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Authors

Logerwell, EA
Ohman, Mark D

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Elizabeth A. Logerwell · Mark D. Ohman

Egg-brooding, body size and predation risk in planktonic marine copepods

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Abstract We investigated the interacting effects of copepod body size and the presence or absence of egg masses on the risk of predation by a visual predator. We conducted selection experiments involving three-spined sticklebacks (*Gasterosteus aculeatus*) and copepods ranging in body mass from 0.5 to 740 $\mu\text{g C}$: *Oithona similis*, *Corycaeus anglicus*, *Pseudocalanus newmani*, *P. moultoni*, *Pseudodiaptomus marinus*, and *Paraeuchaeta elongata*. We found that sticklebacks selected ovigerous females of the two smallest-bodied species of copepods (*Oithona similis* and *Corycaeus anglicus*). In contrast, the fish showed no significant selection for ovigerous females of the remaining, larger-bodied species. Unexpectedly, egg mass position (i.e., in a ventral, dorsal or lateral location on the urosome) appeared to influence predation risk more than did body size, resulting in higher predation risk for the cyclopoid and poecilostomatoid species than for the calanoid species we tested. Although the sticklebacks showed no statistically significant preference for ovigerous females of any of the four calanoid species, for each species the overall proportion of ovigerous females ingested was slightly greater than 0.50. Thus, whether body size influences the susceptibility of egg-brooding calanoid copepods to predation remains an open question.

Key words Copepods · Predation risk · Egg-brooding · Fish predation · Body size

E.A. Logerwell (✉) · M.D. Ohman
Marine Life Research Group, Scripps Institution of Oceanography,
La Jolla, CA 92093-0227, USA

Present address:

E.A. Logerwell, Southwest Fisheries Science Center,
P.O. Box 271, La Jolla, CA 92038, USA,
e-mail: elogerwell@ucsd.edu
Fax: +1-619-5467003

Introduction

The hypothesis underlying most studies of the evolution of life history traits is that directional changes in a trait are constrained by trade-offs (Roff 1992). For example, the advantage of a particular reproductive strategy may depend on the trade-off between the costs to adults and the benefits to offspring (cf. Kiørboe and Sabatini 1994). For planktonic copepods that brood eggs rather than broadcast spawn, the benefit to offspring is thought to be increased egg survival. The mortalities of brooded eggs of marine copepods appear to be at least an order of magnitude lower than those of broadcast eggs (Kiørboe and Sabatini 1994), perhaps due to fewer losses from suspension-feeding predators in the water column as well as reduced sinking of eggs to the benthos in shallow waters (e.g., Peterson and Kimmerer 1994). The cost of the egg-brooding strategy is likely to be, at least in part, increased predation on adult females, since the large and often pigmented egg masses can result in increased conspicuousness of egg-bearing females to visual predators (Hairston et al. 1983; Vuorinen et al. 1983; Bollens and Frost 1991). A decrease in the escape ability of females carrying eggs may also contribute to increased predation mortality of adult females (Winfield and Townsend 1983; Svensson 1992).

In a synthesis of information on marine copepod female body size and reproductive investment Ohman and Townsend (1998) found a striking pattern. A comparison of the body size distribution of copepod species that brood eggs versus species that broadcast spawn revealed a gap in the size distribution of brooding species that is not present in the distribution of broadcast spawners. Whereas there is only one brooding species between 10 and 100 $\mu\text{g C}$, there are 41 species of broadcast spawners in this intermediate size range (Fig. 1). The goal of the research presented here was to investigate whether predation plays a role in maintaining this “brooder’s gap”.

Ohman and Townsend (1998) suggested that the increased predation risk associated with carrying egg masses, particularly in epipelagic waters, may explain

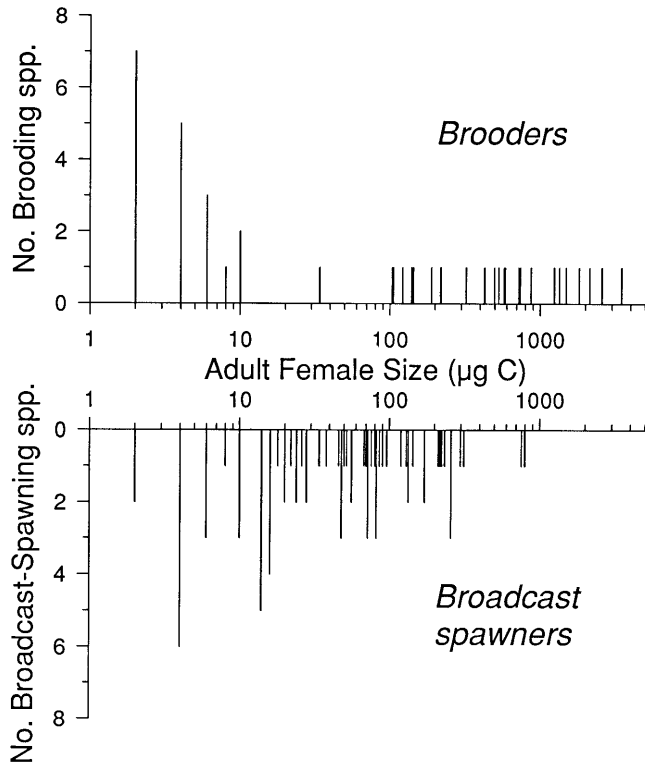


Fig. 1 Size frequency distributions of adult female calanoid and cyclopoid copepods, for egg-brooding and broadcast spawning species found in epi-, meso- and bathypelagic waters throughout the world ocean. Body sizes grouped into 2- μ g C increments (from Ohman and Townsend 1998)

why virtually no intermediate-sized copepod species adopt the brooding strategy. The largest-bodied species of egg-brooding copepods either occupy meso- and bathypelagic waters or perform diel vertical migrations and thus may reduce predation risk despite the presence of potentially conspicuous egg masses. Very deep diel vertical migrations may be less common in intermediate-sized copepods because of limitations on daily ambits. The smallest-bodied epipelagic species may be able to adopt a brooding strategy because the increase in conspicuousness to visual predators resulting from an increase in overall body size and/or pigments in the eggs could be less than it is for larger-bodied species, presumably because the smallest species are very difficult for predators to see with or without egg masses. Ohman and Townsend (1988) thus hypothesized that the predation risk associated with carrying eggs should increase steeply with copepod body size. This hypothesis requires that there is not a significant decrease in the size of the egg mass proportional to body size as body size increases. However, Mauchline (1988) suggested that among several species of calanoid copepods (epi-, meso-, and bathypelagic) brood volume scaled to body volume allometrically, with an exponent of 0.823. In contrast to the hypothesis of Ohman and Townsend (1998), this allometric scaling could result in a smaller increase in conspicuousness due to the presence of egg masses for larger-bodied species, compared to smaller-bodied species.

We conducted a series of experiments with three-spined sticklebacks (*Gasterosteus aculeatus*) preying on six copepod species over a wide range of body sizes. The copepods tested included five small-bodied species below the brooder's gap and one large-bodied species well above the gap, *Paraeuchaeta elongata*. Our goal was to observe whether predation risk associated with carrying egg masses increased with body size, as predicted by Ohman and Townsend (1998), or whether the predation risk of larger-bodied ovigerous copepods was less than that of smaller-bodied ovigerous copepods, as predicted by allometric scaling of brood volume to body volume (Mauchline 1988).

Materials and methods

This study was conducted at Friday Harbor Laboratories, Friday Harbor, Washington during summer (May through September) 1997. Sticklebacks (*Gasterosteus aculeatus*) were collected in Argyle Lagoon, San Juan Island, Washington. The experimental fish ranged in size from 40 mm to 60 mm standard length, indicating that they were adults (Hart 1973). After capture, fish were held in 50-l plexiglass tanks with flow-through sea water and fed a combination of live copepods and flake fish food. Most fish acclimated to holding tanks in three or four days, as indicated by feeding on the copepods offered.

The following copepod species were collected in the channel between San Juan Island and Lopez Island, Washington: *Oithona similis* Claus, *Corycaeus anglicus* Lubbock, *Pseudocalanus newmani* Frost, and *P. moultoni* Frost. Two other species used in the experiments were collected elsewhere: *Pseudodiaptomus marinus* Sato, collected in Mission Bay (San Diego, California); and *Paraeuchaeta elongata* (Esterly), collected in Dabob Bay, Washington. Twenty adult females of each species, preserved in formaldehyde-seawater, were measured to determine total length (Table 1). Body mass of each species (μ g C) was obtained from previously published studies (Gophen and Harris 1981; Uye et al. 1983; Yen 1983; Sabatini and Kiørboe 1994; Kiørboe and Sabatini 1995).

Predation trials were conducted in 20-l glass aquaria. After all fish were fed live copepods, one fish was placed in an aquarium and allowed to acclimate for two hours. Live copepods of one of the six species collected were then placed in the tank in equal proportions of ovigerous and non-ovigerous females. A total of 50 copepods was usually offered, but in some cases there were fewer (Table 1). Fish were observed during feeding, with care given not to disturb fish with noise or movement. Most fish fed readily in the presence of the observer. After 25 strikes were observed (or a number equaling half the total number of copepods offered), the fish was removed from the experimental tank. The duration of predation trials ranged from 1.5 min to a maximum of 30 min when the trial was terminated regardless of the number of strikes observed (6 out of 31 trials were of maximum duration). The experimental aquarium was rinsed and drained slowly with a 6-mm-diameter tygon tube siphon ending in a funnel covered with fine mesh (75 μ m). The last approximately 200 ml of water was removed from the tank with a large pipette and the number of uneaten copepods, ovigerous and non-ovigerous, was counted. Four to six replicate predation trials were conducted for each copepod species (Table 1), and each replicate involved a different stickleback individual.

An egg-loss control was conducted for all copepod species tested. This consisted of placing a known number of ovigerous females (7–18) in an experimental aquarium without a fish, followed by the draining protocol described above. None of the ovigerous females of *Corycaeus anglicus*, *Pseudocalanus newmani*, *P. moultoni*, or *Paraeuchaeta elongata* lost their egg masses. Only 1% of ovigerous females of *Oithona similis* and *Pseudodiaptomus marinus* lost their egg masses. Thus it was not likely that loss of eggs during retrieval of copepods would result in apparent predation preference for ovigerous females.

Because copepods were offered to sticklebacks in equal numbers, preference for ovigerous (or non-ovigerous) females was indicated by fish ingesting copepods of a given type in proportions greater than 0.50. The significance of the proportions of ovigerous and non-ovigerous copepods ingested by fish during the predation trials was tested using the heterogeneity G -test (Sokal and Rohlf 1995). G_H was first calculated and compared to a χ^2 -distribution in order to test whether the outcomes of the replicate trials for each species were homogeneous. Then G_P was calculated and compared to a χ^2 -distribution in order to test whether the data as a whole fit the expected proportions (0.50 ovigerous and 0.50 non-ovigerous). The two tests are used together because an observed frequency in pooled data that does not deviate from the expected frequency can be a result of heterogeneous frequencies among the replicates that cancel each other out (Sokal and Rohlf 1995).

Results

Sticklebacks ingested 13–84% of the copepods offered (Table 1). Because the duration of the experiments was determined from observations of strikes by the fish, deviations from the target ingestion, 50% of the copepods offered, were likely due to inconsistency in discerning

successful from unsuccessful strikes. In addition, some strikes were apparently not observed at all.

In all but one trial, sticklebacks ingested more ovigerous than non-ovigerous copepods of the two smallest-bodied species, *Oithona similis* and *Corycaeus anglicus*. In contrast, sticklebacks consumed roughly equal proportions of ovigerous and non-ovigerous copepods of the four larger-bodied species, *Pseudocalanus newmani*, *P. moultoni*, *Pseudodiaptomus marinus* and *Paraeuchaeta elongata* (Table 1). G_H for all six sets of trials was not significant, indicating that the proportions of ovigerous and non-ovigerous copepods ingested were uniform among the trials within a species (Sokal and Rohlf 1995). Thus, proportions in pooled data that are not statistically different from 0.50 are not likely due to extremely low and extremely high proportions that cancel each other out. The overall proportions of ovigerous copepods ingested (calculated by pooling data from all trials) were greatest for *Oithona similis* and *Corycaeus anglicus* (Table 1). G_P was statistically significant for only these two species, indicating that the proportions of copepods ingested deviated significantly from the expected.

Table 1 Summary of predation trials. Sticklebacks were offered copepods in a 1:1 ratio of ovigerous to non-ovigerous females totaling the amounts shown. The proportion of ovigerous copepods

ingested shown is pooled over all trials. Deviations of pooled frequencies were tested with G_P

Species	Body mass ($\mu\text{g C}$)	Total length (mm)	Copepods offered	% Copepods ingested	Non-ovigerous ingested	Ovigerous ingested	Proportion ovigerous ingested	G_P
<i>Oithona similis</i>	0.5	0.80	50	46	4	19	0.69	5.9*
			50	20	4	6		
			50	32	5	11		
			36	58	9	12		
<i>Corycaeus anglicus</i>	2.4	1.00	50	54	7	20	0.70	10.4**
			46	28	7	6		
			50	34	4	13		
			50	42	5	16		
			44	20	2	7		
<i>Pseudocalanus newmani</i>	4.7	1.28	46	43	7	13	0.54	0.8
			50	30	4	11		
			50	44	11	11		
			50	36	8	10		
			50	56	14	14		
<i>Pseudocalanus moultoni</i>	5.1	1.52	50	36	8	10	0.56	3.2
			50	76	19	19		
			50	46	13	10		
			50	84	20	22		
			50	64	11	21		
<i>Pseudodiaptomus marinus</i>	5.5	1.32	40	40	6	10	0.52	0.1
			50	70	17	18		
			50	22	6	5		
			50	18	4	5		
			50	20	5	5		
<i>Paraeuchaeta elongata</i>	740	5.77	50	66	15	18	0.52	0.2
			40	38	7	8		
			40	13	2	3		
			40	48	11	8		
			40	13	1	4		
			32	59	8	11		$df=1$

* $P < 0.05$, ** $P < 0.01$

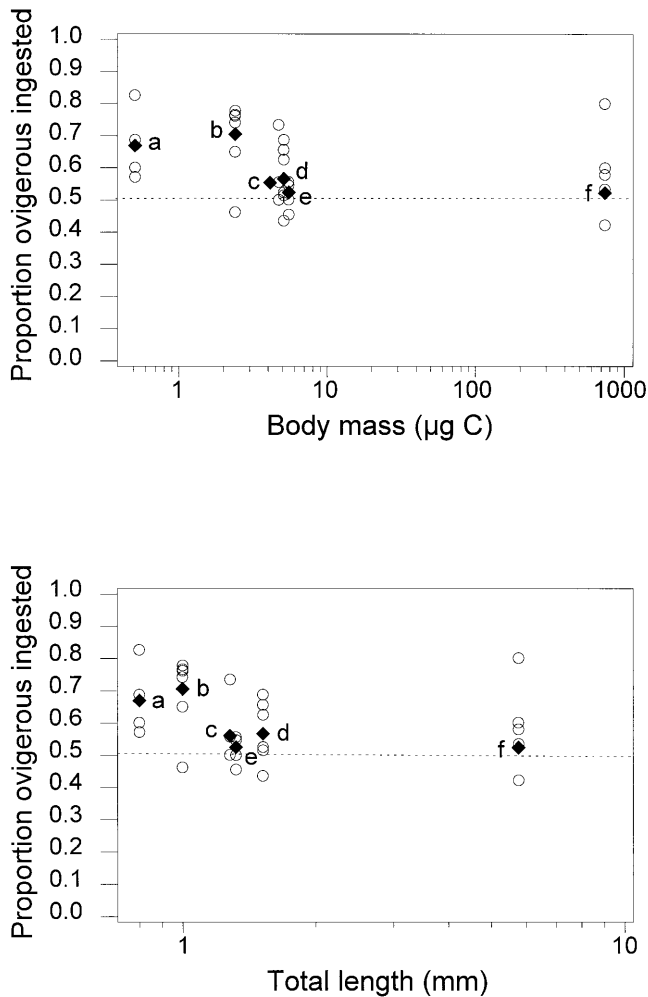


Fig. 2a,b Proportion of ovigerous copepods ingested by sticklebacks for each species tested. **a** X-axis is the adult female body mass of each species ($\mu\text{g C}$). **b** X-axis is the adult female total length of each species (mm). For both graphs, *open circles* represent the proportion in each trial, *solid diamonds* represent the proportion in all trials combined. The *dashed line* marks the proportion expected (0.50) if fish have no preference for ovigerous individuals (species codes: *a* *Oithona similis*, *b* *Corycaeus anglicus*, *c* *Pseudocalanus newmani*, *d* *Pseudocalanus moultoni*, *e* *Pseudodiaptomus marinus*, *f* *Paraeuchaeta elongata*)

Figure 2 shows that the predation risk due to carrying eggs, as measured by the proportion of ovigerous copepods ingested by fish, initially decreased with body size. Figure 2 also shows that although the pooled proportions were significantly greater than 0.50 only for the two smallest-bodied species of copepod, among the four larger-bodied species the replicate proportions were greater than 0.50 for the majority of trials (14 out of 21).

Discussion

This series of predation experiments with six copepod species differing by over three orders of magnitude in body mass showed that three-spined sticklebacks (*Gas-*

terosteus aculeatus) preferentially preyed on ovigerous females of the two smallest-bodied copepod species (*Oithona similis* and *Corycaeus anglicus*). In contrast, sticklebacks showed no significant preference for ovigerous or non-ovigerous females of the remaining, larger-bodied species (*Pseudocalanus newmani*, *P. moultoni*, *Pseudodiaptomus marinus*, and *Paraeuchaeta elongata*).

Although previous studies have shown that carrying egg masses increases the risk of predation by fish (Hirston et al. 1983; Bollens and Frost 1991), there is also evidence that in some situations carrying egg masses does not result in increased predation risk. For instance, the species of predator may influence whether egg masses result in increased predation risk. Winfield and Townsend (1983) showed, experimentally, that an "inefficient" fish predator (roach) had significantly more successful attacks on ovigerous cyclopoids (*Cyclops vicinus*) than on non-ovigerous cyclopoids, whereas an "efficient" predator (bream) showed only a marginal increase in attack efficiency on ovigerous cyclopoids. The experiments of Svensson (1992) showed that zebrafish selectively preyed on ovigerous calanoid copepods (*Eudiaptomus gracilis*), but that roach showed no preference for ovigerous or non-ovigerous copepods. Selection for ovigerous over non-ovigerous individuals has also been shown to depend on the density of copepods offered. Vuorinen et al. (1983) found that sticklebacks selected ovigerous females only at the higher of two experimental densities – no selection was observed at the lower, "natural", density of copepods. Our study suggests that ovigerous females of some species of egg-brooding copepods experience increased predation from a fish predator, whereas females of others do not. Thus, the importance of egg masses in determining female mortality should perhaps not be considered an *a priori* condition when studying life history and migratory strategies of copepods.

Although our experiments showed that sticklebacks did not prey preferentially on ovigerous females of the larger-bodied copepods, this pattern may not always translate to lower predation pressure in the field. Our fish's ability to capture ovigerous females may have been limited by mouth gape (Zaret 1980), particularly when offered the largest-bodied copepod, *Paraeuchaeta elongata*. In addition, the size of the experimental tanks may have artificially reduced the difference between fish predation on ovigerous and non-ovigerous females of *Paraeuchaeta*. The reactive distance, the maximum distance at which prey are detected, of sticklebacks to *Daphnia magna* of different sizes has been measured in the laboratory (Gibson 1980). The mean reactive distance to small *Daphnia* (length 1.4 mm) was 7.6 cm. The tanks used in our experiments were 41 cm long, 25 cm deep and filled to a depth of 20 cm. Thus, the reactive distance of sticklebacks to the small and medium-sized copepods (*Oithona* to *Pseudocalanus*, 0.8 mm to 1.5 mm total length) can be expected to be generally contained within the experimental tanks. In the experiment of Gibson (1980), the mean reactive distance to large *Daphnia*

(length 2.4 mm) was 14.1 cm. Because *Paraeuchaeta elongata* is about 2.5 times larger (in length) than the large *Daphnia*, we multiplied 14.1 cm by 2.5 to estimate the reactive distance of sticklebacks to *Paraeuchaeta*, with the result being a reactive distance of 35 cm. Thus, a portion of a fish's reactive field to the largest copepod used in our experiments would have been outside our experimental tanks. This means that the difference between the stickleback's encounter frequency with ovigerous versus with non-ovigerous *Paraeuchaeta* was very likely lower than the actual difference sticklebacks would experience in situ. Finally, the small number of replicate trials, four to six per copepod species, may not have been adequate to reveal the "natural" patterns.

The results of our experiments did not support the hypothesis that the predation risk associated with egg masses should increase steeply with copepod body size, as predicted by Ohman and Townsend (1998). The results are more consistent with a decrease in conspicuousness associated with carrying eggs, as predicted from the allometric (<1) scaling between brood volume and body size (Mauchline 1988). However, an unexpected pattern emerged regarding predation risk among copepod taxa that suggests additional hypotheses. The paired egg masses of *Oithona similis*, a cyclopoid, are positioned laterally on the urosome. The egg mass of *Corycaeus anglicus*, a poecilostomatoid, is positioned dorsally on the urosome. In contrast, the single egg masses of the four calanoid species for which sticklebacks showed no selective predation are held ventrally, as is the case for all calanoid egg-brooders (Ohman and Townsend 1998). It may be that egg masses in a lateral or dorsal position break up the outline of the copepod body and enhance the apparent size of females more than egg masses held ventrally. Alternatively, lateral or dorsal egg masses may restrict escape ability more than do egg sacs in a ventral position, resulting in higher predation risk for cyclopoid and poecilostomatoid species than for calanoid species. There may also be an interaction between swimming behavior and the effect of egg masses on predation risk. Whereas calanoids swim in a relatively smooth pattern, cyclopoids and poecilostomes move through the water in short bursts (Zaret 1980; Paffenhöfer 1998), a swimming behavior that is likely to make them more conspicuous compared to calanoids (Ibrahim and Huntingford 1989) and could more severely hinder the escape ability of ovigerous females. Previous studies involving detailed observations of the predation sequence offer some support for a difference in escape abilities of cyclopoids versus calanoids. Winfield and Townsend (1983) found that the strike efficiency of fish preying on ovigerous cyclopoids, *Cyclops vicinus*, was 3 times greater than that of fish preying on non-ovigerous cyclopoids. They suggest that this was a consequence of egg sacs impairing the copepod's acceleration and maneuverability. In contrast, Svensson (1992) found that although ovigerous calanoids (*Eudiaptomus gracilis*) had a higher encounter rate with a fish predator, there was no difference in escape success of ovigerous and non-ovigerous females of this species.

While acknowledging the potential role of differences in egg mass position among the copepod orders Calanoida, Cyclopoida and Poecilostomatoida, we would still expect ovigerous females of larger-bodied calanoids such as *Paraeuchaeta elongata* to experience greater predation risk than smaller-bodied calanoids. Although the sticklebacks in our experiments showed no statistically significant preference for ovigerous females of any calanoid species, in the majority of trials involving calanoids (14 out of 21) the proportion of ovigerous females ingested was greater than 0.50 and for each of the four calanoid species the overall proportion of ovigerous females ingested was slightly greater than 0.50. Given this pattern in the data and the potential for predator gape-limitation during our experiments, we suggest that whether body size influences the susceptibility of egg-brooding copepods to predation – and thus explains the brooder's gap – remains an open question.

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