

Salinity fronts shape spatial patterns in zooplankton distribution in Hangzhou Bay

Yepeng Xu^{1, 2}, Yiqi Wang³, Lin Zhan^{1, 2}, Yijun Ou^{1, 2}, Kangning Jia^{1, 2}, Ming Mao^{1, 2}, Xuyu Zhu⁴, Zhibing Jiang^{1, 2, 3, 5, 6}, Yuanli Zhu^{1, 2, 3, 6}, Wei Huang^{1, 2, 3, 5, 6}, Ping Du^{1, 2, 3, 5, 6*}, Jiangning Zeng^{1, 2, 3, 6}, Lu Shou^{1, 2, 3, 5, 6}, Feng Zhou^{3, 6}

¹ Key Laboratory of Marine Ecosystem Dynamics, Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou 310012, China

² Key Laboratory of Nearshore Engineering Environment and Ecological Security of Zhejiang Province, Hangzhou 310012, China

³ State Key Laboratory of Satellite Ocean Environment Dynamics, Ministry of Natural Resources, Hangzhou 310012, China

⁴ Nantong Marine Environmental Monitoring Center, Ministry of Natural Resources, Nantong 226002, China

⁵ Key Laboratory of Ocean Space Resource Management Technology, Ministry of Natural Resources, Hangzhou 310012, China

⁶ Observation and Research Station of Marine Ecosystem in the Yangtze River Delta, Ministry of Natural Resources, Zhoushan 316021, China

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Abstract

Ocean fronts play important roles in nutrient transport and in the shaping ecological patterns. Frontal zones in small bays are typically small in scale, have a complex structure, and they are spatially and temporally variable, but there are limited data on how biological communities respond to this variation. Hangzhou Bay, a medium-sized estuary in China, is an ideal place in which to study the response of plankton to small-scale ocean fronts, because three water masses (Qiantang River Diluted Water, Changjiang River Diluted Water, and the East China Sea current) converge here and form dynamic salinity fronts throughout the year. We investigate zooplankton communities, and temperature, salinity and chlorophyll *a* (Chl *a*) in Hangzhou Bay in June (wet period) and December (dry period) of 2022 and examine the dominant environmental factors that affect zooplankton community spatial variability. We then match the spatial distributions of zooplankton communities with those of salinity fronts. Salinity is the most important explanatory variable to affect zooplankton community spatial variability during both wet and dry periods, in that it contributes >60% of the variability in community structure. Furthermore, the spatial distributions of zooplankton match well with salinity fronts. During December, with weaker Qiantang River Diluted Water and a stronger secondary Changjiang River Plume, zooplankton communities occur in moderate salinity (MS, salinity range 15.6 ± 2.2) and high salinity (HS, 22.4 ± 1.7) regions, and their ecological boundaries closely match the Qiantang River Diluted Water front. In June, different zooplankton communities occur in low salinity (LS, 3.9 ± 1.0), MS (11.7 ± 3.6) and HS (21.3 ± 1.9) regions. Although the LS region occurs abnormally in the central bay rather than its apex because of the anomalous influence of rising and falling tides during the sampling period, the ecological boundaries still match salinity interfaces. Low-salinity or brackish-water zooplankton taxa are relatively more abundant in LS or MS regions, and the biomass and abundance of zooplankton is higher in the MS region.

Key words: zooplankton, spatial distribution, salinity fronts, Hangzhou Bay

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1 Introduction

Oceanic fronts are narrow three-dimensional structures that dynamically partition water masses of different properties. They are characterized by pronounced gradients in hydrographic features such as temperature and salinity (Liu et al., 2022; Zhou et al., 2021). Because of their abrupt nature, fronts are typically

discontinuous. The spatial scale over which they occur can range from a few meters to several thousand kilometers. Temporally they can be transient, persisting for a few days only, to, for many oceanic fronts, being quasi-stationary and occurring seasonally; some persistent fronts also occur (Belkin et al., 2009). Frontal zones in small bays are typically narrower and shallower than lar-

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*Corresponding author, E-mail: duping@sio.org.cn

ger-scale fronts, and cover ranges of a few hundred meters to several kilometers. Additionally, the frontal zones of small bays can be structurally more complex than larger-scale fronts (Hernández-Moresino et al., 2017). Hangzhou Bay, a small shallow coastal bay in the East China Sea, has a complex ecosystem that is influenced by multiple sources, including runoff from rivers, tidal movements, and seawater intrusion from East China Sea. It represents an ideal location in which to study frontal zones in small bays (Jia et al., 2022).

As vital components of marine ecosystems, zooplankton can be highly sensitive to changes in the environment such as in temperature, salinity, and chlorophyll *a* (Chl *a*) concentration. Zooplankton also plays an important role in ecosystems (Liu et al., 2023), constitutes a significant part of the marine food web, and significantly impacts energy transfer and nutrient cycling (Du et al., 2023; de Puelles and Molinero, 2008).

Significant physical, chemical, and biological differences exist among water masses originating from various sources within Hangzhou Bay (Zhang et al., 2022; Yan et al., 2021). These differences substantially impact the distribution and community structure of zooplankton in the bay's waters (Sun et al., 2016). Several studies on the distribution and community structure of zooplankton in Hangzhou Bay and adjacent waters have been reported during last four decades (Zhu, 1988; Chen et al., 1992; Xu et al., 2003; Sun et al., 2016). In the 1980s, a comprehensive study on the ecological characteristics of zooplankton communities in Hangzhou Bay has been made (Zhu, 1988). Chen et al. (1992) analyzed the biomass, species composition and community structure of zooplankton in the north shore of Hangzhou Bay. In waters around Yangshan Islands in Hangzhou Bay, Xu et al. (2003) studied the distribution characteristics of zooplankton. Sun et al. (2016) pointed out that monsoon and the dissolved inorganic nitrogen (DIN) input from freshwater discharge of Qiantang River and Changjiang River resulted in temporal and spatial variations of environmental gradient in Hangzhou Bay, which significantly influenced the structure of mesozooplankton community. Several studies have investigated the response of plankton communities to frontal zones. Hernández-Moresino et al. (2017) reported structural differences in a mesozooplankton community in San Jose Bay between mixed and stratified environments in the frontal zone to be caused mainly by stratification and coastal upwelling. In the Zhujiang River Estuary in southern China, Zhou et al. (2020) found that variations in environmental factors within the plume front area resulted in significant spatial differences in the distribution of phytoplankton communities; Li et al. (2019) pointed out that the salinity gradient contributed to the diversity and distribution of tintinnid ciliates. As mentioned above, previous studies have explored the relationships between zooplankton and environmental factors in Hangzhou Bay, as well as the relationship between zooplankton and fronts in other bays. However, how zooplankton communities respond to frontal zones formed by water masses from different sources in Hangzhou Bay remains poorly known. Because the main fronts in this bay differ in salinity and temperature (Jia et al., 2022; Cao et al., 2021), we hypothesized that zooplankton communities in this region were similarly shaped by these two environmental variables. To test this hypothesis, we related environmental variables to zooplankton communities in Hangzhou Bay in June and December of 2022. Our results contribute to an improved understanding of the ecological response of zooplankton communities to hydrographic fronts and nutrient transport in estuarine and coastal waters.

2 Materials and methods

2.1 Study area

Hangzhou Bay, a typical trumpet-shaped estuary, is located close to the southern side of the Changjiang River Estuary. The bay width at its entrance is approximately 100 km, but it narrows to less than 20 km at its western end (Su and Wang, 1989). Hangzhou Bay is located along a meso-tidal coast, with an average tidal range of ~2.5 m at its entrance, but with a tidal range that increases rapidly towards the interior of the bay, leading to the formation of the famous Qiantang River tidal bore within the Qiantang River Estuary segment west of the bay's apex (Yu et al., 2022; Su and Wang, 1989). The tidal bore typically reaches a height of 1–2 m, with occasional peaks to 3 m, and a tidal range that can extend to 9 m (Hu et al., 2019).

Within Hangzhou Bay, there is a year-round northeast-southwest oriented frontal zone that is composed of a diluted-water secondary front of Changjiang River in the northern part of the bay, and a diluted-water front from the Qiantang River at the bay's apex. These two fronts separate during low tide in the dry season, but they form a continuous line at other times (Jia et al., 2022; Su and Wang, 1989). The wet period in Hangzhou Bay occurs in June when both the Qiantang and Changjiang rivers experience their highest freshwater input levels throughout the year. The dry period extends from October to December, during which time the freshwater input from the Qiantang and Changjiang rivers is at its lowest throughout the year (Fig. 1).

2.2 Sample collection and analysis

Two surveys were conducted at 22 stations during June 18th to 22nd, 2022 (wet season) and December 12nd to 20th, 2022 (dry season) aboard the R/V *Zheluyugong99001* in Hangzhou Bay (Fig. 2). Zooplankton were sampled by plankton net (diameter 31.6 cm, mesh size 160 μ m, length 140 cm) equipped with a flow meter, hauled vertically from the sea bed to the surface. Net-contents were fixed in a buffered 5% formalin solution in 1-L plastic bottles. The volume of filtered water was estimated using a digital flow meter.

In the laboratory, zooplankton were filtered over a mesh (160 μ m) and weighed with a 0.1 mg electronic balance after picking out sundry items. Zooplankton abundance (ind./m³) was calculated by dividing the number of zooplankters by the volume of filtered water. Zooplankton biomass (mg/m³) was determined by dividing the sample wet weight by the volume of filtered water. Taxonomic identification and enumeration were performed beneath a Zeiss SteREO Discovery V8 stereomicroscope. Adult zooplankton, crustacean larvae, and other larvae were identified to species, family, and class levels, respectively.

Temperature and salinity were measured using a Sea-Bird 911 CTD (Sea-Bird Electronics Inc., USA). Seawater was collected from surface, and samples for Chl *a* were processed by filtering 100 mL of water through 0.7- μ m GF/F filters (Whatman). Chl *a* retained on these filters was analyzed using a Turner Design Fluorometer after extraction in 90% acetone for 24 h at –20°C.

2.3 Data analysis

Before analysis, a Bray–Curtis similarity matrix was constructed, and zooplankton species abundance data for each station were square-root transformed. To characterize zooplankton communities, cluster analysis was then performed on the transformed data set. Clusters are depicted separately on station maps for each season. One-way analysis of similarity (ANOSIM) was used to test for any significant differences between community

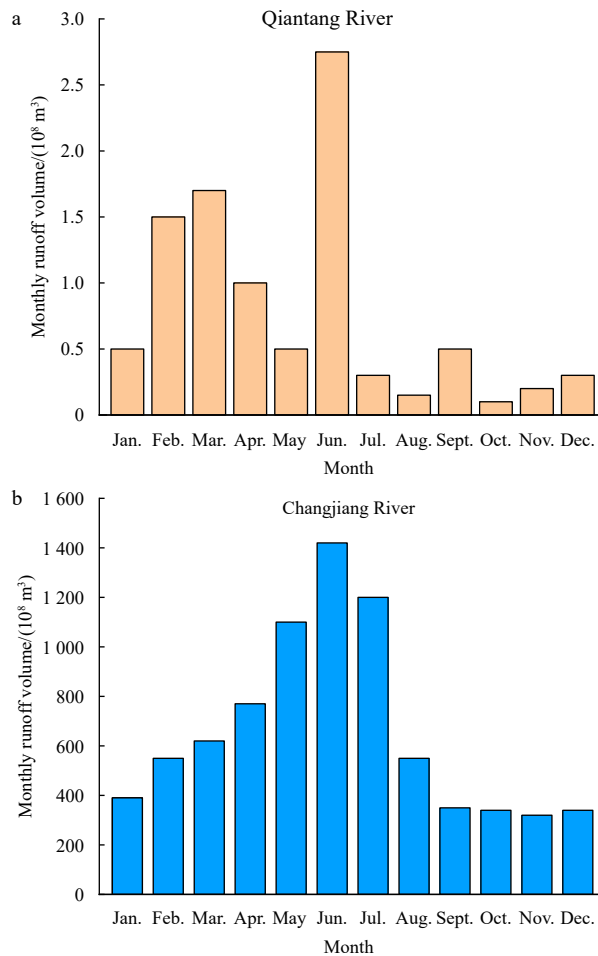


Fig. 1. Monthly flow data for the Qiantang and Changjiang rivers in 2022. Changjiang River flow data are sourced from the Datong station; Qiantang River flow data are sourced from the Zhuji station.

groups. Similarity percentage (SIMPER) was employed to identify the dominant species contributing most to the similarity between groups. Differences in abundance and biomass of zooplankton and dominant species between ecological groups for these two seasons were tested by non-parametric Kruskal–Wallis tests. Relationships between zooplankton community structure and environmental variables were analyzed by canonical correspondence analysis (CCA), before which a detrended correspondence analysis (DCA) was performed.

Cluster analysis, analysis of similarities (ANOSIM), and similarity percentage (SIMPER) analysis were performed using Primer 6 (Plymouth Marine Laboratory, UK). Results of cluster analysis, and the spatial and temporal distributions of temperature, salinity, and Chl *a* were visualized using Surfer 18. The non-parametric Kruskal–Wallis test was performed using IBM SPSS Statistics 27. Correlation analysis was performed using Canoco 5.

3 Results

3.1 Environmental variables

Surface water temperatures were higher in June, at (25.08 ± 1.11) °C than December, at (11.55 ± 1.70) °C, while seawater surface salinity was higher in December (20.94 ± 3.41) and lower in June (12.24 ± 5.58). Seawater surface Chl *a* was higher in June at

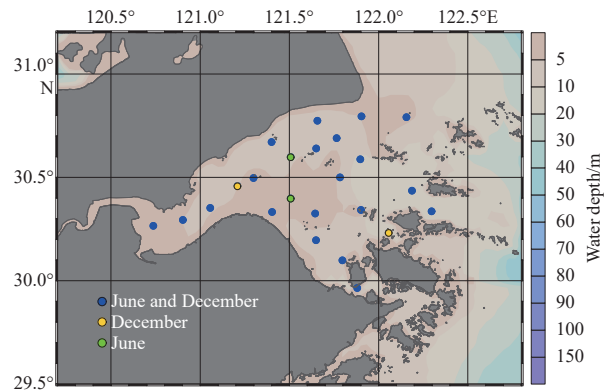


Fig. 2. Sampling stations in the Hangzhou Bay, June and December, 2022.

(1.90 ± 1.21) µg/L than during December at (1.04 ± 0.56) µg/L (Table 1).

Surface water temperatures ranged 22.10–27.40 °C in June, and decreased from northeast to southwest (Fig. 3a). Surface water temperatures in December ranged 7.70–15.22 °C, and decreased from south to north (Fig. 3b). Surface salinity ranged 2.42–23.69 in June, with a low-salinity patch in the middle of the bay and high-salinity patches at the bay’s apex and entrance (Fig. 3c). In December, surface salinity ranged 12.48–25.32, and increased from west to east (Fig. 3d). Surface Chl *a* ranged 0.17–5.61 µg/L in June, with lower concentrations at the bay’s apex and entrance, and higher concentrations in the central bay (Fig. 3e). In December, surface Chl *a* ranged 0.12–2.05 µg/L, and generally decreased from west to east (Fig. 3f).

3.2 Zooplankton community

3.2.1 Spatial and temporal variation in zooplankton communities

In June, four zooplankton communities were identified by cluster analysis at 53% similarity (Fig. 4). Differences in community structure between groups were significant except for Groups A and C (Table 2). The distribution of zooplankton communities in June generally corresponded with the distribution of salinity. Average salinities experienced by Groups A, B, C, and D were 3.87 ± 1.03, 11.38 ± 1.29, 11.87 ± 4.09, and 21.33 ± 1.90, respectively (Fig. 5).

In December, cluster analysis identified four zooplankton communities at 38% similarity (Fig. 4). Average salinities for Groups A, B, C, and D were 15.63 ± 2.20, 20.60 ± 1.59, 22.57 ± 1.72, and 23.19, respectively (Fig. 5). ANOSIM results indicate that differences in zooplankton communities between Groups A, B and C were significant (Table 2).

3.2.2 Spatial and temporal variation in zooplankton abundance and biomass

Kruskal–Wallis test results reveal zooplankton abundance to be significantly higher in June at (1 771.9 ± 1 930.9) ind./m³ than in December at (30.7 ± 31.8) ind./m³ (*p* < 0.001). Similarly, zooplankton biomass was also significantly higher in June at

Table 1. Seasonal means of environmental parameters in June and December, 2022

	June	December
Surface temperature/°C	25.08 ± 1.11	11.55 ± 1.70
Surface salinity	12.24 ± 5.58	20.94 ± 3.41
Chl <i>a</i> concentration/(µg·L ⁻¹)	1.90 ± 1.21	1.04 ± 0.56

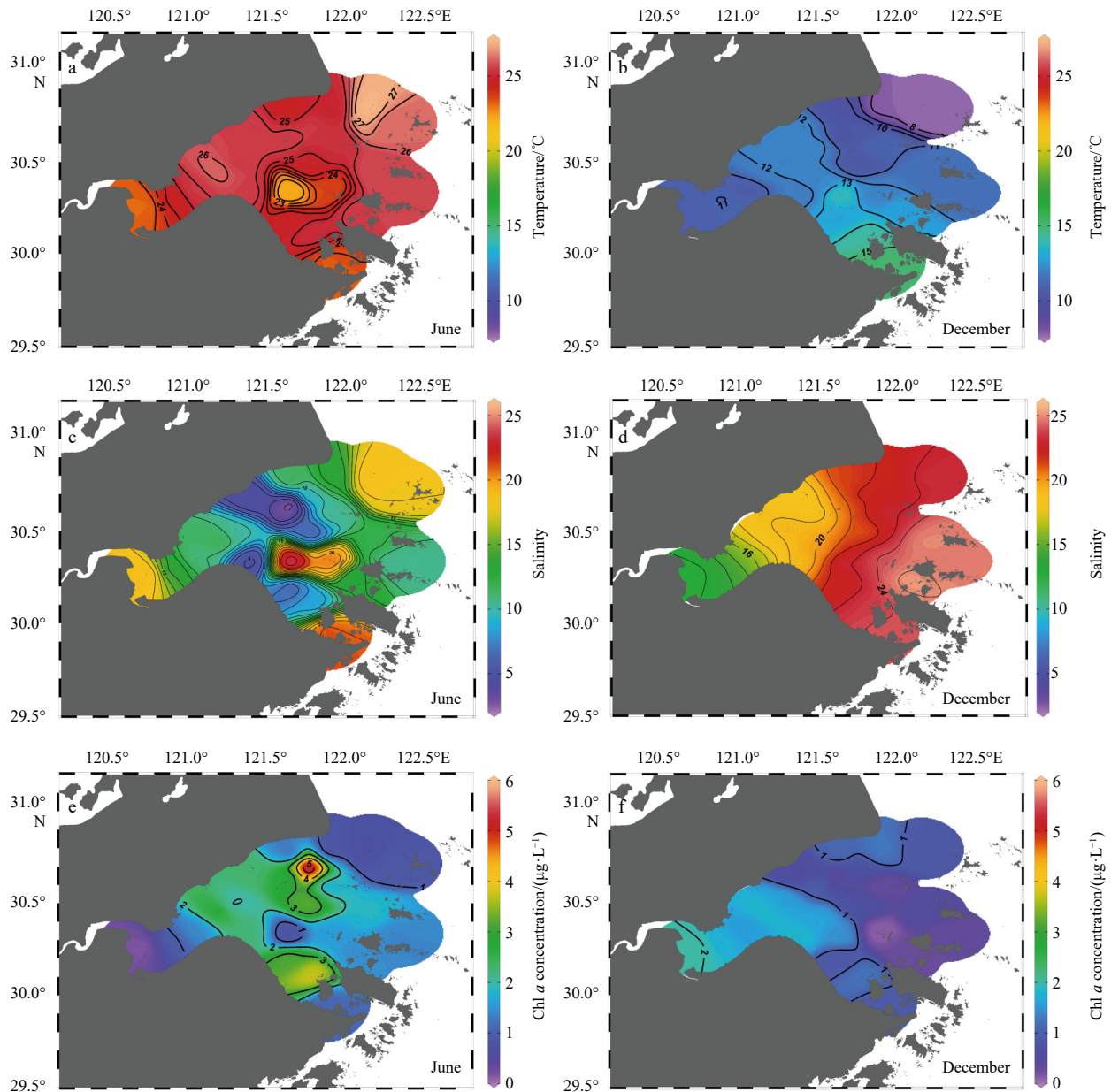


Fig. 3. Spatial distributions of environmental variables: surface temperature (a, b), surface salinity (c, d), and surface Chl *a* (e, f) for June and December, respectively.

(697.8 ± 750.7) mg/m^3 than in December at (30.3 ± 26.4) mg/m^3 ($p < 0.001$).

In June, the abundances and biomasses of zooplankton in Group B were significantly higher than values for Group D ($p = 0.001$). In December, the biomass of zooplankton in Group A was significantly higher than it was for Group B ($p = 0.041$) (Table 3).

3.2.3 Spatial variation in dominant species

SIMPER analysis revealed that in June, the species that contributed most to dissimilarities between Groups A and D, B and D, C and D, and B and C was *Paracalanus parvus* (22.16%, 19.24%, 21.22%, 12.22%, respectively), while that species to contribute most to dissimilarities between Groups A and B, and A and C was *Labidocera euchaeta* (10.39%, 12.54%, respectively). In December, for Groups A and C, and B and C, the taxon that contributed most to dissimilarities was trochophore larvae (11.61%, 21.18%, respectively); for Groups A and B, and A and D, this was

Sinocalanus sinensis (11.82%, 11.08%, respectively); and for Groups B and D, and C and D, these were *Centropages sinensis* (19.03%) and *P. parvus* (14.86%), respectively.

Based on Kruskal-Wallis test results for June, the relative abundance of *L. euchaeta* was significantly higher in Group A than it was in Group D; that of *P. parvus* was significantly higher in Groups C and B than in group A; that of *Temora turbinata* was significantly higher in Group D than in Groups A–C; and those of *Oithona brevicornis* and Gammaridea sp. were significantly higher in Group A than in Group B (Table 4). In December, those of *Acartia pacifica*, *S. sinensis*, *Pseudodiaptomus poplesia*, and Gammaridea sp. were significantly higher in Group A than in Groups B–D (Table 4).

3.3 Relationships between zooplankton communities and dominant environmental variables

In June, salinity was the dominant environmental variable to

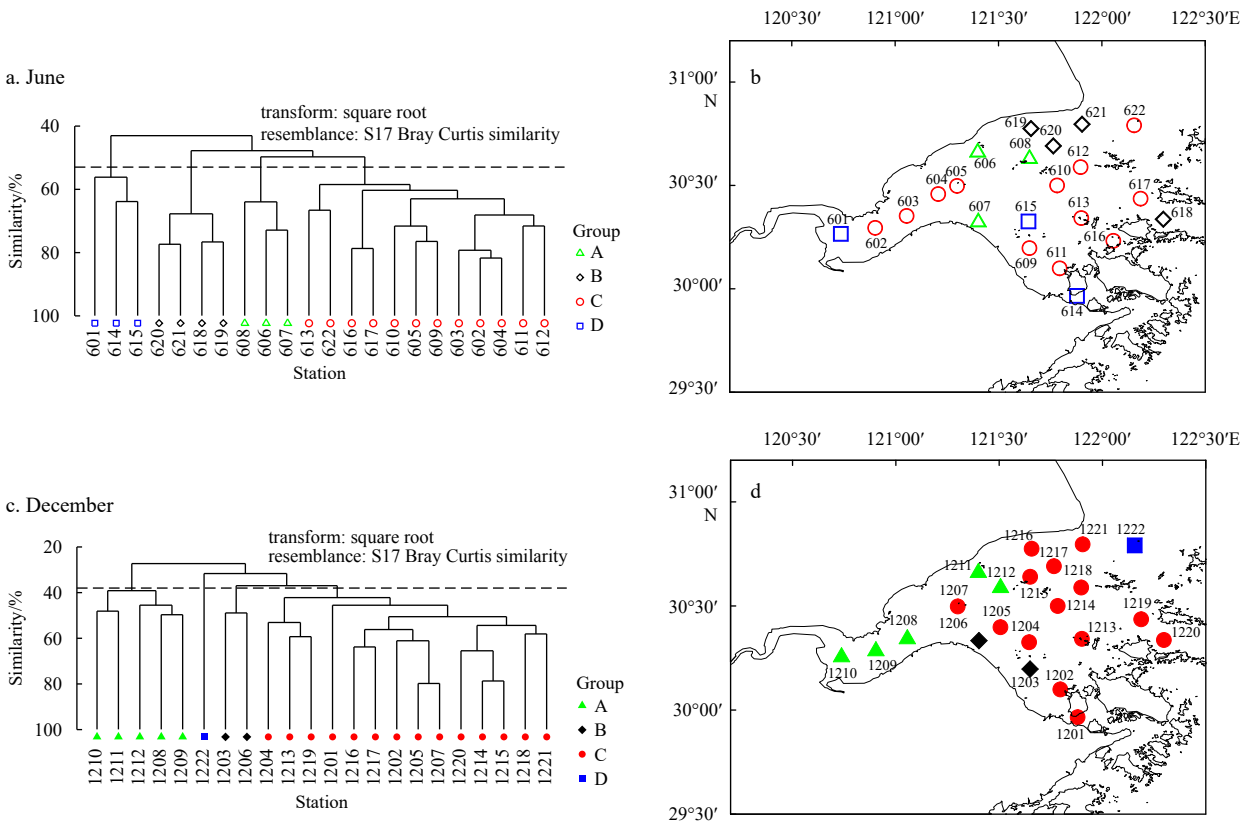


Fig. 4. Zooplankton communities based on taxon abundance datasets for June and December, 2022, within Hangzhou Bay. Four community groups occurred in both June (hollow shapes, a, b) and December (solid shapes, c, d). Groups: A, green triangles; B, black rhombus; C, red circles; D, blue squares.

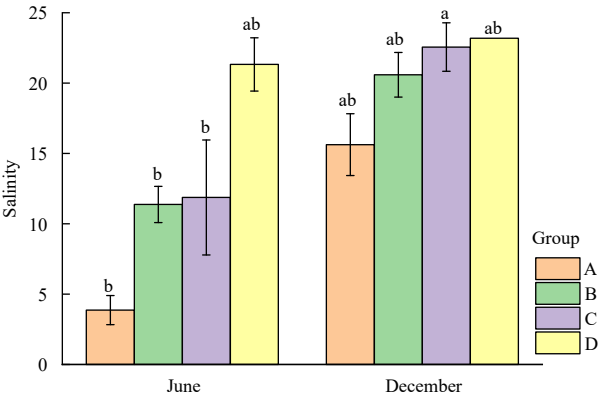


Fig. 5. Salinity in surface waters for stations with zooplankton community Groups A–D, June and December 2022, within Hangzhou Bay. The a and b indicate significant differences between groups.

affect the zooplankton communities (the contributions of temperature and Chl *a* were relatively weaker). In December, salinity again appeared to be the dominant environmental variable affecting zooplankton communities (Table 5, Fig. 6).

4 Discussion

4.1 Salinity as a dominant factor affecting the spatial and temporal distributions of zooplankton communities

In the present study, salinity contributes >60% of the variability

Table 2. Results of the analysis of similarities (ANOSIM) on zooplankton communities between community Groups A–D, for June and December 2022, within the Hangzhou Bay

June						
	A&B	A&C	A&D	B&C	B&D	C&D
<i>R</i>	0.712	1	1	0.862	0.833	1
<i>P</i>	0.002	0.1	0.029	0.002	0.001	0.029
December						
	A&B	A&C	A&D	B&C	B&D	C&D
<i>R</i>	0.745	0.776	1	0.627	1	0.758
<i>P</i>	0.048	0.001	0.167	0.008	0.333	0.067

Note: *R* indicates the statistical value, and *P* indicates the significance level.

Table 3. Spatial and temporal variation in zooplankton abundance (ind./m³) and biomass (mg/m³) for community Groups A–D, for June and December 2022, within the Hangzhou Bay

June				
	Group A	Group B	Group C	Group D
Abundance	790.8 ± 217.1 ^{ab}	889.5 ± 733.7 ^a	922.6 ± 346.3 ^{ab}	318.8 ± 95.9 ^b
Biomass	321.6 ± 117.7 ^{ab}	1727.2 ± 382.1 ^a	392.7 ± 174.7 ^{ab}	154.2 ± 28.7 ^b
December				
	Group A	Group B	Group C	Group D
Abundance	43.0 ± 10.4	10.9 ± 3.5	35.1 ± 38.3	6.7
Biomass	50.5 ± 17.2 ^a	8.2 ± 0.8 ^b	31.7 ± 27.0 ^{ab}	9.9 ^{ab}

Note: The a and b indicate significant differences between groups.

ity in community structure, serving as the dominant factor affecting spatial variation in the distributions of zooplankton com-

munities in June and December. Salinity also serves as a primary factor affecting spatial variation in the distribution of zooplankton communities in many other estuaries (Venkataramana et al., 2023; Lucena-Moya and Duggan, 2017; Taglialatela et al., 2014; Mouny and Dauvin, 2002). This result likely reflects variation in the salinity tolerances of different zooplankters in each of the identified groups (Huynh and Gray, 2020). Different zooplankters have distinct physiological adaptations, including cell osmoregulation capabilities, the ability to balance ions, and metabolic adaptations (Charmantier et al., 1998; Yancey et al., 1982). Some zooplankters can maintain osmotic equilibrium by regulating the concentration of solutes within and outside of their cell membranes to maintain a stable physiological state in condi-

tions of variable salinity (von Weissenberg et al., 2022; Castellano et al., 2018). These physiological characteristics influence their survival and reproductive capacities in environments that experience different salinities (Shang et al., 2005). However, this result is different from Sun et al. (2016), which pointed out the DIN significantly influenced the structure of mesozooplankton community. The reasons are as follows. Firstly, we studied zooplankton with a size of 160 μm and above, while Sun et al. (2016) studied 505 μm and above. The dominant species and abundance levels differ between the two zooplankton communities, resulting in their different responses to salinity. Secondly, we acknowledge the significant variability in nutrients levels, such as DIN, in Hangzhou Bay (Wu et al., 2019). These nutrient levels often

Table 4. Spatial and temporal variation in the relative abundances (%) of dominant zooplankter species in Groups A–D, for June and December 2022, within Hangzhou Bay

Taxa	Dominant species	June			
		Group A	Group B	Group C	Group D
Copepoda	<i>Acartia</i> larva	3.0 $\pm$ 0.5	7.0 $\pm$ 4.2	12.5 $\pm$ 11.3	10.4 $\pm$ 7.5
	<i>Acartia pacifica</i>	0.7 $\pm$ 0.7	0.4 $\pm$ 0.3	8.1 $\pm$ 9.3	0.5 $\pm$ 0.5
	<i>Calanidae</i> larva	2.5 $\pm$ 2.1	2.5 $\pm$ 2.0	1.3 $\pm$ 0.8	1.5 $\pm$ 0.1
	<i>Labidocera euchaeta</i>	25.6 $\pm$ 7.8 ^a	1.3 $\pm$ 0.8 ^{ab}	2.0 $\pm$ 1.6 ^{ab}	0.7 $\pm$ 0.4 ^b
	<i>Labidocera</i> larva	1.8 $\pm$ 1.1 ^{ab}	0.1 $\pm$ 0.1 ^b	3.2 $\pm$ 2.2 ^a	0.5 $\pm$ 0.5 ^{ab}
	<i>Paracalanus parvus</i>	12.3 $\pm$ 6.1 ^b	52.2 $\pm$ 18.1 ^a	42.9 $\pm$ 15.4 ^a	25.2 $\pm$ 5.7 ^{ab}
	<i>Temora turbinata</i>	0.0 $\pm$ 0.0 ^b	0.0 $\pm$ 0.0 ^b	0.2 $\pm$ 0.4 ^b	6.9 $\pm$ 3.8 ^a
	<i>Tortanus derjugini</i>	10.1 $\pm$ 5.6	6.6 $\pm$ 3.7	6.7 $\pm$ 7.4	1.7 $\pm$ 0.7
	<i>Tortanus vermiculus</i>	4.9 $\pm$ 5.3	1.1 $\pm$ 0.8	1.1 $\pm$ 1.1	0.0 $\pm$ 0.0
	<i>Corycaeus dahl</i>	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.3 $\pm$ 0.9	2.5 $\pm$ 2.2
Mysidacea	<i>Oithona brebicornis</i>	7.9 $\pm$ 4.3 ^a	0.3 $\pm$ 0.1 ^b	1.3 $\pm$ 1.2 ^{ab}	0.7 $\pm$ 0.7 ^{ab}
	<i>Oithona</i> larva	12.8 $\pm$ 6.3	2.9 $\pm$ 1.0	5.1 $\pm$ 4.1	2.9 $\pm$ 2.1
	<i>Liella pelagicus</i>	3.7 $\pm$ 3.8	0.0 $\pm$ 0.1	0.2 $\pm$ 0.3	0.4 $\pm$ 0.6
Amphipoda	<i>Gammaridea</i> sp.	2.4 $\pm$ 2.2 ^a	0.0 $\pm$ 0.0 ^b	0.1 $\pm$ 0.2 ^{ab}	0.7 $\pm$ 0.7 ^{ab}
Planktonic larva	Brachyura zoea	0.1 $\pm$ 0.2	0.7 $\pm$ 0.4	0.9 $\pm$ 1.3	4.1 $\pm$ 3.7
	Metazoa zoea	0.0 $\pm$ 0.0	0.0 $\pm$ 0.1	0.0 $\pm$ 0.1	2.2 $\pm$ 2.8
	Copepoda zoea	2.7 $\pm$ 2.1	19.4 $\pm$ 20.6	4.1 $\pm$ 3.5	2.3 $\pm$ 1.0
	Trochophore larva	0.0 $\pm$ 0.0 ^b	0.9 $\pm$ 0.5 ^b	4.9 $\pm$ 3.0 ^a	29.0 $\pm$ 13.0 ^a
Taxa	Dominant species	December			
		Group A	Group B	Group C	Group D
Copepoda	<i>Acartia pacifica</i>	15.1 $\pm$ 17.9 ^a	0.0 $\pm$ 0.0 ^b	1.8 $\pm$ 1.9 ^b	0.0 ^b
	<i>Paracalanus crassirostris</i>	1.2 $\pm$ 1.5	0.0 $\pm$ 0.0	1.3 $\pm$ 2.6	0.0
	<i>Calanus sinicus</i>	4.4 $\pm$ 4.4	4.8 $\pm$ 4.8	1.5 $\pm$ 2.2	0.0
	<i>Sinocalanus sinensis</i>	17.8 $\pm$ 17.0 ^a	0.0 $\pm$ 0.0 ^b	0.2 $\pm$ 0.6 ^b	0.0 ^b
	<i>Centropages sinensis</i>	2.8 $\pm$ 1.9	31.1 $\pm$ 2.2	6.1 $\pm$ 6.8	0.0
	<i>Calanidae</i> larva	3.7 $\pm$ 1.5	0.0 $\pm$ 0.0	2.4 $\pm$ 2.5	0.0
	<i>Labidocera</i> larva	1.0 $\pm$ 1.9	0.0 $\pm$ 0.0	1.1 $\pm$ 2.2	0.0
	<i>Paracalanus parvus</i>	17.5 $\pm$ 19.9	44.3 $\pm$ 5.7	46.8 $\pm$ 15.9	30.8
	<i>Subeucalanus subcrassus</i>	1.7 $\pm$ 2.1	8.3 $\pm$ 8.3	0.2 $\pm$ 0.5	0.0
	<i>Pseudodiaptomus poplesia</i>	2.6 $\pm$ 2.4 ^a	0.0 $\pm$ 0.0 ^b	0.0 $\pm$ 0.0 ^b	0.0 ^b
	<i>Tortanus derjugini</i>	6.9 $\pm$ 4.6	0.0 $\pm$ 0.0	1.2 $\pm$ 1.5	15.4
	<i>Oithona similis</i>	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.9 $\pm$ 1.9	0.0
	<i>Oithona brebicornis</i>	2.7 $\pm$ 2.2	4.8 $\pm$ 4.8	1.9 $\pm$ 3.2	0.0
	<i>Oithona</i> larva	5.2 $\pm$ 9.3	0.0 $\pm$ 0.0	1.4 $\pm$ 2.1	0.0
	<i>Eutrope acutifrons</i>	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.9 $\pm$ 2.3	7.7
Mysidacea	<i>Orientomysis laticauda</i>	1.6 $\pm$ 1.8	0.0 $\pm$ 0.0	0.4 $\pm$ 1.4	0.0
Cumacea	<i>Leucon nasica</i>	3.9 $\pm$ 6.9	0.0 $\pm$ 0.0	0.3 $\pm$ 1.0	0.0
Amphipoda	<i>Gammaridea</i> sp.	5.1 $\pm$ 4.7 ^a	0.0 $\pm$ 0.0 ^b	0.1 $\pm$ 0.3 ^b	0.0 ^b
Planktonic larva	Copepoda zoea	3.3 $\pm$ 6.5	0.0 $\pm$ 0.0	0.2 $\pm$ 0.5	38.5
	Trochophore larva	0.0 $\pm$ 0.0 ^b	0.0 $\pm$ 0.0 ^b	27.6 $\pm$ 21.2 ^a	7.7 ^a

Note: Dominant species are defined as those with a relative abundance >5% in at least one community group. Different lowercase letters (a, b) in the same index indicate significant differences among groups ($p < 0.05$).

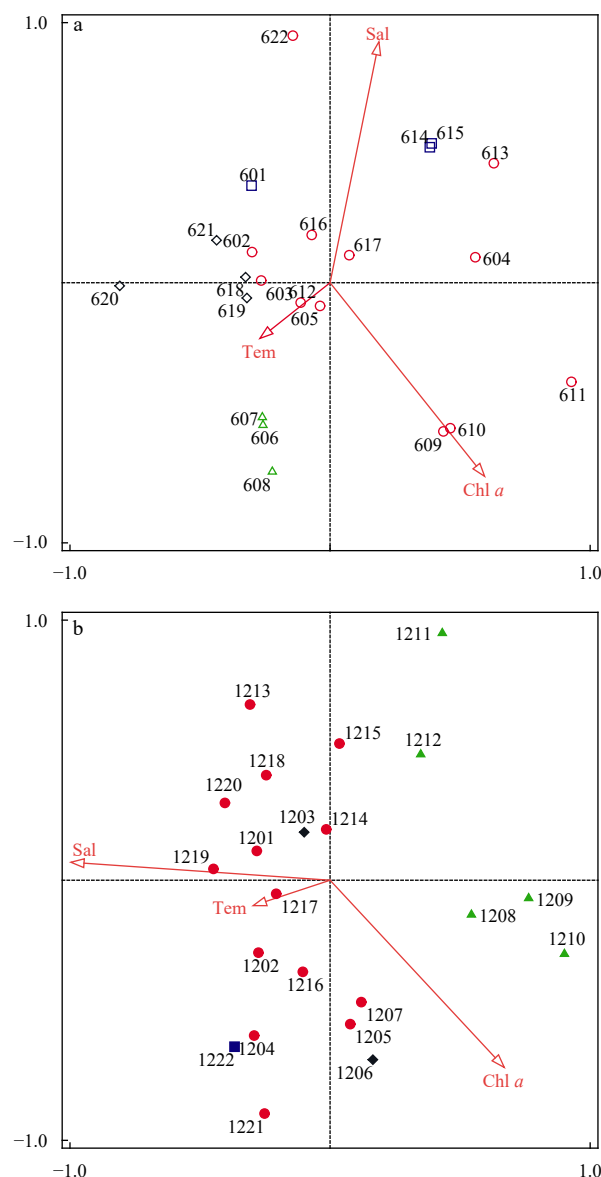
Table 5. Explanatory powers of the three environmental variables for the community structures

	Environmental variable	Explain/%	Contribution/%	<i>p</i>
June	Salinity	15.5	68.9	0.002
	Temperature	3.6	16.1	0.458
	Chl <i>a</i> concentration	3.4	15.0	0.580
December	Salinity	24.6	66.9	0.002
	Temperature	7.4	20.2	0.048
	Chl <i>a</i> concentration	4.8	12.9	0.176

change synchronously with salinity, exhibiting a negative correlation (Chen et al., 2018). Our study did not analyze DIN, due to its indirect impact on mesozooplankton, as mentioned in Sun's discussion, which is one of the reasons our results differ from Sun et al. (2016).

The sampling periods of June and December correspond to Hangzhou Bay's wet and dry periods, respectively (Fig. 1). The Qiantang and Changjiang rivers, and East China Sea water masses converge in Hangzhou Bay. Because of the different contributions of these three water masses at different times of the year, the salinity of waters in Hangzhou Bay differs between these two seasons (Sun et al., 2016). We report salinity to range 2.42–23.69 in June and 12.48–25.32 in December. Based on differences in the salinity ranges of the various groups, we divided zooplankton communities into those inhabiting low salinity (Group A), moderate salinity (Groups B and C), and high salinity (Group D) in June. Similarly, zooplankton communities were categorized into moderate salinity (Group A) and high salinity (Groups B–D) in December (Fig. 5). Spatial differences in the distributions of zooplankton communities are caused mainly by the differences in dominant taxa.

One species, *P. parvus*, tolerant of a wide range in salinity and temperature (Zhang et al., 2016), played a significant role as a key contributing species, and was generally more abundant in all regions during June and December (Table 6). *Labidocera euchaeta*, a nearshore low-salinity species, was more abundant in the low salinity region during June. Another nearshore low-salinity species, *A. pacifica* was more abundant in moderate salinity regions during both June and December (Table 6)—possibly because of distinct salinity preferences (~10 for *L. euchaeta* and 15–25 for *A. pacifica*), with salinities for *L. euchaeta* being more suitable for growth at higher temperatures (Guo et al., 2008; Huang and Zheng, 1984). The estuarine/brackish-water-dwelling *S. sinensis* was dominant in the moderate salinity region during December (Table 6), possibly because *S. sinensis* grows better at lower temperatures (Guo et al., 2008; Lin et al., 2001). The moderate salinity region was most influenced by interactions between water masses, which provided a diverse environment, and contributed to higher taxon abundance and biomass, such as the elevated

**Fig. 6.** Relationships between three environmental variables and zooplankton communities in June (a) and December (b). Sal: salinity, Tem: temperature.

abundance and biomass zones in Groups B and C in June, and in Group A in December (Table 3). This phenomenon is consistent with the occurrence of ocean fronts at the Changjiang River Estuary (Liu et al., 2022).

Table 6. Relative abundances of representative dominant species in different salinity regions during June and December 2022, within the Hangzhou Bay

Species	June			December	
	Relative abundance/%			Relative abundance/%	
	LS	MS	HS	MS	HS
<i>Paracalanus parvus</i> *	12.3 ± 6.1	45.2 ± 16.6	25.2 ± 5.7	17.5 ± 19.9	45.6 ± 15.0
<i>Labidocera euchaeta</i> ▲	25.6 ± 7.8 ^a	1.8 ± 1.5 ^{ab}	0.7 ± 1.4 ^b	\	\
<i>Acartia pacifica</i> ▲	0.7 ± 0.7	6.2 ± 8.7	0.5 ± 0.5	15.1 ± 17.9	1.5 ± 1.9
<i>Sinocalanus sinensis</i> ■	\	\	\	17.8 ± 17.0 ^a	0.2 ± 0.6 ^b

Note: Salinity regions: LS, low; MS, moderate; HS, high. Ecotype: *, euryhaline; ▲, nearshore low-salinity; ■, estuarine brackish-water. \ represents no data.

4.2 Relationships between spatial patterns in the distribution of zooplankton communities and salinity fronts

Hangzhou Bay water masses are derived from inputs of the Qiantang and Changjiang rivers, and the outer sea (Sun et al., 2016; Su and Wang, 1989). Depending on the direction of a monsoon, most of the Changjiang River Plume flows northeast into the East China Sea during warm seasons, and southeast into this sea during cold seasons. A small portion of the Changjiang River Plume—the secondary Changjiang River Plume—exists continuously and flows around the promontory of the Changjiang River, entering Hangzhou Bay (Su and Wang, 1989). A northeast-southwest-oriented salinity front in Hangzhou Bay also occurs throughout the year, composed of the Qiantang River Diluted Water front and Changjiang River Diluted Water secondary front (Su and Wang, 1989).

The distributions of zooplankton throughout Hangzhou Bay in June were generally consistent with those of salinity fronts (Figs 3c, 4b). However, the distribution of salinity over the sampling period in June proved to be somewhat anomalous, having been affected by processes associated with rising and falling tides between June 18 and 22. Tides represent the periodic movement of seawater caused by the gravitational forces of celestial bodies, primarily the moon and the sun (Feng et al., 1999). In estuarine areas, the rise and fall of these tides can cause strong disturbances in the hydrodynamics of the water column as fresh- and seawaters mix (House et al., 1998). The strong southerly monsoon in June causes outer seawaters to significantly influence Hangzhou Bay. Additionally, the Changjiang River Plume flows northeastward during this time, and it is less strong than the secondary Changjiang River Plume (Zhu et al., 1998). Compared with the normal pattern where salinity increases from the west to the east, the areas with salinity anomalies in Fig. 3c were mainly associated with sampling locations on June 18 (higher salinity) and 19 (lower salinity) (Fig. 7). These correspond to sampling during a rising tide on June 18, and a falling tide on June 19. There was a close relationship between the tidal patterns and salinity fronts in June. During the rising tides on June 18, the intense exchange between offshore and nearshore waters led an abnormally high salinity area forming in the bay's apex (Stations 601–605), where zooplankton communities were attributed to Groups C and D (Figs 3c, 4b). Among them, there is a significant variation in salinity gradient between Stations 601 and 602, forming a front (Figs 8a, 8b and 9a). During the falling tides on June 19, Qiantang River Diluted Water led to an abnormally low salinity area forming in the central bay (Stations 606–608), where zooplankton communities were attributed to Group A (Figs 3c, 4b). A dominant taxon in Group A, the low-salinity species *L. euchaeta*, was relatively, significantly more abundant in Group A than it was in Groups B–D (Table 4), and fronts formed on both sides of this group (Figs 8a, 8b and 9a). Over the ensuing three days (June 20–22), the exchange between offshore and nearshore waters decreased, causing previously formed fronts to disappear. This transitioned into two fronts, differentiating Groups B, C, and D (Figs 8a, 8b and 9a).

We report differences in salinity in December among Groups B, C, and D to be small, but for the salinity of Group A to be markedly lower (Fig. 5). In December, because of the influence of the northern monsoon, the Changjiang River Plume flows southeastward, and a stronger presence of the secondary Changjiang River Plume is felt (Liu et al., 2008). We attribute the relatively homogeneous environment with reduced salinity gradient for Groups B–D to the presence of a weaker Qiantang River Diluted Water and stronger secondary Changjiang River Plume. The

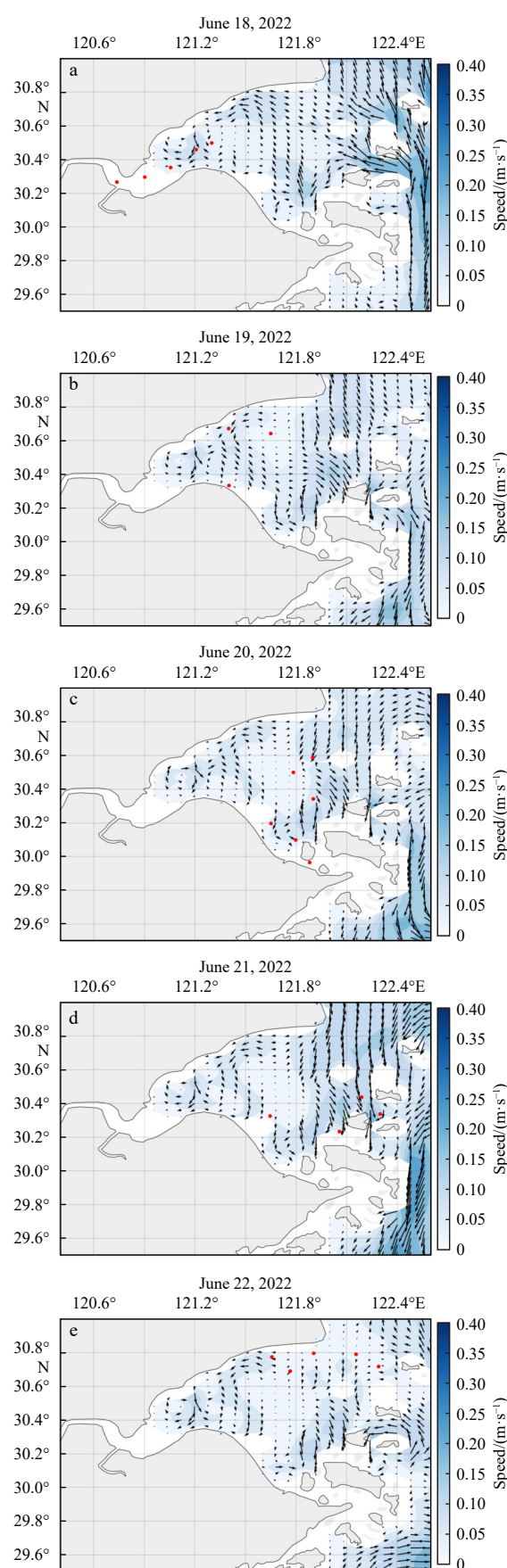


Fig. 7. Distribution of sea surface current fields in the Hangzhou Bay for each sampling day during June 2022.

Changjiang River Diluted Water secondary front extends through Groups B–D, while the Qiantang River Diluted Water front is less prominent (Figs 8c, 8d and 9b). *Sinocalanus sinensis*, a dominant zooplankton taxon in Group A, is an estuarine/brackish-water-dwelling species that manifested significantly higher relative abundances compared with values in Groups B–D (Tables 4, 6). As a result, an ecological boundary is formed between Group A and Groups B–D, which closely matches the location of the Qiantang River Diluted Water front (Figs 8c, 8d and 9b).

5 Conclusions

We report spatial and temporal variation in the distributions of zooplankton communities in Hangzhou Bay to be influenced primarily by salinity during both June and December. The spatial distribution of zooplankton communities match those of salinity fronts. December zooplankton communities are dispersed in MS and HS regions, with zooplankton community boundaries aligning well with the Qiantang River Diluted Water front. While the influence of rising and falling tides contributed to formation of an LS region in the middle of the bay in June, the zooplankton community boundaries during this time continuing to correspond to

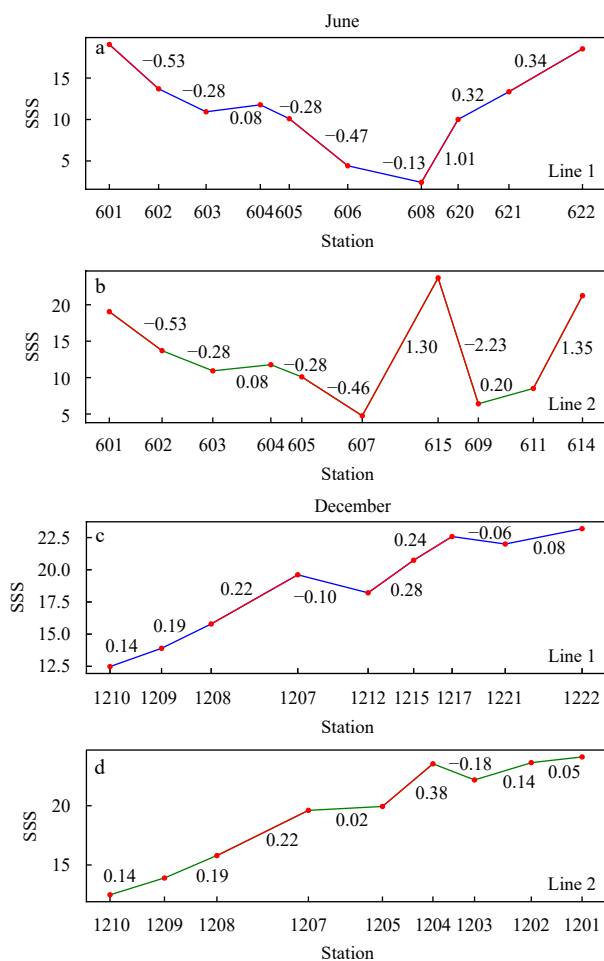


Fig. 8. Sea surface salinity versus distance (SSS vs. distance) along two lines crossing salinity fronts in June (a, b) and December (c, d). The spacing between stations are set according to distance proportion. The number next to each segment of the poly-line represents the slope. The red line indicates a significant salinity gradient between two stations, indicating the presence of a front.

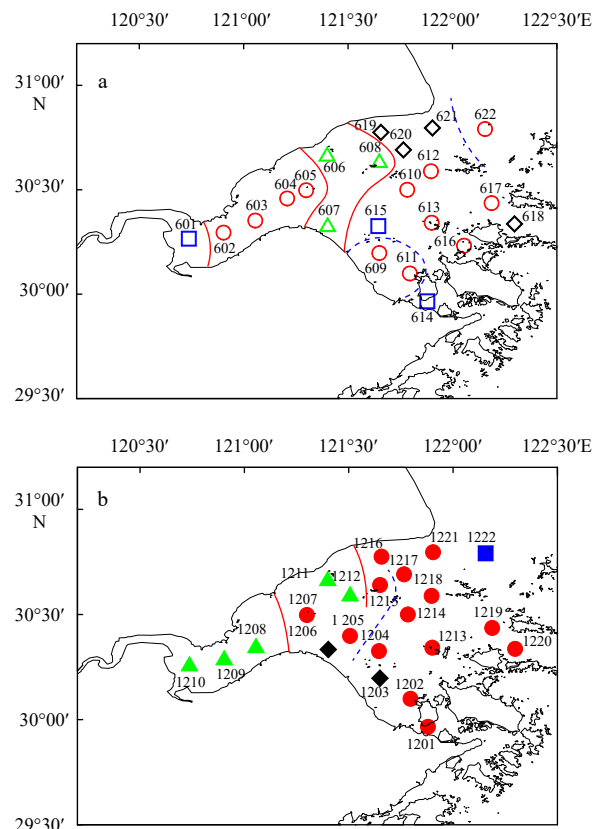


Fig. 9. Approximate locations of fronts in June (a) and December (b). The solid red line and dashed blue line in June represent the fronts during falling and ebbing tides. Lines in December: solid red, Qiantang River Diluted Water front; dashed blue, Changjiang River Diluted Water secondary front.

a salinity interface. The relative abundances of low-salinity or brackish-water species are also higher in LS and MS regions, with the abundance and biomass of zooplankton notably higher in the MS region.

The study reported small-scale fronts within a bay to have a number of features in common with large-scale ocean fronts, in that the spatial distribution of zooplankton communities and their high biomass occur at the interface. We also report structural variability in small-scale fronts within bays or coastal waters, in that they are sensitive to tidal phenomena. Therefore, to better understand the spatial and temporal distributions of coastal zooplankton communities, nutrient transport and the physical environment neighboring the fronts should be more rigorously investigated.

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