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Egg strings in *Euchirella pseudopulchra* (Aetideidae) and comments on constraints on egg brooding in planktonic marine copepods

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Abstract

Adult female *Euchirella pseudopulchra* Park, 1976 from the California Current System bear a pair of unusual linear ovisacs or ''egg strings.'' Each membrane-bound, single file row of eggs contains 11–14 relatively large ova. Calculations suggest that the geometric arrangement of single file rows of eggs could facilitate oxygen diffusion in O_2-deficient waters. The presence of ventrally carried egg masses in *E. pseudopulchra* and other members of the Calanoida appears to be associated with evolutionary loss of the fifth swimming legs (P5) in the adult female. We hypothesize that loss of the female P5 would improve hydrodynamic thrust during escape responses and reduce the probability of loss of ventrally brooded ova. We re-examine the relationship between egg size and body size for planktonic marine calanoid and cyclopoid copepods from the mesopelagic and epipelagic zones and compare the advantages of brooding versus broadcast-spawning life histories. The size distribution of adult females of 43 egg-brooding copepod species is bimodal, comprising a number of small-bodied species and large-bodied species, with only one intermediate-sized species (between 10–100 µg C). The size distribution of 75 broadcast spawners includes a large number (41) of intermediate-sized species. The interrupted size distribution of the egg-brooding species probably reflects enhanced predation risk to intermediate-sized copepods of carrying attached egg masses in the epipelagic zone. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Copepoda; egg sacs; reproductive investment; oocygen diffusion; body size distributions; predation risk

1. Introduction

Despite growing knowledge of the copepod fauna of meso- and bathypelagic regions of the ocean, many elements of the life history of these species remain incompletely described. Among the most basic of life history parameters are measures of reproductive investment by adult females: egg size, clutch size, mode of reproduction, egg viability, and the rate of release and development of ova. Collection techniques for deeper-dwelling copepods are frequently inappropriate for assessment of these parameters because coarse net meshes result in the loss of free eggs and the long periods of time required to retrieve animals from depth, together with abrasion in nets, often cause females to be damaged and egg masses to be lost.

Recent monographs treating significant numbers of deeper-dwelling species reflect this problem. Spe-

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cific information on egg morphology and reproductive mode is scant or lacking completely in the valuable monographs on the Euchaetidae (Park, 1994), the Arietellidae (Ohtsuka et al., 1994), and the Aetideidae (Markhaseva, 1996). In his work on the genus *Euchirella*, Vaupel Klein (1982) reported that ''Females carrying egg sacs were not met with in the present material but in various specimens remnants of the ruptured membrane were observed, attached to the genital area''. G.O. Sars described and depicted many members of the Aetideidae, but only occasionally observed intact eggs or egg masses. For example Sars (1924-1925) made no comments on egg morphology in *Euchirella pulchra*, closely related to the species reported on here. He reported clusters of many ova from *Euchirella messinensis* but found them attached to only 2 specimens. On some specimens of *E. brevis* he found short ovisacs with 1 or 2 eggs in a row. Sars also depicted a single pair of exceptionally large eggs attached to *Valdiviella insignis*, but found them on only 1 individual.

During the course of other investigations we discovered curious elongate egg masses in a member of the family Aetideidae, *Euchirella pseudopulchra* Park, 1976, collected in the upper 550 m of the California Current System. Here we describe the morphology of these ''egg strings'' and suggest a possible adaptive value of the egg string morphology. We also combine our new observations from *E. pseudopulchra* with information from other sources to explore the relationship between female body size and reproductive investment (as egg size) for a spectrum of epi-, meso- and bathypelagic copepod species. Previous efforts to understand the scaling relationships of reproduction with body size in copepods have been biased toward epipelagic species (Sazhina, 1987; Kiørboe and Sabatini, 1995). A notable exception is the work of Mauchline (1988, 1992), who addressed the deeper dwelling fauna. However, to date, no synthesis of such information has been made combining both the surface and deeper dwelling, free-living copepod fauna. Our analysis uncovered an interrupted size distribution of egg-brooding species that implies a size-dependent predation risk and may constrain the habitat depths occupied by egg brooders. In addition, we hypothesize a causal relationship between the presence of ventrally brooded egg masses and the loss of the female fifth swimming legs in the order Calanoida.

2. Methods

Adult female *Euchirella pseudopulchra* were collected in the San Diego Trough (bottom depth $\sim$ 1200 m) with a 1 m^2, 333 μm mesh MOCNESS net (Wiebe et al., 1985) towed at 0.75 m s^{-1}. Specimen 1 was collected at 32° 50′ N, 117° 39′ W, in a haul between 401–0 m at 1248–1356 local time on 13 June 1992. Specimen 2 was collected at 32° 37′ N, 117° 34′ W, in a haul between 554–0 m at 0100–0221 local time on 22 May 1994. As these hauls were not closing we do not know the depth provenance of the animals collected, but we assume them to be mesopelagic based on related species (e.g., Mauchline, 1988) and collection of one additional egg string. Animals were fixed in 1.8% borate-buffered formaldehyde and eggs and females later measured in this preservative with an ocular micrometer. Entire samples were examined for *E. pseudopulchra*, including several other samples from these cruises, and only these 2 individuals were found. Prosome lengths were 3.28 and 3.32 mm for the 2 specimens, total lengths 3.92 and 4.00 mm. Video micrographs were made with a CCD video camera and video printer. An additional free egg string was collected with a 333 μm mesh vertical closing net (Brown and Honegger, 1978) at 33° 04′ N, 117° 31′ W, in a haul between 400–200 m at 0703–0712 local time on 21 December 1992. This sample was frozen in liquid N$_2$ aboard ship upon collection.

The relationship between egg size and body size of adult females was described in units of organic C, for free-living planktonic marine calanoids and cyclopoids. If sizes were not originally reported in these units, the following conversions were used: female C = 0.45 × dry mass (Båmstedt, 1986), female dry mass = 0.17 × wet mass (Båmstedt, 1986), and egg C (μg) = 1.4 × 10^{-7} × (egg volume, μm^3) (Kiørboe and Sabatini, 1995). Egg sizes and female sizes came from Lee et al. (1971); Fulton (1973); Ikeda (1974); Yen (1983); Kimmerer (1984); Sazhina (1987); Ohman (1987); Bradford et al. (1988); Mauchline (1988); Smith and Lane (1991); Ward and Shreeve (1995); Kiørboe and Sabatini (1995),

and a mean diameter of 460 μm for eggs of *Paraeuchaeta elongata* (M.D.O., unpublished). Sazhina (1987) reported some species of *Clausocalanus* as egg brooders and others as broadcast spawners and although we find this unusual we follow her designations. Guisande and Harris (1995) illustrate that egg size, organic content, and viability can be quite variable within a single copepod species, but the larger-scale interspecific relations reported here will not be significantly altered by such within-species variations.

3. Results

We found elongate, linear, single file rows of eggs (''egg strings'') associated with both adult female *E. pseudopulchra* collected. Specimen 1 (Fig. 1) bore a pair of egg strings, one with 8 visible eggs, the other with 7. The distal region of both egg string membranes had constrictions clearly indicating the prior presence of additional ova. The observed ova combined with these vacated positions totalled 11 or 12 ova per string, for a total inferred clutch size for this female of 22 or 24 eggs. The egg string mem-

brane was remarkably sticky, making it difficult to free a probe used to manipulate the string. Specimen 2 (Fig. 2A) had one empty egg string membrane attached to the ventral side of the genital segment. This membrane had 10 visible constrictions, for an egg number of at least 11. In the plankton sample in which this female was found was also one free egg string (Fig. 2B,C) which we conclude originated from specimen 2. No other adult female of this species, or other likely source, was found in the sample. The free egg string had 6 visible ova interspersed with 6 vacant pouches from which eggs appeared to have hatched. The fourth visible egg was in a state of incomplete development. The total inferred clutch size of this female was 23–24 eggs. The coupler, or attachment site of the egg string to the female genital segment, is visible in Fig. 2C, along with the robust egg string membrane. Specimen 2 bore 60–70 stalked peritrich ciliates (40–50 μm cell diameter, 40–70 μm stalk length) on the prosome, swimming legs, and anal segment of the urosome, but none were attached to the egg strings.

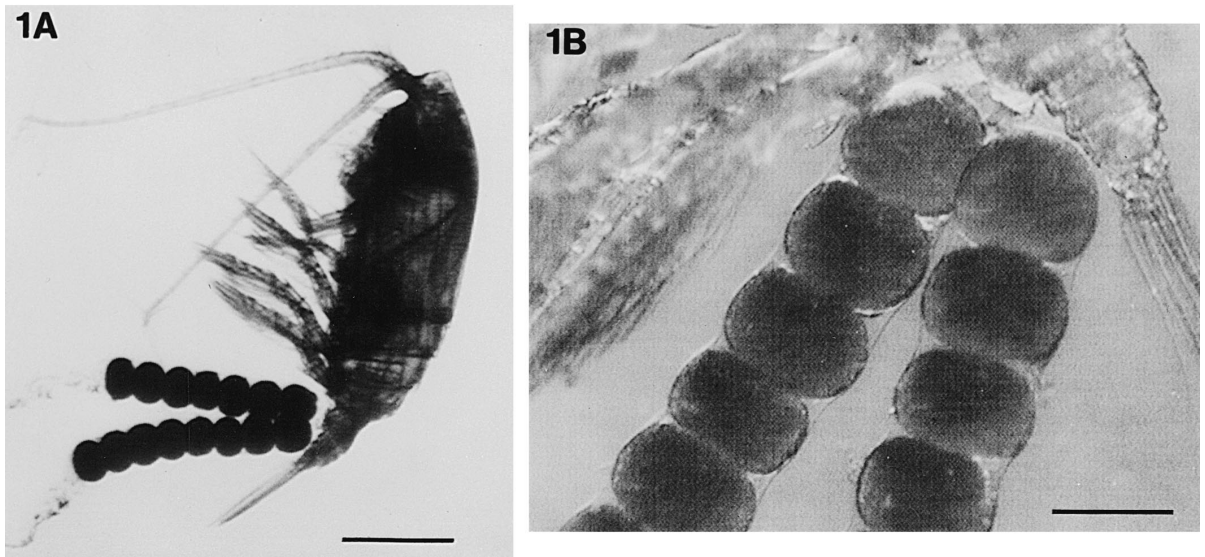A fifth egg string, nearly identical to the preceding, was found in a sample that had been frozen at

Fig. 1. Egg strings from *Euchirella pseudopulchra*, specimen 1. (A) Note distal end of the egg string membrane which previously contained additional ova (scale = 1 mm). (B) Enlargement (scale = 300 μm).
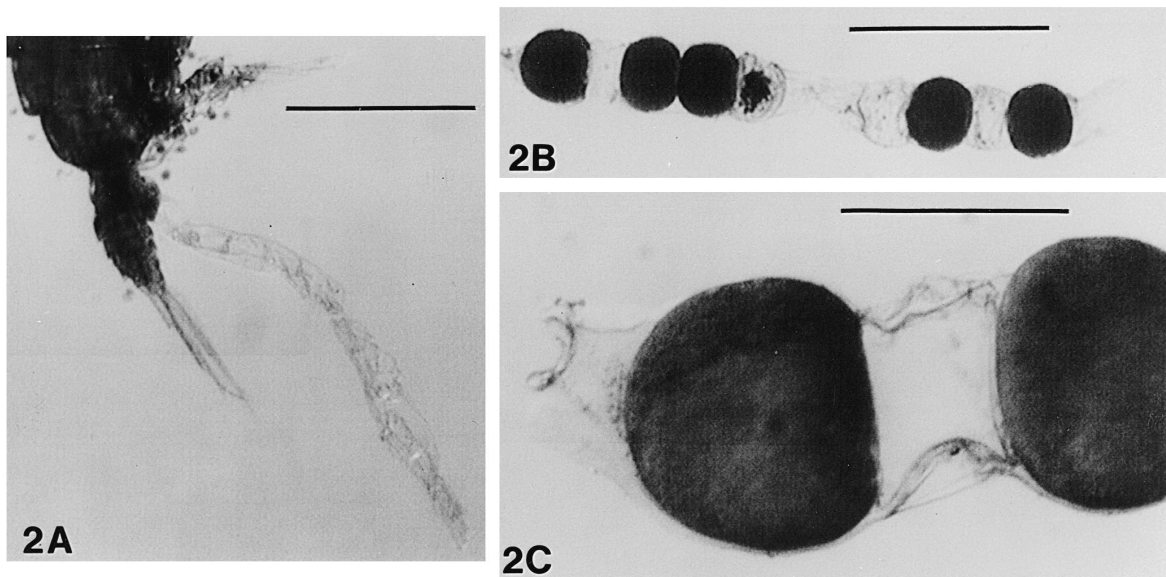
Fig. 2. Egg strings from *Euchirella pseudopulchra*, specimen 2. (A) Egg string membrane, from which eggs have hatched. Note constrictions delineating previous boundaries between individual ova. Prosome, swimming legs, and urosome bear stalked peritrich ciliates (scale = 1 mm). (B) Detached egg string, showing 6 ova and vacant positions from which eggs have hatched. Fourth egg from left in state of incomplete development (scale = 1 mm). (C) Enlargement of detached egg string illustrating coupler to female genital segment at left and vacant position between eggs 1 and 3, from which egg has hatched (scale = 300 μm).

sea. This egg string had the same shape, robust outer membrane enclosing all eggs, distinctive coupler illustrated in Fig. 2C, and same egg dimensions ($P > 0.10$) as the eggs previously described. When freshly thawed these eggs had a light brown-purplish hue. 12 eggs and 2 vacant egg pouches were visible in this string, for an inferred egg number of 14. Each ovum had at least 16 visible blastomeres. No second egg string, or adult female *Euchirella*, was found in this sample, which was a non-quantitative sample collected for other purposes. However, based on the highly distinctive morphology we believe that it originated from this genus.

Eggs within strings were somewhat compressed, with a diameter of 364 ± 4 μm (mean ± 95%; $N = 30$, range 332–384 μm) and height of 281 ± 14 μm (range 212–370 μm). When extruded from the egg string membrane the eggs round up to a nearly spherical shape. Based on egg geometry, the calculated biovolume was $26.0 \pm 1.5 \times 10^6$ μm^3 and estimated C content was 3.65 μg C. From linear measurements of adult females and conversion from biovolume to C ($C = 0.0765 \times$ wet mass; see Section 2), the estimated C content of adult female *E. pseudopulchra* was approximately 220 μg C.

The relation between egg size and adult female size is illustrated in Fig. 3A for *E. pseudopulchra* and 42 other species of egg-carrying calanoid and cyclopoid copepods (''brooders'') ranging in size from *Oithona davisae* (0.23 μg C) to *Valdiviella insignis* (3476 μg C). This relation is essentially isometric, with a mass exponent of 0.967 (Table 1). Nearly all the variance in egg size was accounted for by variability in female body size ($r^2 = 0.962$, $P < 0.001$). *E. pseudopulchra* eggs, although large in absolute dimensions, are just as would be predicted for the relatively large body size of the females. All of the species smaller than 10 μg C (species of *Oithona, Dioithona, Eurytemora, Pseudocalanus, Clausocalanus*, and *Pseudodiaptomus*) are epipelagic, while those larger than 100 μg C (species of *Euchaeta, Paraeuchaeta, Euchirella, Pseudochirella, Gaidius, Euaugaptilus, Valdiviella*) are either meso- or bathypelagic in habitat, or show diel
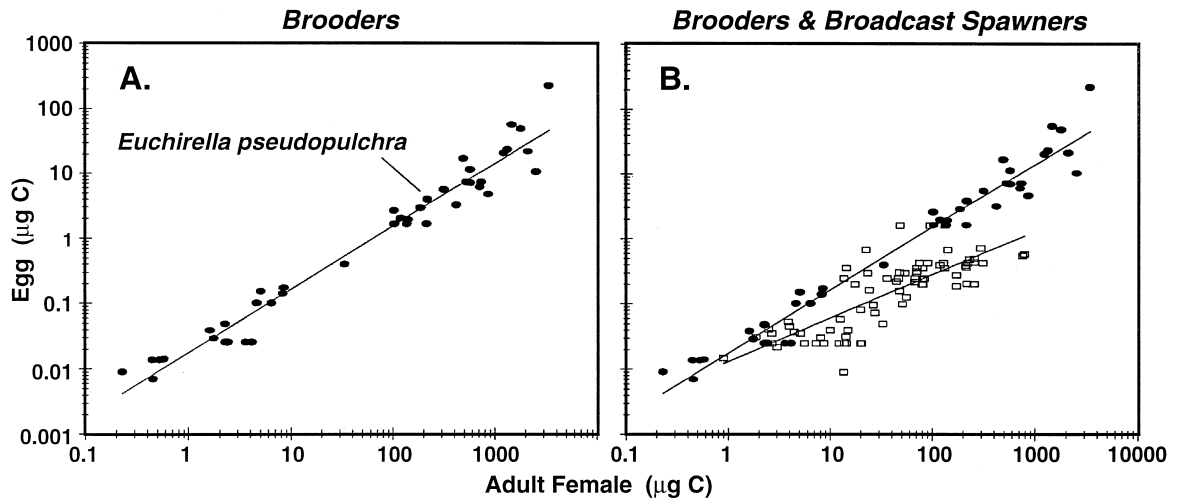
Fig. 3. Relationship between egg size and adult female body size, for marine calanoid and cyclopoid copepods. (A) Egg-brooding species ($N = 43$ species) and (B) egg-brooding ($\cdot$) and broadcast-spawning ($\square$, $N = 75$). Lines illustrate Model I regressions (see Table 1).

vertical migrations below the surface layer. Epipelagic and deeper-dwelling animals are equally well described by a common regression relation.

The relation between egg size and adult female size of egg-brooding species is compared with that of species that release their eggs freely into the water column ("broadcast spawners") in Fig. 3B. The egg sizes of broadcast spawners, members of the Calanoida ranging in size from *Acrocalanus inermis* (0.90 μg C) to *Rhincalanus gigas* (800 μg C) also show a strong relationship with female size, but with a significantly lower ($P < 0.0001$, ANCOVA) mass exponent (0.666, Table 1) reflecting allometric scal-

ing and considerably more scatter in the relationship ($r^2 = 0.629$, $P < 0.001$).

Although there is broad overlap in the range of sizes of brooding and broadcast-spawning species, the size distributions of adult females are distinctly different (Fig. 4; $P < 0.01$, Kolmogorov–Smirnof

Table 1
Regression relationships between egg size (Y, Log_{10}(μg egg C)) and adult female body size (X, Log_{10}(μg female C)), for egg-brooding and broadcast-spawning species of marine calanoid and cyclopoid copepods

	Slope ± 95%	Intercept ± 95%	r^2	P value
Egg brooders ($N = 43$ spp.)				
Model I	0.967 ± 0.061	−1.756 ± 0.127	0.962	< 0.001
Model II	0.986 ± 0.061	−1.788		
Broadcast spawners ($N = 75$ spp.)				
Model I	0.666 ± 0.119	−1.884 ± 0.202	0.629	< 0.001
Model II	0.839 ± 0.119	−2.156		

The fits of both Model I and Model II regressions (Sokal and Rohlf, 1995) are reported.
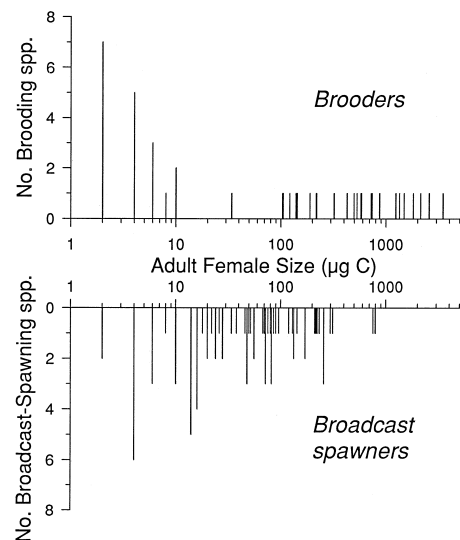

Fig. 4. Size frequency distributions of adult female calanoid and cyclopoid copepods, for egg-brooding and broadcast-spawning species. Body sizes grouped into 2 μg C increments.

test). Egg brooding species are bimodal, with a cluster of smaller taxa and a cluster of larger taxa, and only a single brooding species in the range of 10–100 μg C (*Euchaeta indica*). In contrast, broadcast-spawning species do not attain the extreme sizes of the brooders and there is a cluster of mid-sized females: 41 broadcast-spawning species occur in the range of 10–100 μg C.

4. Discussion

The egg strings of *Euchirella pseudopulchra* differ appreciably from the morphology of agglomerated, multi-layered egg clusters more typically found in egg-brooding marine planktonic calanoid and cyclopoid copepods. The present arrangement of eggs in elongate, single file rows of eggs does not appear to be reported for other free-living calanoids, although it has been observed in some Siphonostomatoid and poecilostomatoid copepods (e.g., Jones, 1985; Huys and Boxshall, 1991). Sars (1918) illustrates ovisacs of several cyclopoid species that appear to be egg strings. The arrangement of 1–2 eggs of *Euchirella brevis* in a row reported by Sars (1924-1925) bears a resemblance to the geometric arrangement observed here and suggests the possibility that in nature *E. brevis* may also have elongate egg strings with appreciably larger clutch sizes than previously reported (Sars, 1924-1925; Mauchline, 1988).

In their diagnosis of the order, Huys and Boxshall (1991) stated that ''It is possible that true egg sacs do not occur within the Calanoida''. Although some species brood eggs without enclosing them within an external membrane, the present results with *E. pseudopulchra* clearly indicate that at least some calanoid species encase eggs within a membranous sac. Membrane bound sacs have also been observed in various other species.

One advantage of the linear geometric arrangement of eggs within egg strings is that most of the surface of each egg is close to the sac membrane and thus to the external environment for gas exchange. If these large eggs were instead arranged within a dense, multi-layered egg cluster, those eggs at the interior of the cluster might experience diminished oxygen concentrations as a consequence of limited oxygen diffusion into the center. Diffusion-limitation of oxygen has been suggested as a selective agent influencing egg mass morphology in benthic invertebrates (Strathmann and Strathmann, 1995).

How thick would a copepod egg mass have to be for the interior to become oxygen deficient? For a spherical egg mass with oxygen transport by molecular diffusion, the time rate of change of oxygen concentration can be described by the rate of radial diffusion minus the respiration rate of the egg mass (see Rubinow, 1975; Fenchel, 1987). If the oxygen concentration within the egg mass is at equilibrium, the respiration rate = the diffusion rate, so:

$$M = \frac{k}{r^2} \frac{\partial}{\partial r}\left(r^2 \frac{\partial \theta}{\partial r}\right) \tag{1}$$

where M is the respiration rate of the egg mass, k the molecular diffusion coefficient for oxygen, r the radius of the egg mass, and θ the oxygen concentration. Eq. (1) can be integrated and solved for the limiting diameter (D') of an egg mass at which the interior oxygen concentration would go to zero (Fenchel, 1987):

$$D' = \sqrt{\frac{24 k \theta_0}{M}} \tag{2}$$

where θ_0 is the ambient (external) oxygen concentration. The volume-specific rate of oxygen uptake by *E. pseudopulchra* eggs can be approximated as $M = 3.5 \times 10^{-5}$ nl O_2 (nl egg volume)$^{-1}$ s^{-1} (from Banse, 1982, regression for unicellular organisms corrected to 8°C using a Q_{10} of 2.0) and the oxygen diffusion coefficient, $k = 2 \times 10^{-5}$ cm^{-2} s^{-1} (Cohen and Strathmann, 1996). For copepods living in oxygenated ocean waters where the ambient dissolved oxygen concentration $\theta_0 = 6$ ml O_2 L^{-1}, the solution of Eq. (2) for the limiting diameter D' is 2.86 mm. While ~ 3 mm may roughly approximate the maximum diameter of egg masses of free-living planktonic copepods, it greatly exceeds the diameter of *E. pseudopulchra* eggs. However, if *E. pseudopulchra* occupied the depths of the oceanic oxygen minimum zone in the NE Pacific where the ambient oxygen concentration $\theta_0 = 0.2$ ml L^{-1}, then D' reduces to 0.52 mm. In such low oxygen conditions, no more than one egg of diameter 0.37 mm could be accommodated before the egg mass interior would

become oxygen deficient. While we do not know that *E. pseudopulchra* evolved in the oceanic oxygen minimum layer, we consider diffusion-limitation to be a plausible constraint on the geometry of this and other copepod egg sacs.

We also observed a general association between the presence of ventrally brooded egg masses and the absence of the fifth swimming legs (P5) in adult female marine calanoids (Table 2). For example, the egg-brooding species of *Euchirella, Pseudochirella, Pseudocalanus, Gaidius, Euchaeta, Paraeuchaeta*, and *Valdiviella* all lack P5s. This pattern holds for 28 of 35 (80.0%) species of egg-brooding calanoid species from Fig. 3A (the 8 cyclopoid species are discussed below). The 7 calanoid exceptions are species of *Clausocalanus, Pseudodiaptomus, Eurytemora*, and *Euaugaptilus*. Although *Clausocalanus* females bear a P5 it is quite reduced in size. *Pseudodiaptomus* females have been observed to press the P5 against the egg mass to facilitate extrusion of nauplii (S.-U. Uye, personal communication), perhaps an aid that is particularly necessary for this genus for reasons unknown. In contrast to egg brooders, only 7 of 75 (9.3%) species of broadcast-spawning marine species from Fig. 3B lack the P5, all of them members of *Eucalanus* sensu lato. *Eucalanus* females have a foreshortened urosome, whose flexure could interfere with the motion of elongate P5s. The differences between brooding/broadcasting marine calanoids in absence/presence of P5 are highly significant ($P < 0.0001$). We appreciate that each of these species should not be treated as independent evolutionary events, but a more sophisticated statistical analysis will await a robust phylogeny of copepod genera.

Since all egg-brooding calanoids carry their eggs ventrally, attached to the genital segment, loss of P5s

would be of considerable benefit. In rapid contractions of the swimming legs during escape responses, contact of elongate P5s with egg masses could result in ineffective power strokes, hence shorter escape distances and increased probability of capture by planktivores. P5 contact could also cause loss of the eggs. Although other constraints may also operate on the evolution of P5 morphology (Vaupel Klein, personal communication), especially since many species that bear P5s have them only as reduced or vestigial structures, we suggest that there would be strong selection for complete loss of the fifth swimming legs in egg brooding Calanoida so as to maximize hydrodynamic thrust and minimize loss of brooded eggs.

Several freshwater calanoids, most notably the diaptomids, do not conform with the pattern of P5 loss among egg brooding taxa. However, a striking feature of the life histories of most freshwater zooplankton taxa, copepods and otherwise, is the preponderance of egg brooding (or production of resting eggs) and paucity of broadcast spawning. This pattern includes not only most freshwater calanoids and all cyclopoids, but also rotifers, cladocerans, anostracans, and mysids (confirmed by N.G. Hairston, Jr.). Apparently, selection for egg brooding in freshwater supersedes the constraints on brooder morphology seen in marine taxa. We infer that the overriding factor in freshwaters is the need to avoid sinking of subitaneous eggs to the benthos in shallow waters of density close to 1.0 g cm^{-3}. This constraint may also explain why the estuarine genus *Eurytemora* departs from the rule of P5 loss for calanoid brooders.

Members of the two other major orders of pelagic marine copepods (Cyclopoida and Poecilostomatoida) carry attached eggs, while females bear (uniramous) P5s. But unlike the calanoids, which brood eggs in a ventral position, in cyclopoids and poecilostomes the gonopores (and thus the egg sacs) are in a lateral or dorsal position on the genital segment (Huys and Boxshall, 1991). Thus the propulsive strokes of the swimming legs would not interfere with their brooded eggs.

In previous analyses of the scaling of egg size with body size in planktonic marine copepods, Mauchline (1988) and Kiørboe and Sabatini (1995) both obtained an exponent close to 1 for brooding species, but these studies emphasized deeper-dwell-

Table 2
Association between ventral egg brooding and the loss of the 5th swimming legs (P5) in planktonic marine calanoid copepods

	Egg-brooding species ($N = 35$ spp.) (%)	Broadcast-spawning species ($N = 75$ spp.) (%)
P5 absent	80	9
P5 present	20	91

The hypothesis of no relationship is rejected ($\chi^2 = 54.93$, $P < 0.0001$).

ing and epipelagic species, respectively, and in both studies many fewer species and a smaller range of body sizes were available. Here we establish with a much larger combined data set that egg sizes of epi-, meso-, and bathypelagic egg brooders all scale in a common manner. Kiørboe and Sabatini (1994) fitted a common regression line to both brooding and broadcast-spawning copepods, then later corrected this to differentiate the two groups (Kiørboe and Sabatini, 1995). Our analysis of broadcast spawners yields an exponent similar to theirs, confirming a scaling with (female mass)$^{0.67}$ or the familiar surface-area related scaling of metabolic processes. The difference between brooders and broadcast spawners in scaling of egg size with body size is well accounted for by the argument of Kiørboe and Sabatini (1995). The more rapid development time of freely broadcast eggs (Sazhina, 1987; Kiørboe and Sabatini, 1994) compensates for their greatly increased mortality rates in comparison with brooded eggs (Kiørboe and Sabatini, 1994; Ohman and Wood, 1996). Because broadcast-spawning females must produce many more individual eggs to compensate for this higher mortality rate per egg, and egg size is inversely related to clutch size (Poulin, 1995), their eggs are smaller in size than those from brooders with similar body sizes.

The occurrence of 41 species of broadcast-spawning copepod species in the size range of 10–100 μg C where only one egg-brooding species occurs suggests a key difference in predation risk between the two types of spawners. Because the presence of egg sacs makes copepods more conspicuous to visually feeding predators (Vuorinen et al., 1983; Bollens and Frost, 1991), virtually none of these mid-sized copepods (some species of _Temora, Centropages, Tortanus, Calanus, Undinula, Calanoides, Pleuromamma, Pontella, Labidocera, Candacia_, and several others) adopts the brooding life history. To be of intermediate body size, the females are constrained to broadcast their eggs. The very small-bodied epipelagic species can carry eggs because the increase in predation risk due to the presence of egg masses will be proportionately less than that for the mid-sized animals. The largest-bodied egg brooding species cannot permanently occupy the epipelagic zone, but survive by dwelling deeper in the water column on a continuous basis or perform diel verti-

cal migrations to reduce predation risk. A specific and testable prediction follows from the interrupted size distribution of egg brooders: the predation risk associated with carrying eggs should increase steeply with the body size of planktonic copepods.

References

Båmstedt, U., 1986. Chemical composition and energy content. In: Corner, E.D.S., O'Hara, S.C.M. (Eds.), The Biological Chemistry of Marine Copepods. Oxford Univ. Press, Oxford, pp. 1–58.

Banse, K., 1982. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. Mar. Ecol. Prog. Ser. 9, 281–297.

Bollens, S.M., Frost, B.W., 1991. Ovigerity, selective predation, and variable diel vertical migration in _Euchaeta elongata_ (Copepoda: Calanoida). Oecologia 87, 155–161.

Bradford, J.M., Ohman, M.D., Jillett, J.B., 1988. Larval morphology and development of _Neocalanus tonsus, Calanoides macrocarinatus_, and _Calanus australis_ (Copepoda: Calanoida) in the laboratory. N.Z. J. Mar. Freshwat. Res. 22, 301–320.

Brown, D.M., Honegger, H.-W., 1978. Design of a rapid-sampling vertical-tow net. Mar. Biol. 45, 93–95.

Cohen, C.S., Strathmann, R.R., 1996. Embryos at the edge of tolerance: effects of environment and structure of egg masses on supply of oxygen to embryos. Biol. Bull. 190, 8–15.

Fenchel, T., 1987. Ecology of Protozoa. The Biology of Free-living Phagotrophic Protists. Springer, New York, pp. 1–197.

Fulton, J., 1973. Some aspects of the life history of _Calanus plumchrus_ in the Strait of Georgia. J. Fish. Res. Bd. Can. 30, 811–815.

Guisande, C., Harris, R., 1995. Effect of total organic content of eggs on hatching success and naupliar survival in the copepod _Calanus helgolandicus_. Limnol. Oceanogr. 40, 476–482.

Huys, R., Boxshall, G.A. 1991. Copepod Evolution. The Ray Society, No. 159, London. pp. 1-468.

Ikeda, T., 1974. Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22, 1–97.

Jones, J.B., 1985. A revision of *Hatschekia* Poche, 1902 (Copepoda: Hatschekiidae) parasitic on marine fishes. N. Z. J. Zool. 12, 213–271.

Kimmerer, W.J., 1984. Spatial and temporal variability in egg production rates of the calanoid copepod *Acrocalanus inermis*. Mar. Biol. 78, 165–169.

Kiørboe, T., Sabatini, M. 1994. Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods. J. Plankton Res. 16: 1353-1366.

Kiørboe, T., Sabatini, M. 1995. Scaling of fecundity, growth and development in marine planktonic copepods. Mar. Ecol. Progr. Ser. 120: 285–298.

Lee, R.F., Hirota, J., Barnett, A.M., 1971. Distribution and importance of wax esters in marine copepods and other zooplankton. Deep Sea Res. 18, 1147–1165.

Markhaseva, E.L. 1996. Calanoid copepods of the family Aetideidae of the world ocean. Trudy Zoologicheskogo Instituta RAN Vol. 268, St. Petersburg. pp. 1-331.

Mauchline, J., 1988. Egg and brood sizes of oceanic pelagic crustaceans. Mar. Ecol. Prog. Ser. 43, 251–258.

Mauchline, J., 1992. Restriction of body size spectra within species of deep-sea plankton. Mar. Ecol. Prog. Ser. 90, 1–8.

Ohman, M.D., 1987. Energy sources for recruitment of the subantarctic copepod *Neocalanus tonsus*. Limnol. Oceangr. 32, 1317–1330.

Ohman, M.D., Wood, S.N., 1996. Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. Limnol. Oceanogr. 41, 126–135.

Ohtsuka, S., Boxshall, G.A., Roe, H.S.J., 1994. Phylogenetic relationships between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera. Bull. nat. Hist. Mus. Lond. (Zool.) 60, 105–172.

Park, T., 1976. A new species of *Euchirella* (Copepoda, Calanoida) from the Pacific coast of North America, with notes on *Euchirella pulchra* (Lubbock). Crustaceana 31, 208–212.

Park, T., 1994. Taxonomy and distribution of the marine calanoid copepod family Euchaetidae. Bull. Scripps Inst. Oceanogr. 29, 1–203.

Poulin, R., 1995. Clutch size and egg size in free-living and parasitic copepods: A comparative analysis. Evolution 49, 325–336.

Rubinow, S.I. 1975. Introduction to mathematical biology. Wiley, N.Y. pp. 1-386.

Sars, G.O. 1918. An account of the Crustacea of Norway. Vol. VI. Copepoda Cyclopoida. Bergen Museum, Bergen. pp. 1-225.

Sars, G.O. 1924-1925. Copépodes particulièrement bathypélagiques provenant des campagnes scientifiques du Prince Albert Ier de Monaco. Res. Camp. Sci. Monaco 69: atlas (1924) pls. 1–127, text (1925) pp. 1–408.

Sazhina, L.I. 1987. Reproduction, growth and production of marine Copepoda. Institute of Biology of the Southern Seas, Ukrainian Academy of Sciences, Kiev. pp. 1–155 (in Russian).

Smith, S.L., Lane, P.V.Z., 1991. The jet off Point Arena, California: Its role in aspects of secondary production in the copepod *Eucalanus californicus* Johnson. J. Geophys. Res. 96, 14849–14858.

Sokal, R.R., Rohlf, F.J. 1995. Biometry. 3rd edn. Freeman, W.H., N.Y. pp. 1–887.

Strathmann, R.R., Strathmann, M.F., 1995. Oxygen supply and limits on aggregation of embryos. J. Mar. Biol. Assoc. U.K. 75, 413–428.

Vaupel Klein, J.C.v., 1982. A taxonomic review of the genus *Euchirella* Giesbrecht, 1888 (Copepoda, Calanoida). II. The type species, *Euchirella messinensis* (Claus, 1863). A. The female of f. typica. Zoologische verhandelingen 198, 1–131.

Vuorinen, I., Rajasilta, M., Salo, J., 1983. Selective predation and habitat shift in a copepod species —support for the predation hypothesis. Oecologia 59, 62–64.

Ward, P., Shreeve, R.S., 1995. Egg production in three species of antarctic calanoid copepods during an austral summer. Deep Sea Res. 42, 721–735.

Wiebe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, J.E., Barber, V., Cowles, T.J., Flierl, G.R., 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Mar. Biol. 87, 313–323.

Yen, J., 1983. Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. Mar. Biol. 75, 69–77.