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Effects of hypoxia on benthic eggs of calanoid copepods in the Southern Sea of Korea

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Global warming is affecting the composition, structure, and function of marine ecosystems. The increase in hypoxic regions due to stratification is a major environmental problem worldwide. Off the southern coast of Korea, hypoxia occurs frequently in summer, and the area of water affected is gradually expanding. In this study, we investigated the effects of hypoxia on the eggs of copepods in the order Calanoida. Data on the distribution and abundance of eggs in benthic sediments were collected from 17 stations, using a piston core sampler (64 mm internal diameter, 50 cm length), from August 1 to 7, 2012. Significant variations in the distribution of calanoid eggs and the occurrence of abnormalities in egg development were found between stations. The abundance of eggs found in the sediments ranged from 0.004 to 2.389 × 10^6 eggs·m^{-2}, with higher abundances identified in hypoxic than in normoxic areas. The proportion of abnormal eggs ranged from 0 to 92.7%. In particular, there were significantly more abnormal than normal eggs in areas where hypoxia occurred ($p < 0.01$). These results show that hypoxia can have a lethal effect on calanoid eggs and further affect population and community dynamics.

KEYWORDS

abnormal development, marine copepods, oxygen, sediment egg bank, chlorophyll

1 Introduction

Worldwide, the concentration of dissolved oxygen in coastal waters has changed dramatically over recent decades, and widespread anthropogenic eutrophication-induced hypoxia is a major environmental problem in coastal systems (Diaz and Rosenberg, 2008; Rabalais et al., 2010; Kodama and Horiguchi, 2011). Hypoxia can be a serious stressor to marine organisms and ecosystems, and low dissolved oxygen concentrations can reduce the range of organisms and suitability of habitats, and even further accelerate community change (Rabalais et al., 2001; Breitburg, 2002; Lai et al., 2022). Vaquer-Sunyer and Duarte (2008) showed that the number of coastal areas where hypoxia has been reported has increased at a rate of 5.5%·$year^{-1}$. Examples of marine regions with permanent, seasonal, periodic, or episodic hypoxia include the Baltic Sea, Black Sea, Gulf of Mexico, Chesapeake Bay, Yangtze River Estuary, Masan Bay, and Gamak Bay (Hagy et al., 2004; Conley et al., 2009; Rabalais et al., 2010; Chen et al., 2015; Choi et al., 2016; Jessen et al., 2017; Du et al., 2018; Choi et al., 2021).

Most marine species of the order Calanoida lay their eggs freely in the water column; relatively few species place them in egg sacs (Hansen, 2019). Marine calanoids may produce subitaneous eggs, which can develop without delay, or diapause eggs, which enter an obligatory refractory phase during which they cannot hatch (Grice and Marcus, 1981; Baumgartner and Tarrant, 2017; Belmonte and Rubino, 2019). Hatching of diapause eggs replenishes the population of copepods in the water column for portions of the year, and the presence of subitaneous eggs is important for maintaining the population during active seasons (Marcus, 1979; Marcus, 1996). Many studies have been reported that the onset of adverse conditions induce quiescence (subitaneous), whereas diapausal eggs are produced during normal conditions (Belmonte, 1992; Onoue et al., 2004; Tachibana et al., 2019; Takayama and Toda, 2019). It has been confirmed that before population biomass declines, females release diapause eggs that can survive for a long time in anoxic sediments (Marcus, 1984; Katajisto, 1996).

Calanoid egg abundances are high in sediments, varying between 10^4 and 10^7 eggs·m^{-2} (Belmonte et al., 1995; Marcus, 1995; Uriarte and Villate, 2006; Choi et al., 2021); high egg abundance is found in bays or estuaries rather than in the open ocean (Masero and Villate, 2004; Glippa et al., 2011). The eggs of marine calanoids sink because they are denser than the surrounding seawater (Tang et al., 1998). The accumulation of a large number of eggs contributes to the recruitment of nauplii (larvae), as well as serves as an “egg bank” for long-term persistence of the species (Marcus, 1984; Marcus et al., 1997; Katajisto, 2006). Most of the sunk calanoid eggs spend weeks to years on the seabed during their benthic resting phase (Marcus and Boero, 1998). Therefore, eggs that quickly sink to the seabed in shallow water habitats can be buried by sedimentation processes and may be exposed to stressful conditions, such as hypoxia and anoxia.

Uye and Fleminger (1976) demonstrated the importance of oxygen in calanoid embryo development, as eggs did not hatch in deoxygenated water, even under favorable temperature conditions. Choi et al. (2021) showed that long-term exposure of calanoid eggs to hypoxic conditions reduces hatching rates and increases the relative proportion of abnormal eggs (unhatched egg or missing egg contents). Marcus et al. (2004) suggested that exposure to hypoxia could substantially reduce egg hatching, which in turn could have considerable impacts on population and community dynamics in coastal systems, which may be exacerbated by prolonged exposure to low oxygen or hypoxic conditions.

The IPCC Assessment Report (AR6) shows that, by the end of the 21st century, the global average sea surface temperature will rise by 1.4–3.7 °C compared to current conditions. Global warming can increase sea level rise, temperature, precipitation and increase coastal hypoxia (Altieri and Gedan, 2015). In the Southern Sea of Korea, there are continuous inputs of industrial wastewater and domestic sewage; consequently, low oxygen or hypoxic conditions arise in summer in some semi-closed bays where the rate of seawater exchange is relatively low (Kim et al., 2006; Lee et al., 2019). Such conditions are expected to have a significant impact on calanoid copepod eggs that form near the bottom.

The study area in South Korea is affected by various ocean currents that change seasonally. These relatively shallow coastal waters are important as spawning grounds for various species of fish and shellfish (Kim and Pang, 2005; Baek et al., 2010; Ko et al., 2010). However, the area is surrounded by populated cities in the southeastern (Masan, Changwon, and Jinhae) and south–central (Yeosu, Namhae) parts of the country, extending up to the east coast, with the establishment of the Imhae Industrial Complex along the Namhae coast (Lee and Min, 1990; Lee and Kim, 2008). As a result, constant hypoxia or anoxia occurs in summer (July to September) in semi-closed bays (Gamak Bay, Jinhae Bay), where the rate of seawater exchange is low.

The response and abundance of mesozooplankton to hypoxia have been the focus of many studies, but there have been relatively few investigations of the relationship between calanoid eggs and hypoxia. Calanoid egg abundance is a key factor in nauplii recruitment and drives the continuation of active populations (Marcus, 1984; Belmonte and Pati, 2007). The occurrence of hypoxic conditions associated with climate change may threaten the existence of zooplankton, which have an important position in food webs. Accordingly, the objectives of this study were to indirectly evaluate the effects of hypoxia on (1) the distribution characteristics of normal and abnormal eggs, and (2) the abundance of calanoid eggs in the Southern Sea of Korea, where hypoxia occurs frequently in summer.

2 Materials and methods

2.1 Study area and environmental variables

Data were collected from a total of 17 stations along the southern coast of South Korea. Four stations (S1 to S4) were located in Jinhae Bay in the north of Geoje, and three stations (S5 to S7) were west of Geoje (Figure 1). Two stations were located in Jinju Bay (S8, S9), north of Namhae. Station S10 was located within Gwangyang Bay, and stations S11 and S12 were located outside Gwangyang Bay. Stations S13 and S14 were located in Gamak Bay, S15 was within the inner bay, S16 in the center, and S17 further out, in Yeoja Bay. The water depth of the survey stations varied from 3 m (S15) to 39 m (S6).

The environmental variables (water temperature, salinity, chlorophyll-*a* fluorescence, and dissolved oxygen [DO] concentration) were measured at these 17 sites, with vertical profiles measures in the field, using a water quality multi-meter (Model 6600; Xylem Inc., Yellow Springs, OH, USA).

2.2 Calanoids in the water column

Zooplankton and sediment samples were collected from August 1 to 7, 2012. Zooplankton samples were collected vertically, from the near-bottom water to the surface layer, using a conical net

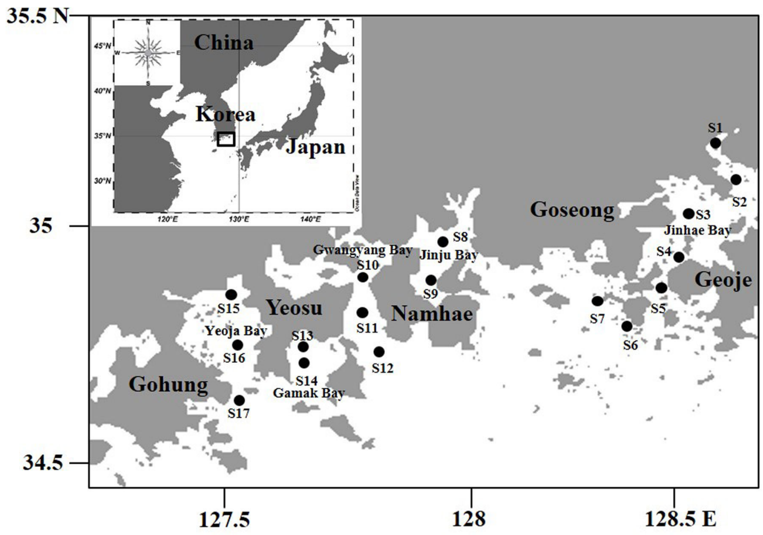

FIGURE 1
Location of 17 sampling stations in the Southern Sea of Korea in summer.

(mouth opening diameter 45 cm, mesh size 200 μm) to filter an adequate water volume. Zooplankton samples were immediately fixed to a final concentration of 5%, using neutralized formalin solution *in situ*. The water volume was measured by attaching a flow meter (model 438115; Hydro-Bios, Altenholz, Germany) to the net mouth and measuring the amount of filtered seawater that passed through the net. Zooplankton were counted using a Bogorov counting chamber using a stereomicroscope (Nikon SMZ 1000; Nikon, Japan), and identified using a high-magnification optical microscope (Nikon ECLIPSE 80i; Nikon, Japan). Calanoid abundance was converted to the number of individuals per cubic meter (individuals·m^{-3}). Only adults were counted.

2.3 Distribution and abundance of eggs in the sediments

The distribution and abundance of calanoid eggs in the sediments, and the ratio of normal and abnormal eggs, were determined at each sediment core collected, using a piston core sampler (64 mm internal diameter, 50 cm length), from August 1 to 7, 2012 (Figure 1). The sediment samples were placed in a dark-treated icebox and immediately transferred to the laboratory. The sediment obtained by cutting the upper 1 cm of each core sediment sample was washed through a 40 μm mesh, and the remaining eggs were recovered from the mesh, fixed in 5% formalin solution, and placed in a conical 50 mL tube (SPL Life Science Co., Ltd., GyunggiDo, Korea). The potential impact of the egg isolation method on egg morphology cannot be ruled out, as it could induce physical and osmotic stresses that may cause abnormal egg shapes. The common sugar floating isolation method, which has been shown to have a direct effect on egg morphology (Lukic et al., 2016), was not used in this study. Therefore, it is important to acknowledge the limitations of the egg isolation method used in this study and its potential impact on the results. After placing 1 mL of the concentrated sample in the Bogorov counting chamber and diluting it with filtered seawater, calanoid eggs were counted as the average of three replicates under a dissecting microscope (Olympus, SZX7, Tokyo, Japan). The egg abundance was converted to eggs per unit area (eggs·m^{-2}), and the proportion of normal and abnormal eggs was simultaneously confirmed while counting the eggs.

Calanoid eggs were identified based on published descriptions (Kasahara et al., 1974; Belmonte et al., 1997). Normal and abnormal calanoid eggs were identified following the procedures of Poulet et al. (1995); Ban et al. (2000) and Choi et al. (2021), and the eggs were photographed using a high-magnification optical microscope (Nikon ECLIPSE 80i; Nikon, Japan). In this study, abnormal eggs were sorted into various categories based on particular characteristics, such as eggs with unusual shapes and leaking egg contents, eggs that failed to develop and hatch, eggs that produced deformed nauplii, and eggs with no cracks but missing egg contents (Figure 2).

2.4 Statistical analysis

We performed Pearson’s test to determine the correlation between the ratio of normal to abnormal eggs and the following parameters: DO concentration, egg abundance, and chlorophyll-*a* concentration. The confidence interval was 95% for each of the correlations. All statistical tests were performed using SPSS version 18.0 (SPSS Inc., Chicago, IL, USA), with a significance level of $p < 0.05$.

3 Results

3.1 Environmental variables

The water temperature in the survey area ranged from 24.3 to 31.1 °C in the surface layer and 15.8 to 30.3 °C in the near-bottom

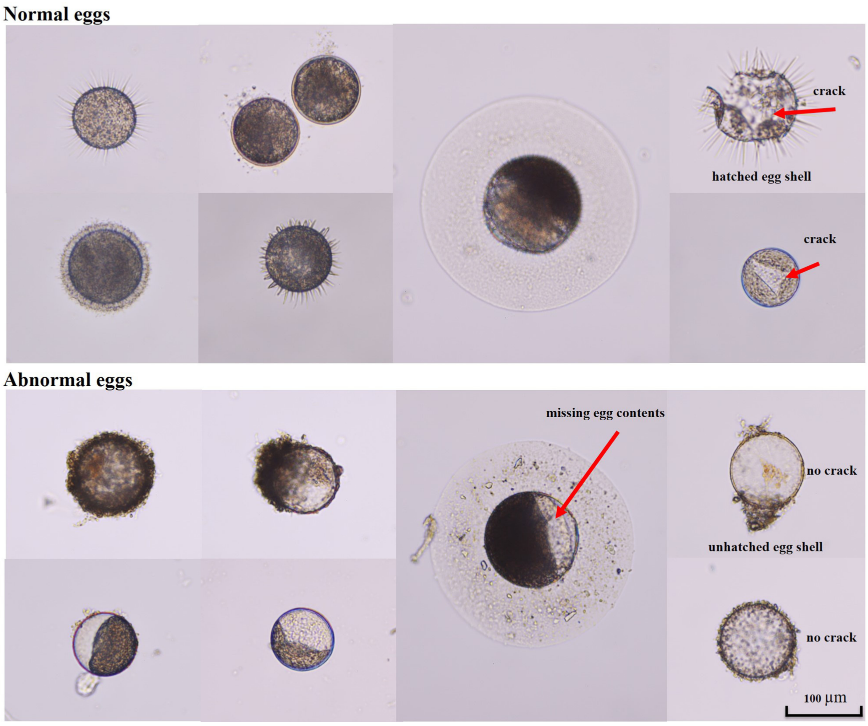

FIGURE 2
Normal and abnormal eggs of calanoid copepod, collected from benthic sediments in the Southern Sea of Korea in summer.

water (Figures 3A, B). Based on measurements at Namhae, the water temperature of the eastern stations (S1 to S7) at the bottom was lower than that of the western stations (S8 to S17), by more than 5 °C on average. The surface and bottom salinities were 29.4 to 32.7 and 29.6 to 34.1, and the average salinity was 31.3 and 32.2, respectively (Figures 3C, D). At S3, located in Jinhae Bay, the salinity of the surface and near-bottom water was significantly different. Salinity of less than 30 was observed in the surface and

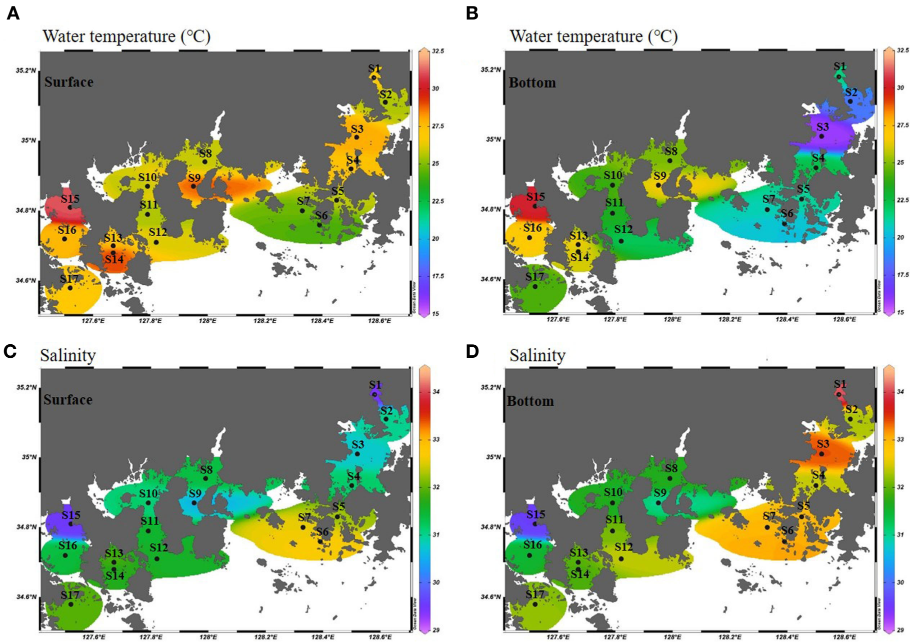

FIGURE 3
Horizontal distribution of water temperature (°C) **(A, B)** and salinity **(C, D)** between the surface (0 m) and near-bottom water (B-1 m) of the Southern Sea of Korea in summer.

near-bottom water in S15, the inner station of Yeoja Bay. The surface layer chlorophyll-*a* concentration in the study area ranged from 1.4 to 26.2 μg·L^{-1}, and that of the near-bottom water ranged from 1.6 to 10.8 μg·L^{-1} (Figures 4A, B). The highest surface and bottom chlorophyll-*a* concentrations were found in S1 (26.2 μg·L^{-1}) and S15 (10.8 μg·L^{-1}), respectively. The range of dissolved oxygen in the surface layer varied between 3.71 and 7.72 mg·L^{-1}, and in the bottom ranged from 0.55 to 5.58 mg·L^{-1} (Figures 4C, D). A low DO concentration of 2 mg·L^{-1} or less was observed at some stations (S1, S2, and S3) in Jinhae Bay.

3.2 Diversity of calanoids in the water column

A total of 12 species of Calanoida were observed in the summer (early August) in the Southern Sea of Korea, and showed different prevalence characteristics depending on the station (Figures 5A, B). *Paracalanus* sp. accounted for more than 63% of the calanoid copepod population in the surveyed area and reached population abundances of more than 1,000 individuals·m^{-3} in S5, S8, and S16. *Acartia erythraea* was absent at three stations (S10, S12, and S17); in contrast, the abundance of this species was found to be greater than 1,000 individuals·m^{-3} at S13. *Acartia erythraea* showed high abundance, especially at the stations in the inner bay (Jinhae, Gamak and Yeoja Bay), and was almost ubiquitous. *Acartia ohtsukai* appeared at S8 and S9 located in Jinju Bay, and S10 located in Gwangwang Bay, and *A. sinjiensis* only appeared at S4, S5, and S6 located nearshore waters of Jinhae Bay. *Tortanus forcipatus* appeared at all of the western stations (S10 to S17), but only at S5 among the eastern stations. *Acartia* sp. accounted for more than 5% of the population of Calanoida in the surveyed area and represented more than 80% of the calanoid species at S1.

3.3 Egg abundance and normal: Abnormal ratio

Overall, the abundance of calanoid eggs was higher at the nearshore stations located in the bay (Figure 6A). Egg abundance ranged from 0.004 to 2.389 × 10^{6} eggs·m^{-2}, being highest at S1 and lowest at S6. An egg abundance of 0.2 × 10^{6} eggs·m^{-2} or more was confirmed at a total of five stations (S1, S9, S13, S15, and S17).

The ratio of abnormal eggs ranged from 0 to 92.7% (Figure 6B). At S1, S2, and S3, the proportion of abnormal eggs accounted for more than 80%. Approximately 54% of eggs collected at station S13, in the nearshore waters of Gamak Bay, were abnormal. At stations located to the west of Geoje (S5, S6, and S7), and the stations located in Gwangyang Bay (S10, S11, and S12), the collected eggs were 100% normal. We found an increasing incidence of abnormal eggs in areas with decreasing DO concentrations ($r^2 = 0.734$, $p < 0.01$) (Figure 7A), indicating a clearly negative correlation between the proportion of abnormal eggs and the DO concentration. The abundance of calanoid eggs was positively correlated with chlorophyll-*a* concentration ($r^2 = 0.485$, $p < 0.05$) (Figure 7B).

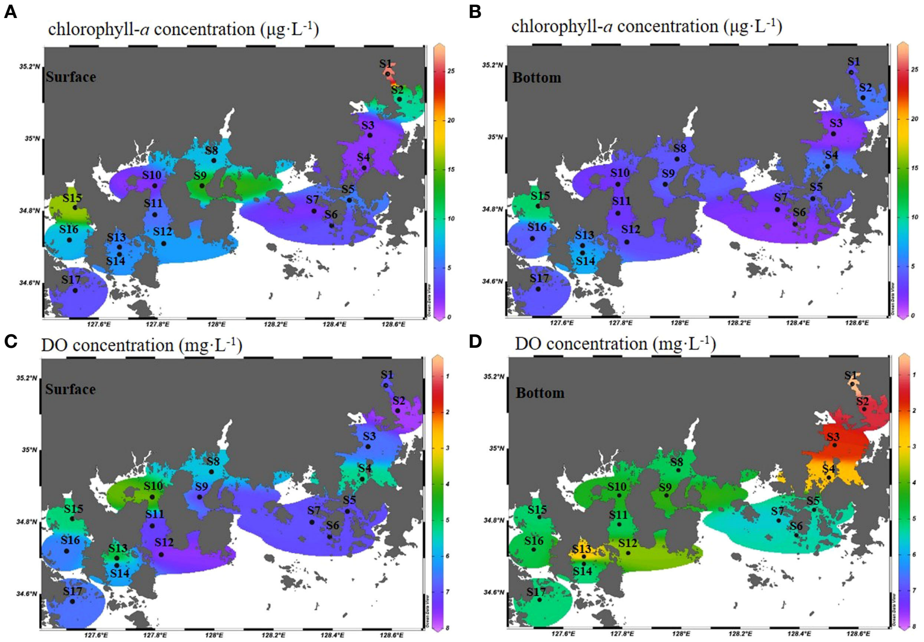

FIGURE 4
Horizontal distribution of chlorophyll-*a* concentrations (μg·L^{-1}) **(A, B)** and dissolved oxygen concentrations (mg·L^{-1}) **(C, D)** between the surface (0 m) near-bottom water (B-1 m) of the Southern Sea of Korea in summer.

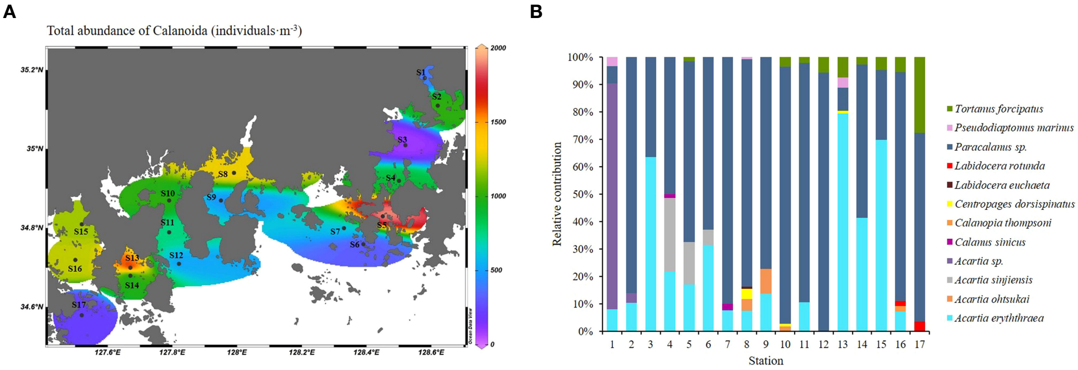

FIGURE 5
Horizontal distribution of Calanoida **(A)** and relative contribution (%) **(B)** of the Southern Sea of Korea in summer.

4 Discussion

The near-bed strata of the water column DO concentration was in the range of 0.55 to 5.58 mg·L^{-1}, and hypoxia was evident at several stations, with a range similar to that previously reported (Choi et al., 2005; Kim et al., 2006). Dead zones created by the depletion of dissolved oxygen in coastal waters are one of the most widespread and harmful anthropogenic threats to marine ecosystems worldwide (Gooday et al., 2009; Rabalais et al., 2010). The decrease in DO concentration in summer and hypoxia of the near-bed water on the southern coast of Korea affected the ratio of normal to abnormal eggs. Previous studies have shown that eggs exhibit varying responses depending on the duration of exposure to low oxygen or anoxic conditions (Invidia et al., 2004; Katajisto, 2004; Nielsen et al., 2006). In laboratory experiments, low DO concentrations have been shown to negatively affect the hatching success of non-diapause calanoid eggs (Marcus and Lutz, 1994; Marcus et al., 1994). Furthermore, Marcus (2001) reported that diapause eggs were able to withstand significant periods of exposure to anoxic conditions and toxic levels of hydrogen sulfide. Only calanoid eggs (as a stage) were considered in the present study. Calanoid eggs can be functionally different: diapausal and quiescent (subitaneous). Thus, a limitation of this study was that subitaneous eggs were not differentiated from diapausal ones; therefore, we cannot draw conclusions on how the functional status of the eggs (subitaneous vs. diapausal) might be correlated with egg abundance and/or abnormalities.

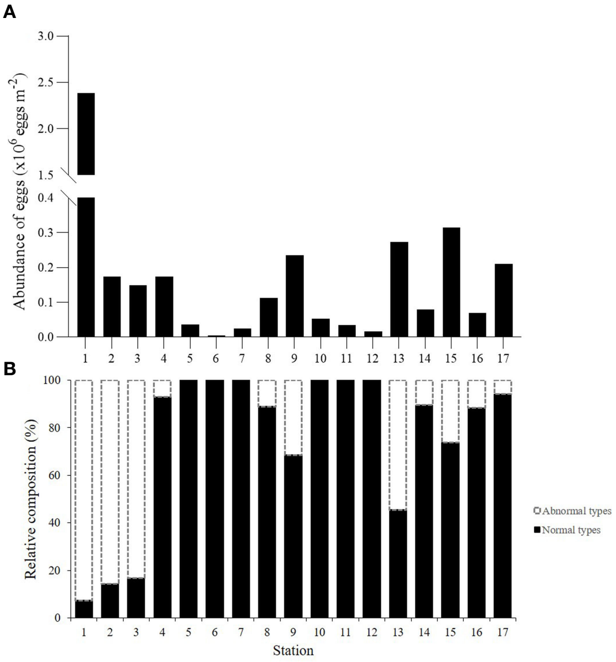

FIGURE 6
The abundance of calanoid eggs **(A)** (y-axis is divided into two parts, each with its own linear scale) and relative composition of normal and abnormal eggs **(B)** in sediments of the Southern Sea of Korea in summer.

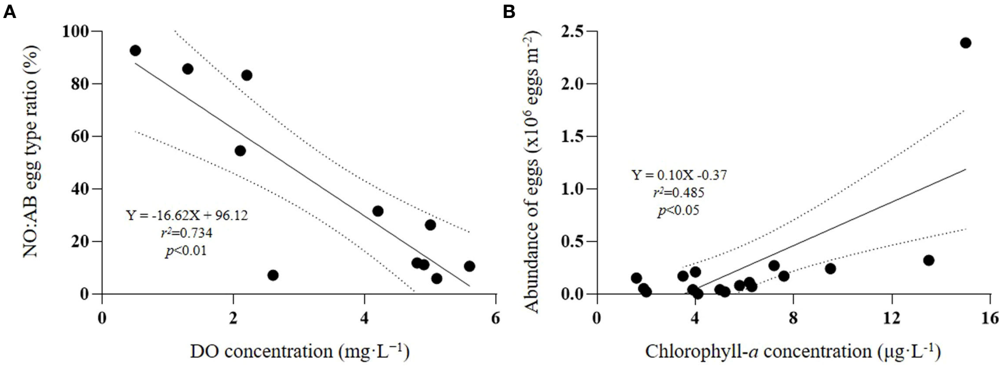

FIGURE 7
Linear regression between normal: Abnormal egg type ratio and near-bottom DO concentration **(A)** and abundance of calanoid eggs and chlorophyll-*a* concentration **(B)**, including 95% confidence intervals (dashed).

The egg abundance (0.004–2.389 × 10^6 eggs·m^{-2}) recorded at the south coast stations was similar to that reported in other studies of marine and estuarine systems (Table 1). There were differences in egg abundance between stations, probably due to differences in sediment heterogeneity. Glippa et al. (2014) also noted high inter-station and replicate variability, which may be a problem of sediment heterogeneity that characterizes the study area. Although the particle size of the sediments was not measured in this study, the particle size of the sediments in Jinhae Bay corresponded to the "very fine" grade, in which 92% of the samples had an average grain size of 8 µm or less. Previous studies confirmed that the average grain size of Jinju Bay was 7–8 µm (Kim et al., 1988; Cho and Lee, 2012). The average grain size of the sediments in was in the range of 7–9 µm in Gwangyang Bay (Ryu et al., 2003), 7.0–8.8 µm in Gamak Bay (Kim et al., 2012), and 8.46 µm in Yeoja Bay (Choi et al., 2007).

We did not identify calanoid eggs at the species level, but a significant number of eggs are believed to originate from Calanoida in the study area. A total of 12 species of marine calanoids have been identified in the plankton along the southern coast of Korea; the predominant species were *Paracalanus* sp., *Acartia* spp. (*A. erythraea*, *A. ohtsukai*, *A. sinjiensis*, and *Acartia* sp. indet.), and *Tortanus forcipatus*. However, not all species eggs are likely to be observed in the sediment samples. For example, *Paracalanus parvus* may not produce dormant eggs (Næss, 1996) and some may have eggs that are too fragile to withstand sediment abrasion (Marcus, 1991). Conversely, it was reported that the eggs of *T. forcipatus* were found to have the strongest chorions compared to other calanoids (Uye et al., 1984). Therefore, the abundance of eggs in the sediments may not reflect the actual abundance of calanoid species in the water column, as the eggs of some species may not be present in the sediment samples.

Low DO conditions have a negative effect on calanoid egg production (Sedlacek and Marcus, 2005), and may cause growth retardation (Richmond et al., 2006). *Acartia tonsa* exposed to hypoxia showed ecologically adaptable behavior by reducing feeding (Elliott et al., 2013). Metabolic activity and respiration in Calanoida decrease significantly with body size (Hirst and Sheader, 1997; Mauchline, 1998). Decreased DO concentrations can lead to decreased metabolism in a variety of zooplankton, as reported in various studies. Our data did not directly show this effect. In our results, egg abundance was positively correlated with the chlorophyll concentration at the hypoxic stations. This is most likely due to the fact that phytoplankton generated in the water column sink to the bottom and are decomposed by microorganisms, thus promoting oxygen consumption (Hoegh-Guldberg and Bruno, 2010). However, it is difficult to describe distribution characteristics by associating only specific variables *in situ*. Marcus et al. (2004) proposed a method to accurately predict the DO reduction effect, considering the interaction effect of temperature and food concentration.

Environmental fluctuations, such as hypoxia and anoxia, occur frequently in the southern coast of Korea. In the present study, in Jinhae Bay and Gamak Bay, where hypoxia occurred, water quality has severely deteriorated; massive algal blooms occurr every year, and hypoxia has increased every year in the near bottom sediment during summer (June-September) (Kim et al., 2006; Lim et al., 2006; Lee et al., 2009). Thus, the population of Calanoida in these two regions (Jinhae and Gamak Bay) may experience higher mortality rates and may show more significant nauplii recruitment from sediment than in other regions investigated in the study. The high egg abundance of calanoids in hypoxic regions identified in this study may be one key for population maintenance under adverse conditions. Despite the high egg abundance observed in hypoxic regions in Jinhae Bay and Gamak Bay, there was no correlation found between the abundance of mature calanoids and egg abundance. This may be due to the presence of diapausal eggs, which are known to accumulate in an egg bank and can persist for multiple seasons or years (Marcus et al., 1994; Marcus, 1996). As such, the high egg numbers found in these hypoxic regions could be a result of diapausal eggs produced in previous years rather than a direct relationship with calanoid abundance.

In the present study, we found that the proportion of abnormal eggs was higher at hypoxic stations, indicating the potential impact of long-term exposure to hypoxia on egg abnormalities (Choi et al., 2021). This is consistent with previous research that has shown that exposure to hypoxic or anoxic conditions can affect the eggs of Calanoida (Katajisto, 2004; Richmond et al., 2006). Marine calanoids lay two types of eggs: subitaneous eggs, which can hatch within hours to days after spawning, and diapause eggs,

TABLE 1 Comparison of calanoid egg abundance in benthic sediments from various locations around the world.

Region	Egg abundance (egg m^{-2})	References
Inland Sea of Japan	$3–10 \times 10^6$	Kasahara et al. (1975)
Alligator Harbor region, Florida	$0–0.073 \times 10^6$	Marcus (1989) *
Northern California coastal waters	$0.12–0.19 \times 10^6$	Marcus (1995)
Tyrrhenian Sea	$0.0016–0.012 \times 10^6$	Belmonte et al. (1995)
Ionian Sea	$0.031–1.07 \times 10^6$	Belmonte et al. (1995)
Adriatic Sea	$0.15–1.19 \times 10^6$	Belmonte et al. (1995)
Baltic Sea	Up to 3.7×10^6	Katajisto (1996)
Màlaga Harbor, Spain	$0.19–6.6 \times 10^6$	Guerrero and Rodriguez (1998)
Estuary of Mundaka, Bay of Biscay	$0.019–0.16 \times 10^6$	Masero and Villate (2004)
Estuary of Bilbao, Bay of Biscay	$0.008–0.009 \times 10^6$	Masero and Villate (2004)
Sällvik, Baltic Sea	1.03×10^6	Viitasalo and Katajisto (1994)
Seine estuary, France	1.42×10^6	Glippa et al. (2011)
Seine estuary, France	$0.6–23.3\times 10^6$	Glippa et al. (2014)
Masan Bay, Korea	$0.59–1.49 \times 10^6$	Choi et al. (2021)
Southern coastal waters, Korea	$0.004–2.389 \times 10^6$	This study

*Only Centropages hamatus eggs were counted.

which must complete a dormancy (refractory) period before hatching (Grice and Marcus, 1981; Glippa et al., 2014; Belmonte and Rubino, 2019). Subitaneous eggs have higher metabolic demands and are unable to tolerate prolonged exposure to hypoxia, unlike diapause eggs, which can survive in deeper layers of sediment (Dahms et al., 2006; Hansen and Drillet, 2013; Roman et al., 2019). Short-term exposure to anoxia did not significantly affect egg hatching success of subitaneous eggs in *Acartia tonsa*; however, hatching generally decreased with increasing exposure time (Nielsen et al., 2006). As the anoxic exposure time increased, egg viability of subitaneous eggs in *A. tonsa* decreased after incubation periods of 15 and 32 days (Invidia et al., 2004). The origin of the eggs in present study was not investigated, and further experiments are needed to determine how the type of eggs affects survival when exposed to long-term anoxic conditions in a laboratory. Nevertheless, the findings of this study demonstrate the potential for hypoxia to cause egg abnormalities in Calanoida.

5 Conclusion

In conclusion, we confirmed that the abundance of calanoid eggs on the southern coast of Korea is similar to what it has been found in other estuaries and coastal waters. In addition, the high rate of abnormal eggs suggested a negative effect of hypoxia and changes in egg morphology due to long-term exposure to hypoxic conditions. Eggs in the sediment may experience strong hypoxic conditions over many years, eventually changing the structure and function of ecosystems and plankton communities. The viability of eggs decreases with increasing exposure to hypoxia, and eggs may not hatch, or may hatch into deformed nauplii, as has also been emphasized by Choi et al. (2021). These changes in eggs have considerable potential to serve as indicators of quality in marine ecosystems, such as hypoxic conditions due to summer climate change. The high prevalence of abnormal eggs can be used as a tool to detect DO stress *in situ*.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

SYC conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft. HYS conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft. KS conceived and performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft. SWJ conceived and performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft. MCJ contributed to funding acquisition, conceptualization of the experiments, data interpretation and discussion, authored or reviewed drafts of the paper, and approved the final draft. All authors contributed to the article and approved the submitted version.

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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.

Publisher's note

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