

Article

Northward Expansion of a Warm-Water Doliolid *Dolioletta gegenbauri* (Uljanin, 1884) into a Temperate Bay, China

Shiwei Wang^{1,2,3,*}, Aiyong Wan^{1,2,3}, Guangtao Zhang^{1,2,3,4} and Song Sun^{1,2,3,4,5}

- ¹ Jiaozhou Bay Marine Ecosystem Research Station, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China; way@qdio.ac.cn (A.W.); gtzhang@qdio.ac.cn (G.Z.); sunsong@qdio.ac.cn (S.S.)
- ² Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao 266071, China
- ³ Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266237, China
- ⁴ University of Chinese Academy of Sciences, Beijing 100049, China
- ⁵ Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China
- * Correspondence: wangshiwei@qdio.ac.cn

Abstract: A warm-water doliolid species *Dolioletta gegenbauri* (Uljanin, 1884) was firstly recorded in Jiaozhou Bay (JZB) during the autumn of 2019–2020. As a warm-water species, its native habitat lies in the East China Sea Shelf, >1000 km south of JZB. Distribution, abundance, stage composition, size frequency distribution, and relationships with environmental factors were studied. Both asexual and sexual reproduction stages were observed. Gonozooids generally dominated the population, indicating an active population development status. Abundance was significantly correlated to temperature. Water temperature in the two consecutive years was among the highest levels during the recent 3–4 decades. The continuous warming trends both in the China coastal seas and JZB likely expanded the biogeographic range. The sub branches of a boundary current, the Kuroshio Current, especially the Yellow Sea Warm Current, may play a central role during the northward extension. Moreover, its feeding, growth, reproduction, and recruitment could also be benefited from the neritic food environment. Finally, when the temperature dropped below 15 °C in the early winter, it disappeared in JZB. The seasonal expansion of *D. gegenbauri* in JZB could be facilitated by current transportation, warming, and the neritic environment.

Keywords: *Dolioletta gegenbauri*; Jiaozhou Bay; warming; boundary current; northward shift



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1. Introduction

Doliolids have the most complex life history even in the pelagic tunicates [1], with not only alternation of sexual and asexual life history stages but also polymorphism in the buds produced asexually by the oozoids [2]. Moreover, it is also marked by the sudden and mystical blooming capability [3] from a “rare species” status [4]. Previous research mainly focused on the abundance or distribution, leaving large knowledge gaps especially in the mechanisms regulating the population dynamics.

The doliolid *Dolioletta gegenbauri* (Uljanin, 1884) is widely distributed in subtropical neritic regions globally, such as in the tropical west and southwest Pacific Ocean, tropical and temperate southwest Indian Ocean, Atlantic Ocean, and the Mediterranean Sea [5]. In Chinese waters, it is generally distributed in the south China Sea [6] and southern East China Sea (ECS) [7–9], recognized as an indicator species of the warm and saline water [10]. Northerly, it was sporadically observed in the Yellow Sea (YS) only in some years [11,12], with restricted distribution in the southern margin area of the YS during summer [13].

D. gegenbauri appeared with considerable density at the Jiaozhou Bay (JZB) in 2019 and 2020, which was the first record of this species since the 1980s when regular (seasonal or monthly) plankton surveys began locally. Adjacent to the YS, JZB is a shallow bay with an

average water depth of 7 m. Surrounded by one of the biggest cities in northern coastal China, it has been under huge pressure from human activities, e.g., shipping, industry, and city sewage water and aquaculture. Besides, it was also influenced by climate change, such as global warming, drought, and marine heatwaves [14]. The zooplankton assemblages in JZB are mainly comprised of cool temperate species [15] but with occasional warm water species intrusions in the recent decades [15–17].

There are several questions with regard to the sudden occurrence remaining unanswered. How was it introduced into JZB? Is it an occasional intrusion event by ballast water or reflecting a broader warm water species expansion process? What are the growth, feeding, and reproduction status in the new habitat? In this study, we report the first observation of *D. gegenbauri* in a temperate bay, >1000 km off the main population. We aim to (1) record the abundance, distribution, life stage, and size compositions as well as the reproductive status and to (2) explore the potential roles of boundary current transportation and the warming background during the northward expansion of this warm water species.

2. Materials and Methods

2.1. Environmental Data

A total of 12–14 survey stations covering JZB and the adjacent YS (Figure 1) were studied each month. Temperature and salinity were measured at each station from 1 m above the seabed to the surface using a CTD profiler (Sea Bird Electronics, SBE-19). Seawater samples (500 mL) for the measurement of Chlorophyll *a* (Chl *a*) concentration were collected from the surface layer (0–1 m) and filtered through GF/F glass-fiber filters. The filters were then extracted in 90% aqueous acetone for 24 h at 0 °C, and the Chl *a* concentration was measured with a Turner Designs Model 7200 fluorometer. In this study, surface Chl *a* concentration was used to represent the food availability for *D. gegenbauri* at each station given the fact that the water column was well-mixed in autumn [14].

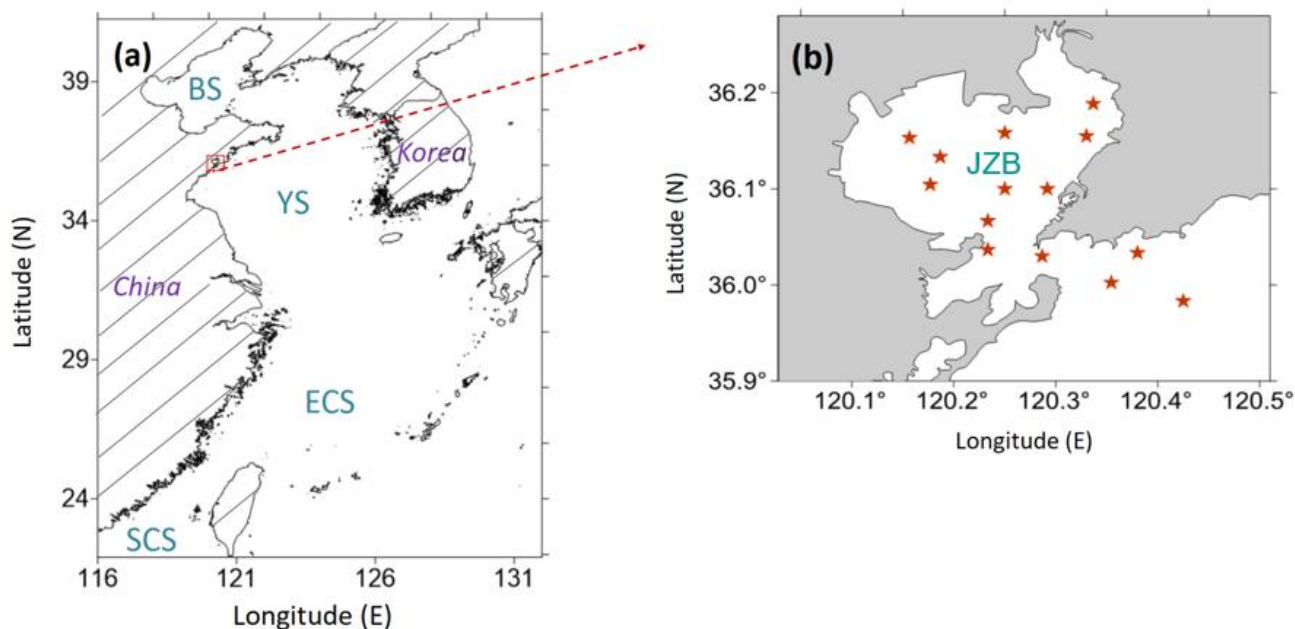


Figure 1. Location and sampling stations of the Jiaozhou Bay. (a). SCC, the South China Sea; ECS, the East China Sea; YS, the Yellow Sea; BS, the Bohai Sea. (b) JZB, the Jiaozhou Bay. '★' represents the 14 stations with zooplankton sampling and environmental measurements for each month during 2004–2020.

Long-term background data on temperature and salinity were acquired from the monthly surveys by the Jiaozhou Bay Marine Ecosystem Research Station (JMERS), which is a long-term monitoring and research department focusing on a set of environmental and

ecological parameters in JZB and the adjacent YS since the 1980s. From the late 1980s to 1990s, zooplankton sampling generally followed a seasonal basis. From 2000 to the present, however, the surveys followed a monthly regular pattern covering the whole bay, and therefore, data from this period were used to reveal the long-term background.

2.2. Sampling

Zooplankton samples for population analyses were captured using a zooplankton net (mouth opening: 0.2 m²; mesh size: 500 µm; total length: 1.8 m) with an adapted cod end (mesh size: 20 µm). Towing was from 1 m above the seabed to the surface, with speed of ~0.2 ms⁻¹. All samples were preserved in 4% formalin seawater. By examining the zooplankton samples and records from the 1990s to 2021, only surveys in October–December 2019 and in October and November 2020 were found with *D. gegenbauri*'s presence in the recent 3–4 decades.

2.3. Body Size, Life History Stage, and Abundance

Body size was measured with the body length (mm) of each life stage. Doliolids in each life stage include both the alternation of sexual (aggregations) and asexual (solitary) generations and the polymorphism of asexual phorozoids and trophozooids. In samples, life history stage of *D. gegenbauri* was identified according to [18]. Quantity and proportion of each observed life stage were also enumerated and calculated.

Abundance of *D. gegenbauri* was quantified as follows:

$$A = N/V$$

where A represents the abundance of each life stage at a station, N represents numbers of individuals of each life stage in each tow, and V is the water volume filtered by each tow. V is estimated by multiplying the rope length (m) outreaching in the water column by the net's opening area (m²).

Pictures of the specimens were taken under the microscopes of a ZEISS V20 and a Revolve RVL-100-G (Discover Echo Inc., San Diego, CA, USA).

2.4. Role of Environmental Factors

To reveal the long-term environmental change, anomalies of temperature and salinity changes during 2000–2020 were calculated as follows. Based on the appearance duration, we chose to compare the temperature and salinity conditions in November of each year. Firstly, water column temperature or salinity means of the 12 or 14 stations in November were calculated. Then yearly mean and the long-term mean as well as the anomaly in each year were calculated. Mann–Kendall trend tests (XLSTAT software) were used to detect the significance of long-term trends. Mann–Whitney *U* tests were applied when comparing the abundance difference between the inner bay and the outer bay.

To understand the regulatory mechanisms of its distribution, relationships between *D. gegenbauri* abundance with temperature, Chl *a* concentration, and salinity were analyzed. Pearson correlations were used with the SPSS software (SPSS for Windows, Version 16.0., SPSS Inc., Chicago, IL, USA). Before statistical analyses, abundance data were log₁₀ transformed to meet the normality demand.

3. Results

3.1. Abundance and Distribution

D. gegenbauri appeared firstly in October 2019, as shown in Figure 2, in which the total zooid density (zooids m⁻³) at each survey station was indicated. As the first occurrence, it was mainly distributed in the outer bay and the bay mouth regions in October 2019 (Figure 2a) (Mann–Whitney *U* test, abundance: inner bay < outer bay, *n* = 24, *p* < 0.05), with a peak abundance of ~25 zooids m⁻³. In November 2019 (Figure 2b), a more evenly distribution was observed over the studied area but with significantly decreased abundance (<5 zooids m⁻³ at each station). There was only one station in the outer bay, with its

presence (Figure 2c) in December 2019. It then disappeared until the next October. The distribution in 2019 indicates a probable outer source, inner bay population development, and retreat in winter.

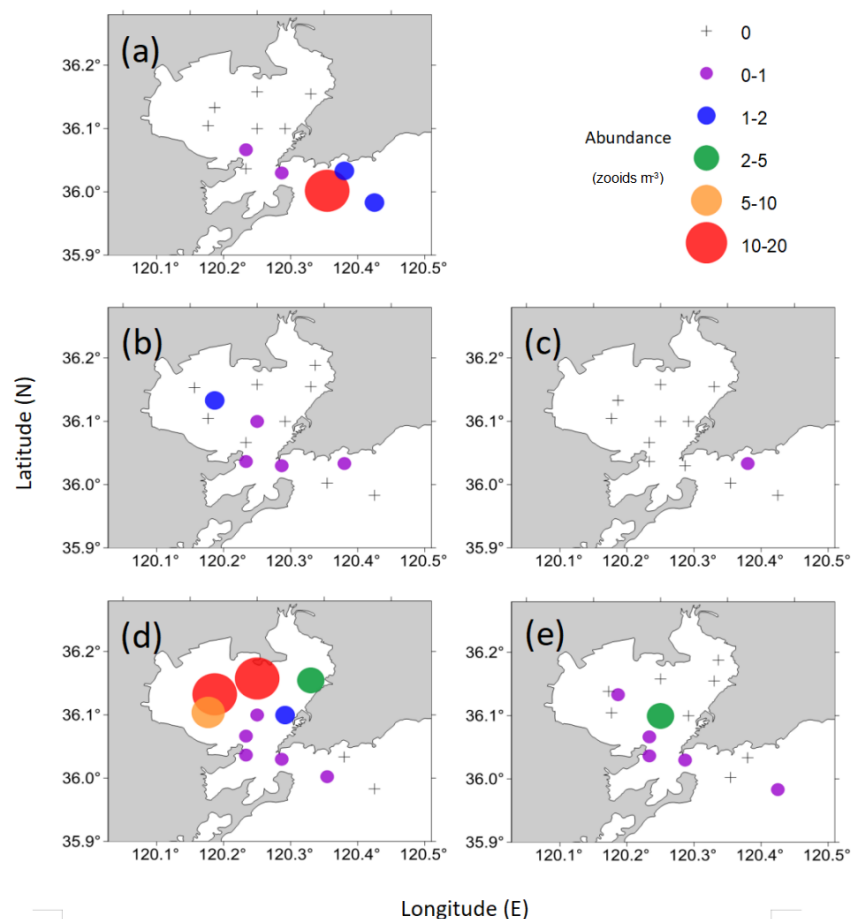


Figure 2. Abundance of *Dolioletta gegenbauri* (zooids m^{-3}) in the Jiaozhou Bay in October 2019 (a), November 2019 (b), December 2019 (c), October 2020 (d), and November 2020 (e). Abundance was summed for all life stages at each station.

In October 2020, however, its distribution center turned into the north part of the inner bay (Mann–Whitney U test, abundance: inner bay > outer bay, $n = 24$, $p < 0.05$) if compared to the result of October 2019. In this month, the maximum abundance was ~ 41 zooids m^{-3} , reaching the highest value during this study (Figure 2d). It implies that its population had likely developed between the surveys of September and October 2020. Similar to that of the previous year, the abundance decreased in November 2020, with the abundance range of 0.3–5.8 zooids m^{-3} (Figure 2e). In December 2020 and thereafter, it vanished in JZB.

3.2. Life History Stage and Body Size Compositions

Both sexual and asexual stages were observed in JZB samples (Figure 3). Life stage compositions in each survey were shown in Table 1. Gonozooids were generally dominating the population, with the mean proportion of each survey ranging between 62.0–87.8%. Then, it was followed by the nurse stage, with the mean proportion varied between 3.0–21.8%. The phorozoid stage was not as frequently observed as the earlier-mentioned two stages, with a mean proportion of 8.4–13.5% when it appeared. The larval stage was only observed at some stations in October 2020, with a mean proportion of 2.0% in the whole surveyed area.

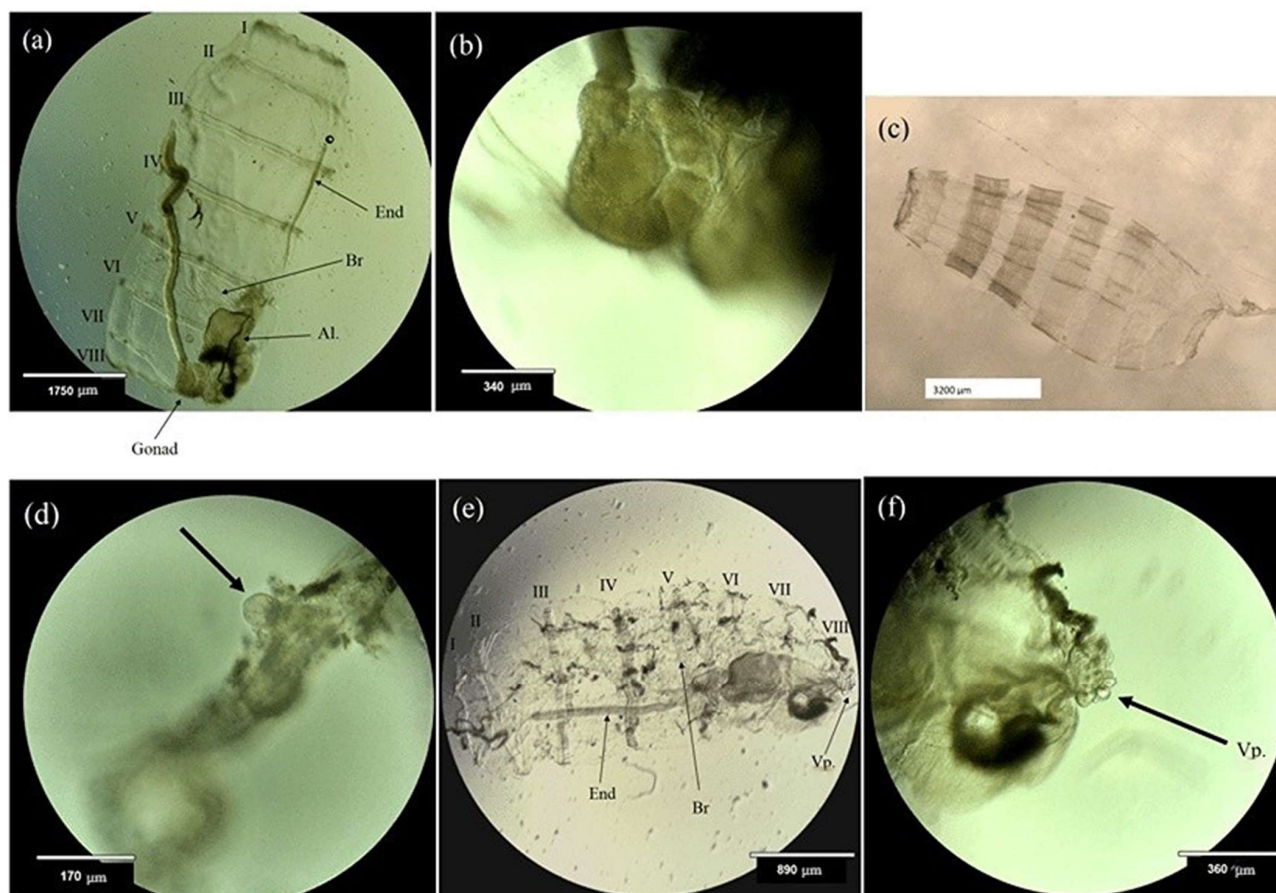


Figure 3. *Dolioletta gegenbauri*. Life cycle stages observed in the Jiaozhou Bay. (a) Gonozooid stage, lateral view. Al., alimentary canal; Br., branchial septum; End., endostyle. (b) Mature gonad of a mature gonozooid. (c) Nurse stage. with sprouting trophozooids (d) with arrow indication. (e) Phorozooid stage with ventral peduncle (Vp.) details in (f), where sprouting gonozooids can be seen.

Table 1. *Dolioletta gegenbauri*. Life stage compositions (% , mean $\pm$ SD) in the Jiaozhou Bay in each survey. $n = 1$ –10, according to the numbers of stations with its presence.

Life Stages	2019			2020	
	Oct	Nov	Dec	Oct	Nov
Nurse	19.8 $\pm$ 7.1	16.2 $\pm$ 10.0	100.0	21.8 $\pm$ 8.3	3.0 $\pm$ 2.6
Gonozooid	70.7 $\pm$ 14.2	83.8 $\pm$ 10.0	NA	62.0 $\pm$ 18.0	87.8 $\pm$ 9.9
Phorozooid	9.5 $\pm$ 7.6	NA	NA	13.5 $\pm$ 9.3	8.4 $\pm$ 9.7
Larva	NA	NA	NA	2.0 $\pm$ 3.8	NA

Early zooids and relatively large trophozooids were not seen in this study, partially due to the coarse mesh size. Only short cadophores were observed in this study. Therefore, only small sprouting trophozooids (~ 100 μ m) were found. Very early nurse was not observed either; only the bigger ones were observed ($\sim >5$ mm).

Size-frequency distribution was studied in October 2020, when the numbers of each life stage were abundant enough. As shown in Figure 5, the body size of gonozooids varied between 1.3–7.2 mm with a mean size of 3.4 mm. A small portion of gonozooids attained the mature size at >6 mm, capable of releasing eggs and/or sperm with sexual reproduction [5]. Phorozooids size varied between 1.8–3.3 mm with the mean size of 2.6 mm. Late nurse zooids were dominant in this survey, and their body size ranged between 5.0–12.5 mm, with a mean of 7.7 mm.

3.3. Temperature and Salinity Long-Term Change

Over the recent 21 years, water temperature in 2019 and 2020 was among the highest levels (Figure 4A). A significant increasing trend from 2000–2019 can be detected (Mann–Kendall trend test, Kendall's tau = 0.47, slope = 0.18, $p = 0.003$). According to Figure 4B, the salinity anomaly showed no significant long-term trend (Mann–Kendall trend test, Kendall's tau = 0.067, slope = 0.015, $p = 0.695$). Our results, together with the water temperature-rising trend in the 1960s to 2000s in JZB [14], indicate a continuous warming background in the past several decades locally.

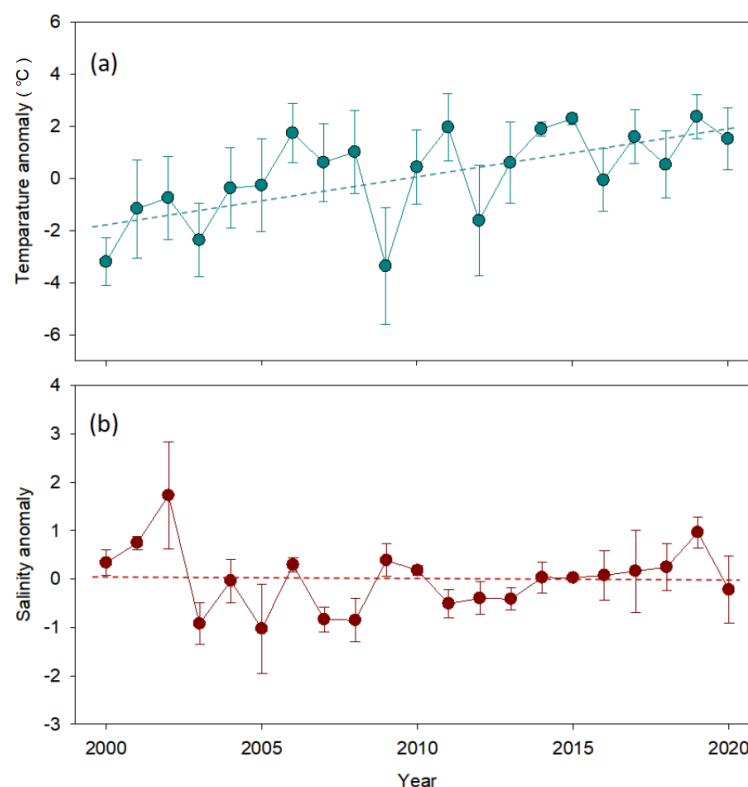


Figure 4. Anomaly of (a) temperature (°C) and (b) salinity (mean $\pm$ SD, $n = 12$ or 14) in November of 2000–2020 in the Jiaozhou Bay. Dashed lines indicate linear curve fits.

3.4. Relationship with Temperature, Salinity and Food

Temperature and salinity ranges when *D. gegenbauri* appeared were different in each year, i.e., 11.4–22.8 °C and 31.9–32.1 in 2019 and 15.5–22.0 °C and 29.6–31.2 in 2020, respectively. Chl *a* concentrations varied between 0.6–4.29 μgL^{-1} and 0.7–3.26 μgL^{-1} in 2019 and 2020, respectively.

As shown in Table 2, *D. gegenbauri* abundance was significantly and positively correlated with temperature but insignificantly with salinity or Chl *a* concentration. In fact, we noticed that the maximum abundance of *D. gegenbauri* was not necessarily coincident with the Chl *a* maximum spatially in each survey. Instead, maximum abundance usually appeared under moderate food availability. To sum up, temperature is a primary factor influencing the abundance or distribution.

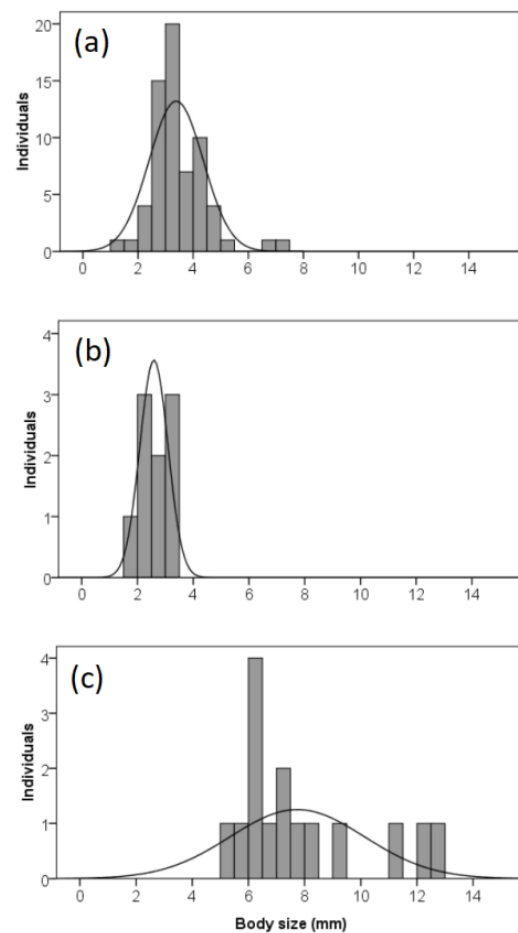


Figure 5. *Dolioletta gegenbauri*. Size (mm) frequency distribution of each life stage in October 2020 in the Jiaozhou Bay. (a) Gonozooids. (b) Phorozoids. (c) Nurse zooids. Normal distribution curve fit is indicated in each panel.

Table 2. Pearson correlations between $\log_{10}$ abundance (zooids m^{-3}) of *Dolioletta gegenbauri* and temperature ($^{\circ}\text{C}$), salinity, and surface Chl *a* concentration ($\mu\text{g L}^{-1}$). A, abundance; T, temperature; S, salinity. “*” indicates the statistical significance ($p < 0.05$).

	Correlation Coefficient	<i>p</i>	<i>n</i>
A vs. T	0.35	0.005 *	64
A vs. S	−0.09	0.496	64
A vs. Chl <i>a</i>	−0.17	0.179	64

4. Discussion

The main population of *D. gegenbauri* is known to occur in the southern East China Sea shelf, with an oceanic origin [7,9,10]. This study records *D. gegenbauri*’s new north limit (36°N), which was $\sim 31^{\circ}\text{N}$ in previous reports [13]. It indicates a northward expansion of $\sim 400\text{ km}$. Reproduction status, body size, and life stage composition suggest that the autumn environment in JZB was suitable for its survival and population development. Appearing as a seasonal dominant species, the population abundance levels in JZB are similar to that in the native habitat in the southern East China Sea [9] but significantly lower than the reported peak abundance in China ($\sim 450\text{ ind. m}^{-3}$, at 29°N) when it bloomed [7]. These results, together with the recorded abundance maxima worldwide [19], suggest a non-blooming but active status in JZB.

From a global perspective, *D. gegenbauri*’s occurrence, dense swarms, or blooming events were usually closely associated with intrusions of boundary currents. In the South

Atlantic Bight (SAB) region [19], where this relationship was most thoroughly studied in decades, one could predict the *D. gegenbauri*'s appearance and blooming scale with predictable boundary currents intrusion. In the Oyashio–Kuroshio mixed water region of the Northwestern Pacific Ocean, *D. gegenbauri* formed dense blooms with an origin from the seed population in the Kuroshio region [4].

In Chinese coastal seas, there is a complex current system, including a series of wind-driven coastal currents, seasonal dominating cold water mass, and sub-branches of warm currents [20,21] (Figure S1). Among them, the Kuroshio Current (KC) is a major boundary current originating from the western tropical Pacific, such as its Atlantic counterpart the Gulf Stream [19]. It intrudes into the shelf of the ECS and even into the YS through seasonal sub-branches. The Yellow Sea Warm Current (YSWC) belongs to be one of the sub-branches, an intermittent and compensated current, which responds to the north monsoon winds from late autumn to early spring [22]. Therefore, warm water or tropical species was usually found intruding into the central YS associated with the YSWC [23,24].

Thus, we hypothesize that *D. gegenbauri* of the oceanic margin origin was transported by the sub-branches of KC and, finally, the YSWC reaching into JZB. This is supported by the strengthening trend of the warm currents. In the past several decades, the warming trend strengthened the intensity of KC, mediated by the intensifying of tropical cyclones [25]. It is also supported by the timing coincidence of its autumn occurrence and the seasonal start of YSWC, as previously mentioned. Actually, summer northward transportation of *D. gegenbauri* could be blocked by both the steady physical structure of the Yellow Sea Cold Water Mass (dominating the central YS) and the Yangtze River Plume (Figure S1), as partially pointed out by previous studies [13,24]. Therefore, restricted distribution in the south of 31° N was observed in summer [13]. Only after the formation of YSWC in autumn, northward expansion could be possible.

Warming may be another necessary factor determining the *D. gegenbauri*'s expansion into JZB. Biogeographical shifts are a ubiquitous response to climate change [26]. In fact, the years 2019 and 2020 were among the warmest years in the recent four decades in JZB [14]. This long-term warming trend is in agreement with those in the Chinese coastal seas [27,28]. It is also in agreement with the observation that global ocean warmth maximized in the consecutive two years 2019–2020 [29,30]. This warming background may expand both the temporal and spatial range of *D. gegenbauri*. Our finding of the positive relationship between abundance and temperature (Table 2) and the record of abundant *D. gegenbauri* in Zhejiang coasts of the ECS in 2019 (personal communications) indicate they could be favored by warming at both the native and introduced habitats. Due to the low energy density of doliolids, it could thrive in a relatively low food concentration when compared with other planktonic groups [3]. Therefore, the lack of a significant relationship between the abundance and Chl *a* concentration (Table 2) is not surprising. Similar insignificance between *D. gegenbauri* abundance and food availability was observed in other regions [4,19,31]. Doliolids were known capable of feeding items ranging from bacteria and phytoplankton to eggs and nauplii of copepods [31]. The neritic food environment in general could benefit *D. gegenbauri*, with generally higher nutrients, higher phytoplankton density, and other food items in JZB than in the oceanic regions [14,15]. This could also be reflected by the relatively high proportion of gonozooids (Table 1), indicating an active population developing status or blooming potential [19].

While seasonally occurring and even dominating in JZB's planktonic food web, its ecological implications were largely unknown. The newly occurring doliolid has imported a potential competitor or prey to the local zooplankton, such as the appendicularian *Oikopleura dioica* [32], which shares a similar niche with *D. gegenbauri* in JZB. It might explain the general absence of *D. gegenbauri* in the inner bay in 2019 but not in 2020. In contrast to the normal status in autumn of 2019, a large-scale diatom bloom lasted in the autumn of 2020, providing sufficient food for both the *O. dioica* and *D. gegenbauri* (Wang et al., unpublished data). Due to the complex and understudied food relationships between

fish, copepods, etc. [1,31,33], the ecological impacts of *D. gegenbauri* in JZB should be addressed with further research efforts.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w14111685/s1>, Figure S1: Diagram of the general autumn–winter current systems in China coastal seas.

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Conflicts of Interest: The authors declare no conflict of interest.

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