Reproductive cycle of the subarctic brooding asteroid

*Leptasterias polaris*

Y. Boivin 1, D. Larrivée 1 and J. H. Himmelman 2

1 Département des sciences fondamentales, Université du Québec à Chicoutimi; Chicoutimi, Québec G7H 2B1, Canada
2 GROQ and Département de biologie, Université Laval; Québec, Québec G1K 7P4, Canada

Abstract

The reproductive cycle of the large brooding sea-star *Leptasterias polaris* Müller and Troschel was examined over an 18-month period in the St. Lawrence Estuary, Québec, Canada. There is a distinct annual cycle with spawning over several months in the autumn. The female has an unusual cycle in that the ovary only slightly decreases in size during spawning, and the size structure of the oocyte population is remarkably stable throughout the year. The major annual change observed in the oocyte population is the development of a small number of 600- to 800-μ oocytes prior to spawning and their loss during spawning. This stability, combined with the lack of evidence of phagocytosis, suggests that oocyte development takes place over many years. By contrast, the developmental cycle of the testis is similar to that of most echinoderms. The large reservoir of oocytes probably guarantees a steady annual recruitment, and brooding during the winter probably minimizes metabolic costs for the female and ensures the release of the juveniles when conditions are favourable in the spring and summer.

Introduction

The subarctic seastar *Leptasterias polaris* is a brooding species abundant in subtidal communities in the northwestern Atlantic. To protect the developing embryos, the female curves all of her six arms so that her body forms a disc over the young, which are attached to bedrock, boulders or cobbles (Emerson, 1973, 1977; Himmelman et al., 1982). She remains on her brood for 4 to 5 months and does not feed during this period (Emerson, 1973).

Giese (1959) described a reproductive cycle as a series of events: activation of the germinal epithelium, cellular proliferation and development, and finally spawning and a resting period. For many marine invertebrates, reproductive events are relatively synchronous within a population and show a pattern which is repeated annually (Thorson, 1949; Chia, 1966; Giese and Pearse, 1974). This is particularly characteristic of invertebrates in cold water regions (Giese and Pearse, 1974), and many species with planktonic larvae carry out gamete development during the winter and spawn in the spring, when temperature and food conditions are optimal for the larvae (Thorson, 1946; Himmelman, 1981). Producing large, yolky eggs, and brooding the young, is an alternate pattern which is particularly common among arctic and boreal species (Thorson, 1946). Asteroïds have evolved a variety of ways for brooding their young (Himmelman et al., 1982). For example, spines or other structures may be modified to form a brooding chamber on the aboral side of the seastar, or the arms may be folded downward to form a brooding chamber between the mouth and the arms. *Leptasterias polaris* and *L. ochotensis similispinis* are the only brooding seastars known to attach their broods to the substratum (Kubo, 1951; Emerson, 1973; Himmelman et al., 1982).

Since brooding species generally produce far fewer eggs than species producing pelagic larvae, the energetic expenditures in producing young may be less. For example, *Leptasterias polaris* produces 1 000 to 3 000 eggs (Himmelman et al., 1982), whereas *Asterias rubens*, a similar-sized seastar having planktotrophic larvae, produces > 2 500 000 eggs (Gemmill, 1914). However, seastars which brood their young under their mouth, including all *Leptasterias* species (Chia, 1966, 1969; Smith, 1971; O'Brien, 1976; Worley et al., 1977), have the constraint of not being able to engage in their usual predation activities during the brooding period.

In the present study, using histological techniques as well as body component indices, we examine the reproductive cycle of *Leptasterias polaris* and its adaptations to the prolonged period of starvation during brooding.

Materials and methods

Sampling. The population of *Leptasterias polaris* Müller and Troschel studied was at Anse à la Barque (Lat.
48°19'05"N; Long. 69°24'53"), near Les Escoumins, Québec, eastern Canada (Fig. 1). Between September 1981 and February 1983, collections of ~30 individuals were made at monthly or bimonthly intervals from a depth of 5 to 15 m and over a surface area of ~2000 m². The seastars were kept cold during transport to the laboratory and were maintained in natural seawater at 2 °C for up to 3 d before being dissected. For each seastar, after making lateral cuts along the arms, the ventral body wall was cut away to expose the internal organs. The gonads and pyloric caeca were removed, and after draining excess water by placing them on absorbant paper for 5 min, were weighed to the nearest 0.005 g. For each individual, one gonad and a portion of the pyloric caeca were fixed in 10% formalin in seawater. The remaining gonad and pyloric caecum tissue was dried at 60 °C for 25 h to determine the percentage water content.

**Body component indices.** Indices of the gonads and pyloric caecum were calculated as a percentage of the total live body weight. For each index the mean and 95% confidence limits were calculated from the arcsine-transformed percentage values. These statistics were then transformed back to percentage values for plotting the indices against time. When indices at different dates were compared statistically, a Student's t-test or an analysis of variance was carried out using the arcsine-transformed percentage values. An examination of the relationship between percentage gonadal weight and total body weight at several different periods of the year showed the percentage gonadal weight to be independent of body weight (Pearson correlation coefficients were <0.016 for females and <0.001 for males) for individuals weighing 20 to 192 g (10 to 31 cm in radius) and only this size range was used in the calculation of body component indices.

**Histology.** The preserved portions of the gonads and pyloric caeca were dehydrated and embedded in paraffin using standard procedures (Gabe, 1968). We made 7-μ thick sections of the gonads at approximately the center of the organ. To aid in obtaining intact sections of the ovaries, which had a very high vitellus content, the specimens embedded in paraffin were placed in a distilled water bath at room temperature for 15 to 30 min prior to sectioning as recommended by Worley et al. (1977). After sectioning, the sections were stained with Masson’s tri-chrome (Gabe, 1968). A number of sections were prepared for ultrastructural analysis. The tissues were fixed in 3.5% glutaraldehyde in sea water for about 5 h, then post-fixed in osmium tetroxide (1% in water for 1 h), dehydrated in alcohol, transferred in propylene oxide, and finally embedded in Epon 812 or Spurr medium (Spurr, 1979). When embedding in Spurr medium, propylene oxide was not used. Sections, 80 to 150 Å thick, were obtained using a Reichert ultramicrotome (Om U2). The sections were stained with uranyl acetate (saturated in 95% ethanol) for 20 min and then by lead citrate (Reynolds, 1963) for 6 min.

Histological observations using a light microscope were made on 7 to 18 individuals of each sex for each sampling date. To determine the size structure of the oocyte population, the mean of two diameter measurements, one perpendicular to the other, was calculated out using the arcsine-transformed percentage values. An examination of the relationship between percentage gonadal weight and total body weight at several different periods of the year showed the percentage gonadal weight to be independent of body weight (Pearson correlation coefficients were <0.016 for females and <0.001 for males) for individuals weighing 20 to 192 g (10 to 31 cm in radius) and only this size range was used in the calculation of body component indices.

**Results**

**Male reproductive cycle**

**Gonadal size.** There was an annual cycle in the size of the testis (Fig. 2). The mean gonadal index of 13.3 for the first