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Reproductive cycle of the subarctic brooding asteroid *Leptasterias polaris*

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Abstract

The reproductive cycle of the large brooding seastar *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). Asteroids 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.

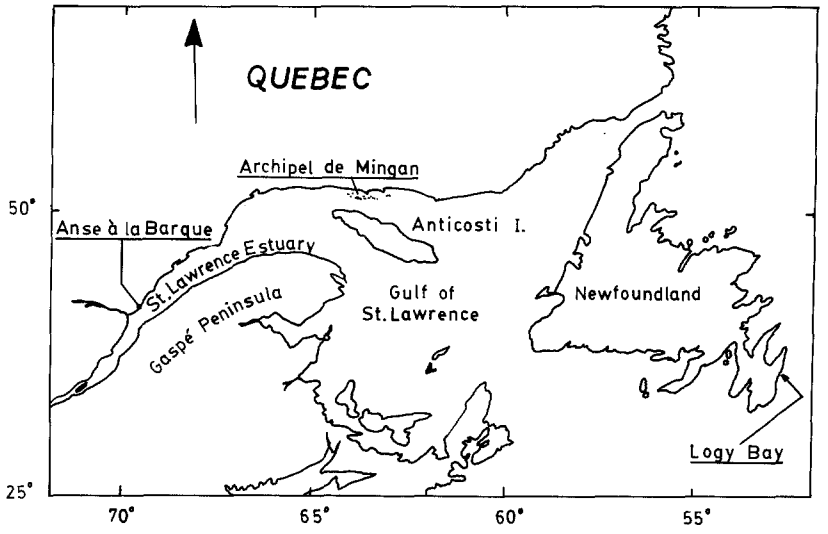

Fig. 1. Map of eastern Canada showing locations referred to in the text

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 ≈ 2 000 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 trichrome (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 for all oocytes sectioned through the nucleolus in a single section from the center of each ovary (Pearse and Giese, 1966; Crump, 1971; Gonor, 1973). The number of oocytes measured ranged from 116 to 649 per sampling date. For each male we calculated the mean thickness of the germinal epithelium, based on three measurements. We also ranked the quantity of spermatozoa in the testicular lumens using five categories, ranging from empty (0) to full (4).

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

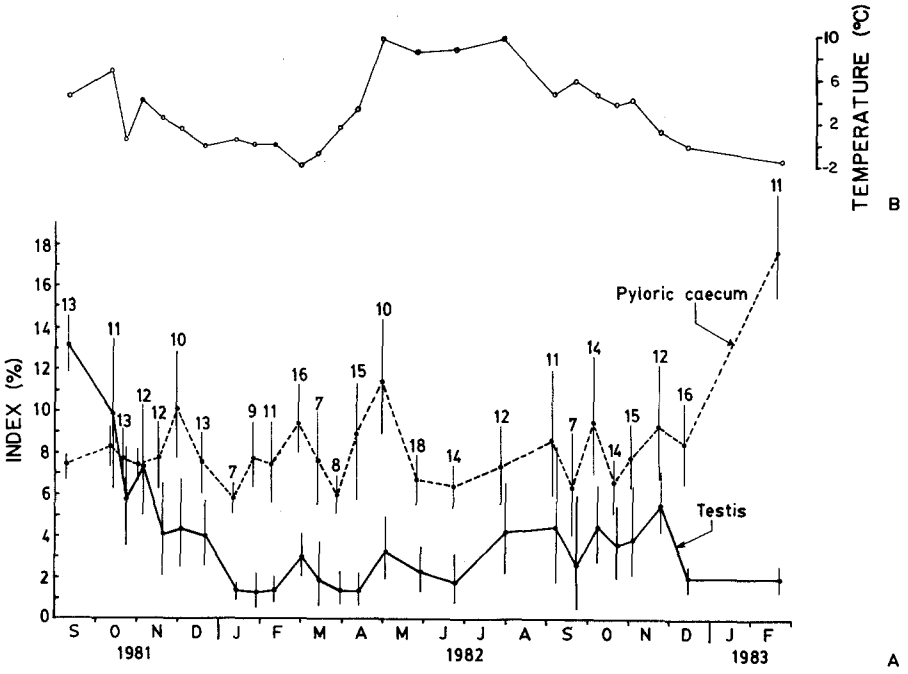

Fig. 2. *Leptasterias polaris.* (A) Variation in the index of the testis and index of the male pyloric caecum during September 1981 to February 1983. The vertical lines represent the 95% confidence limits and the numbers indicate the sample size for each data. (B) Water temperature at each sampling

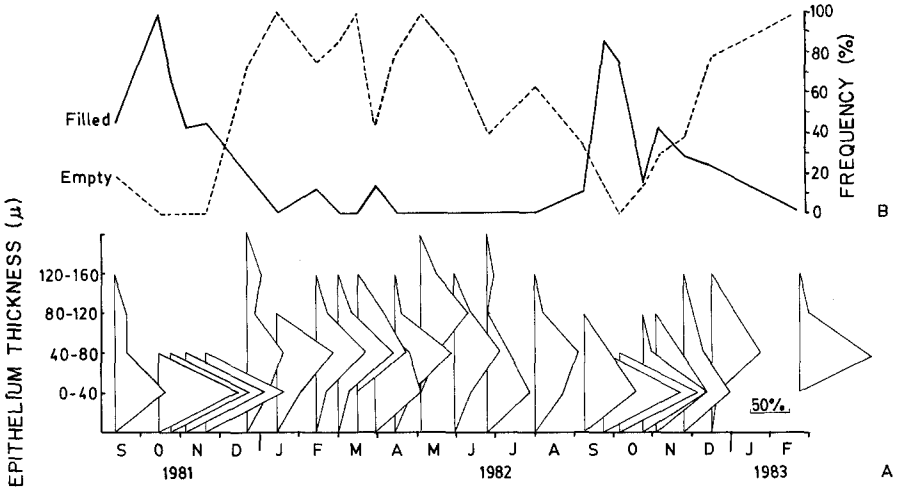

Fig. 3. *Leptasterias polaris.* (A) Distribution of the germinal epithelium thickness frequencies in the testis. (B) Changes in the frequency of the male individuals with the testicular lumen empty or filled with spermatozoans. (Intermediate categories make up the difference between the sum of the full and empty categories and 100%)

sample in early September 1981 was the highest value encountered during the study. Following this there was a significant decline ($P<0.01$) to a minimum of 1.3 in January 1982, suggesting that spawning had occurred. During a preliminary dive on 18 July 1981, no brooding individuals were found. They were first observed when the first collection was made on 10 September 1981 and were common by October 1981. The testicular index remained generally low from January through June 1982, although there were irregular and significant ($P<0.05$) variations, and then generally higher values occurred during July through November 1982. The peak attained in November 1982 was 5.8, less than half the peak in September 1981. Between November and December 1982 there was an abrupt and significant ($P<0.05$) decrease to a minimum in December 1982. While this decrease to the winter minimum clearly indicated that spawning was finished, the testicular index did not indicate when spawning began. Brooding individuals were first observed on 23 October 1982, thus more than a month later than in 1981. A one way *a-posteriori* analysis of variance comparing the samples from the different dates (groups) showed that there were no significant changes ($P>0.05$) in the water content of the testis throughout the study period. The mean percentage water content for all of the individuals collected was 81.6% (95% confidence interval = 7.65–86.3, $n=322$).

Pyloric caecum index. The size of the male pyloric caecum showed irregular variations and there was no recognizable annual cycle (Fig. 2). While the variations were significant ($P<0.05$) at numerous points, an inverse relationship with the cycle in testicular size, as might occur if the caecum supplied materials for producing spermatozoa, was not evident. As for the testis there were no significant seasonal (analysis of variance, $P<0.05$) variations in the water content of the pyloric caeca ($\bar{X}=70.0\%$; C.I. = 63.8–75.8; $n=322$).

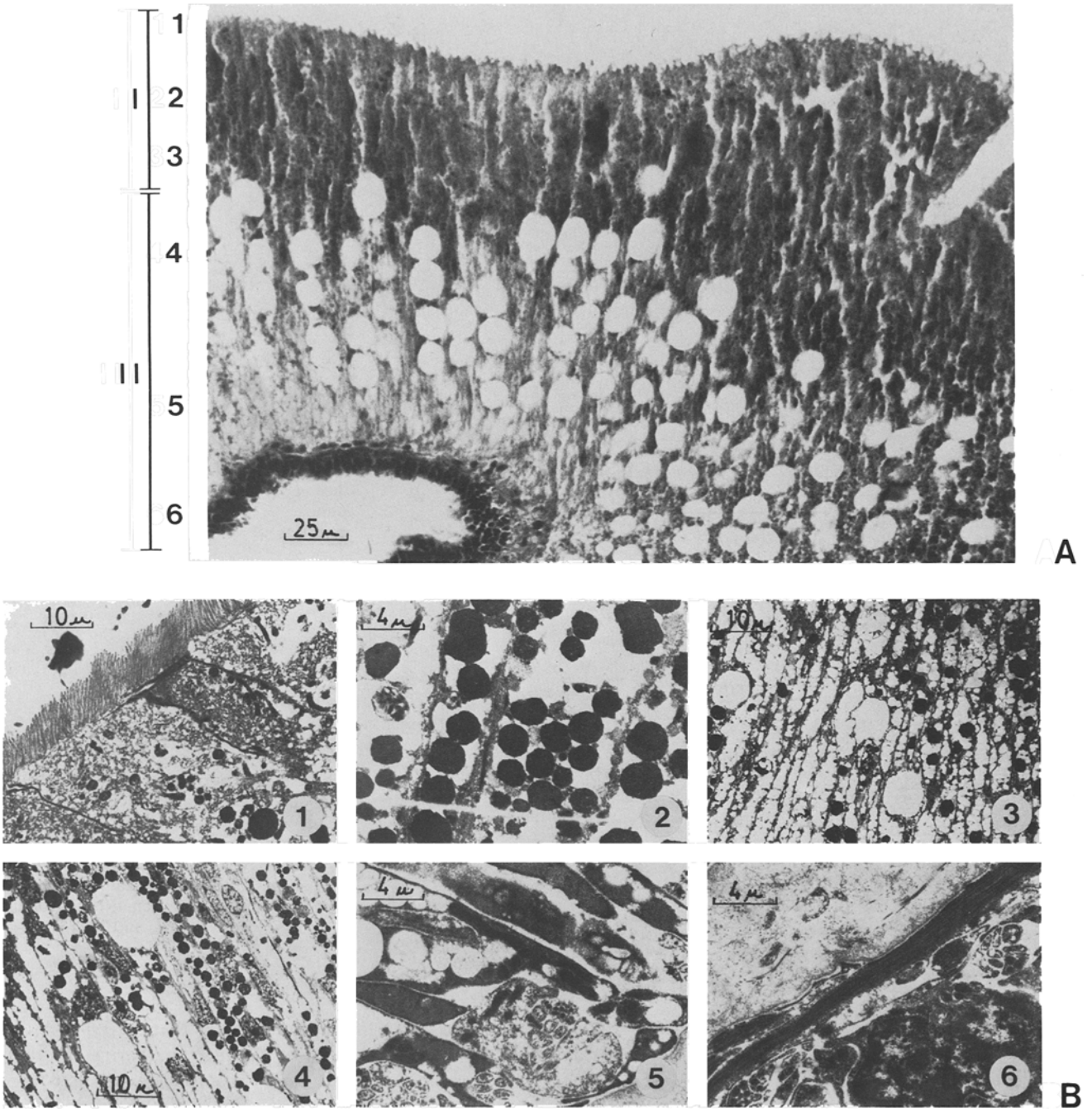

Fig. 4. *Leptasterias polaris.* (A) Light micrograph of the pyloric caecum wall showing an outer darkly staining zone (I) and inner zone with large clear vesicles (II). (B) Electron micrographs showing details of the five portions of the wall indicated in the light micrograph (A)

Histology of the testis. There was a distinct annual cycle in epithelium thickness and in the quantity of spermatozoa in the lumen (Fig. 3). In 1981, the percentage of males with a germinal epithelium $<40\,\mu$ in thickness increased from 80% in September to 100% in October and November. In December, following spawning, individuals with an epithelium $>40\,\mu$ in thickness and a thin layer of spermatogonia appeared (Fig. 3). They predominated thereafter until late September to early October 1982 when 100% of the individuals again had a thin epithelium. In both years in September to early October, coinciding with the thinning of the epithelium, the frequency of individuals with testicular lumens full of spermatozoa increased to nearly 100%. Subsequently the percentage of individuals with full lumens decreased and reached 0% in January or February. The frequency of individuals with empty lumens showed the opposite pattern (Fig. 3). Thus, the thickening of the germinal epithelium in December marked the beginning of spermatogenesis and by July it could measure up to $160\,\mu$ in thickness. Then in July, with differentiation and release of spermatozoa into the lumen, there was a thinning of the epithelium to $\approx 5\,\mu$. The high frequency of

individuals with a thin epithelium and a full lumen in late September to early October marked the peak of the spermatogenic cycle. After sperm release there was a renewed growth of the epithelium marking the beginning of a new cycle.

Histology of the pyloric caecum. Histological observations of the pyloric caecum showed two main structural zones: (I) from the interior of the lumen to a darkly stained area where the nuclei were aligned and (II) the remaining tissue characterized by large clear vesicles (Fig. 4). The interior brush border cells of Zone I may be responsible for the transfer of exogenous nutritive material to the interior, whereas the cells of Zone II may process and store it. When the pyloric caecum was large (index $\approx$ 12), there was a regular arrangement of the brush border cells and the nuclear and stained areas were close to the brush border cells. By contrast, when the pyloric caecum was small (index $\approx$ 4), the brush border cells appeared fragmented and the nuclear and pigmented areas were further away. Also, there were fewer large clear vesicles in Zone II. These observations suggest that the pyloric caecum has a storage function.

Female reproductive cycle

Gonadal size. While there was an annual cycle in the ovarian index following roughly the same pattern as that of the testicular index, there were a number of differences (Fig. 5). The most striking was the reduced amplitude of the cycle in ovarian size. During the 18-month study period the percentage weight of the ovary varied from 2.8 to 4.8, compared to 1.5 to 13.3 for the testis. In the autumn of 1981, while there was a significant ($P < 0.05$) drop in the testicular index by mid-October (Fig. 2), the ovarian index showed little variation until after 9 November when it dropped significantly ($P < 0.05$) to the annual minimum (Fig. 5). Thus, the ovarian index did not indicate when spawning began. The minimum for the testicular index was not reached until two months later. The relative size of the ovary remained remarkably stable from November 1981 to late June 1982 and then showed a progressive increase to a peak in early September 1982. This peak was almost identical in magnitude to the index observed in early September 1981. Subsequently, over the period when brooding individuals appeared in the field, there was a gradual decrease in mean ovary size, although the decrease was not significant ($P > 0.05$) until December 1982. The percentage water content of the ovary showed no significant seasonal variations (analysis of variance, $P > 0.05$) ($\bar{X} = 71.6\%$, C.I. = 66.7–76.3, $N = 335$); and was significantly less (paired Student's t-test, $P < 0.005$) than the percentage water content of the testis.

Pyloric caecum index. While the size of the pyloric caecum of the female, like that of the male, did not show a distinct annual cycle, some trends were apparent (Fig. 5). For example, there was a general decrease between October 1981 and late January 1982, followed by an increase in May 1982. The decrease coincided with the period when brooding individuals were most abundant and the increase with the disappearance of brooding individuals in the field. This cycle was not repeated in the following year as the pyloric caecum index was relatively stable between July and December 1982. The percentage water content of the pyloric caecum did not show significant changes over time (analysis of variance, $P > 0.05$) ($\bar{X} = 66.4\%$, C.I. = 63.3–69.3, $n = 335$); and was significantly less paired (Student's t-test. $P < 0.005$) than the percentage water content of the pyloric caecum of the male.

Histology of the ovaries. The oocyte frequency distribution was stable throughout the year, with cells measuring 0 to 200 μ in diameter always predominating and a gradual decrease in frequencies with increasing size (Fig. 6). The most evident seasonal change was in the abundance of very large oocytes, measuring 600 to 800 μ in diameter. They were present from September through November 1981 and disappeared in December 1981. Their disappearance was only shortly after the ovarian index dropped to its minimum (Fig. 5), thus suggesting these large oocytes were released during spawning. Oocytes >600 μ were virtually absent from December 1981 through April 1982 and then were present between May and late November 1982. Finally, they again disappeared in December 1982 at the same time as the ovary reached minimum size. Thus, the size structure of oocyte populations showed

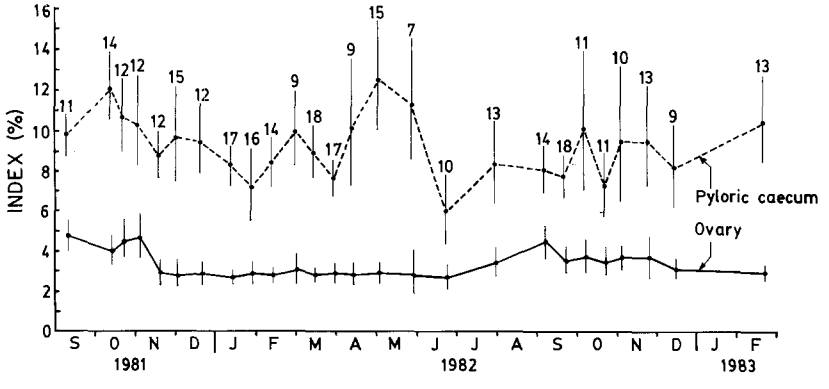

Fig. 5. *Leptasterias polaris.* Variation in the index of the ovaries and index of pyloric caecum during September 1981 to February 1983. The vertical lines represent the 95% confidence limits and the numbers indicate the sample size for each date

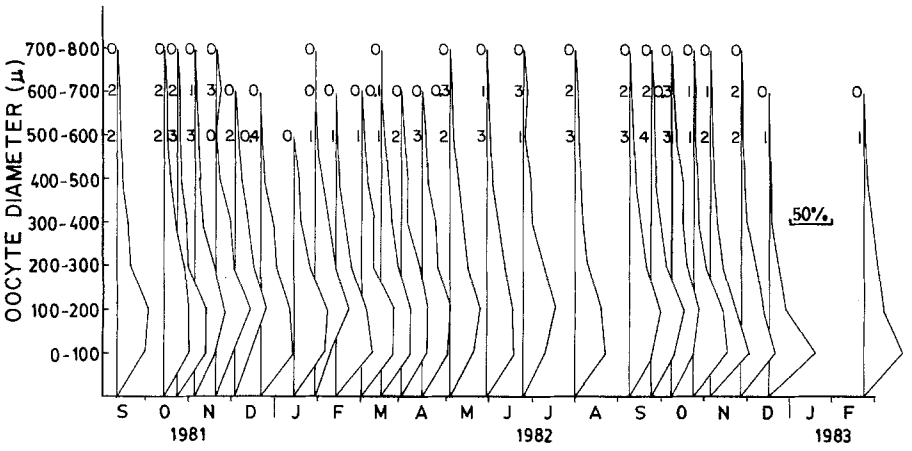

Fig. 6. *Leptasterias polaris.* Size-frequency polygons of oocyte diameter. The number associated with polygons represents the exact percentage at this level

remarkedly little annual variation except that the 600- to 800-μ oocytes appeared in May and disappeared at the end of spawning in December. These large oocytes represented at most 4% of the oocyte population.

We could distinguish four stages of oogenesis from histological observations (photographs of stages given by Boivin, 1985). In the first, the pre-meiotic generative stage, there was cellular proliferation generating clusters of secondary oogonia. In the second stage, there was a slow transformation of oogonia of 20 μ in diameter into oocytes of approximately 100 μ in diameter. These two stages lasted less than 5 months. The third stage was the vegetative growth phase (prophase I) or endogenous vitellogenesis. It started when the primary oocytes of 100 μ in diameter detached from the germinal epithelium and continued until they had reached 600 μ in diameter. As vitellogenesis progressed, the nuclear membrane became more folded, and a clear perinuclear zone and numerous nuclear pores developed. These characteristics became more pronounced and attained their maximum at the end of vitellogenesis and in addition the cytoplasm became filled with electron dense vesicles. The duration of vitellogenesis was probably much longer than one year. The fourth stage was characterized by the elaboration of clear vesicles in the peripheral cytoplasm and by a decrease in the size of the nucleus. It lasted about three months. When the cells reached 600 to 800 μ in diameter they were ready for spawning. Examination using both light and electron microscopy revealed no evidence of phagocytosis.

Histology of the pyloric caecum. The pyloric caecum of the female showed the same histological changes in relation to caecum size as described for the male.

Discussion

Reproductive cycle

As in most marine invertebrates, the gonadal development of *Leptasterias polaris* follows a distinct annual pattern. The cycle in gonadal size is most pronounced in the males. Coinciding with spawning in the autumn of 1981, there was a 12% drop in percentage gonadal weight. However, in 1982 the gonads did not attain a very large size and the percentage testicular weight decreased only by 3% during spawning. Such annual variations in gonadal production are common in marine invertebrates. For example, they have been documented in the seastar *Pisaster ochraceus* (Mauzey, 1966; Chia, 1969; Ferguson, 1975) and the urchin *Strongylocentrotus purpuratus* (Lawrence *et al.*, 1966), and are generally considered to be due to variations in food availability (Himmelman, 1978; Town, 1980; Lawrence and Lane, 1982). The histology of the testis shows a marked annual pattern. There is no rest period after spawning, but rather as spawning is finishing in late November and December the germinal epithelium thickens. It remains developed until late August and September when it suddenly becomes thin. At this time the lumen of the testis fills with spermatozoa and the males are ready for spawning. The above cycle of testicular events is similar to that found in many marine invertebrates, including those with pelagic larvae.

The gonadal cycle of female *Leptasterias polaris* differs markedly from that of the male and from cycles reported for other echinoderms. Firstly, the amplitude of the cycle is greatly reduced. The maximum variation in ovarian weight during two successive spawning periods was only 2% of the total body weight. Other differences are evident from the histological observations. There is little annual change in the size structure of oocyte populations, and a generally unimodal distribution skewed towards the smaller size cells is found throughout the year. The only distinct annual change is the disappearance of cells 600 to 800 μ in diameter in December when spawning finishes. By contrast, non-brooding species, as well as several brooding species of *Leptasterias* (Chia, 1966; Smith, 1971; Menge, 1975; Strathmann and Strathmann, 1982), show marked annual changes in oocyte populations, with passage of oocytes from the smaller to the larger size classes coinciding with an annual production of gametes.

We hypothesize that the oocyte populations are stable because oogenesis is a prolonged process and only a relatively small number of oocytes are spawned annually.

Observations by light and electron microscopy show no phagocytosis at any period during the year. As 600- to 800-μ oocytes never represent more than 3 to 4% of the oocyte population, few oocytes are released during spawning. Since there is no phagocytosis, the remaining cells ($<600\,\mu$) are probably retained and maintained, which suggests that oogenesis occurs over a prolonged period. A period of oogenesis of > 1 year has already been suggested for the congeneric species, *Leptasterias hexactis* (Chia, 1966), *L. pusilla* (Smith, 1971) and *L. tenera* (Worley *et al.*, 1977; Hendler and Franz, 1982). An alternative explanation for the stable oocyte populations would be that there is continuous reproduction, as has been suggested for the seastar *Ctenodiscus crispatus* (Shick *et al.*, 1981). However, the absence of 600- to 800-μ oocytes between December and May, and the absence of brooding individuals in the field in June, July and August show that this is not the case. In *L. polaris*, the reserve of cells remaining in the gonad after spawning would be sufficient for more than ten annual spawnings. A similar situation is that of oogenesis in the bullfrog *Xenopus laevis* (Callen *et al.*, 1980). Each year oocytes mature from a stock of oocytes which appears to be present before the females reach sexual maturity and which is sufficient for the 20 years of adult life.

An inverse relationship between the annual cycles in the size of the pyloric caeca and gonads has been reported for a number of seastars and it is suggested that the pyloric caecum stores material for later transfer to the gonads (Chia, 1969; Nimitz, 1971; Menge, 1975). In fact, Smith (1971) showed that there is a decrease in the size of the pyloric caecum coincident with rapid oocyte growth in the brooding species *Leptasterias pusilla*. While no well defined pattern was observed during our study, the decrease between October 1981 and January 1982 could indicate the use of materials stored in the pyloric caeca during brooding, and the increase between February and May 1982 may be related to the end of brooding and the resumption of active foraging (Fig. 6). During our study, the production of large oocytes began before all individuals had completed brooding. Since we did not separate brooding and non-brooding individuals when making collections, we cannot state that for a given individual the production of large oocytes can begin before brooding stops. However, this seems probable since large oocytes are produced when females are maintained in cages without food (J. Moffat, Université du Québec à Chicoutimi, unpublished data). Further, Chia (1969) showed that *L. hexactis* can produce large oocytes before feeding is resumed. In our study, the irregularity of seasonal variations in the size of the pyloric caecum of the male gave no indication that its metabolism is coordinated with testicular development.

Regulation of gamete production

Spawning in *Leptasterias polaris* lasts several months. In our study the first brooding individuals were observed in early September 1981 and in late October 1982, and the gonads were depleted of mature oocytes in December in both years. The most abrupt histological event in the testis is the sudden thinning of the germinal epithelium and the filling of the lumen of the testis with spermatozoa in September. Emerson (1973) reported that brooding begins in January in Logy Bay, eastern Newfoundland, several months later than at Anse à la Barque in the St. Lawrence Estuary. Since the two populations are at approximately the same latitude, photoperiod can be excluded as an environmental factor controlling spawning. Our measurements showed that temperatures dropped to $\approx 6\,^{\circ}C$ in September at Anse à la Barque. In contract, at Logy Bay the annual temperature maximum (≈ 11–$12\,^{\circ}C$) occurs in September and there is a slow decline thereafter, reaching $6\,^{\circ}C$ in late October (Steele, 1974). Since spawning lasts several months it may not simply be provoked by an environmental change, such as is common in many species with pelagic larvae (Himmelman, 1981). Given that *L. polaris* is a brooding species, spawning probably involves behavioural changes such as the aggregation of males and females and the search for suitable substrates for brooding. Environmental factors may stimulate behavioural changes leading to spawning, rather than directly stimulating spawning.

The most marked annual change in the histology of the ovary is the production of 600- to 800-μ oocytes, which begins in May. The production of these large cells even when seastars are experimentally starved (J. Moffat, unpublished data) suggests that this process is independent of food conditions. It may be stimulated by a sharp rise in temperature during the spring (Fig. 2 B) or by photoperiod.

Reproductive strategy

The increased frequency of brooding species in northern waters is a well known phenomenon in marine invertebrates and has probably evolved in response to the rigorous climatic conditions and short period of planktonic food availability (Thorson, 1946). The reproductive cycle of the female *Leptasterias polaris* is evidently related to its brooding habit. In comparison with species with pelagic planktotrophic or lecithotrophic larvae, brooding species produce far fewer larvae. Our histological analysis indicates that only a very small proportion of the oocyte population is released during spawning, and Himmelman *et al.* (1982) reported that *L. polaris* weighing 100 to 200 g brood 1 000 to 3 000 larvae. Most brooding species, including other *Leptasterias* species, are relatively small (Chia, 1966; Smith, 1971; Menge, 1975; Strathmann and Strathmann, 1975), but *L. polaris* can attain a diameter of 50 cm. However, in spite of its large size, *L. polaris* produces low numbers of eggs.

The unusual features of the female reproductive cycle of *Leptasterias polaris* appear to have evolved to limit energetic expenditures and guarantee a stable annual recruitment. Because only a small proportion of the large

reservoir of 100- to 600-μ oocytes is annually converted into prespawning oocytes (600–800 μ) in the months prior to spawning, annual variations in food availability probably have little effect on the production of ova. This may be particularly important given the relatively short period, from the end of brooding and the beginning of the subsequent brooding period, when they can actively forage. While we did not observe a distinct annual cycle in the size of the pyloric caecum, during the first year there was some indication that this organ may have provided materials sustaining the female during brooding and oocyte production.

The timing of brooding may also be advantageous. The fact that it occurs during the coldest months of the year probably minimizes maintenance expenditures during brooding. Many species produce gametes during the winter so that the larvae released in the early spring can profit from a longer period of favourable environmental conditions (Thorson, 1946; Himmelman, 1981). In the same way, *Leptasterias polaris* broods during the winter and the young start their independent life at the beginning of the period of elevated temperatures and abundant food in the form of newly recruited organisms.

In contrast with the female, the reproductive cycle of the male resembles the general pattern for echinoderms and does not suggest that particular strategies have evolved in response to severe climatic conditions. Possibly such adaptations are not necessary since males can forage throughout the year. As we observed, there can be marked differences between years in spermatozoa production similar to those occurring in non-brooding species. If males and females are close to one another during spawning, fertilization may be assured even if there is not a large production of spermatozoa.

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