 2018	23:10–0:17	0.00°	88.01° E	500	
EI7		20 Nov. 2018	19:11–20:56	5.00° S	88.01° E	487	
EI8		22 Nov. 2018	20:45–22:19	10.00° S	88.01° E	503	
EI9		27–28 Nov. 2018	23:02–0:40	15.00° S	88.01° E	496	
EI10		26 Nov. 2018	2:11–3:53	20.00° S	88.01° E	491	
South Pacific Ocean (KH19-6)		SP1	11 Nov. 2019	0:05–1:47	10.19° S	100.01° W	494
		SP2	13 Nov. 2019	0:59–01:59	14.59° S	95.44° W	521
	SP3	15–16 Nov. 2019	23:45–1:45	20.00° S	90.00° W	525	
	SP4	16 Nov. 2019	21:10–22:20	24.43° S	90.29° W	506	
	SP5	19 Nov. 2019	23:55–0:43	30.07° S	89.99° W	498	

using the ^{15}N - ^{13}C dual inlet technique that combines $^{15}\text{N}_2$ gas dissolution (Mohr et al. 2010) with a ^{13}C primary production assay (Hama et al. 1983) according to Sato et al. (2022) and Horii et al. (2023). Depth-integrated nitrogen fixation and primary production were calculated using trapezoidal integration. Details of the sampling and water properties are presented in Table 1 and S1, respectively.

2.2 Euphausiid community structure analysis

All adult euphausiids at each station were sorted in the laboratory and identified to the lowest possible taxonomic level according to Baker et al. (1990) and Brinton et al. (2000) under a stereomicroscope (Nikon SMZ-745 T). The genus *Nematoscelis* is described as *Hansarsia* in the present study,

according to Shaw et al. (2023). *Thysanopoda astylata* and *T. aequalis* were merged as one species because of the absence of subtle morphological differences between the two species. The total length of euphausiids was measured from the tip of the rostrum to the end of the telson. The abundance of each species was standardized as individuals (ind.) 1000 m^{-3} . Species richness (N, total number of species), Shannon index (H' ; Shannon 1948), and Simpson's diversity index (D [compliment]; Simpson 1949) were computed to evaluate euphausiid species diversity. To detect the regional differences in euphausiid abundance and species diversity, the Kruskal–Wallis test with Dunn post hoc test or Mann–Whitney U test was conducted when data sets were non-normally distributed. Otherwise, a one-way analysis of variance (ANOVA) with Fisher's least significant difference post-hoc test was used. To investigate the relationship between euphausiid abundance and species diversity and the environment, correlations among euphausiid abundance, species diversity, and environmental parameters were tested using Spearman's rank correlation. All analyses were performed using the IBM SPSS Statistics 23 (Zar 1999).

For further community analyses, to avoid spurious associations among rare species, only species comprising more than 3% of the total euphausiid abundance at any station were included. To evaluate the relationship among euphausiid assemblages in the study area, cluster analysis (group average) and non-metric multidimensional scaling ordination based on the Bray–Curtis similarity index were employed on $\log(x + 1)$ -transformed euphausiid abundance data. To assess the similarity within the potential clustered groups and the dissimilarity between groups and verify the “representative species” that typified every clustered

group, similarity percentages analysis (SIMPER) was executed (Clarke 1993). Euphausiid species that contributed to the similarity/dissimilarity within/between groups majorly (displaying higher *Av.Sim* or *Av.Diss* values) and consistently (larger *Sim/SD* or *Diss/SD* ratios) were determined as “representative species” of the defined clustered groups.

To explore the effects of environmental drivers on euphausiid community structure in the low latitudes (except NP3), sea surface temperature (SST), sea surface salinity (SSS), depth-averaged (0–500 m) temperature and salinity (T_{500} ; S_{500}), depth-averaged (0–250 m) DO (DO_{250}), MLD, surface Chl-*a*, integrated Chl-*a* from 0 to 250 m, integrated nitrogen fixation, surface primary production, and integrated primary production were assessed using distance-based linear model (DistLM) analysis. To determine the best combination of these predictor variables to explain the variation in the euphausiid community, models were constructed using the BEST selection procedure (all possible variable combinations) under the Akaike Information Criterion (AIC) with 9999 permutations. Finally, distance-based redundancy analysis (dbRDA) was used to visualize the impact of the fitted environmental parameters ascertained by DistLM on the representative euphausiid species. All analyses were performed using PRIMER version 7 with the PERMANOVA + add-on package (Anderson et al. 2008).

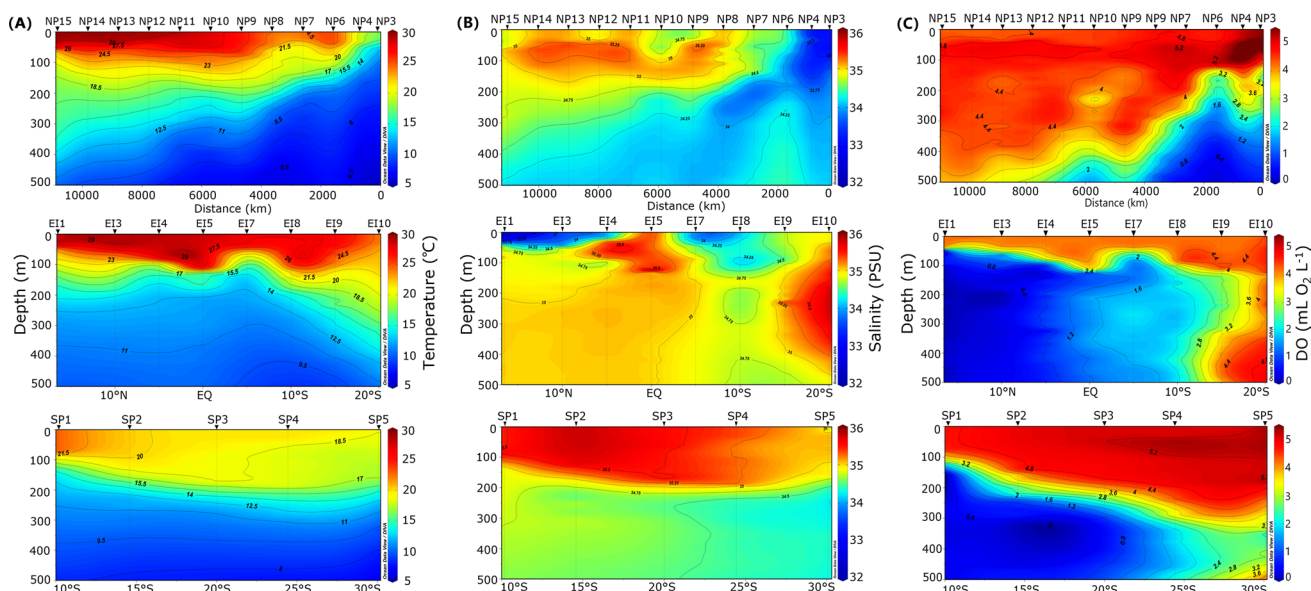


Fig. 2 Vertical sections of **A** water temperature ($^{\circ}\text{C}$), **B** salinity (PSU), and **C** DO ($\text{mL O}_2\text{ L}^{-1}$) at 0–500 m across the three study sites

3 Results

3.1 Environmental conditions

Located at relatively higher latitudes, NP3–4 demonstrated distinctively lower temperatures and salinities than other stations in the subtropical and tropical areas (Fig. 2A and B, Fig. S1). NP6, on the outer edge of NPSG, also presented unique intermediate thermohaline conditions. As for the low-latitude area, stations in the South Pacific were characterized by a significantly lower average SST (20.6 °C) than the eastern Indian (average of 27.8 °C) and other NPSG stations (NP7–15; 27.8 °C; Kruskal–Wallis; $p < 0.05$) and a relatively higher average SSS. The South Pacific water was also well-mixed, whereas a prominent temperature gradient in the upper 200 m was observed in NPSG and the eastern Indian Ocean (Fig. 2A). Moreover, the water mass of the eastern Indian Ocean displayed lower salinity in the upper 100 m (except at EI5), which was different from that of NPSG with higher salinity (Fig. 2B and Table S1). Another notable feature of the eastern Indian stations was a significantly lower average DO_{250} (2.4 mL

$O_2 L^{-1}$) compared to the NPSG stations (average 4.5 mL $O_2 L^{-1}$) and the South Pacific stations (average 4.2 mL $O_2 L^{-1}$; Kruskal–Wallis; $p < 0.05$). Hypoxic conditions ($< 1 mL O_2 L^{-1}$) were observed in the shallow layers at the northern Indian stations and SP1 (49–145 m).

The surface Chl-*a* concentration was similar across the three ocean regions. However, the average integrated Chl-*a* from 0 to 250 m was significantly lower in the South Pacific (17.1 mg m^{-2}) than in the NPSG area (29.7 mg m^{-2}) and eastern Indian Ocean (27.9 mg m^{-2} ; Kruskal–Wallis; $p < 0.05$). Deeper subsurface chlorophyll maxima (below 100 m) were obtained at stations in the subtropical zone, particularly in western NPSG (NP11–15; average 128 m). Furthermore, a regional pattern of Chl-*a* was evident in each ocean (Fig. 3A). The average surface Chl-*a* levels of stations EI1–4 and SP1–2 were significantly higher than the southern EI7–10 and SP3–5 (One-way ANOVA, $p < 0.05$). The western NPSG stations displayed a relatively greater average integrated Chl-*a* concentration (33.5 mg m^{-2}) than the eastern NPSG stations (25.9 mg m^{-2}). Additionally, the average integrated primary production (PP) was significantly lower in the NPSG region (0.21 g C $m^{-2} d^{-1}$) than in the eastern Indian (0.73 g C $m^{-2} d^{-1}$) and South Pacific

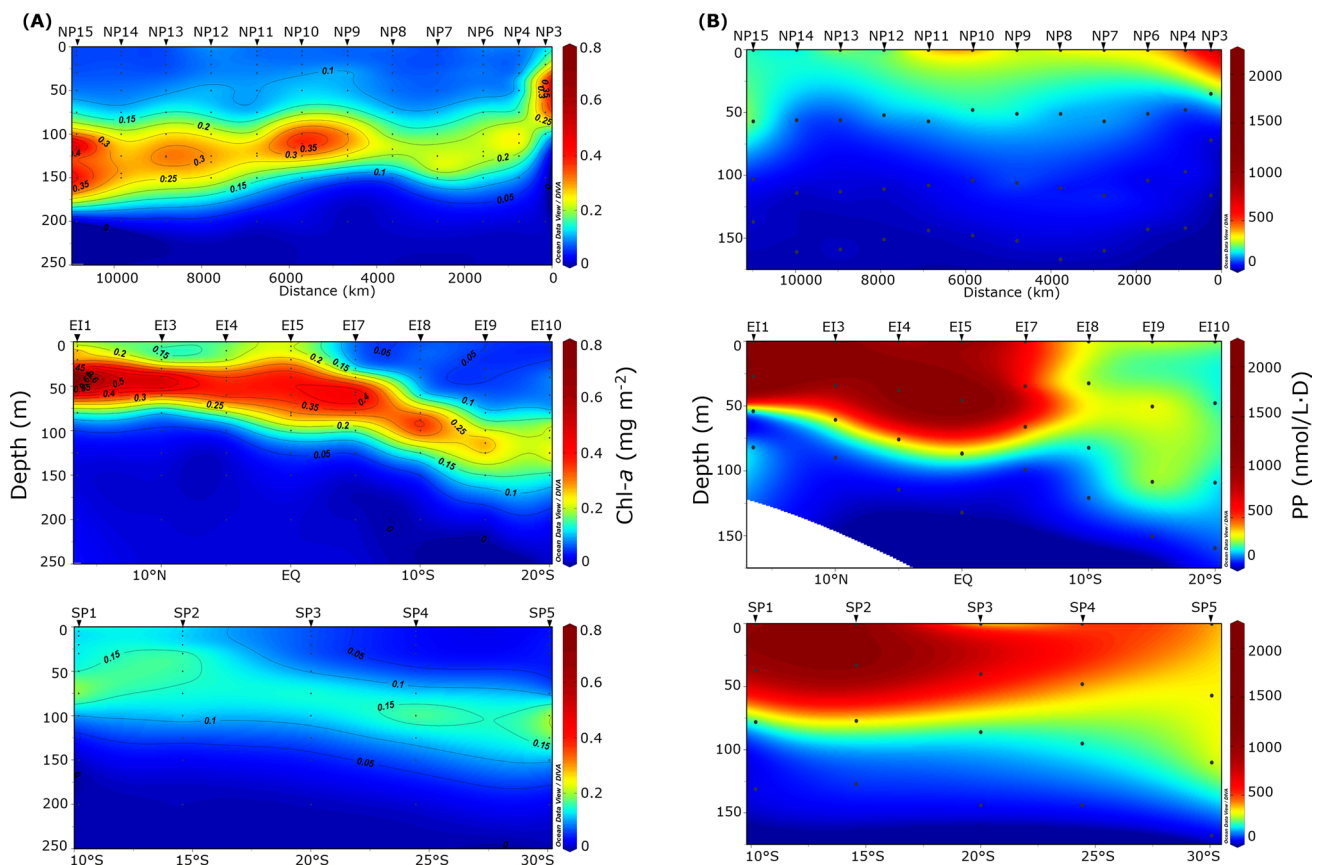


Fig. 3 Vertical sections of **A** chlorophyll *a* concentration ($\mu g/L$) at 0–250 m and **B** primary production level ($nmol/L \cdot D$) across the three study sites

Oceans ($0.70 \text{ g C m}^{-2} \text{ d}^{-1}$; One-way ANOVA, $p < 0.05$). Like the regional pattern of Chl-*a*, the northern stations in the eastern Indian and South Pacific Oceans had significantly higher average surface and integrated PP than the southern stations (one-way ANOVA, $p < 0.05$). However, the eastern NPSG displayed a higher average surface and integrated PP than the western NPSG, in contrast to the integrated Chl-*a* pattern in the NPSG region. The integrated nitrogen fixation of the NPSG region was significantly greater (average $91.1 \text{ } \mu\text{mol N m}^{-2} \text{ d}^{-1}$) than that of the low-latitude South Pacific ($16.0 \text{ } \mu\text{mol N m}^{-2} \text{ d}^{-1}$) and the eastern Indian Oceans ($45.7 \text{ } \mu\text{mol N m}^{-2} \text{ d}^{-1}$; Kruskal–Wallis; $p < 0.05$).

3.2 Abundance and diversity of euphausiids

A total of 41 euphausiid species (including nine rare species) from six genera were identified in the study area (Table S2): thirteen species of *Euphausia*, nine of *Stylocheiron*, eight of *Thysanopoda*, six of *Hansarsia*, three of *Nematobrachion*, and two of *Thysanoessa*. The average length (mean \pm SD) of identified euphausiid species ranged from 4.9 ± 0.1 (*S. submii*) to 29.3 ± 2.6 mm (*T. orientalis*). The total abundance of adult euphausiids significantly varied among stations from $13.9 \text{ ind. } 1000 \text{ m}^{-3}$ at NP13 to $1893.3 \text{ ind. } 1000 \text{ m}^{-3}$ at EI1 (Fig. 4A). Moreover, euphausiid abundance was strongly and positively correlated with surface PP, integrated PP, and surface Chl-*a* and negatively correlated with DO_{250} (Table 2). Specifically, the eastern Indian Ocean with a higher integrated PP and lower DO level possessed a significantly greater euphausiid abundance (average $462.4 \text{ ind. } 1000 \text{ m}^{-3}$) than the North Pacific ($71.6 \text{ ind. } 1,000 \text{ m}^{-3}$; SP: $214.7 \text{ ind. } 1000 \text{ m}^{-3}$). A southward-decreasing gradient of euphausiid abundance was observed in the eastern Indian Ocean, consistent with the surface Chl-*a* tendency. Euphausiid abundance in the NPSG region followed the same pattern as the surface and integrated PP, showing a significantly higher abundance in eastern NPSG (NP6–10; peaked at NP10) than in western NPSG (Mann–Whitney *U*; $p < 0.05$).

In contrast to the euphausiid abundance pattern, the eastern Indian Ocean presented a relatively lower euphausiid species number and diversity (mean \pm SD; $N = 12.8 \pm 6.3$, $H' = 1.5 \pm 0.7$, $D = 0.6 \pm 0.2$) than the North Pacific ($N = 14.3 \pm 3.2$, $H' = 2.0 \pm 0.5$, $D = 0.8 \pm 0.2$) and South Pacific Oceans ($N = 16.6 \pm 2.5$, $H' = 2.1 \pm 0.4$, $D = 0.8 \pm 0.1$). Correspondingly, euphausiid species diversity was negatively associated with surface PP, integrated PP, and surface Chl-*a*, and the species number was negatively related to surface Chl-*a* and PP. A positive correlation between species diversity and DO concentration was observed (Table 2). Moreover, within the lower latitudes, there was a general increasing trend in euphausiid species diversity from the equator to $\sim 20^\circ\text{S}$ both in the eastern Indian Ocean and the South Pacific. Further, stations settled in the subtropical

gyres (latitude $\sim 20\text{--}30^\circ$) showed significantly higher H' and D than the tropical stations (One-way ANOVA, $p < 0.05$, Fig. 4B).

3.3 Euphausiid community structure related to environmental factors

Based on the abundance and composition of euphausiids at each station, cluster analysis helped delineate three major groups of euphausiid communities in the study area at a 22% similarity level, the CC, subtropical, and tropical groups (Fig. 5). The CC group containing only NP3 at a higher latitude, dominated by *Euphausia pacifica* (Fig. 4A), was considerably different from the other two groups (at a 10% similarity level); therefore, it was considered an outgroup. The subtropical group consisting of stations NP4–15, EI9–10, and SP3–5 displayed significantly lower euphausiid abundance and higher euphausiid species number and diversity than the tropical group comprising stations EI1–8 and SP1–2 (Fig. 4B; One way ANOVA, $p < 0.05$). These two groups were further divided into three subgroups at a 45% similarity level (subtropical: marginal NPSG, central NPSG, and austral eastern Indian Ocean [EI]–South Pacific [SP] subgroups; tropical: Bay of Bengal [BoB], equatorial EI–SP, and equatorial EI subgroups; Fig. 5). The equatorial EI subgroup only contained station EI5 at the equator whereas other stations located in the equatorial region of the South Pacific (SP1–2) and the eastern Indian Ocean (EI4 and EI7–8) were included in the equatorial EI–SP subgroup.

DistLM analysis revealed that most of the assessed environmental variables significantly influenced the low-latitude euphausiid community structure individually ($p < 0.05$), especially DO_{250} (Pseudo $F = 12.13$; $p < 0.01$), surface PP (Pseudo $F = 10.71$; $p < 0.01$), and total PP level (Pseudo $F = 10.02$; $p < 0.01$) (Table S3). Moreover, the combination of SST, SSS, S_{500} , DO_{250} , surface Chl-*a*, surface PP, integrated PP, and integrated nitrogen fixation optimally accounted for euphausiid community structure patterns across the study area ($R^2 = 0.72$). According to the RDA ordination, these environmental variables explained 40.7% and 13.4% of the total variance in euphausiid communities on Axis1 and Axis2, respectively (Fig. 6). The subtropical and tropical groups bore strong connections to integrated PP and DO_{250} , which were highly correlated with Axis1. The secondary structure of the two euphausiid communities was mainly affected by surface PP, Chl-*a*, and thermohaline conditions. Within the subtropical community, the austral EI–SP subgroup correlated with higher salinity, distinct from the marginal and central NPSG subgroups associated with warmer and less saline water. For the tropical community, the equatorial EI and BoB subgroups with higher surface PP and SST were clearly separated from the equatorial EI–SP subgroup (Fig. 6 and Fig. 5C).

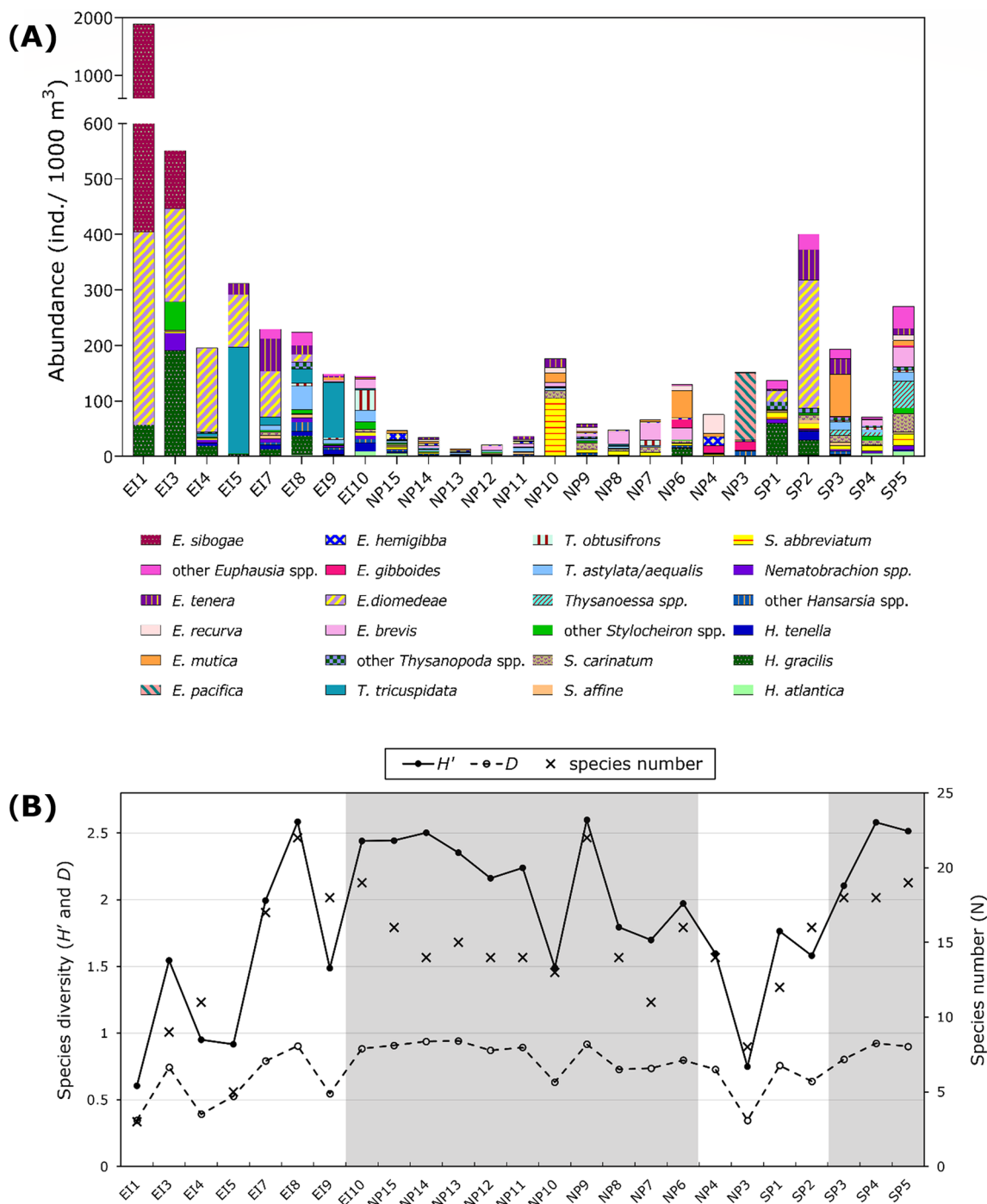


Fig. 4 **A** Euphausiid species composition and abundance (individuals/ 1,000 m³) at each sampling station. Different colors indicate different euphausiid species. **B** Euphausiid species diversity (H' and

D) and total species number (N) of each station. Subtropical stations with higher species diversity are shaded

3.4 Representative euphausiid species in subtropical and tropical areas

SIMPER analysis revealed that *E. brevis*, *E. mutica*, and *Stylocheiron abbreviatum* were primary contributors to the internal similarity of the subtropical community (higher *Av.*

sim values; Table 3). All three species occupied > 10% of the total subtropical community abundance (high *Av.abund* value), and they were evenly distributed (high *Sim/SD* ratio) at the subtropical stations (Fig. 4A and Table 3). However, *S. abbreviatum* was scarce (< 5 ind. 1000 m⁻³) at most stations, yet only overwhelmingly abundant at NP10, in contrast to *E.*

Table 2 Spearman correlation coefficients between euphausiid abundance and species diversity indices (N: number of species, H' : Shannon index, D : Simpson's diversity index) and environmental variables

	SST (°C)	T_{500} (°C)	MLD (m)	SSS (PSU)	S_{500} (PSU)	DO_{250} (mL L ⁻¹)	Surface Chl- <i>a</i> (µg L ⁻¹)	Total Chl- <i>a</i> (mg m ⁻²)	Surface PP (nmol/L·D)	Total PP (g C m ⁻² d ⁻¹)	Total N ₂ (µmol N m ⁻² d ⁻¹)
Total abundance	-0.250	-0.270	0.304	-0.244	0.414*	-0.631**	0.376	-0.135	0.730**	0.817**	-0.218
N	-0.251	0.206	0.048	0.242	0.025	0.326	-0.709**	-0.385	-0.536**	-0.260	-0.107
H'	0.058	0.325	-0.241	0.336	-0.136	0.563**	-0.678**	-0.153	-0.655**	-0.528**	-0.060
D	0.223	0.416	-0.245	0.388	-0.080	0.523**	-0.627**	-0.028	-0.649**	-0.591*	-0.098

SST: sea surface temperature. SSS: sea surface salinity. T_{500} , S_{500} : depth-averaged (0–500 m) water temperature, salinity. DO_{250} : depth-averaged (0–250 m) dissolved oxygen concentration. Total Chl-*a*: depth-integrated (0–250 m) chlorophyll-*a* concentration. Total N₂, PP: depth-integrated (light depth 0.1–100%) nitrogen fixation and primary production

Bold numbers indicate a significant correlation (* $p < 0.05$; ** $p < 0.01$)

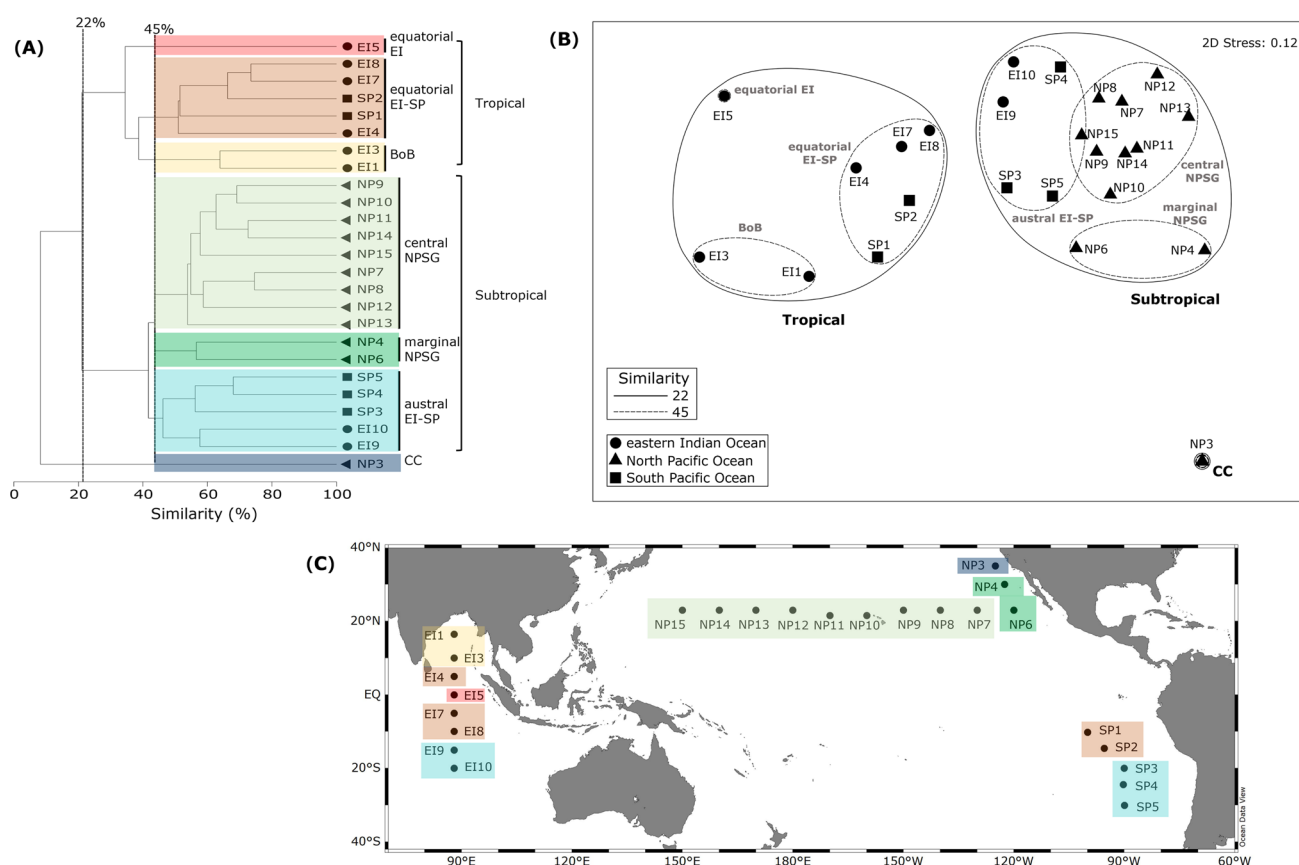


Fig. 5 **A** Dendrogram derived by cluster analysis on the euphausiid community using $\log(x+1)$ -transformed species abundance data and the Bray–Curtis similarity index. **B** Multidimensional scaling

ordination plot overlapping clustered analysis suggesting similarities between euphausiid communities. **C** Geographic distributions of different clustered groups

brevis and *E. mutica* (Fig. 4A and Table S2). Furthermore, the heterogeneous distribution of specific euphausiid species shaped the secondary structure of the subtropical euphausiid community. The absence of *E. hemigibba* only in the austral EI-SP, relatively greater abundances of *Hansarsia atlantica*

and *S. carinatum* in the south hemisphere, and higher density of *E. brevis* in central NPSG segregated the austral EI-SP subgroup and other two subgroups; the absence of *T. astylata/aequalis* together with the prevalence of *E. hemigibba* and *E. mutica* at the edge of NPSG, in addition to the

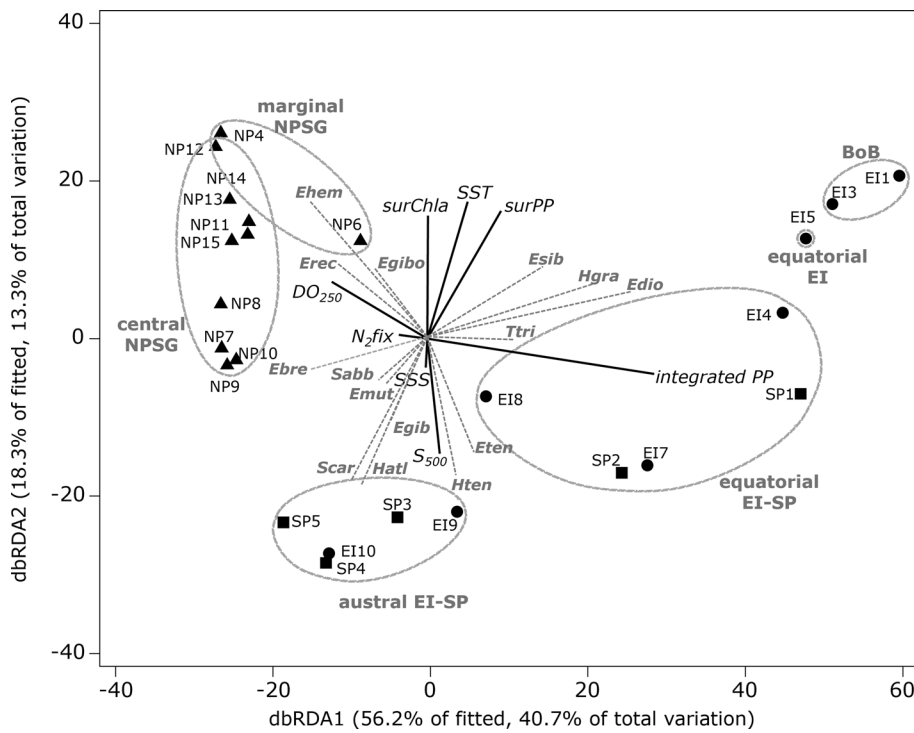


Fig. 6 Distance-based redundancy analysis (dbRDA) triplot illustrating the fitted distance-based linear model for low-latitude euphausiid community groups (except for NP3) and representative euphausiid species in the study area. Percentages (%) suggest the proportion of the fitted variation and the total variation in the Bray–Curtis resemblance matrix explained by dbRDA axes. The environmental variables that significantly explain the variation in low-latitude

euphausiid communities identified by the model are indicated as vectors in solid lines. Representative species were annotated by vectors as gray dashed lines. (Esib: *E. sibogae*; Hgra: *H. gracilis*; Edio: *E. diomedea*; Eten: *E. tenera*; Hten: *H. tenella*; Egib: *E. gibba*; Hatl: *H. atlantica*; Scar: *S. carinatum*; Emut: *E. mutica*; Sabb: *S. abbreviatum*; Ebre: *E. brevis*; Erec: *E. recurva*; Ehem: *E. hemigibba*; Egibo: *E. gibboides*)

Table 3 Results of SIMPER analysis indicating species contributions to the average similarity of the subtropical and tropical groups (cutoff for low contributions: 60%)

Clustered group	Species	Av.abund	Av.Sim	Sim/SD	Contrib%
Subtropical (average similarity: 46.80)	<i>T. astylata/aequalis</i>	1.65	5.79	1.60	12.13
	<i>E. brevis</i>	1.79	5.60	1.18	11.74
	<i>E. mutica</i>	1.68	4.61	1.43	9.67
	<i>S. abbreviatum</i>	1.65	4.60	1.48	9.65
	<i>S. carinatum</i>	1.46	3.50	0.99	7.33
	<i>H. tenella</i>	0.99	3.22	1.78	6.75
	<i>E. hemigibba</i>	0.99	3.10	0.80	6.51
Tropical (average similarity: 43.50)	<i>E. diomedea</i>	4.51	16.37	2.41	36.47
	<i>H. gracilis</i>	3.44	11.30	2.80	25.19

Species were listed in the order of *Av.Sim* indicating how much they contributed to the Bray-Curtis similarity within each group. *Av. Abund*: average log-transformed abundance, *Av. sim*: average similarity, *Sim/SD*: similarity over standard deviation of similarity, *Contrib%*: contribution to the total within group similarity

dominance of *E. gibboides* and *E. recurva* in the subarctic-subtropical transition zone of NP, promoted discrepancy between the marginal and central NPSG euphausiid communities (Fig. 4A and Table S4).

Euphausia diomedea and *H. gracilis*, which were always observed simultaneously, typified the tropical euphausiid population (Fig. 4A and Table 3). Both species were discovered at every station in the tropical group; however, *E. diomedea* (accounting for 28.3% of the tropical euphausiid

abundance) was more abundant than *H. gracilis* (10.4%; Fig. 4A). Within the tropical community, the equatorial EI assemblage that was significantly occupied by *T. tricuspidata* differed considerably from the BoB and equatorial EI-SP assemblages (Figs. 4A and 5A). *Euphausia sibogae* uniquely characterized the BoB population, and the higher abundance and frequent occurrence of *E. tenera* and *H. tenella* in the equatorial area also intensified the dissimilarities between the equatorial EI-SP and other subgroups

Table 4 Representative species identified in the subtropical and tropical areas of the present study with the known geographical distribution

Region	Species	Geographical distribution and abundance center
Subtropical	<i>E. gibboides</i>	NP subarctic-subtropical transition zone
	<i>E. recurva</i>	NP subarctic-subtropical transition zone
	<i>E. brevis</i>	Central subtropical gyre
	<i>E. mutica</i>	Marginal subtropical gyre
	<i>S. abbreviatum</i>	Cosmopolitan in low latitudes, surged when PP is high
	<i>E. hemigibba</i>	NPSG endemic and dominant in marginal NPSG
	<i>S. carinatum</i>	Cosmopolitan in low latitudes
	<i>H. atlantica</i>	Subtropics
Tropical	<i>E. diomedea</i>	Tropics
	<i>H. gracilis</i>	Tropics
	<i>T. tricuspidata</i>	Cosmopolitan in low latitudes, surged when PP is high
	<i>E. sibogae</i>	BoB endemic
	<i>H. tenella</i>	Cosmopolitan in low latitudes
	<i>E. tenera</i>	Cosmopolitan in low latitudes, dominant in equatorial area

(Fig. 4A and Table S5). The distribution characteristics of the representative euphausiid species that established the subtropical and tropical euphausiid communities are summarized in Table 4.

4 Discussion

The present study successfully provides a holistic account of euphausiid community structure at low latitudes covering the Pacific and Indian Oceans, complementing the three previous seminal studies regarding biogeography (Brinton 1962, Brinton and Gopalakrishnan 1975) and ecology of euphausiids (Letessier et al. 2011a). As we posited, integrated primary production (PP) was the most critical environmental driver controlling the euphausiid community structure in low latitudes. PP significantly correlated with the euphausiid abundance and species diversity. Euphausiid species displayed distinct distribution patterns based on their association with PP, dividing the low-latitude population into subtropical and tropical groups.

4.1 Primary productivity affecting euphausiid abundance and species diversity in low latitudes

At the marine food web base, primary productivity is a critical determinant of the abundance of higher trophic levels, including zooplankton and fish (Matsuzaki et al. 2018; Capuzzo et al. 2022; Behrenfeld et al. 2019). The higher integrated PP rates triggered by mesoscale eddies in the Bay of Bengal, equatorial eastern Indian Ocean, and tropical South Pacific off Peru are known to sustain the large tropical assemblages of euphausiid abundance (Gordon et al. 2017; Stramma et al. 2013; Czeschel et al. 2018; Hu et al. 2022). However, low rates of PP limited by the short nutrient supply in the subtropical gyres significantly restrained the

subtropical population (Begon et al. 2014; Steinberg et al. 2008).

The characteristic high euphausiid species diversity in the subtropics in the present study agreed with the admitted latitudinal gradient of the global biodiversity pattern (Gaston 2000) and the modeling results of Letessier et al. (2011a) in the Pacific Ocean, in which the highest euphausiid species richness was observed in the western NPSG and center of SPSG. The euphausiid species diversity in the present study was negatively correlated with the surface/total PP significantly, indicating the niche partitioning resulting from a stable vertical distribution structure or varied feeding preferences of coexisting euphausiid species was a vital driver of higher diversity in the oligotrophic regions (Hayward and McGowan 1979; Longhurst 1985). Since the species number and evenness were high at subtropical stations, finer-scale niche partitioning among euphausiid species, reflecting different responses to food resource availability, is expected in subtropics. Additionally, the higher stability of the subtropical gyre centers facilitated the increased zooplankton species diversity (Brinton 1962; Letessier et al. 2011a).

Our study detected no clear correlation between any diversity indices and seawater temperature, agreeing with the observations of McWilliam (1977) in the Indian Ocean. One explanation for the “divergence” between our results and the high temperature-high diversity link of Letessier et al. (2009, 2011a) was that the responses of zooplankton species diversity to environmental drivers displayed remarkable spatial scale dependencies. Studies above were performed in considerably broad latitudinal gradients with apparent temperature changes (up to 60° difference in latitude, and 20 °C difference in SST). Yet, most of our study sites were concentrated in the low latitudes (with < 10 °C differences in SST). Unsurprisingly, species diversity was positively correlated with SST concerning only the NPSG area, including station NP4 of low temperature (Spearman correlation = 0.673, $p < 0.05$; Fig. S2).

4.2 Ecology and biogeography of representative euphausiid species in low latitudes

The correlations between PP level and representative euphausiid species indicated their feeding strategies or functional responses to adapt to changing food and environmental conditions (Gentleman et al. 2003; Bachiller et al. 2016), further influencing the euphausiid community structure. For example, filter-feeding omnivorous *Euphausia* species would consume more heterotrophic prey than autotrophic one in a lower phytoplankton density environment (Perissinotto et al. 2000; Stuart and Pillar 1990; Henschke et al. 2016; Zhou et al. 2021). Hence, subtropical *E. brevis* correlating with integrated/surface PP negatively should be more carnivorous than tropical *E. diomedea* (Fig. 6). Zhou et al. (2021) discovered that gut contents of *E. brevis* contained mainly copepods and mixotrophic dinoflagellates due to the lower PP contributed by picophytoplankton. By contrast, *E. diomedea* was likely to utilize more eukaryotic phytoplankton such as diatoms, phototrophic dinoflagellates, and pelagophytes that contributed to the enhanced PP in the equatorial eastern Indian Ocean (Isaji et al. 2022) and the tropical South Pacific (Rousseaux and Gregg 2012; Bruland et al. 2005). Within the subtropical assemblage, *E. hemigibba* associated with surface PP positively displayed an herbivory tendency compared to *E. brevis* (Zhou et al. 2021). This led *E. hemigibba* and *E. brevis* to dominate the relatively productive marginal NPSG and the oligotrophic central NPSG, respectively.

Unlike *Euphausia*, the raptorial *Stylocheiron* and versatile *Hansarsia* (capable of raptorial feeding and weak filter feeding; Gopalakrishnan 1975) are not subject to the low encounter rate with food particles in oligotrophic environments (Prowe et al. 2019; Ge et al. 2022), thereby showing cosmopolitan distributions in the low latitudes. Of interest was the elevated abundance of the mesopelagic *S. abbreviatum* (Wiebe et al. 2016) at NP10 near the Hawaii islands. To some extent, increased new production and vertical carbon flux supported by nitrogen fixation favored them through the bottom-up control of the food web (Fig. 6, Nagatomo et al. 2023). Ongoing research regarding the feeding ecology of the representative species would offer more details for advancing the current knowledge of euphausiid distribution patterns in low-latitude ecosystems.

Dissolved oxygen (DO) affected the low-latitude euphausiid community structure significantly, in addition to PP. Most representative subtropical euphausiid species correlated positively with DO (Fig. 6), underlying their weak ability to adapt to a lower DO concentration than the tropical ones. Investigations on euphausiids' hypoxia tolerance were mainly conducted in the world's three major Oxygen Minimum Zones (OMZs), in which subtropical representatives of the present study were hardly detected. Only *E. gibboides*

and *E. recurva* could use the OMZ during the day as a refuge from predators in the Gulf of California (Ambriz-Arreola et al. 2017) and the Southwest Atlantic Ocean (Werner and Bucholz 2013), respectively. This corresponded to their higher abundance and absence of other subtropical species in the eastern NPSG margin with a shallower upper boundary of the low-oxygen zone (Fig. 4A, Table S1). On the contrary, the superior hypoxia adaptation of tropical *E. diomedea*, *H. gracilis*, and *E. tenera* allowed them to inhabit the oxygen-depleted northern Indian Ocean and the eastern tropical Pacific (Antezana 2009; Tremblay et al. 2020; Seibel et al. 2016).

4.3 Sampling limitations

Quantitative sampling of euphausiids is sometimes difficult because of their net avoidance behavior (Brinton 1967; Wiebe et al. 2013; Gislason et al. 2023). The Matsuda-Oozeki-Hu Trawl, with an ability of working at a relatively higher towing speed, showed a superiority in collecting macroplanktonic crustaceans compared to other gears (Yamamura and Yasuma 2010). The abundance and distribution of representative euphausiid species were comparable with previous reports (Brinton 1962, Brinton and Gopalakrishnan 1975; Brinton et al. 2000). Although the coarse mesh size tends to result in an underestimation of smaller species and larvae, our study mainly focused on the adult euphausiids, and the average total length of identified euphausiid species was consistent with Brinton et al. (2000) (Table S2, Fig. S3). This indicates that the bias from a larger mesh opening was minor. Future studies with multiple tows at each station and modified trawls with strobe light systems should be implemented to minimize the impact further. Additional sampling stations along the latitudinal gradient across the equatorial Pacific Ocean and the South Pacific subtropical gyre are expected to include more environmental gradients.

5 Conclusions

The present study revealed that the euphausiid community structure, numerical abundance, and species diversity pattern in the subtropical and tropical zones across the Indian and Pacific Oceans were most significantly influenced by primary productivity rates in the water column. Our results indicate that food resources appear more critical than seawater temperature in shaping euphausiids' community structure in an oligotrophic ecosystem with subtle hydrography gradients. A closer examination of the feeding habits and conditions of euphausiids could offer more insights for assessing and predicting their responses to the changing environment.

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Declarations

Conflict of interest The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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