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Egg size and composition in *Ceratoserolis* (Crustacea: Isopoda) from the Weddell Sea*

Andrew Clarke and Deborah J. Gore

British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, UK

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Summary. Samples of ovigerous female *Ceratoserolis trilobitoides* carrying newly spawned (stage A1) eggs in the marsupium were obtained from Borge Bay, Signy Island (South Orkney Islands), the continental shelf near Elephant Island (South Shetland Islands), and two sites in the inner Weddell Sea. The dry mass of a newly spawned egg was greater at the inner Weddell Sea sites even when the larger size of the females from the Weddell Sea and the positive relationship between egg size and female size were taken into account. Larger eggs contained more yolk, and there was a slight but significant tendency for larger eggs to have a lower percentage nitrogen content. Eggs from *Ceratoserolis meridionalis* were smaller in size than sympatric *Ceratoserolis trilobitoides*, but of similar composition. The reason for a greater investment per egg by females at higher latitudes is not clear, but it may be related to a slightly longer development period, itself associated with the lower water temperatures in the inner Weddell Sea.

Introduction

A tendency for cold water marine invertebrates to avoid pelagic feeding larval stages was first noted by 19th century naturalists, particularly those working in Scandinavian waters. These early observations were summarised and extended significantly through detailed studies of reproduction in southerly cold temperate species by scientists of the *Challenger* expedition (Thomson 1878; Murray 1985). Most early attention had been directed at echinoderms; however 50 years later the Danish biologist Gunnar Thorson, working with a large collections of benthic Marine invertebrates collected during a 24 month study at Franz Josef Fjord, East Greenland, proposed that high latitude species from many groups reproduced mainly through benthic embryonic development, thereby avoiding pelagic feeding stages (Thorson 1936). This argument was later developed (Thorson 1950) and then extended by Mileikovsky (1971), who named the tendency to avoid pelagic larval stages at high latitudes *Thorson's Rule.*

More recent work, particularly on echinoderms, at McMurdo Sound has shown that pelagic larvae are produced by many Antarctic species, although a high proportion of these are lecithotrophic (and hence non-feeding) larvae (McClintock and Pearse 1986; Bosch and Pearse 1990). It is clear that Thorson's Rule, at least in its simplistic form, is in need of revision (for a recent full discussion of this see Pearse et al. 1991).

Egg size and larval development type are correlated: production of a large non-feeding larva or development directly to a small adult generally requires more reserves and hence a larger egg, whereas pelagic feeding (planktotrophic) larvae often hatch from a small egg (for a detailed review of these correlations in opisthobranchs see Hadfield and Miller 1987). The general trend from small planktotrophic larvae at lower latitudes to either direct development or larger, non-feeding larvae at higher latitudes would thus suggest a latitudinal cline in egg size with larger eggs at higher latitudes. A latitudinal cline in egg size is now well established (Thorson 1936, 1950; Mileikovsky 1971; Clarke 1979). However most studies to date have concerned a comparison of different species with a given taxonomic group (genus, family or order). More recently attention has been directed at clinal variation in egg size *within* species, and this is now well documented in caridean shrimps (*Pandalus borealis*: Clarke et al. 1991; *Chorismus antarcticus* and *Notocrangon antarcticus*: Clarke 1979; Gorny et al. 1992) and the barnacle *Balanus balanoides* (Patel and Crisp 1960).

Wägele (1987) has shown that the mean size of eggs in the isopod *Ceratoserolis trilobitoides* increases from 2.97 mm at King George Island and the South Orkney Islands, to 3.09 mm at Camp Bay and 3.55 mm at Gould Bay in the Weddell Sea. These measurements were the longest axis of formalin-preserved eggs sampled from early in embryonic development (stages A1–B1). Egg size is of considerable evolutionary and ecological importance, for

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Offprint requests to: A. Clarke

it is a measure of the investment by the female parent in each individual offspring. In this context it is particularly important to establish that an increase in egg volume represents a real increase in investment of resources per egg (as against, for example, simply differences in the degree of egg swelling after spawning). Note that the changes in female investment per egg (that is, egg size) are independent of overall investment by the female (reproductive output: Clarke 1987).

Studies of echinoderms have shown that when comparing species with different mean egg sizes, larger eggs contain more yolk (Turner and Lawrence 1979; Lawrence et al. 1984). Comparison within species have revealed no significant correlation in species with small eggs (McEdward and Carson 1987) but a strong correlation in species with larger eggs (McEdward and Chia 1991). In the Arctic deep-water prawn *Pandalus borealis*, the larger eggs produced by females at higher latitudes have been shown to contain more yolk (Clarke et al. 1991).

During Leg 3 of the European *Polarstern* Study (EPOS), samples of female *Ceratoserolis trilobitoides* carrying recently spawned eggs were collected from several sites. These were taken as part of a much larger study of egg size and composition in caridean shrimps but the opportunity was taken to see whether the latitudinal variations in egg size reported by Wägele (1987) reflected changes in investment per egg.

Taxonomic note

Wägele (1986) has shown clearly that, as first suggested by Hodgson (1910), the species previously described as *Serolis cornuta* and *Serolis trilobitoides* are synonymous, forming a polymorphic species widely distributed in the Southern Ocean. Wägele (1986) also followed Cals (1977) in placing this species in a new genus, *Ceratoserolis*, containing three species: *meridionalis*, *pasternaki* and *trilobitoides*. This revised taxonomy has yet to become established in the literature. However in a recent study Brandt (1988) proposed dividing the previously monogeneric family Serolidae into eight genera, although accepting that many current descriptions are inadequate and a full taxonomic or phylogenetic analysis of this group will require considerable further work. The species examined in this study are thus *Ceratoserolis trilobitoides* (Eights 1883) (synonyms *Serolis trilobitoides*, *Serolis cornuta*) and *Ceratoserolis meridionalis* (Bruce 1908) (synonym *Serolis meridionalis*).

Material and methods

Ovigerous female *Ceratoserolis trilobitoides* were collected by bottom trawl or Agassiz trawl during Leg 3 of EPOS (expedition Antarktis VII/4 of *RV Polarstern*) at the following stations (all in 1989):

Stn 212	15 Jan	60°50′S 55°39′W	400 m	Elephant Island
Stn 241	1 Feb	75°03′S 28°00′W	450 m	Halley Shelf
Stn 273	13 Feb	73°35′S 21°04′W	200 m	Westkapp

A further sample was collected on 19 Dec. 1990 by beam trawl from 100 m depth in Borge Bay, Signy Island, South Orkney Islands (60°41′S, 45°34′W), and taken to the British Antarctic Survey Research Station for examination. Data from three ovigerous female *Ceratoserolis meridionalis* taken at Station 261 (in 800 m depth on the Halley Slope at 74°36′S, 29°41′W) during EPOS are also included for comparison.

Eggs were removed gently from the marsupium, placed immediately in cold seawater, examined under a stereomicroscope to determine stage of development and photographed alongside a stainless steel sphere (ball bearing) of precisely known size for scale. The long and short axes of each egg were later measured by image analysis (IMS Video System III) and the volume calculated assuming the eggs to be ellipsoid. Known numbers of eggs were carefully drained of excess seawater and dried at 60°C for 24 h. The dried eggs were weighed, and carefully homogenised. Subfractions of the dry material were then used to determine ash content (following ignition at 500°C for 12 h) and elemental (C, H, N) composition. For CHN composition triplicate samples were analysed in a Carlo Erba 1106 elemental analyser using acetanilide as standard. All chemical analyses were restricted to newly spawned, undifferentiated eggs (stage A1: Wägele 1987).

For the females serolids, the width of the 4th pereonal segment (maximum width) was measured to the nearest 0.1 mm with digital calipers and then dry mass, ash content and CHN composition were determined as for the eggs.

Results

Fecundity

At only two sites, Borge Bay (Signy Island) and Elephant Island, were sufficient females collected to examine the relationship between fecundity and female size. These relationships were

$$\text{Fec} = (7.82 \pm 2.25)\,\text{W} - 270.2 \quad (n = 14,\ \text{F} = 12.08), \text{ and}$$
$$\text{Fec} = (6.81 \pm 2.33)\,\text{W} - 199.1 \quad (n = 10,\ \text{F} = 8.52)$$

at Borge Bay and Elephant Island respectively (where Fec is the number of eggs being brooded and W the width of the female in mm). Both relationships were significant ($P < 0.05$). The slopes of these relationships do not differ ($F = 0.10$, $P > 0.05$) whereas the elevations do differ significantly ($F = 8.89$, $P < 0.01$) with females from Elephant Island tending to produce more eggs than similarly sized females from Borge Bay, although the raw data overlap (Fig. 1). The relationship for 14 females sampled from Borge Bay in 1990 also differs in elevation ($F = 10.8$, $P > 0.001$) but is similar in slope $F = 0.10$, $P > 0.05$) to that obtained for 90 females sampled from Borge Bay in 1978/1979 by Luxmoore (1982). Fecundity is usually a linear function of female mass (and hence a roughly cubic function of length or width) but the variability and the unusual flattened shape of serolids mean that fitting a logarithmic relationship does not improve the fit.

Egg size/mass relationships

As reported by Wägele (1987) there was considerable variation in egg size between females. The relationship between egg dry mass and egg volume was strongly linear