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Occurrence of the calanoid copepod *Acartia* (*Odontacartia*) *ohtsukai* in Laizhou Bay, the Bohai Sea, China, and its relationship with environmental factors

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In this study, we examined the short-term variation in the abundance of copepod *Acartia* specimens, identified previously as *Acartia pacifica*, in Laizhou Bay, an estuarine bay in the southern Bohai Sea in northern China. Monthly samples were collected from May 2011 to April 2012, excluding December 2011 and January to February 2012 due to ice. Based on its morphological characteristics, *Acartia ohtsukai* was distinguishable from *A. pacifica* for the first time in Laizhou Bay. *A. ohtsukai* was sporadically present from summer to autumn, with the highest abundance and occurrence in September. It appeared in June when the water temperature was above 20°C, and disappeared in November when the water temperature decreased to less than 10°C. During the surveyed months, *A. ohtsukai* was more commonly found inshore with salinity less than 28 than offshore in the bay. Correlation analysis revealed that temperature and chlorophyll a concentration significantly influenced the monthly variations in *A. ohtsukai* abundance. We also compared the occurrence of *A. ohtsukai* with that of three species from the genus *Tortanus* (*Tortanus derjugini*, *Tortanus forcipatus*, and *Tortanus spinicaudatus*) in Laizhou Bay. The coexistence of *A. ohtsukai* and *T. derjugini* in the bay suggests that their ecological habitats are similar to those of brackish-water species.

KEYWORDS

Acartia pacifica, *Acartia ohtsukai*, copepod, Laizhou Bay, Bohai Sea

1 Introduction

The genus *Acartia* Dana, 1846 (Copepoda, Calanoida, Acartiidae) is widely distributed in coastal areas and estuaries globally. They can be indicators of hydrological conditions and respond to climate warming (Rice et al., 2015; Rice and Stewart, 2016; Borkman et al., 2018) in terms of their phenology, abundance, body size, and distribution pattern. Furthermore, many *Acartia* species are dominant in estuarine zooplankton communities (Wang et al., 2002; Borkman et al., 2018; Zuraire et al., 2018), and they are crucial as secondary producers, transferring energy through the food web to the fish stock, especially small pelagic fish such as anchovies and sprats, in the coastal ecosystems. The species *Acartia* (*Odontacartia*) *ohsukai* is present in the estuarine and coastal waters of Korea, China, Vietnam, and Japan (Razouls et al., 2005–2023). It seasonally dominates the zooplankton community (Youn and Choi, 2008; Choi et al., 2021a) and is a good potential live prey for fish larvae through mass culture (Choi et al., 2021b). *Acartia* *ohsukai* was originally identified as a separate species from its sibling species *Acartia pacifica* based on morphological and genetic differences (Ueda and Bucklin, 2006). These two *Acartia* species also have different habitat preferences. *A. ohsukai* is a brackish species found along the coasts of the Northwest Pacific (Ueda and Bucklin, 2006; Moon et al., 2008; Sakaguchi et al., 2011), while *A. pacifica* is a coastal euryhaline species broadly distributed in offshore waters of the Indo-West Pacific (Ueda and Bucklin, 2006; Moon et al., 2008).

The population of *A. ohsukai* in Ariake Bay, Japan, is considered a continental relict (Ueda and Bucklin, 2006) and is geographically segregated from the *A. pacifica* population in Gwangyang Bay, Korea (Moon et al., 2008). While *A. ohsukai* has been frequently reported in bays and estuaries in Japan and Korea (Ueda and Bucklin, 2006; Moon et al., 2008; Youn and Choi, 2008, 2012; Kang, 2011; Park et al., 2013; Lee et al., 2017, 2020; Choi et al., 2019, 2021a, 2021b; Seo et al., 2021), and in Iraqi water (Jebir et al., 2021), its occurrence in the Chinese offshore waters is limited compared to that in the neighboring regions. On the other hand, *A. pacifica*, which is often confused with *A. ohsukai*, is recognized as a common species on Chinese coasts, ranging from the Bohai Sea in the north to the South China Sea in the south (Chen and Zhang, 1965; Liu, 2008). It has also been reported in river mouths or estuaries with lower salinities, such as the Yellow River estuary and the turbid zone of the Yangtze River estuary (Liu et al., 2012; Feng and Liu, 2019).

The low salinity tolerance of *A. pacifica* observed in Chinese waters is inconsistent with its typical marine habitats in the NW Pacific (Steuer, 1915; Ueda and Bucklin, 2006). To address this inconsistency, researchers have investigated specimens previously identified as *A. pacifica* from various regions in China. Liu (2007) reported high genetic similarity and morphological resemblance between samples identified as *A. pacifica* in Xiamen Harbor and *A. ohsukai* specimens in Ariake Bay, Japan (Ueda and Bucklin, 2006). Wang et al. (2011) suggested that the *A. pacifica* previously recorded in Jiaozhou Bay of the South Yellow Sea should be *A. ohsukai* based on molecular sequencing. Moreover, Shih et al. (2022a) revised the species identification of *A. pacific* described by

Chen and Zhang (1965) to *A. ohsukai* on the China *Acartia* species list.

Laizhou Bay, one of the three largest bays in the Bohai Sea in North China, is a typical estuarine bay that receives runoff from more than ten rivers, including the Yellow River. The bay has a water salinity usually below 30–32, due to the influx of freshwater (Xia et al., 1991; Wang and Wu, 2018). Researchers have shown *A. pacifica* to be the dominant planktonic copepod species in Laizhou Bay during summer and autumn (Bi et al., 2001; Liu et al., 2012; Wang and Wu, 2018), while *A. ohsukai* has not been reported in the region thus far. Correct identification of various *Acartia* species is essential for comprehending their geographic distribution and responses to changes in marine ecosystems. Given the low-salt conditions in the bay, which may not be suitable for the oceanic species *A. pacifica*, we re-examined samples collected in Laizhou Bay from 2011 to 2012. We focused on specimens initially identified as *A. pacifica*. We also investigated the influence of environmental factors on the distributions of these species in the bay. We aimed to clarify the classification of *Acartia* species and their habitat characteristics related to water conditions in Laizhou Bay, contributing to a better understanding of the *Acartia* species diversity and zoogeographic distribution in the region.

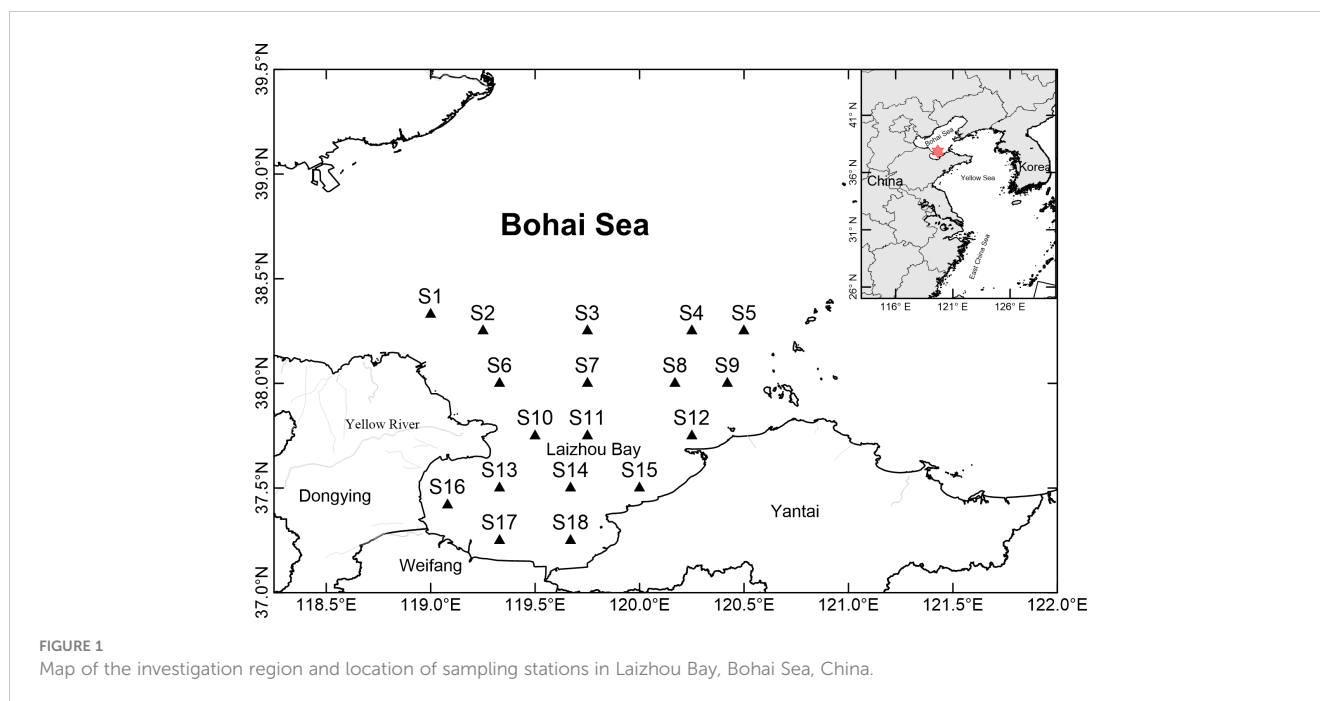
2 Materials and methods

2.1 Study area

Laizhou Bay is a semiclosed bay in the southern Bohai Sea, China. It has a bowl-shaped structure and an average depth of less than 10 m. The bay covers an area of approximately 7000 km² and has a coastline of 320 km. The mouth of the bay is 96 km long, stretching from the Yellow River estuary (37°39'N, 119°16.6'E) in the west to Gaojiao of Kaimu Island (37°41'N, 120°13'E) in the east (Figure 1). Laizhou Bay receives water from more than ten rivers, including the Yellow River, the largest river in northern China. The bay has shallow topography and receives great input from river water, resulting in low salinity and high nutrient levels. A northwesterly coastal current flows into the bay, creating a counterclockwise circulation pattern that facilitates water exchange, along with the tidal influences (Jiang et al., 2018). During summer, the increased discharge from the Yellow River can create an eastward plume at the river mouth, affecting the adjacent sea. During the rainy season, the average salinity in the bay can decrease to less than 26. In winter, the Laizhou Bay zone experiences sea ice due to the combined effects of cold air, shallow water, and low salinity (Zhang et al., 2013).

2.2 Sample collection

From May 2011 to April 2012, monthly sampling was conducted in the bay area between 37.25°N and 38.75°N, 119°E and 120.75°E. Samples from December 2011 to February 2012 were excluded due to the presence of ice (Zhang et al., 2013). A total of eighteen stations were set (see Figure 1). At each station, vertical tows were made using a conical plankton net with a mesh size of 160 μm and a mouth



diameter of 32 cm from the bottom to the surface layer. The volume of filtered water was estimated using a flow meter (Hydrobios, Germany) attached to the net mouth. Copepod samples were immediately fixed and stored in a buffered formaldehyde seawater solution at a final concentration of approximately 5%. Surface water temperature and salinity data were obtained from the Oceanographic Data Center, Chinese Academy of Sciences (CASODC) (<http://msdc.qdio.ac.cn>, accessed on 19th January 2024). The dissolved oxygen (DO) concentration and pH were measured at each station using YSI ProPlus (USA). Chlorophyll a (chl. a) concentration data were obtained from the OCEAN PRODUCTIVITY website (<http://www.science.oregonstate.edu/ocean.productivity/index.php>, Oregon State University, accessed on 25th September 2018).

Specimens of *Acartia*, previously identified as *A. pacifica*, were sorted from the samples and dissected under a stereomicroscope (Olympus SZX16, Japan). The developmental stages of the *Acartia* species were classified as copepodites (copepodids I-V) and adults following the criteria outlined by Li and Fang (1990). Prosome length (PL) was determined to the nearest 0.01 mm using a measuring reticule calibrated with a stage graticule on a dissecting microscope. Genetic analyses were not performed on the specimens due to the extended storage period of over a decade. Additionally, copepod specimens of the genus *Tortanus* were also sorted for further analysis, considering their possible coexistence with *A. ohtsukai* in estuarine waters, as suggested by Ueda and Bucklin (2006) and Moon et al. (2008).

2.3 Statistical analysis

The abundance of *Acartia* was measured as individuals per cubic meter (ind. m⁻³) at each station. Correlation analyses

were conducted to investigate the impact of environmental factors (water temperature, salinity, DO, pH, and chl. a concentration) on the occurrence of *Acartia*. A statistical significance level of 0.05 was used. To account for autocorrelation among environmental factors, partial correlation analysis was performed with temperature as the control variable. The original abundance of *Acartia* was log-transformed. Principal component analysis (PCA) was used to determine the relationships between the factors and log-transformed *Acartia* abundance. The ordination component scores and the variable loading coefficients were plotted based on Pearson's correlation matrix using STATISTICA 12.0 (StatSoft, Inc., Tulsa, OK, USA). Distribution contour and post maps were generated using Surfer 10.0 (Golden Software, Inc, USA) to visually represent the temporal and spatial distributions of *Acartia*.

3 Results

3.1 Morphological description

The adult female *Acartia* specimens had prosome lengths (PLs) ranging from 850 μ m to 1100 μ m, with a mean of 957 ± 301 μ m. As Shown in Figure 2, the fifth pediger of the female had acute, slightly curved lateral projections and posterodorsal spines on each side. The genital double somite is as long as its width and has two dorsal spines. The cauda rami were relatively long, with a length/width ratio of approximately three or more. On the first antennule, the second segment had a short spine on the distal half of the dorsal surface, while the fourth and fifth segments had subterminal spines dorsally. The length of the fifth leg was approximately 1.5 times greater than the width of the fifth leg.

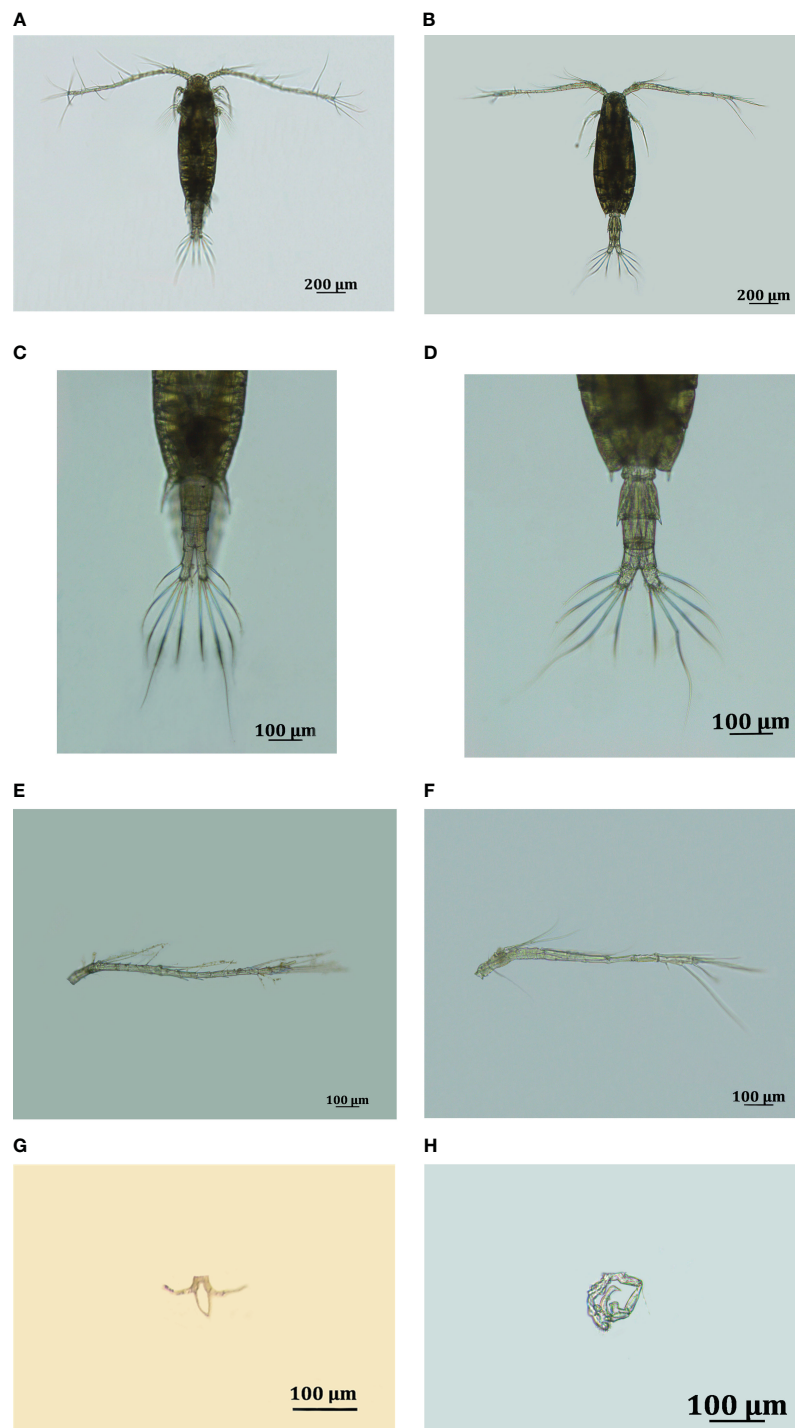


FIGURE 2

Photographs of *Acartia ohtsukai* sampled in Laizhou Bay, Bohai Sea, showing the (A) habitus (dorsal view), (B) urosome (dorsal view) and (C) antennule (right), (D) fifth leg of female and (E) habitus (dorsal view), (F) urosome (dorsal view) and (G) antennule (right), (H) fifth leg of male, respectively.

For adult males, the prosome length ranged from 835 μm to 1100 μm , with a mean of $835 \pm 216 \mu\text{m}$. The caudal ramus was approximately 1.5 times longer than its width. The length of the first exopod segment of the left fifth leg was approximately equal to that of the second exopod segment of the left fifth leg and shorter than the length of the first exopod

segment of the right fifth leg. The second exopod segment of the right fifth leg was as long as its width and had a square medial projection.

Based on the above observations, the morphological characteristics of the specimens were consistent with the descriptions of *Acartia ohtsukai* by Ueda and Bucklin (2006).

3.2 Abundance and developmental compositions

During the nine-month surveys conducted in Laizhou Bay, the presence of *A. ohtsukai* was first observed sporadically in June (Figure 3). Its abundance gradually increased throughout July and August, peaking in September at a mean abundance of 557 ± 1423 ind m^{-3} . However, there was a noticeable decline in October, with the abundance decreasing to less than 3 ind m^{-3} . By November, *A. ohtsukai* had almost disappeared from the surveyed area.

From July to November, both female and male adults of *A. ohtsukai* coexisted. The female-to-male (F/M) ratio was approximately equal in July (1.35) and September (0.97). However, there was a noticeable female bias in adults during August and October, with F/M ratios of 3.90 and 4.52, respectively. Copepodite individuals appeared later than adults and dominated the population accounting for more than 50% of the total population from July to September.

3.3 Spatial distribution

Figure 4 illustrates the distribution pattern of *A. ohtsukai* in the bay. The species is mainly concentrated at the base of the bay and is rarely found in the central part of the bay. In June, *A. ohtsukai* was found only found at station S16 near the bay base. In July and August, the species began spreading from the bottom to the center and mouth of the bay. It was present in approximately 33% of the surveyed stations. In September, *A. ohtsukai* had the highest

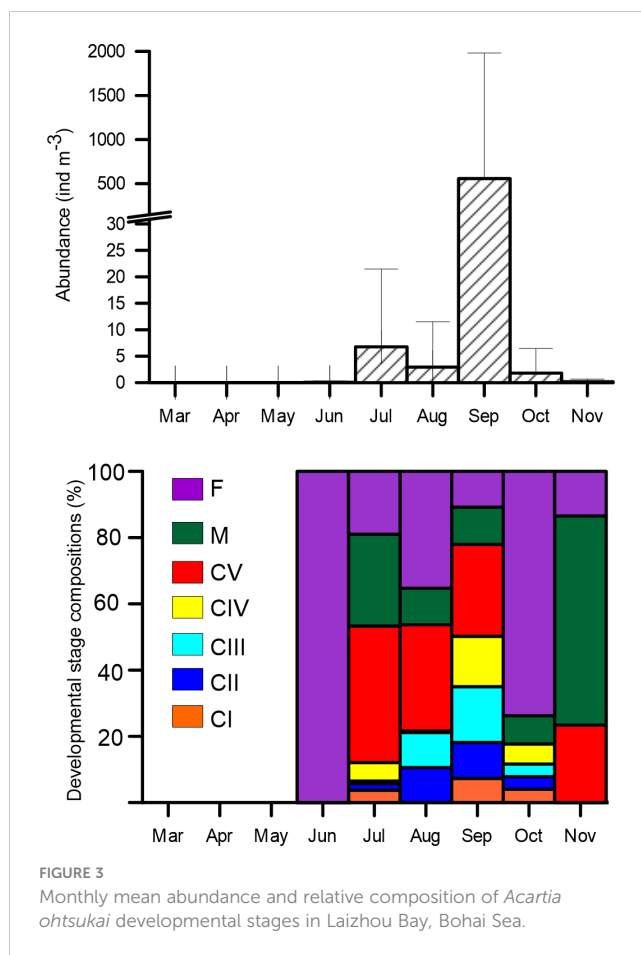


FIGURE 3 Monthly mean abundance and relative composition of *Acartia ohtsukai* developmental stages in Laizhou Bay, Bohai Sea.

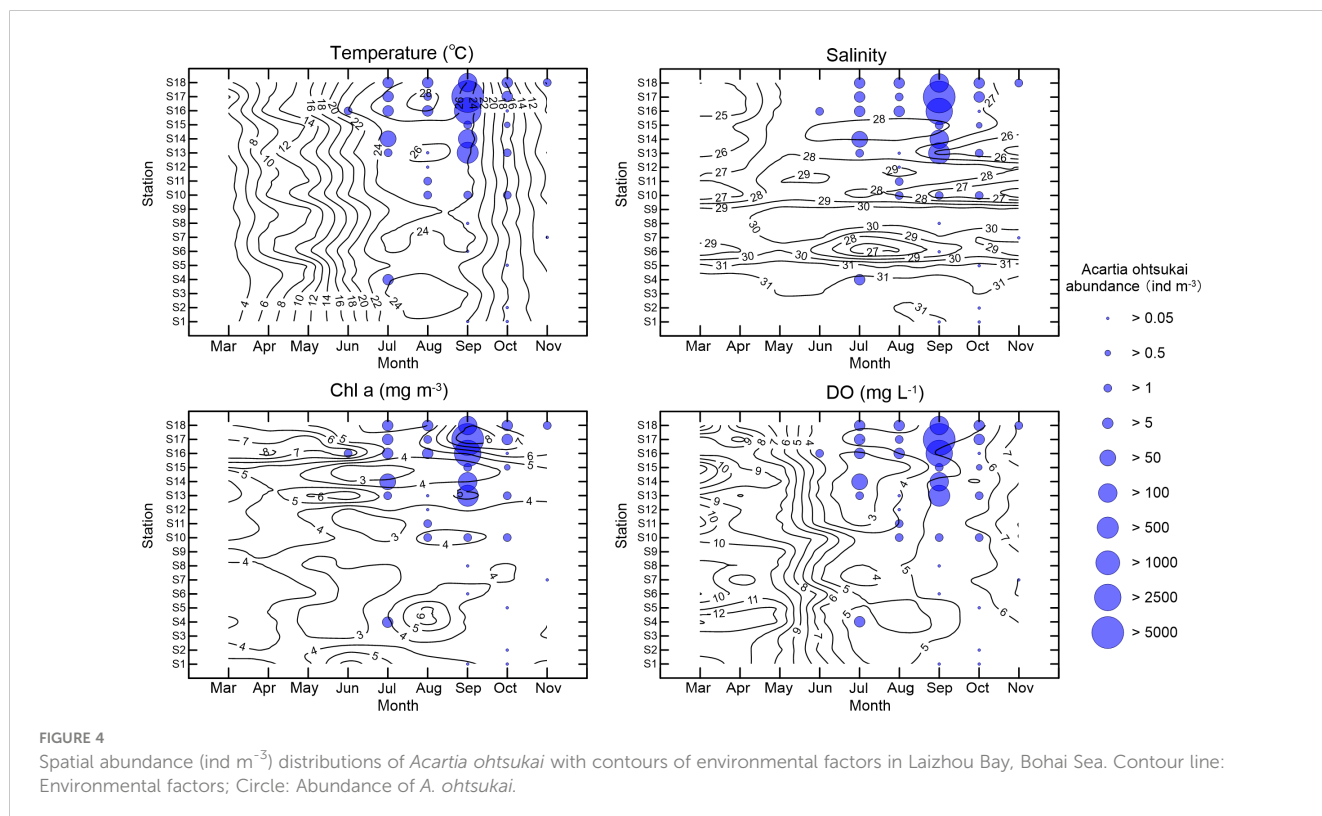


FIGURE 4 Spatial abundance (ind m^{-3}) distributions of *Acartia ohtsukai* with contours of environmental factors in Laizhou Bay, Bohai Sea. Contour line: Environmental factors; Circle: Abundance of *A. ohtsukai*.

occurrence rate (55%). The distribution of *A. ohtsukai* was remarkably heterogeneous, with higher densities observed at the bottom of the bay than at the central part. The highest abundance of *A. ohtsukai*, with more than 5000 ind m⁻³ was observed at Station No.17. The neighboring stations No.16 and No.13 also had relatively higher abundances, with 3022 and 907 ind m⁻³, respectively. However, at other stations, the abundance of *A. ohtsukai* was less than 5 ind m⁻³. In October, the abundance of *A. ohtsukai* was less than 5 ind m⁻³ at all stations, although the occurrence rate (50%) was similar to that in September. In November, the species gradually disappeared from the bay and was sporadically found at only two stations.

3.4 Relations with environmental effects

ANOVA showed significant differences in water temperature, salinity, chlorophyll, dissolved oxygen levels, and pH among the months and stations. Table 1 presents the correlation analysis results, indicating that water temperature, salinity, and chl. a concentration significantly impacted the abundance of *A. ohtsukai*. Importantly, there were seasonal variations in the correlation coefficients. A positive correlation between water temperature and *A. ohtsukai* abundance was observed in June and August, while a negative correlation with salinity was found in September and October. In June, there was a highly significant positive correlation between the chl. a concentration and *A. ohtsukai* abundance, which decreased from September to October.

Figure 4 illustrates the relative distributions of the environmental factors and *A. ohtsukai*. *A. ohtsukai* was observed at stations with temperatures above 20°C in June and disappeared when the temperature decreased below 10°C in November. On average, *A. ohtsukai* occurred in waters with an average temperature of 24.9°C, a salinity of 27.4, and an average chl. a concentration of 7.33 mg m⁻³. Stations with *A. ohtsukai* abundances exceeding 500

TABLE 1 Correlation coefficients between log-transformed *Acartia ohtsukai* abundance and environmental factors.

Month	Temperature	Salinity	Depth	chl. a	pH	DO
June	0.53*	0.17	0.05	0.52*	0.11	0.04
July	0.29	-0.08	-0.35	0.02	-0.33	-0.45
August	0.52*	-0.1	-0.11	-0.03	-0.28	0.05
September	0.26	-0.27	-0.44	0.71**	-0.03	-0.24
October	-0.41	-0.20	-0.28	0.71**	0.32	-0.02
Months from June to December	0.14	-0.16	-0.19	0.41**	0.11	0.10

*Statistically significant at p<0.05; ** highly significant at p<0.01.

ind m⁻³ were characterized by temperatures above 23°C, salinities below 28, and chl. a concentrations above 8 mg m⁻³.

We identified three *Tortanus* species, namely, *T. derjugini*, *T. forcipatus*, and *T. spinicaudatus*. No copepods of the genus *Sinocalanus* were observed in the samples. Figure 5 illustrates that *Tortanus* sp. was present from May to October, with the highest abundance occurring at station S17 in September. Over 46% of the *Tortanus* occurrences coincided with those of *A. ohtsukai*. The highest abundance of *T. derjugini* occurred in September at station S17, which was the same as that of *A. ohtsukai*. *T. spinicaudatus* had the greatest number of occurrences (18), occurring from May to September. *T. derjugini* rarely occurred at only two stations in August and September, but it had the highest total abundance. *T. forcipatus* appeared in September and disappeared in October, making it the latest occurring species. Due to the infrequent occurrence and small sample sizes, data from the three *Tortanus* spp. were combined for correlation analysis. Correlation analysis revealed a strong correlation between the total abundance of *Tortanus* sp. and that of *A. ohtsukai* (Spearman rank R = 0.25, p = 0.01<0.05).

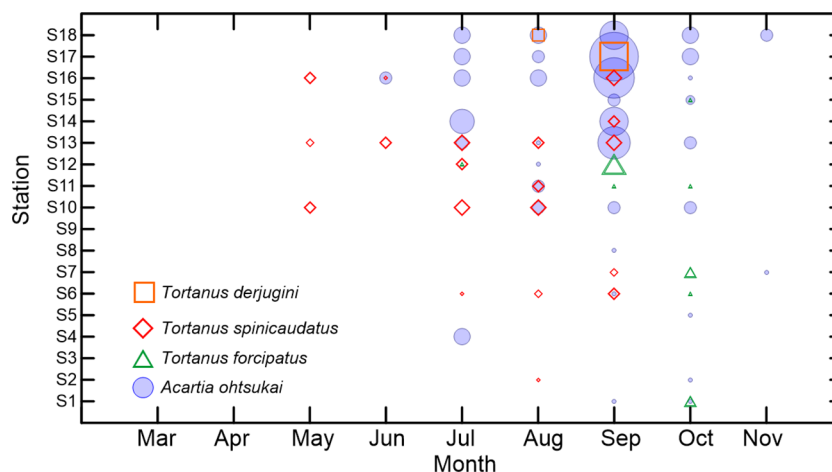


FIGURE 5 Occurrence distributions of *Tortanus derjugini*, *T. forcipatus*, and *T. spinicaudatus* among months and stations in Laizhou Bay, Bohai Sea. The scale legend of the symbols is similar to that in Figure 4.

Figure 6 presents a biplot illustrating the results of PCA for environmental factors during summer and autumn. The two-axis ordination diagram explains more than 65% of the variance, with the first two principal components explaining 36.63% and 28.68% of the variance, respectively. The biplot indicates that the scores on Axis I were mostly influenced by factors such as chl. a, salinity, and depth, which were closely related to *Acartia* abundance. The loadings of factors on Axis II indicate that the scores on the second component were mostly influenced by temperature, pH, and dissolved oxygen (DO). However, *A. ohtsukai* contributed only slightly (6%) to the variability of Axis II. Therefore, chlorophyll, salinity, and depth appeared to be more sensitive to *A. ohtsukai* than to the other three factors from June to November. Additionally, the principal discriminating endpoints between the abundances of *Acartia* and *Tortanus* were closely distributed, indicating a similar response to environmental factors.

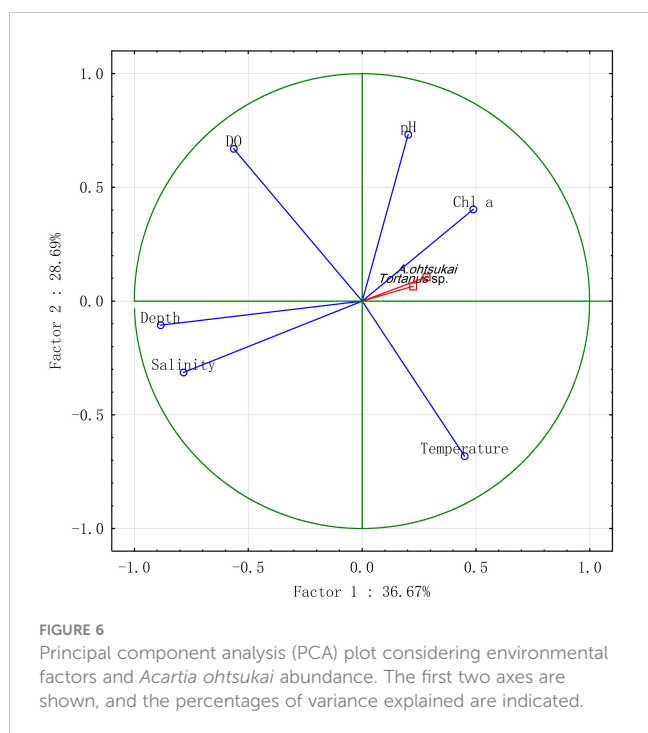
4 Discussion

4.1 Species determination

A. ohtsukai is not commonly reported along the Chinese coasts, unlike its closely related species *A. pacifica*, which has been extensively reported in coastal or estuarine waters in China since the 1950s. However, after Ueda and Bucklin (2006) described *A. ohtsukai* as a distinct species, Chinese researchers re-examined *Acartia* specimens from estuaries and coasts. According to morphology and genetic sequences, specimens previously identified as *A. pacifica* in Jiaozhou Bay in the southern Yellow Sea (Wang et al., 2011) and in Xiamen Harbor in the East China Sea (Liu, 2007) should be reclassified as *A. ohtsukai*. There have been no records of *A. ohtsukai* in Laizhou Bay. Although we did not perform

genetic analysis on the *Acartia* specimens due to their preservation in formaldehyde for more than a decade, the results indicated that *Acartia* specimens collected in 2011 from Laizhou Bay, previously identified as *A. pacifica*, should be considered *A. ohtsukai* based on their morphology, specifically the characteristics of the caudal rami and antennule in females and the urosomal somites and the fifth leg in males, as described by Ueda and Bucklin (2006).

Copepods belonging to the genus *Acartia* are prevalent and widely distributed in estuarine and coastal waters worldwide. However, each species has specific temperature and salinity requirements, limiting its spatial-temporal distribution (Kasahara et al., 1975; Bradford, 1976; Kang, 2011; Peck et al., 2015). Therefore, ecological habits, along with morphological characteristics and genetic sequences, are crucial for determining *Acartia* species. *A. ohtsukai* predominantly resides in river mouths, estuaries, and harbors temperate waters during the hot season, particularly in areas with abundant freshwater inputs (Ueda and Bucklin, 2006; Youn and Choi, 2008; Park et al., 2013; Jebir et al., 2021). This species exhibits limited tolerance to low temperatures, requiring a minimum water temperature of 16.5°C (Youn and Choi, 2008) and tolerating a maximum of 29°C (Ueda and Bucklin, 2006). *A. ohtsukai* also exhibits favorable tolerance to low salinity and is found in waters with a minimum salinity of 0.8 (Sakaguchi et al., 2011) and a maximum salinity of 32 (Choi et al., 2021a). The optimal temperature and salinity for its population density are suggested to be approximately 25~26°C (Youn and Choi, 2008; Kang, 2011; Choi et al., 2019) and below 30~32 (Ueda and Bucklin, 2006; Moon et al., 2008; Kang, 2011), respectively. On the other hand, *A. pacifica* is mostly found on temperate and tropical coasts during warm seasons (summer and autumn). It can tolerate a minimum water temperature of 12°C (Moon et al., 2008) and a maximum exceeding 29°C (Zuraire et al., 2018). *A. pacifica* has a high salinity tolerance, with a minimum of 21 (Kang, 2011) and a maximum of 36.5 (Greenwood, 1981) in its habitat. Typically, the *A. pacifica* population occurs in waters with temperatures above 22°C (Greenwood, 1981; Kang, 2011; Zuraire et al., 2018) and salinities greater than 30~32 (Greenwood, 1981; Ueda and Bucklin, 2006; Moon et al., 2008). A study conducted in Gwangyang Bay revealed a distinct separation of *A. ohtsukai* and *A. pacifica* in response to changes in salinity (Moon et al., 2008). *A. ohtsukai* is primarily a brackish species in estuarine waters with salinities less than 30~32 during the summer, while *A. pacifica* is relatively hypersaline and is found in offshore waters with salinities greater than 30~32 during the warm season. As a result, the two congener copepods are suggested to be distinguished by their salinity preferences (Kang, 2011). Laizhou Bay, characterized by its shallow topography and abundant river input, has low salinity levels. The salinity during the study period was lower than 31.5 (Figure 4), which may not be optimal for the survival of typical *A. pacifica*. Moreover, there was a negative correlation between the abundance of *A. ohtsukai* and salinity during the abundant months of September and October (Table 1). There was also a preference for relatively low salinity (< 28) (Figure 4), which is consistent with the temperature and salinity characteristics of the ecological habitats of *A. ohtsukai* in Korean and Japanese waters (Ueda and Bucklin, 2006; Moon et al., 2008; Soh, 2010; Kang, 2011).



4.2 Effects of environmental factors

In this study, we found that *A. ohtsukai* in Laizhou Bay appeared sporadically and seasonally during the summer and autumn, similar to bays and estuaries in Korea (Kang, 2011; Choi et al., 2021a) and Jiaozhou Bay in the South Yellow Sea (Zhong and Xiao, 1992a, 1992b; Sun et al., 2012). The seasonality of *A. ohtsukai* emergence and population increase is likely linked to the production and hatching of resting eggs. These eggs remain on the surface substrate during winter and hatch when temperatures become favorable. Research by Zhong and Xiao (1992a) supports this hypothesis. The initial surge in *Acartia* sp. larvae was not a result of normal reproduction but the hatching of dormant eggs (Zhong and Xiao, 1992a; Wang et al., 2005). The hatching of dormant eggs is strongly influenced by water temperature (Uye, 1985). Incubation experiments demonstrated that *A. ohtsukai* had high spawning rates and hatching success at temperatures of 25°C and 30°C and salinities of 27 (Choi et al., 2021b). In Jiaozhou Bay, southern Yellow Sea, the species exhibited a high rate of dormant egg hatching at 15°C (Zhong and Xiao, 1992a) and continued spawning when the water temperature ranged between 8°C and 24°C. The highest egg production rate occurred at a temperature of 23°C (Sun et al., 2011). Moreover, *A. ohtsukai* mortality was relatively low at 20–30°C across a salinity range of 20–33 (Choi et al., 2021b). Therefore, water temperature is likely to be the crucial factor triggering the population increase of this species. Our data, presented in Table 1, show significant positive correlations between species abundance and temperature during the early seasons of occurrence. Additionally, as presented in Figure 4, *A. ohtsukai* first emerged in June when the water temperature was above 20°C, then decreased as the water temperature decreased below 20°C and disappeared when the temperature decreased below 10°C. This may be due to the high mortality rate of *A. ohtsukai* females at the same temperature, as reported by Choi et al. (2021b).

In addition, the concentration of chl. a was also significantly correlated with the distribution of *A. ohtsukai* in Laizhou Bay (Table 1). The density of *A. ohtsukai* was highest inshore where the chl. a concentrations were relatively high (>8 mg m⁻³) (Figure 4). Similarly, the chl. a concentration was suggested to influence the occurrence of *Acartia erythroa* in Incheon and Ulsan (Kang, 2011). A high chl. a concentration of (>10 mg L⁻¹) was recommended for maintaining relatively high species richness and diversity of *Acartia* sp. during summer (Choi et al., 2021a). The low concentration of suitable food in seawater compared to that in estuaries may explain the failure of *A. tonsa* to develop in coastal waters with lower chl. a concentrations <1 µg L⁻¹ ppm (Paffenhöfer and Stearns, 1988). The chl. a concentration also affects the daily production of *Acartia omorii* in Ilkang Bay, Korea (Kang et al., 2007), and the spawning rate of the copepod *Acartia hongii* in Gyeonggi, Korea (Youn and Choi, 2007), which in turn affects population size.

Exposure to hypoxic conditions (< 2.0 mg L⁻¹ dissolved oxygen) negatively affects egg production, developmental rate, and size at maturity in *Acartia tonsa*, especially during the summer when the copepod population is most abundant and growing rapidly

(Richmond et al., 2006). *A. ohtsukai* has been observed to avoid hypoxic waters with naturally depleted DO (Kang, 2011). However, in this study, the distribution of *A. ohtsukai* in the bay cannot be explained by DO as a limiting factor, as the bay has a relatively high DO concentration (>3.0 mg L⁻¹). Although *A. ohtsukai* did not occur in the waters with the highest DO concentration, its density was found in waters with a DO concentration above 4 mg L⁻¹, similar to that of *A. ohtsukai* in ports of Korea, which occurred within a relatively narrow range of DO concentrations from 4.30 to 9.32 mg L⁻¹ (Kang, 2011).

4.3 Coexistence with *Tortanus* sp.

Ueda and Bucklin (2006) reported that *A. ohtsukai*, a continental relict species, coexisted with *S. sinensis* and *T. derjugini*/*T. dextrilobatus* in turbid estuaries within Ariake Bay, Japan. Similar patterns of coexistences were observed in Korean estuaries (Moon et al., 2008). In this study, we identified three species of the genus *Tortanus* in Laizhou Bay: *T. forcipatus*, *T. spinicaudatus*, and *T. derjugini*. These species are common in East Asian continental waters during the warm season, with *T. forcipatus* and *T. spinicaudatus* preferring coastal waters and *T. derjugini* being restricted to estuaries (Chen and Zhang, 1965; Ohtsuka et al., 1995; Soh, 2010; Shih et al., 2022b). *S. sinensis* was not found in our samples, possibly because this species mainly occurs in the innermost part of the oligohaline water where the salinity is less than 15 (Youn and Choi, 2008; Suzuki et al., 2013; Seo et al., 2021), which is outside the scope of our survey area. Our results indicated that *T. forcipatus*, *T. derjugini*, and *T. spinicaudatus* overlap temporally and geographically with *A. ohtsukai*, particularly *T. derjugini*, which was observed at the same station as *A. ohtsukai* in September (Figure 5). This suggests that they have similar ecological habits to warm-season and estuarine species (Soh, 2010). The coexistence of *T. derjugini* and *A. ohtsukai* may be due to their shared optimum water temperature of approximately 15°C for dormant egg hatching in their growth cycles (Kasahara and Uye, 1979; Zhong and Xiao, 1992a), while *T. forcipatus* emerges later than *A. ohtsukai*, probably due to its higher optimum water temperature (>15°C) for dormant egg hatching at 25°C (Kasahara et al., 1975; Kasahara and Uye, 1979). Nevertheless, our findings showed that *T. derjugini* occurs rarely and does not completely overlap in spatial and temporal distribution with *A. ohtsukai* in Laizhou Bay. Seo et al. (2021) also reported that *A. ohtsukai* and *T. dextrilobatus* appeared in the same seasons from spring to autumn in the Tamjin River estuary, but *T. derjugini* appeared only in the spring. Sakaguchi et al. (2011) observed the co-occurrence of three continental relict species, *A. ohtsukai*, *S. sinensis*, and *T. derjugini*/*T. dextrilobatus*, in estuaries in southern and western Korea but not in estuaries in western Japan. Suzuki et al. (2013) suggested that these semi-endemic species may have different preferences for estuarine habitat factors, such as turbidity and food concentration, in addition to temperature and salinity, leading to different distribution patterns over time and space on the southeastern coasts of the Eurasian continent and in neighboring waters.

A. ohtsukai and *Tortanus* sp. were present in Laizhou Bay during the warm season, and their populations were concentrated at the base of the bay. They first appeared at the western base of the bay near the river mouth in early summer and then spread from west to east and from the inner to the middle bay from July to September. Finally, they retreated to the base of the bay in late autumn and winter. This indicates that the inner bay serves as the source of replenishment for their populations. The seasonal occurrence patterns of the populations are consistent with the dynamics of low-salt runoff water in Laizhou Bay. The hydrology in Laizhou Bay is mostly influenced by the Yellow River and coastal river runoff, Bohai Sea waters, and monsoons (Jiang et al., 2018). The water salinity on the west side at the base of the bay remains low due to runoff from the Yellow River and land runoff along the coast throughout the year, which provides a continuous brackish habitat for *A. ohtsukai* and *Tortanus* sp. In late spring and early summer, when the water temperature rises, the resting eggs of *A. ohtsukai* and *Tortanus* sp. on the west base of the bay hatch and form pelagic populations. During the rainy seasons of summer and early autumn, the low-salt water expands from the base of the bay to the middle and outer bay due to the increase runoff from the Yellow River, land runoff, and the southeastern monsoon. Consequently, the *A. ohtsukai* and *Tortanus* sp. populations also extend to the middle bay with runoff. During the dry seasons of autumn and winter, the low-salinity water retreats southward to the bay bottom, and the relatively high-salinity water of the Bohai Sea enters the bay from the eastern part of the mouth of the bay in a compensatory way. As a result, the *A. ohtsukai* and *Tortanus* sp. also retreat toward the bay base and disappear in the middle and outer bay.

5 Conclusion

Laizhou Bay, which has relatively low salinity, provides a suitable habitats for brackish-water organisms. The *Acartia* specimen previously identified as *Acartia pacifica* in Laizhou Bay is *Acartia ohtsukai*, based on its habitat and morphological characteristics. Monthly surveys indicate that *Acartia* species are present in Laizhou Bay during the warm seasons of summer and autumn. They are found near the river mouth where the chl. a concentration is high, the water temperature exceeds 20°C, and the salinity is below 28. These findings align with the habitat preference of *A. ohtsukai* as a brackish-water species, as described by Ueda and Bucklin (2006). Water temperature may also function in the occurrence of *A. ohtsukai*, while the chl. a concentration influences its distribution. The co-occurrence of *A. ohtsukai* with three *Tortanus* species in Laizhou Bay was observed, although there were spatial and seasonal variations among the *Tortanus* species.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

TZ: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. DW: Formal analysis, Visualization, Writing – review & editing. YL: Data curation, Writing – review & editing. MN: Formal analysis, Writing – review & editing. ZC: Formal analysis, Writing – review & editing. JW: Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Bi, H. S., Sun, S., Gao, S. W., and Zhang, G. T. (2001). The ecological characteristics of zooplankton community in the Bohai Sea II. The distribution of copepoda abundance and seasonal dynamics. *Acta Ecol. Sin.* 21, 177–185. doi: 10.3321/j.issn:1000-0933.2001.02.001
- Borkman, D. G., Fofonoff, P., Smayda, T. J., and Turner, J. T. (2018). Changing *Acartia* spp. phenology and abundance during a warming period in Narragansett Bay, Rhode Island, USA: 1972–1990. *J. Plankton Res.* 40, 580–594. doi: 10.1093/plankt/fby029
- Bradford, J. M. (1976). Partial revision of the *Acartia* subgenus *Acartiura* (Copepoda: Calanoida: Acartiidae). *New Zeal. J. Mar. Fresh.* 10, 159–202. doi: 10.1080/00288330.1976.9515606
- Chen, Q. C., and Zhang, S. Z. (1965). The planktonic copepods of the Yellow Sea and the East China Sea, I. Calanoida. *Studia Marina Sin.* 7, 20–131.
- Choi, S. Y., Lee, E. H., Soh, H. Y., and Jang, M.-C. (2021b). Effects of temperature and salinity on egg production, hatching, and mortality rates in *Acartia ohtsukai* (Copepoda, Calanoida). *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.704479
- Choi, S. Y., Seo, M. H., Shin, K., Jang, M. C., and Soh, H. Y. (2019). Spatial distribution of *Acartia* (Copepoda, Calanoida) species in the southern coastal waters of Korea during summer. *Korean J. Environ. Biol.* 37, 299–308. doi: 10.11626/KJEB.2019.37.3.299
- Choi, S. Y., Seo, M. H., and Soh, H. Y. (2021a). Short-term variation in abundance of four *Acartia* species (Copepoda, Calanoida) in a eutrophic bay. *PeerJ* 9, e10835. doi: 10.7717/peerj.10835
- Feng, Y., and Liu, Z. (2019). Environmental determinants of zooplankton assemblages during summer hypoxia in the Changjiang Estuary and its adjacent waters, China. *Reg. Stud. Mar. Sci.* 32, 100838. doi: 10.1016/j.rsma.2019.100838
- Greenwood, J. G. (1981). Occurrence of congeneric pairs of *Acartia* and *Pseudodiaptomus* species (Copepoda, Calanoida) in Moreton Bay, Queensland. *Estuar. Coast. Shelf Sci.* 13, 591–596. doi: 10.1016/S0302-3524(81)80060-6
- Jebir, A. M., Ajeel Shaker, G., and Khalaf Talib, A. (2021). Ecological study of zooplankton in South Shatt Al-Arab River, Southern Iraq. *J. Biol. Stud.* 4, 1–23. doi: 10.62400/jbs.v4i1.5609
- Jiang, H., Liu, D., Song, X., Ma, Y., Wang, Y., Liu, A., et al. (2018). Response of phytoplankton assemblages to nitrogen reduction in the Laizhou Bay, China. *Mar. Pollut. Bull.* 136, 524–532. doi: 10.1016/j.marpolbul.2018.09.042
- Kang, H. K., Kang, Y. J., and Park, C. (2007). Production of *Acartia omorii* (Copepoda: Calanoida) in Ilkwang Bay, southeastern coast of Korea. *J. Mar. Syst.* 67, 236–244. doi: 10.1016/j.jmarsys.2006.05.014
- Kang, J. (2011). The occurrence of *Acartia* species and their environmental characteristics at three ports in Korea. *Ocean Sci. J.* 46, 219–237. doi: 10.1007/s12601-011-0018-7
- Kasahara, S., Onbe, T., and Kamigaki, M. (1975). Calanoid Copepod eggs in sea-bottom muds. III. Effects of temperature, salinity and other factors on the hatching of resting eggs of *Tortanus forcipatus*. *Mar. Biol.* 31, 31–35. doi: 10.1007/BF00390645
- Kasahara, S., and Uye, S. (1979). Calanoid copepod eggs in sea-bottom muds. V. Seasonal changes in hatching of subitaneous and diapause eggs of *Tortanus forcipatus*. *Mar. Biol.* 55, 63–68. doi: 10.1007/BF00391718
- Lee, E. H., Choi, S. Y., Seo, M. H., Lee, S. J., and Soh, H. Y. (2020). Effects of temperature and pH on the egg production and hatching success of a common Korean copepod. *Diversity* 12, 372. doi: 10.3390/d12100372
- Lee, E. H., Seo, M. H., Yoon, Y. H., Choi, S. D., and Soh, H. Y. (2017). Environmental factors affecting zooplankton community in Gwangyang Bay. *Korean J. Environ. Biol.* 35, 631–639. doi: 10.11626/KJEB.2017.35.4.631
- Li, S., and Fang, J. C. (1990). *Marine planktonic copepod larvae in China Seas* (Beijing: China Ocean Press), 115–118.
- Liu, C. C. (2007). Molecular phylogeny of two *Acartia* species in China Southeast Coastal Seas (Xiamen, China: Xiamen University).
- Liu, R. Y. (2008). *Checklist of marine biota of China Seas* (Beijing: Science press).
- Liu, A. Y., Song, X. K., Liu, L. J., Ren, L. H., Jin, Y., Liu, Y. H., et al. (2012). Community structure of zooplankton in Laizhou bay in summer. *Mar. Sci.* 36 (10), 61–67.
- Moon, S. Y., Ohtsuka, S., Ueda, H., and Soh, H. Y. (2008). *Acartia* (*Odontartia*) *ohtsukai* ueda and bucklin 2006 (Copepoda, Calanoida, Acartiidae): first record of its occurrence in Korean waters and habitat segregation from its sibling species *A. pacifica* steue. *Zootaxa* 1841, 61–64. doi: 10.11646/zootaxa.1841.1.5
- Moon, S. Y., Seo, M. H., Shin, Y., and Soh, H. Y. (2012). Seasonal variation of mesozooplankton communities in the semi-enclosed Muan Bay, Korea. *Ocean Polar Res.* 34, 1–18. doi: 10.4217/OPR.2012.34.1.001
- Ohtsuka, S., Ueda, H., and Lian, G. (1995). *Tortanus derjugini* Smirnov (Copepoda: Calanoida) from the Ariake Sea, western Japan, with notes on the zoogeography of brackish-water calanoida copepods in East Sea. *Bull. Plankton Soc. Japan* 42, 147–162.
- Paffenhöfer, G. A., and Stearns, D. E. (1988). Why is *Acartia tonsa* (Copepoda, Calanoida) restricted to nearshore environments? *Mar. Ecol. Prog. Ser.* 42, 33–38. doi: 10.3354/meps042033
- Park, E. O., Rahman, M. S., Seo, M. H., Kim, J. J., and Soh, H. Y. (2013). Distribution patterns of Calanoid Copepods along the Seomjin River Estuary in Southern Korea during summer. *Korean J. Environ. Biol.* 31, 165–171. doi: 10.11626/KJEB.2013.31.2.165
- Peck, N., Peters, J., Diekmann, R., Laakmann, S., and Renz, J. (2015). Interactive effects of temperature and salinity on population dynamics of the calanoid copepod *Acartia tonsa*. *J. Plankton Res.* 37, 197–210. doi: 10.1093/plankt/fbu093
- Razouls, C., Desreumaux, N., Kouwenberg, J., and de Bovée, F. (2005–2023) (Sorbonne University, CNRS). Available online at: <http://copepodes.obs-banyuls.fr/en> (Accessed December 20, 2023).
- Rice, E., Dam, H., and Stewart, G. (2015). Impact of climate change on estuarine zooplankton: surface water warming in Long Island Sound is associated with changes in copepod size and community Structure. *Estuaries Coasts* 38, 13–23. doi: 10.1007/s12237-014-9770-0
- Rice, E., and Stewart, G. (2016). Decadal changes in zooplankton abundance and phenology of Long Island Sound reflect interacting changes in temperature and community composition. *Mar. Environ. Res.* 120, 154–165. doi: 10.1016/j.marenvres.2016.08.003
- Richmond, C., Marcus, N. H., Sedlacek, C., Miller, G. A., and Oppert, C. (2006). Hypoxia and seasonal temperature: Short-term effects and long-term implications for *Acartia tonsa* Dana. *J. Exp. Mar. Biol. Ecol.* 328, 177–196. doi: 10.1016/j.jembe.2005.07.004
- Sakaguchi, S. O., Ueda, H., Ohtsuka, S., Soh, H. Y., and Yoon, Y. H. (2011). Zoogeography of planktonic brackish-water calanoid copepods in western Japan with comparison with neighboring Korean fauna. *Plankton Benthos Res.* 6, 18–25. doi: 10.3800/pbr.6.18
- Seo, M. H., Kim, H. J., Lee, S. J., Kim, S. Y., Yoon, Y. H., Han, K. H., et al. (2021). Environmental factors affecting the spatiotemporal distribution of copepods in a small mesotidal inlet and estuary. *Diversity* 13, 389. doi: 10.3390/d13080389
- Shih, C., Chen, Q. C., Lan, Y. C., Hsiao, S. H., and Weng, C. Y. (2022a). Key to the species of Acartiidae *Acartia* occurring in the China Seas. *J. Mar. Sci. Tech.* 30, 119–145. doi: 10.51400/2709-6998.2593
- Shih, C.-T., Chen, Q.-C., Lan, Y.-C., Hsiao, S.-H., and Weng, C.-Y. (2022b). Key to the species of Tortanidae *Tortanus* occurring in the China Seas. *J. Mar. Sci. Tech* 30, 884–909. doi: 10.51400/2709-6998.2679
- Soh, H. Y. (2010). *Invertebrate fauna of Korea. Volume 21, number 3. Arthropoda: Crustacea: Copepoda: Calanoida, Cyclopoida, Marine Planktonic Copepods* (Incheon: National Institute of Biological Resources, Republic of Korea), 18–23.
- Steuer, A. (1915). Revision de gattung *acartia* dana. *Zoologischer Anzeiger* 45, 392–397.
- Sun, X., Sun, S., Li, C., and Wang, M. X. (2012). Seasonal change in body length of important small copepods and relationship with environmental factors in Jiaozhou Bay, China. *Chin. J. Ocean. Limnol.* 30, 404–409. doi: 10.1007/s00343-012-1140-9
- Sun, X. H., Sun, S., Li, C. L., and Zhang, G. T. (2011). Seasonal and spatial variability in egg production, abundance and production of small copepods in and near Jiaozhou Bay, China. *J. Plankton R.* 33, 741–750. doi: 10.1093/plankt/fbq135
- Suzuki, K. W., Nakayama, K., and Tanaka, M. (2013). Distinctive copepod community of the estuarine turbidity maximum: comparative observations in three macrotidal estuaries (Chikugo, Midori, and Kuma Rivers), southwestern Japan. *J. Oceanogr.* 69, 15–33. doi: 10.1007/s10872-012-0151-7
- Ueda, H., and Bucklin, A. C. (2006). *Acartia* (*Odontartia*) *ohtsukai*, a new brackish-water Calanoid Copepod from Ariake Bay, Japan, with a redescription of the Closely Related *A. pacifica* from the Seto Inland Sea. *Hydrobiologia* 560, 77–91. doi: 10.1007/s10750-005-9513-0
- Uye, S. (1985). Resting egg production as a life history strategy of marine planktonic copepods. *Bull. Mar. Sci.* 37, 440–449. doi: 10.3354/meps08635
- Wang, M. X., Cheng, F. P., Li, C. L., and Sun, S. (2011). DNA barcoding of zooplankton in the Jiaozhou Bay for species identification. *Haiyang Yu Huzhao* 42, 702–710. doi: 10.1080/0144929X.2011.553739
- Wang, G., Jiang, X., Li, S., Wu, L., and Wu, D. (2005). A potential source of recruitment of *Acartia pacifica* nauplii: viable benthic resting eggs. *Acta Oceanol. Sin.* 24, 151–158. doi: 10.1029/2003JC002236
- Wang, J., and Wu, Q. (2018). *Fishery resource and habitat in Laizhou Bay* (Beijing: Chinese Aquaculture Press), 11–54.
- Wang, R., Zhang, H. Y., Wang, K., and Zuo, T. (2002). Distribution and population dynamics of *Paracalanus parvus*, *Paracalanus crassirostris*, and *Acartia bifilosa* (Copepoda, Calanoida) in the Bohai Sea. *Chin. J. Oceanol. Limn.* 20, 348–357. doi: 10.1007/BF02847926
- Xia, D. X., Wang, W. H., Liu, C. X., Han, L. Z., and Zheng, P. Y. (1991). *China's coastal embayment Vol. 3: Bays of Northern and Eastern Shandong Peninsula* (Beijing: China Ocean Press), 9–26.

- Youn, S. H., and Choi, J. K. (2007). Egg production of the copepod *Acartia hongii* in Kyeonggi Bay, Korea. *J. Mar. Syst.* 64, 217–224. doi: 10.1016/j.jmarsys.2006.05.017
- Youn, S. H., and Choi, J. K. (2008). Distribution pattern of zooplankton in the Han River estuary with respect to tidal cycle. *Ocean Sci. J.* 43, 135–146. doi: 10.1007/BF03020694
- Zhang, X. L., Zhang, Z. H., Xu, Z. J., Li, G., Sun, Q., and Hou, X. J. (2013). Sea ice disasters and their impacts since 2000 in Laizhou Bay of Bohai Sea, China. *Nat. Haz.* 65, 27–40. doi: 10.1007/s11069-012-0340-0
- Zhong, X. F., and Xiao, Y. C. (1992a). Resting eggs of *Acartia bifilosa* Giesbrecht and *A. pacifica* Steuer in Jiaozhou Bay. *Mar. Sci.* 16 (5), 55–59.
- Zhong, X. F., and Xiao, Y. C. (1992b). Seasonal cycles of abundance of three copepod species population in Jiaozhou Bay. *Mar. Sci.* 16 (1), 44–48.
- Zuraire, M., Cob, Z. C., Toda, T., Othman, B. H. R., and Yoshida, T. (2018). Seasonal changes in abundance of four *Acartia* species (Copepoda, Calanoida) in the coastal waters of Peninsular Malaysia; relationship with monsoon transition. *Reg. Stud. Mar. Sci.* 22, 101–111. doi: 10.1016/j.rsma.2018.06.007