Costs of brood maintenance and development in the seastar *Neosmilaster georgianus* from Anvers Island, Antarctica

MARC SLATTERY, *Department of Biology, University of Alabama, Birmingham, Alabama 35294*
ISIDRO BOSCH, *Department of Biology, State University of New York, Geneseo, New York 14454*

Parental investment of marine invertebrates that protect their offspring through development to a juvenile stage (that is, brooders) includes both direct and indirect energetic costs. Direct costs, for instance, might include the energy initially allocated to eggs as provisional reserves for development (Turner and Dearborn 1979) or to produce larger juveniles (Lawrence, McClintock, and Guille 1984). Indirect energy costs might include a reduced capacity to feed while holding a brood or even starvation in cases where females carry broods in their oral cavities and are prevented from feeding (Emlet, McEdward, and Strathmann 1987).

The total energy costs associated with brood protection will be related to the duration of the brooding period. Slow developmental rates and prolonged periods of brood protection are well-known characteristics of antarctic invertebrates (Pearse, McClintock, and Bosch 1991). Therefore, a relatively high cost of reproduction might be expected in this fauna. The purpose of this study was to examine the costs of brooding and brood development in the seastar, *Neosmilaster georgianus*. These large (having a radius of 51.4 centimeters) forcipulate asteroids are widespread in shallow subtidal communities of the Antarctic Peninsula (Dearborn and Fell 1974). *Neosmilaster georgianus* exhibits reproductive asynchrony within populations, an unusual pseudocopulatory spawning behavior, and extended periods of brood protection during which the female is unable to feed (Slattery and Bosch in press).

Collections of *Neosmilaster georgianus* were made, during the 1991 field season at Palmer Station, from depths of 2–15 meters (m). Wet and dry weights of the whole body, body wall, pyloric caeca, and gonads of 31 female and 5 male seastars were measured.
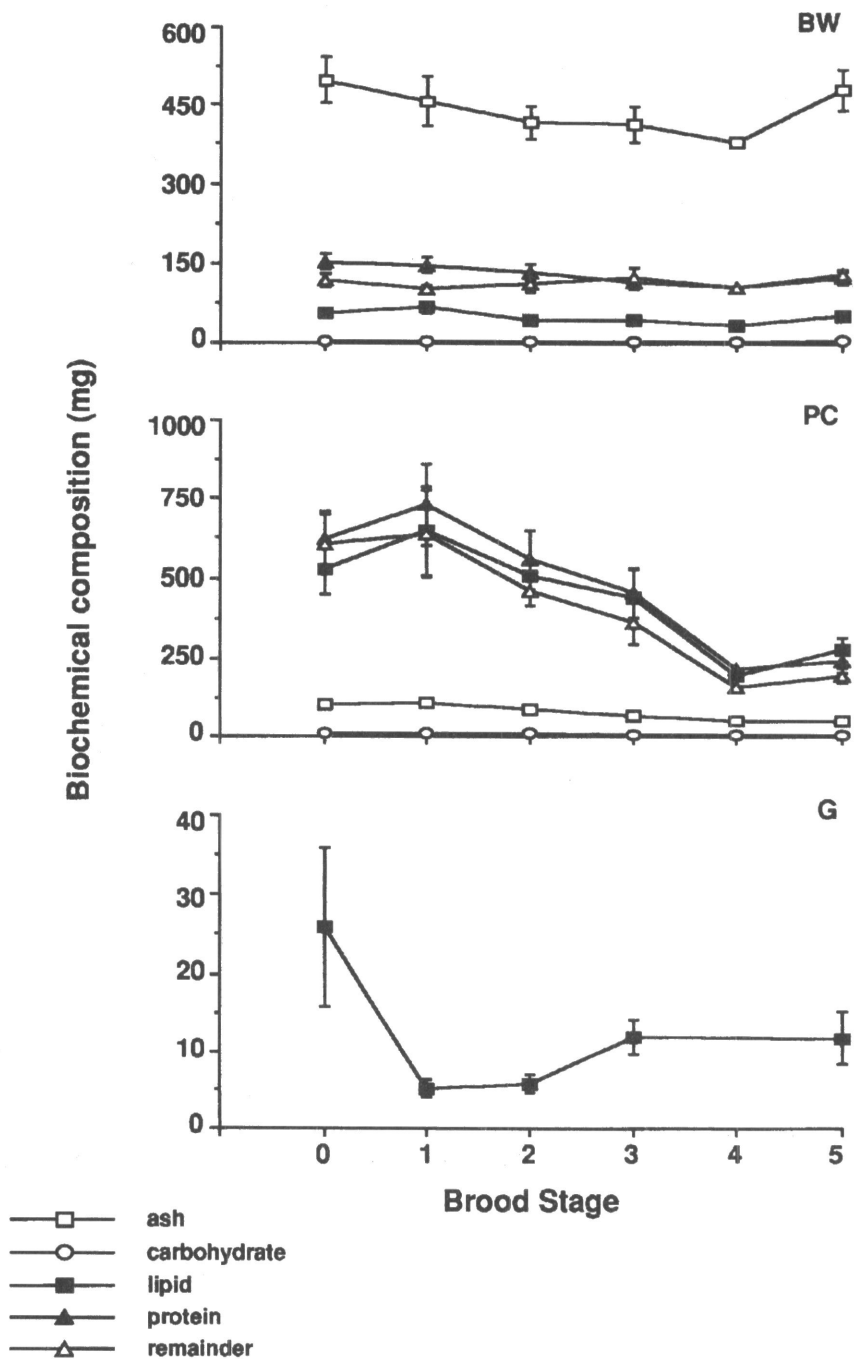

Figure 1. Biochemical composition of the body wall (BW), pyloric caeca (PC), and gonad (G) for brooding *Neosmilaster georgianus* females throughout brood stages 1 to 5. Stage 0 individuals indicate a prespawned condition. Each point represents the mean ±1 standard deviation (N=7, 5, 5, 7, 1, and 6 for stages 0 to 5, respectively).

Wet organ indices (ratio of wet body components to the whole body) were determined for all individuals. The percentage of biochemical composition (ash, carbohydrate, lipid, and protein) of the dry body components was also determined using methods detailed in Lawrence and Guille (1982). The energetic content of the different body components was determined from the tissue biochemical composition using energy-equivalent coefficients calculated by Brody (1945). The energetic content of females holding each brood stage was compared to determine costs associated with brooding-induced starvation (figure 1).

The stage-specific energy content of the body wall, pyloric caeca, and gonads of females holding broods was compared to estimate the costs associated with brooding-induced starvation. There were no significant changes in the composition of the body wall. Lipid levels in the pyloric caeca, the principal storage organ of seastars, were initially twice that reported in temperate and tropical species and comparable to other antarctic seastars (Lawrence and Guille 1982; McClintock and Pearse 1987). All biochemical constituents and the energy content within the pyloric caeca exhibited significant ($P<0.001$) declines with stage of brood development, an indication that nutrients were being redistributed to other parts of the body. In temperate seastars, a major part of these energy reserves is allocated to the production of new eggs in preparation for the next reproductive event (Chia 1969). In *N. georgianus*, the stage-specific lipid content of the gonads of brooding females did not change significantly after spawning (figure 1) nor was there significant growth of existing, early-stage oocytes (Slattery and Bosch unpublished data). Thus, the resources of the pyloric caeca are utilized for maintenance during the long brood cycle (approximately 1 year) and not in preparation for future reproductive events. On the basis of the extended periods required for oocyte production in antarctic echinoderms (18 months or more: Pearse, McClintock, and Bosch 1991), we predict that species such as *N. georgianus*
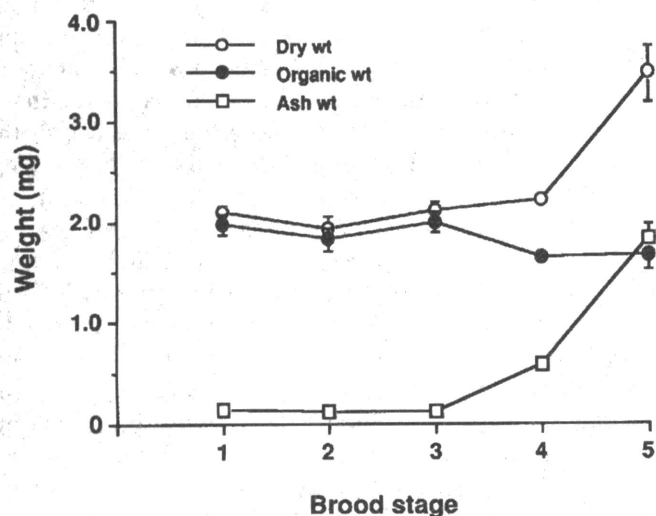
may have a lower frequency of reproduction compared to their temperate and tropical counterparts, which typically produce annual broods.

Broods of all females were removed, counted, and categorized into one of five groups based on developmental stage. (Prespawned individuals were classed a stage 0.) Broods were dried and ashed for organic composition, lyophilized for biochemistry, or fixed for sectioning. Samples were weighed on a Cahn microbalance prior to and after ashing in a muffle furnace, and the organic weight was determined by subtraction (figure 2). Biochemical tests were conducted on pooled whole embryos and juveniles, of like developmental stage, to provide adequate sample weights for analyses. Thin-sections were examined via light and transmission electron microscopy to determine the purpose of an amorphous membranaceous tubule interconnecting individuals within all stage 2 broods.

Brooded individuals exhibited a significant ($P<0.0001$) increase in dry weight with a coincident significant ($P<0.004$) decrease in organic weight during development from stages 1 to 5. These overall changes were consistent with a trend for decreased lipid and protein during the onset of ossification (stage 4 and 5) in the developing offspring (data not shown). A slight increase in organic weight, lipid content, and consequently energy levels occurred in early development (stage 1 to 3), though this change was relatively small compared to the losses that occurred during the ossified stages. These results suggest, in contrast to antarctic echinoderm embryos examined by Lawrence, et al. (1984), that *N. georgianus* produces large eggs in part to offset energetic demands of development. These early embryonic changes were coincident with the development of membranaceous tubules that effectively joined brood mates, forming clusters of up to 40 individuals. Histological evidence showing the movement of lipid and other material through these tubules suggest they are a means of "cannibalizing" broodmates for energy to fuel development. A trend toward a 25 percent decrease in the numbers of siblings per brood between spawning and the separation of brood clusters (stage 0 through 3) supports our interpretation of sibling cannibalism. In fact, similar structures connecting brood mates occur in a deep-sea asteroid, *Leptasterias tenera* (Hendler and Franz 1982), and two antarctic seastars, *Diplasterias brucei* and *Notasterias armata* (Bosch personal observation), suggesting this unusual process of supplementing the initial parental investment in eggs is not be unique to *N. georgianus*.

Figure 2. *Neosmilaster georgianus* juvenile growth throughout brood stages 1 to 5. Each point represents the mean ±1 standard deviation (N=10).

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Epipelagic communities in the northwestern Weddell Sea: Results from acoustic, trawl, and trapping surveys

R.S. Kaufmann, K.L. Smith, Jr., R.J. Baldwin, *and* R.C. Glatts, *Marine Biology Research Division, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92093-0202*

B.H. Robison *and* K.R. Reisenbichler, *Monterey Bay Aquarium Research Institute, Pacific Grove, California 93950*

Until recently, little was known about the community inhabiting the underside of seasonal sea ice in the Antarctic. Increasing understanding of this unique environment has given rise to a number of questions about the under-ice community and its interactions with other portions of the antarctic fauna, especially those of the underlying water column and the above-ice community, including seabirds and marine mammals. In particular, the discovery of mesopelagic species in the guts of surface-feeding seabirds foraging in areas of open water (for example, leads and polynyas) amidst heavy pack ice (Ainley et al. 1986; Ainley, Fraser, and Daly 1988) has presented the startling possibility of trophic coupling between two apparently disjunct communities. Although many of the mesopelagic species found in bird guts are known to migrate vertically on a daily basis (Torres et al. 1985; Torres and Somero 1988), most have not been caught at depths of less than 100 meters (m) in open water (Lancraft, Torres, and Hopkins 1989); whereas the seabird species sampled are not known to forage deeper than 5 m (Ainley et al. 1986).

There are numerous difficulties in examining the ecology of under-ice fauna, including the logistic intractability of the environment and the distribution and behavior of the animals themselves. The animals, most commonly krill (*Euphausia superba*), tend to be found in close association with the under-ice surface and are known to actively avoid sampling gear (O'Brien 1987; Marschall 1988). As part of a short-term feasibility study to evaluate the possibility of using free-vehicle (independent of a ship or any surface mooring) acoustic instruments to monitor the abundance, vertical distribution, and size distribution of animals in the upper 100 m of the water column beneath seasonal pack ice, two upward-looking, split-beam acoustic arrays were deployed at each of two locations (four deployments total) in the northwestern Weddell Sea during early October 1992: in ice-covered water at 61°32.54'S 41°54.28'W and 61°30.62'S 41°39.44'W and in open water at 60°14.96'S 49°47.74'W and 60°13.13'S 49°50.62'W (figure 1). These instruments were moored on the bottom and positioned approximately 100 m beneath the sea surface in areas with bottom depths of 1,050–1,100 m. Each instrument operated at a frequency of 72 kilohertz and was programmed to ensonify an 8,600-cubic-meter conical section of the water column [100 m vertically upward from the transducer with 20-centimeter (cm) vertical resolution and a beam angle of 5°] every 5 seconds for 1 minute, with intervals of 6 minutes between 12-ping groups over a deployment duration of 2 days. In the ice-covered area, two lines of baited minnow traps (for the collection of scavenging animals) were deployed concurrently at depths of 0, 10, 50, 100, and 200 m through holes drilled in the ice. A similar trap array was deployed from a floating buoy at the open-water site. In both the ice-covered and open-water areas, the upper 250 m of the water column was also sampled during the day and at night using an opening-closing Tucker trawl (two nets with a 10-square-meter mouth opening). The Tucker trawl was successfully employed 11 times in the pack ice and three times in open water.

Acoustic targets were more abundant at the open-water location than at the ice-covered site, 10.0 and 7.6 targets per