Article

On the Predation of Doliolids (Tunicata, Thaliacea) on calanoid Copepods

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Abstract: The main goal of this contribution was to determine the effect of predation of the often abundant to dominant doliolid *Dolioletta gegenbauri* (Tunicata, Thaliacea) on the abundance of co-occurring planktonic copepods by feeding on their eggs. Previous oceanographic investigations revealed that doliolids had ingested eggs of small calanoid copepods. The ecological significance of such feeding could not be quantified completely because the environmental abundance of such eggs was not known. In this study, the eggs and nauplii of the neritic calanoid *Paracalanus quasimodo* (Crustacea, Copepoda) were offered to gonozooids and phorozooids of *D. gegenbauri* with a 6–6.5 mm length together with three species of phytoplankton; i.e., simulating diet conditions on the shelf. We hypothesized that copepod eggs of a similar size as food particles would be readily ingested whereas small nauplii, which could escape, would hardly be eaten by the doliolids. Our results revealed that doliolids have the potential to control small calanoids by ingesting their eggs at high rates but not their nauplii or later stages. Late copepodid stages and adults of co-occurring calanoid species could cause less mortality because they prey less on such eggs than doliolids of a similar weight. However, certain abundant omnivorous calanoid species with pronounced perception and/or capture abilities can prey successfully on the nauplii of small calanoids.

Keywords: copepod eggs; nauplii; doliolids; calanoid copepods

1. Introduction

Mortality among planktonic copepods in the ocean is particularly pronounced for eggs and nauplii [1–5]). Laboratory studies on *Calanus helgolandicus* [6], on four species of calanoids [7], and on two species of calanoids [8] revealed pronounced predation on eggs and/or nauplii of calanoid copepods.

During a seven-day oceanographic study in January/February of 1990 on the southeastern shelf of the United States of America, about 12% of the fecal pellets of the doliolid *Dolioletta gegenbauri* (Tunicata, Thaliacea) contained eggs of the calanoid genus *Paracalanus* [9]. The researchers' calculations showed that the feeding rates of large gonozooids of nearly 7 mm in length (in situ, about one such large doliolid L^{-1}) resulted in a noticeable suppression of that calanoid genus: the oceanographic data indicated that large parts of the water column where doliolids were abundant showed low abundances of *Paracalanus* copepodid stages and adults. A model of the effects of doliolids on the plankton community structure on the southeastern shelf showed significantly that the presence of doliolids was followed by a larger decrease in copepods than did a decrease in food supply to the copepods [10].

D. gegenbauri has been found during much of the year on the southeastern U.S. shelf at a range of abundances, often surpassing 1000 zooids m^{-3} [9,11]. It is also abundant in other regions of the eastern seaboard of the USA [12] (at 1500 zooids m^{-3}; [13] at thousands of individuals m^{-3}). This doliolid species has been encountered abundantly off the Mississippi Delta [14], in the northern Gulf of Mexico [15], and off southern California [16] and further north [17]. High abundances were found in the Inland Sea of Japan, usually

>2000 zooids m^{-3} with a maximum of 48 zooids L^{-1} [18] (Nakamura 1998), and in the Kuroshio [19,20]).

Our main question after observing oceanographically the effects of doliolids on small copepod abundance [9] was: to what extent can doliolids actually affect the abundances of small calanoids? We designed experiments to offer eggs and nauplii of *Paracalanus quasimodo* to large gono- and phorozooids of *D. gegenbauri* in the presence of environmental concentrations of several phytoplankton species because to comprehensively understand in situ feeding processes, potential food organisms ought to be offered together [7]. We hypothesized that eggs of small planktonic copepods could be readily ingested while they were still in the water column. We also hypothesized that the nauplii would hardly fall prey to doliolids because they would perceive the weak feeding current produced by the doliolids and therefore would escape.

2. Materials and Methods

The doliolid *D. gegenbauri* was collected at different times of the year on the southeastern shelf of the USA, as was the calanoid *Paracalanus quasimodo*, which releases its eggs directly into the water. We utilized a plankton net with a 50 cm mouth diameter and a 200 μm mesh to collect zooplankton gently in oblique tows; i.e., near the surface to near the bottom to near the surface at ship speeds not surpassing 0.5 kn. The 4 L of codend contents were gently immersed in large seawater-filled buckets to avoid damaging the doliolids and copepods. Sorting of doliolids and copepods into freshly collected Niskin bottle water (from 20 m depth) on board the ship occurred in a temperature-controlled room at 20 °C; they were then placed in glass jars with 1.9 and 3.8 L volumes. Back in the laboratory, both the doliolids and copepods were immediately placed in their jars on a plankton wheel rotating at nearly 0.5 rpm. Here, doliolids and copepods were simultaneously offered three species of phytoplankton: the flagellates *Isochrysis galbana* and *Rhodomonas* sp. and the diatom *Thalassiosira weissflogii* at average total concentrations ranging from about 50 to 60 μg C L^{-1} at 20 °C in a light–dark cycle of 12 h:12 h.

The doliolids and copepods were reared in separate jars for the ensuing experiment [21]. Food concentrations were quantified with a Coulter Beckman Multisizer IV (Brea, CA, USA) using an orifice with a 140 μm diameter. Quantifications with the Coulter counter were regularly checked and confirmed with phytoplankton samples that had settled in 10 mL chambers and were counted with a Leitz Dialux (Wetzlar, Germany) inverted microscope. Food concentrations were expressed in units of carbon; i.e., μg C L^{-1}. *I. galbana* had an average cell volume of ~50 μm^3 with 200 μg C mm^{-3} of cell volume; *Rhodomonas* had an ~300 μm^3 cell volume with 160 μg C mm^{-3}; and *T. weissflogii* had an ~1000 μm^3 cell volume with 80 μg C mm^{-3}. Food concentrations in each jar were quantified daily and adjusted in a manner that resulted in an average concentration of ~50 to 60 μg C L^{-1} over 24 h.

Doliolids were kept in the laboratory for weeks to months, growing and reproducing in 3.8 L jars on the rotating wheel. Their water was renewed to about 75% every 4–5 days. *P. quasimodo* was reared through several generations in jars with a 1.9 L volume and also offered those three phytoplankton species, but near a 30 to 40 μg C L^{-1} total. Prior to our experiments, doliolid zooids of a similar size were placed in one jar the day prior to each experiment and we ascertained whether they escaped well.

Each of the six experiments of *D. gegenbauri* feeding on eggs of *P. quasimodo* was started early in the morning using new algal suspensions in GFC-filtered seawater, 50% of which was water in which the doliolids had been previously. Females of *P. quasimodo* produced eggs overnight that were rapidly counted. Each of these experiments lasted 4 to 4.5 h and offered on average 208 eggs L^{-1} (starting concentration) plus phytoplankton to three *D. gegenbauri* gonozooids of a 6–6.5 mm length in a 960 mL jar. The initial and final egg concentrations were counted in 25 mL settling chambers in triplicate. Phytoplankton concentrations were quantified at the start and end of each experiment. Doliolid fecal pellets were collected at the end of each experiment. The production of eggs of *P. quasimodo* started after 17:00 h the previous day when about 10 to 15 females were placed into a

1.9 L jar containing *I. galbana* and *T. weissflogii* at an average total concentration of about 50 µg C L^{-1}. By 08:00 h the next morning, no nauplii had hatched; by 12:00 h, an occasional nauplius was found.

When offering nauplii of *P. quasimodo,* three large phorozooids (two experiments) or gonozooids (four experiments) were placed in a 960 mL jar containing the three phytoplankton species (*I. galbana*, *Rhodomonas* sp., and *T. weissflogii*) which served as food for both the doliolids and the nauplii. We usually offered 100 nauplii of varying stages or 75 nauplii and 25 copepodid stage I of that copepod species for about 4.5 h to large phorozooids (6–6.5 mm length), and later to large gonozooids (6–6.5 mm length) of that doliolid. Prior to these experiments, those zooids had been in 1.9 L vessels and were offered those three phytoplankton species. The nauplii ranged in age from mainly Nauplius stage III to VI. Since so few nauplii were ingested, we decided to check each doliolid fecal pellet collected at the end of each experiment to determine whether it contained a nauplius.

For each of the feeding experiments on nauplii, 43 to 90 intact zooid fecal pellets of *D. gegenbauri* (i.e., all pellets produced during the experimental period) were individually checked for ingested nauplii, copepodid stages, and exuviae under a light microscope (AxioScope A1, Zeiss, Jena, Germany). Each pellet was transferred with a glass pipette to a slide and covered with a coverslip. The tip of a narrow needle was gently pressed on the coverslip to release the enclosed food items. Microphotographs of intact and smashed pellets, as well as the food items of interest, were captured at 100- to 400-fold magnification using a 5 MP digital CCD camera (AxioCam Mrc 5, Zeiss, Jena, Germany) and the software AxioVision 4.1.

Feeding rates and average food concentrations were determined according to Frost (1972) [22]. Statistical analyses were conducted according to Zar (1974) [23] using the Kruskal–Wallis test, a nonparametric single-factor analysis of variance by ranks for K ≥ 2 independent samples [24].

3. Results

Doliolids feeding on copepod eggs. We conducted six separate experiments offering on average 208 eggs L^{-1} to three large gonozooids of *D. gegenbauri* (6–6.5 mm length) over an average period of 4.5 h together with three phytoplankton species (Figure 1). The Kruskal–Wallis test showed that the clearance rates for the three phytoplankton species and the copepod eggs did not differ significantly ($p < 0.005$). The eggs were readily ingested (Figure 1). Photographs of fecal pellets from these experiments were taken to document the ingestion of those eggs amidst the phytoplankton cells (Figure 2A,B). Although the concentration of copepod eggs (208 L^{-1}) was high, it did not contain much particulate matter (5.24 µg C L^{-1}) when using data from [25] as compared to the simultaneously offered phytoplankton, which represented the concentrations of a well-developing intrusion onto the southeastern shelf of the US [26].

Doliolids offered nauplii of *P. quasimodo*. As our field results [9] did not show that nauplii of *P. quasimodo* were ingested by large gonozooids of *D. gegenbauri*, we decided to evaluate in specific feeding experiments whether that finding was indeed true. A total of six experiments were conducted in which each of three zooids (6–6.5 mm length) were fed mainly on nauplii and the three phytoplankton species (Figure 3). The clearance rates for phytoplankton were not significantly different from each other (Figure 3, Kruskal–Wallis test, $p < 0.05$) but were significantly higher than those for the nauplii of *P. quasimodo* (Kruskal–Wallis test $p > 0.005$). The *D. gegenbauri* gonozooids in each jar captured a total of between one to four nauplii during the 4–4.5 h experimental periods. The clearance rates for nauplii of *P. quasimodo* were on average 2.0 mL *D. gegenbauri* zooid^{-1} h^{-1} (Figure 3).
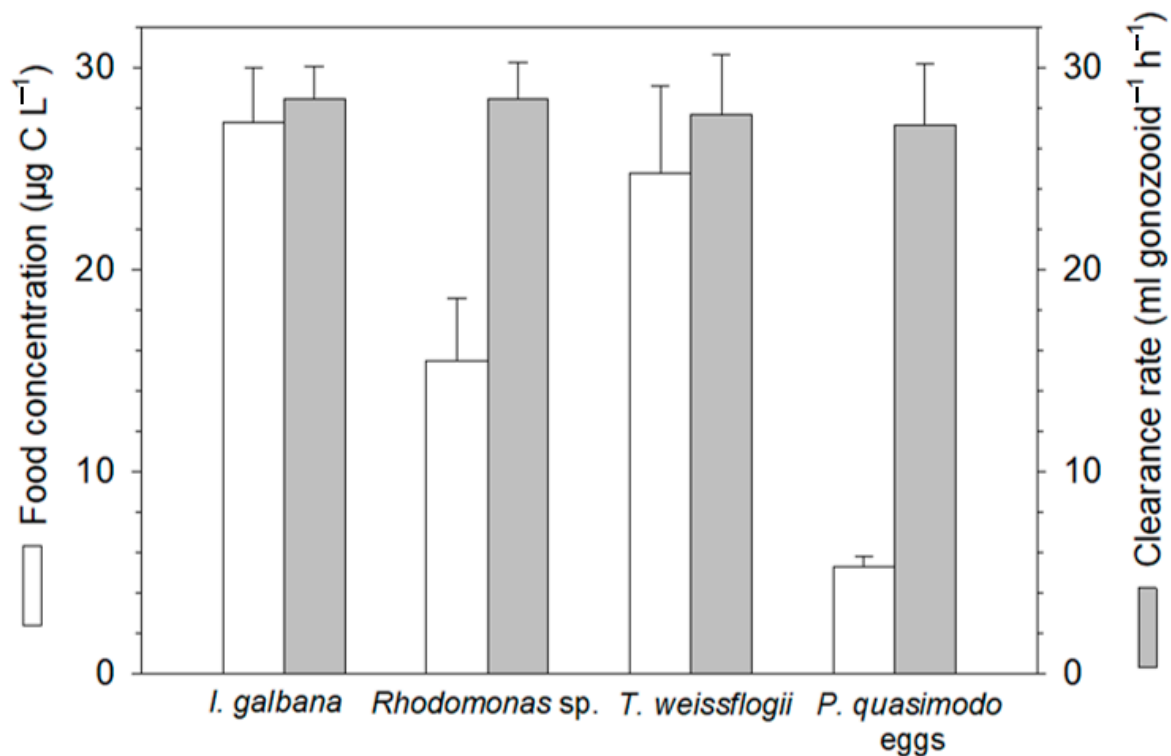
Figure 1. *Dolioletta gegenbauri.* Clearance rates of gonozooids of 6–7 mm length simultaneously offered eggs of *Paracalanus quasimodo* and cells of the three phytoplankton taxa (*Isochrysis galbana*, *Rhodomonas* sp., and *Thalassiosira weissflogii*) at 20 °C.

To recognize nauplii in pellets, they had to be squeezed for microscopical observation (Figure 2C–E). The nauplii we offered ranged from Nauplius stage III to VI. Those clearance rates for nauplii would amount to a clearance rate of 2.0 mL large gonozooid^{-1} h^{-1}, which would be 7.4% of the rates on eggs (Figure 1). Our photographs revealed *P. quasimodo* eggs (Figure 2A,B) and juvenile stages in pellets (Figure 2C–E). Large gonozooids were able to ingest exuviae (e.g., Figure 2F) that were compressed in the feeding net prior to passing the esophagus, which measured 60 to 70 μm in diameter.
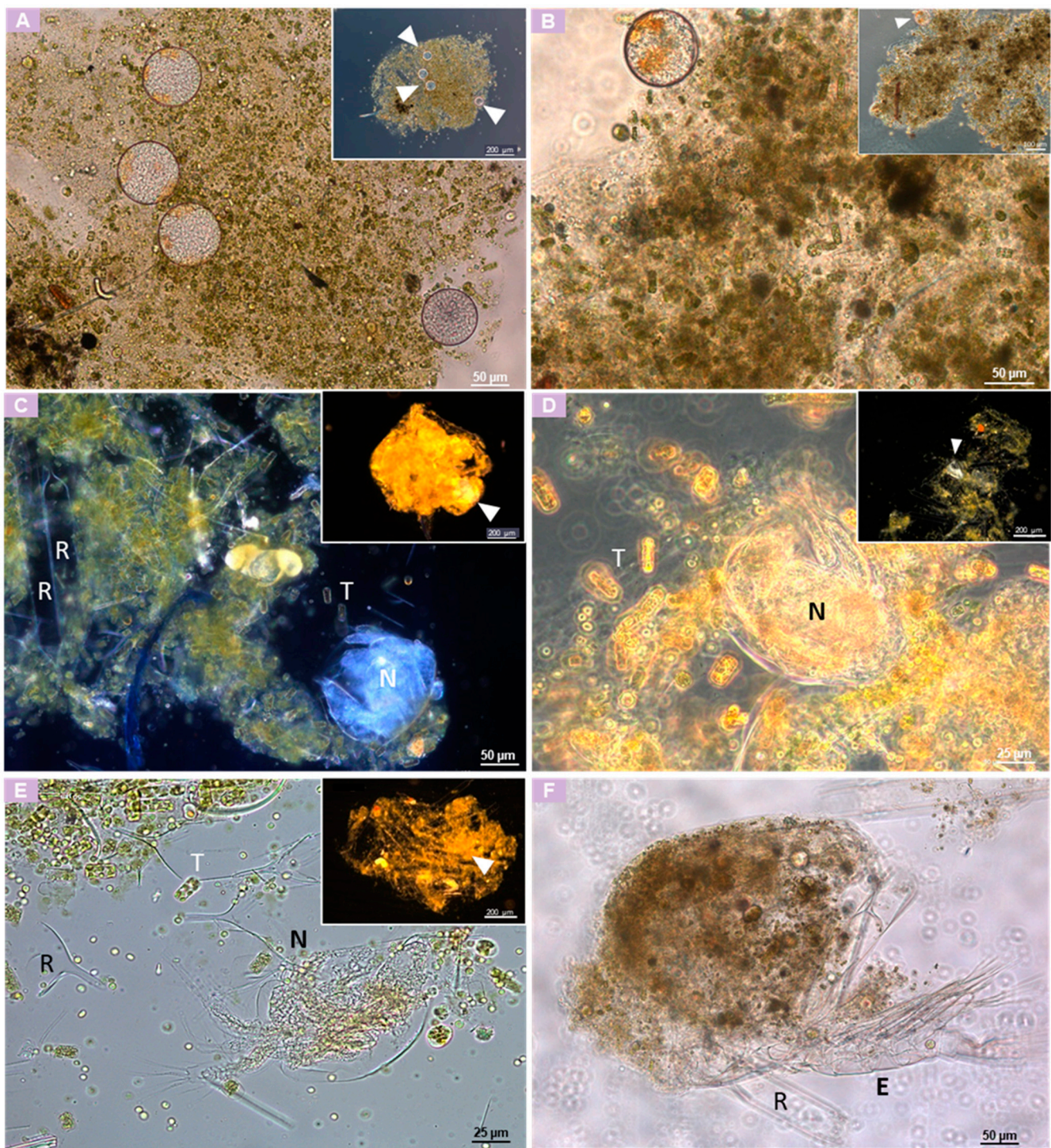
Figure 2. Light microscope photographs of fecal pellets of *Dolioletta gegenbauri* containing intact eggs (**A**,**B**) and juvenile stages (**C**–**E**) of the small calanoid copepod *Paracalanus quasimodo*. The inserts show the intact doliolid pellets. The white arrows indicate the hardly recognizable ingested zooplankton food items (eggs, nauplii, and copepodids of *P. quasimodo*) that were only detectable after the pellets were smashed (see food items at larger magnifications). (**A**,**B**) Phase-contrast micrographs of doliolid fecal pellets containing four and one *P. quasimodo* eggs with diameters ranging from 60 to 65 μm. (**C**–**E**) Dark-field and phase-contrast micrographs of smashed doliolid fecal pellets showing their nauplii (N) "unwrapped". (**F**) Phase-contrast micrograph of a doliolid fecal pellet containing a several hundred micron long exuvia of a copepodid of *P. quasimodo*. T = intact digested cells of *Thalassiosira weissflogii*; R = empty cells of *Rhizosolenia alata*. E = exuvia.
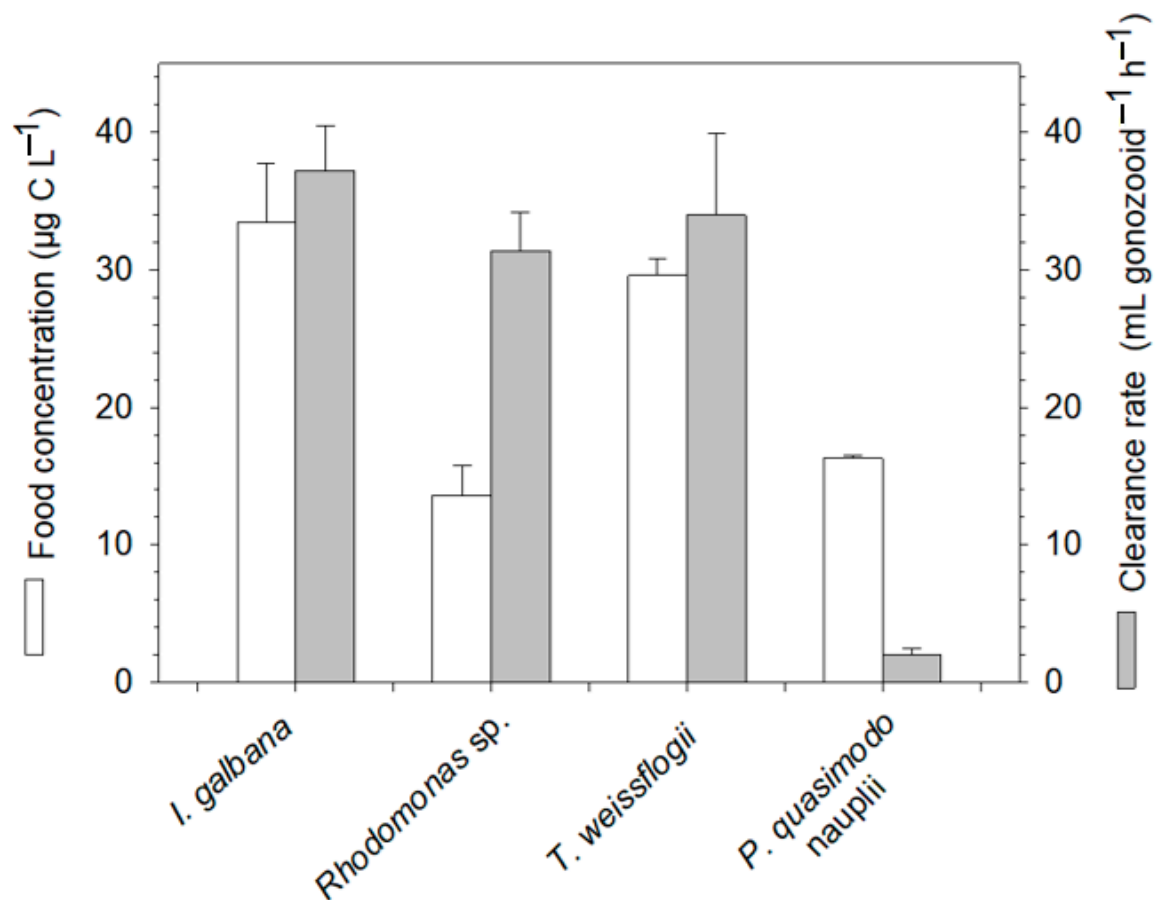
Figure 3. Zooids (phorozooids and gonozooids) of *Dolioletta gegenbauri* (6–6.5 mm body length) feeding simultaneously on three species of phytoplankton and nauplii of *Paracalanus quasimodo*. Arithmetic means and standard errors are given (*n* = 6).

4. Discussion

We will first discuss the ecological effects of doliolid predation on calanoid eggs and nauplii, then compare those findings with predation results from omnivorous calanoid genera that co-occur with doliolids on subtropical shelves, and end with general conclusions on the effects of doliolid predation on continental shelf food webs.

Feeding of doliolids on eggs and nauplii of small copepods. The assumption of Paffenhöfer et al., 1995 [9] that doliolid feeding could significantly affect the abundance of the calanoid copepod *P quasimodo* came from their field observations on the vertical abundance and distribution of *Paracalanus* spp. copepodids and adults versus that of doliolids. Their abundance was inverse: a higher abundance of *D. gegenbauri* co-occurred with a low abundance of *Paracalanus* spp. Those investigators found no nauplii in the guts or pellets of doliolids. The authors' calculations showed that the doliolid assemblage at times cleared 25% or more of the upper water column of ingestible particles per day. That was considered a conservative estimate.

Our results revealed that large doliolids ($\geq$6 mm length) ingested *P. quasimodo* eggs at rates that were nearly identical to those rates on co-occurring phytoplankton (Figure 1). What did this finding imply? The clearance rate of gonozooids of a 6–6.5 mm length on eggs was 28.6 mL zooid^{-1} h^{-1}, which would amount to 686 mL d^{-1}. As the eggs of *P. quasimodo* would hatch within ~15–18 h of being released, such a doliolid would spend that time at the clearance rate of ~514 mL for that period of 18 h; this implies that about 50% of those eggs would be ingested by one large doliolid L^{-1}. The extent of such predation depends on abundance and size of the zooids. Even a small *D. gegenbauri* zooid of a 4.5 mm length that was able to ingest cells up to 60 μm in diameter and clearing 350 mL d^{-1} at

20 °C [27] would clear 233 mL in 16 h, and thus would ingest near 25% of small copepod eggs. The effect of doliolids of >4 mm length would be a function of their clearance rate as a population, which repeatedly amounted to more than 500 gonozooids/phorozooids m^{-3} in the winter of 1990 [9].

Overall, *D. gegenbauri* should influence to a varying extent the abundance of small calanoids on subtropical shelves. Aside from the genus *Paracalanus*, the calanoids *Temora turbinata, T. stylifera, Clausocalanus furcatus*, and *Centropages furcatus/velificatus* also often occur abundantly on the SE shelf [26] and produce eggs of a similar size, and therefore could fall prey to *D. gegenbauri*.

Having copepod eggs ingested and released within pellets revealed that many of those eggs appeared undamaged (Figure 2A), as we had also observed for diatoms of different sizes [28]. Those pellets remained for several to many hours in the water column [29]. During that time, the nauplii would most likely hatch. We do not know whether the hatching nauplii were affected by the digestion process, as the eggs appeared undamaged externally. Having hatched, the nauplii would attempt to move out of the pellet. We observed one ingested nauplius that attempted this. Our oceanographic study [9] seemed to support the assumption that a high percentage of ingested eggs would not lead to surviving nauplii.

Doliolids produce slow-moving feeding currents by displacing water and particles therein toward their mouth [30]. Even nauplii with continuously moving appendages such as *Paracalanus* most likely will perceive the shear in such feeding currents and escape. Some nauplii may not be able to do so and thus could be ingested (Figure 3). Overall, the clearance rate of *D. gegenbauri* on nauplii of *Paracalanus* that was calculated in our experiments was only 2.0 ml gonozooid/phorozooid^{-1} h^{-1}, implying minimal effects of doliolids on nauplii and later stages.

Comparing the effects of doliolids with those of calanoid copepods on eggs and juveniles of calanoids. The intermittent high abundance of larger doliolids [31] (from about 1000 m^{-3} on) should affect the abundance of egg-releasing smaller calanoids. It appeared that eggs and nauplii were more vulnerable than later juvenile stages of calanoid copepods: Eggs cannot perceive predators and cannot escape, while nauplii can perceive and escape fairly well; however, copepodid stages have superior perception (extended first antennae with 3D-arranged setae) and escape capabilities, and therefore are not as vulnerable to predation by omnivorous copepods as nauplii [32]. Doliolids are effective at preying on calanoid eggs but not on calanoid nauplii. Different species of omnivorous calanoids vary in their capability to prey on eggs and nauplii of other species and their own (Table 1): females of the calanoid *Calanus helgolandicus*, which usually create a feeding current, remove eggs at a far higher rate than its nauplii [6] (Table 1). Those rates are usually lower than those on larger phytoplankton cells by a closely related species [33] (Table 1): while phytoplankton is perceived via chemosensory mechanisms in a calanoid feeding current [34], eggs do not produce a chemical signal like phytoplankton. They may either be perceived by mechanosensory mechanisms, or, if not perceived individually, could arrive at the mouth together with phytoplankton, which provide the signal for ingestion [35].

The almost continuously moving *Temora longicornis* clears eggs at a higher rate than nauplii, whereas two species of the genus *Centropages*, which are considered ambushers, clear nauplii at a higher rate than eggs [7]. Our observations (Paffenhöfer and Knowles, unpubl. observations) revealed that *T. stylifera* females move almost continuously while creating a feeding current. They thus provide a mechanical warning signal to nauplii while ingesting much of the phytoplankton and most likely some calanoid eggs (Table 1). *Centropages velificatus* adults, however, create a feeding current only briefly before starting to sink motionless for longer periods. They are not perceived by slowly swimming nauplii while ingesting only small amounts of phytoplankton due to brief feeding current activity (Table 1): *C. velificatus* adults ingested 7 nauplii day^{-1} at 30 nauplii L^{-1} and 13 nauplii d^{-1} at 60 nauplii L^{-1} [8]. These findings supported the results of Boersma et al., 2014 [7] of feeding on nauplii by congeners, revealing differences between doliolids and co-occurring

copepod genera: while omnivorous calanoids can perceive and capture nauplii and eggs, doliolids do not rely on perceiving their prey; they instead create a feeding current that displaces particles with an ~1 to >50 μm diameter toward themselves and ingest them. Most of the copepod rates were obtained with adult females. It remains to be determined to which extent earlier copepodid stages could be carnivorous and to which extent potential predators and their prey operate in similar depth ranges.

Table 1. Average clearance rates on copepod eggs and nauplii and phytoplankton by calanoid copepods and doliolids (n.d.—not determined).

Species and Stage	Temperature (°C)	Clearance Rate (mL^{-1} Copepod^{-1} Day^{-1})			References
		Eggs	Nauplii	Phytoplankton	
Calanus helgolandicus female	13–15	320	>102	n.d.	Bonnet et al., 2004 [6]
Temora longicornis female	10	161	>120	n.d.	Boersma et al., 2014 [7]
Centropages hamatus female	10	94	<195	n.d.	
Centropages typicus female	10	159	<224	n.d.	
Temora stylifera female	20	n.d.	139	<360	Paffenhöfer and Knowles unpubl.results
Centropages furcatus/velificatus female	20	n.d.	230	>60	
Calanus helgolandicus female	15	n.d.	n.d.	530	Paffenhöfer 1971 [33]
Dolioletta gegenbauri Gonozooids/Phorozooids	20	648	69	670	This paper

Data from a previous cruise [36] revealed that during the summer, on average, the genus *Paracalanus* occurred at 1429 copepodid stage II (C II) to adult m^{-3} in warm surface waters and at 3030 CII to adults m^{-3} in cooler bottom layers. At the same time, the potential predators *Centropages furcatus/velificatus* were 287 C II to adult m^{-3} in surface waters and 84 m^{-3} in cooler bottom layers. The doliolid *D. gegenbauri* occurred at a low abundance during those cruises, decreasing from 424 to 8 zooids m^{-3} [37]. This species is usually found during the summer in larger numbers only in cooler bottom layers and in the thermocline.

Data on the actual vertical distribution of nauplii in the ocean are sparse: during the summer of 1979, several cross-shelf transects using a 30-micron mesh for sampling the entire water column with a pump revealed the following [38] when sampling the warm upper mixed layer, the thermocline, and the cold bottom layers consecutively. Nauplii occurred between 7 and 100 L^{-1}. At 11 stations, they were most abundant five times in the upper mixed layer, four times in the thermocline, and twice in the intrusion of cold water. While *Paracalanus* spp. occurred from about 3000 to 11,000 m^{-3} and *Temora turbinata* from near 1000 to 5000 m^{-3} (C I to adults), doliolids were sparse, amounting to 60 to nearly 300 zooids m^{-3} over the following two weeks, and therefore should have had hardly any effect through predation on the copepods' eggs. However, one week later *D. gegenbauri* had increased to 620 to 1230 gono/phorozooids m^{-3} in the thermocline and had intrusion at two stations, which had the potential to affect the populations of *Paracalanus* spp. and *T. turbinata*.

Our time-series findings from a two-month oceanographic coverage (weekly) of the southeastern shelf off northern Florida and southern Georgia showed abundances of 20–250 *D. gegenbauri* zooids m^{-3} on part of the shelf by mid-July and maxima of 500–1000 zooids m^{-3} two to three weeks later, which diminished afterward [26]. In comparison to the winter of 1990 [9], these summer doliolid abundances should have had a limited effect on the populations of small copepods, which were dominated by *T. turbinata*

repeatedly reaching maxima between 1000 to 10,000 (mainly juveniles) m^{-3}. There were no data on the sizes of *D. gegenbauri* during all those summer studies. The very high abundances of *T. turbinata* could have diminished doliolid reproduction, as they could have grabbed doliolid larvae and thus killed them (grabbing behavior of Temoridae, pers. observation, G.-A. Paffenhöfer for copepodids and adults).

The clearance rates of *D. gegenbauri* on phytoplankton of about 640 to 670 mL gonozooid (body weight of 35 µg C)$^{-1}$ d^{-1} were slightly above the rates of nearly 600 mL gonozooid (body weight of 35 µg C)$^{-1}$ d^{-1} feeding at 60 µg C L^{-1} of phytoplankton [27] (and also the rates shown in Figure 1) We may attribute such differences to variability when cultivating these doliolids.

Doliolids do not appear to choose particles based on their chemical quality and composition. They could affect calanoid reproduction more than similarly sized calanoids: Our study provided a glimpse into what extent planktonic copepods and doliolids will affect zooplankton communities via predation on copepod eggs. However, the short residence time of small calanoid eggs in the water column prior to hatching (15–18 h) implied only short periods of vulnerability in situ as compared to nauplii, which will exist for about 4–8 days in the water column prior to molting to copepodid stage I (C I). Then they are less vulnerable to predation [32]. In essence, eggs would be mainly vulnerable to doliolid occurrence while nauplii would be sensitive to copepodids and adult calanoids (omnivory) on a subtropical shelf. Other studies revealed that the far less abundant but larger outer-shelf and oceanic salps are considered carnivores [39,40] as observed in their gut contents.

General Conclusions. Earlier results [10,41] and ours indicated that doliolids can have significant influences on food web processes on subtropical continental shelves: they can ingest anything from a nearly one micron width to a >60 micron maximum dimension. Such food particles include detritus such as fecal pellets [41], which are displaced by a gentle current into a doliolid's mouth and settle on the mucous filter. However, in comparison to copepods, the doliolid digestion process is limited [42]. The fecal pellets contain aggregated or not or partly digested small cells [28] (e.g., *Isochrysis galbana*), which as individual cells are not perceived by copepods and can now, as a pellet, be ingested and used by calanoids. At the same time, such doliolid pellets sink slower than similarly sized copepod pellets [29], depriving the seafloor of food particles as those are ingested by suspension feeders in the water column [43] (e.g., heterotrophic dinoflagellates). In comparison to most copepod fecal pellets, the doliolid pellets contain considerable amounts of nitrogen [43], which, compared with copepod pellets, can support growth of those zooplankters ingesting them. Doliolids do not uniformly digest and utilize phytoplankton as many calanoids do, which destroys the cells when they enter the esophagus and then utilizes the cells' contents to a high percentage. Doliolids do not persist permanently in abundance on continental shelves as voracious predators such as hydromedusae with extended tentacles ingest and digest them readily (unpubl. results by L. Frazier and G.-A. Paffenhöfer, shipboard and laboratory observations). As addressed in [1,2], we wanted to inquire to what extent different copepod species (calanoids and cyclopoids) and smaller doliolid zooids actually affected a community's copepod composition via predation on eggs, aside from predation on juveniles (nauplii), of which we already have some knowledge [7,8]. That research will also include obtaining information on the residence times of sinking copepod eggs in the water column and their vertical position when being released.

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