

Reproductive ecology of the Antarctic bivalve *Lissarca notorcadensis* (Philobryidae)

Robert S. Prezant,¹ Merrill Showers,¹ Ray L. Winstead¹ and Carol Cleveland²

¹Department of Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania 15705-1090, U. S. A.

²Invertebrate Zoology Section, Gulf Coast Research Laboratory, Ocean Springs, Mississippi 39564, U. S. A.

Abstract. The reproductive ecology of museum deposited specimens of the small philobryid Antarctic bivalve *Lissarca notorcadensis* was examined. Common to southern polar waters, the philobryids are typically epifaunal in habitat. *L. notorcadensis*, collected from sites adjacent to the Antarctic Peninsula, are found frequently attached byssally to cidaroid echinoid spines. While 95% of all mature clams display either ova or sperm, there is a quantitative shift in populations examined from male to female dominance with some indications of proterandry. *L. notorcadensis* are synchronous pallial brooders producing 9-15 shelled offspring regardless of adult female size. Juveniles that have already produced dissoconch shell, apparently crawl from the parental infrabranial chamber directly onto the same spine as their parent. The newly released juveniles lack fully developed digestive diverticula but are sustained by residual yolk reserves. Possible adaptations for brooding in the adult include an absence of the anterior adductor muscle thereby increasing pallial volume, and filibranch ctenidia that allow compact brood development. We suspect that these iteroparous bivalves release their broods in late austral winter to early summer. A single distinct collection from a site close to South Georgia reflects differences between zoogeographic areas.

As environmental threats to the relatively pristine ecosystem of Antarctica grow, it is imperative that we examine its present malacofauna and ecological "sanctity". The philobryid bivalves are a common and widely distributed group of southern polar molluscs (Powell, 1960; Tevesz, 1977) with intriguing reproductive biologies. Primarily thought to be dioecious, the philobryids brood their young in their infrabranial chamber well past prodissoconch stages (Prezant, 1990). The circumantarctic philobryid *Lissarca notorcadensis* Melvill and Standen has been reported to have a small prodissoconch I and a large prodissoconch II (Prezant, 1990), a pattern more characteristic of bivalves producing planktotrophic larvae (Jablonski and Lutz, 1980; 1983). The proposed discrepancy in larval shell form could be a retention of a primitive character from a nonbrooding ancestry. Philobryids, while Tertiary in origin (Morton, 1978), have in fact an interesting mix of apomorphic and plesiomorphic characters (outlined in Tevesz, 1977; Morton, 1978).

The Philobryidae are known poorly. Tevesz (1977) defines the family as filibranch bivalves with a posteriorly directed, ventral ciliary tract and a ligament pit situated between two rows of denticles (the provinculum). According to Tevesz (1977) there are eight valid, extant genera, distinguishable by variations in their ligament pit, denticles, adult hinge teeth, external shell ornamentation, and adductor muscles. The family is also characterized by nonfused mantle lobes, lack of siphons, reduction or absence of anterior adductor muscle, and the capacity to brood young to a juvenile stage. There has, to date, been only a single detailed report

on the reproductive ecology of any philobryid. Richardson (1979) reported on the reproductive ecology of a shallow water population of *Lissarca miliaris* (Philippi) from Borge Bay, Signy Island, Antarctica. Other than this, Dell (1964), reported about 400 "young shells" associated with the ctenidia of the Antarctic philobryid *Philobrya capillata* Dell. An incidental report on philobryid reproduction is given in Bernard (1897). *L. notorcadensis*, while sometimes found as an epibiont on kelp holdfasts, gorgonians, hydroids, sponges, and large solitary ascidians, is frequently found byssally attached to cidaroid echinoid species [especially species of the genus *Ctenocidaris* (J. H. Dearborn, pers. comm.)] (Fig. 1). The present paper details some aspects of the reproductive biology of *L. notorcadensis* from deeper Antarctic waters.

Viviparity in antarctic fauna appears to be a common phenomenon but understanding of this stems from studies of relatively few species (see Pearse *et al.*, 1991). In the very early 1900s, Giard (1905) suggested that antarctic organisms would tend to have a disproportionately large number of brooders that bypassed larval stages. Thorson (1950) proposed that the large number of polar brooders could be attributed to the short austral summers and restricted food supplies. Undoubtedly, the philobryids are well adapted to brooding but this may not be an adaptation to polar conditions but instead could be a conservative trait reflective of the group's phylogeny. Possible adaptations of adult female philobryids for brooding young to late stage juveniles include the absence of an anterior adductor muscle, filibranch ctenidia with a reduced outer demibranch, and a one way flow of pallial water

currents originating along the anterior portion of the mantle cavity. The relationship between small adult size and internal brooding is discussed by Strathmann and Strathmann (1982). This paper has a more narrow focus and attempts to explore the overall reproductive ecology of a single, small antarctic

species with respect to brood size, maturation characteristics, and distribution within habitat.

METHODS

Specimens of *Lissarca notorcadensis* were obtained from the Smithsonian Oceanographic Sorting Center of the U. S. National Museum. Voucher specimens have been accessed into the Smithsonian Institution, U. S. National Museum of Natural History (USNM Cat. #860303). Specimens were collected during expeditions of the early to mid-1970s and included the following: Islas Orcadas Cruise 575 from 12 May 1975 using a 10' Blake Trawl at depths of 132 - 143 m from 53°38.0'S/038°01.8'W; 2 June 1975 using a 5' Blake Trawl at depths of 161 - 210 m from 56°23.8'S/027°24.6'W; and 31 May 1975 using a 5' Blake Trawl at depths of 121 - 228 m from 56°42.8'S/026°69.7'W; and the HERO Cruise of 3 January 1972 using a Blake Trawl at a depth of 110 m from 64°47.3'S/64°07.4 to 64°06.3'W. Locations are denoted on a station map (Fig. 2). More specific information on the Islas Orcadas cruise can be found in DeWitt (1976). Most of these cruises were under the supervision of Dr. John H. Dearborn, University of Maine. While only spine material was available to us and positive identification of the specific host proved difficult, it is most likely that the host echinoid was one of three common cidaroids present at these collection sites: *Ctenocidaris geliberti*, *C. perrieri* or *C. speciosa* (J. Dearborn, pers. comm.). Specimens were preserved originally in 10% formalin and transferred to isopropyl

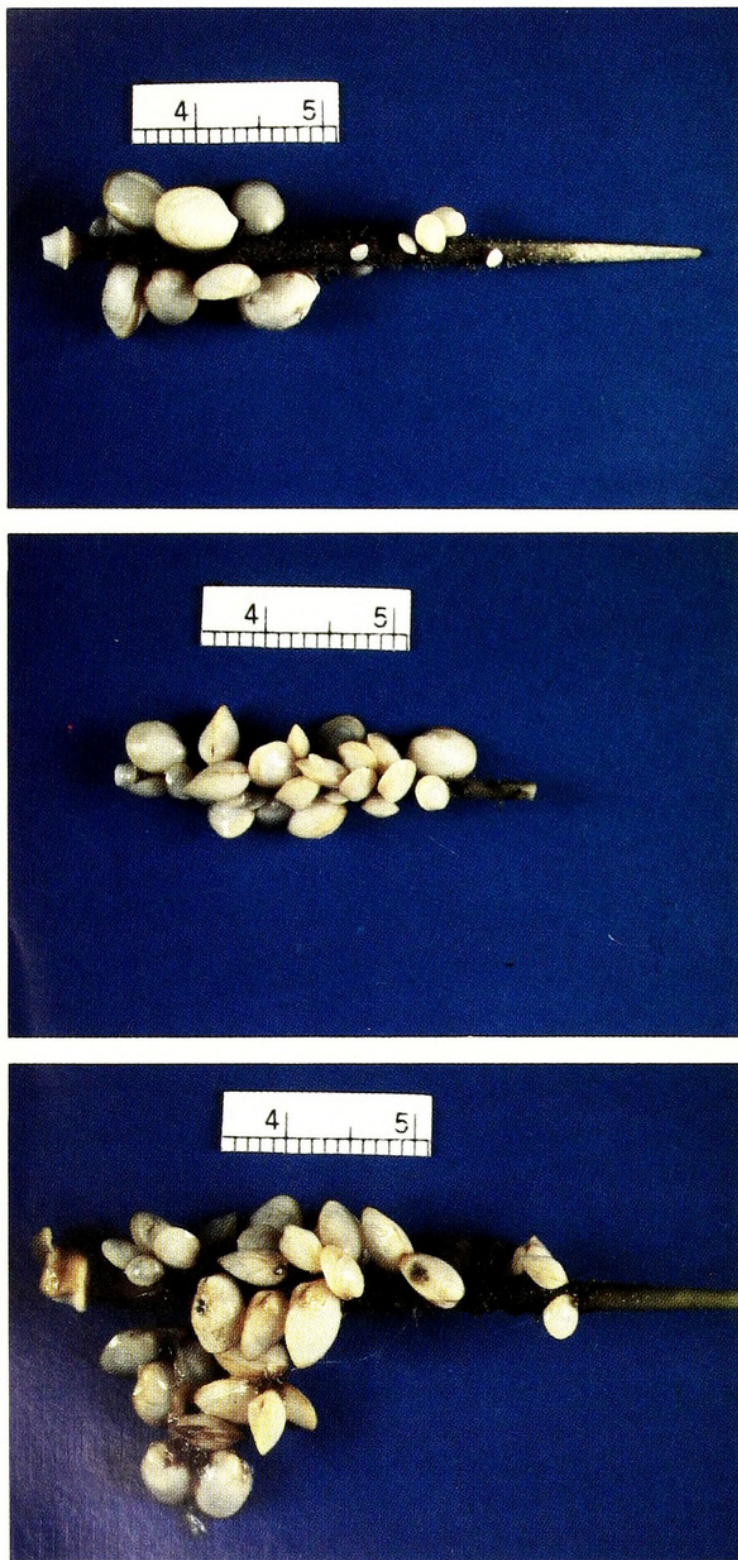


Fig. 1. *Lissarca notorcadensis* attached to sea urchin spines. Various distributions and concentrations are displayed by these three "typical" examples of spines recovered.

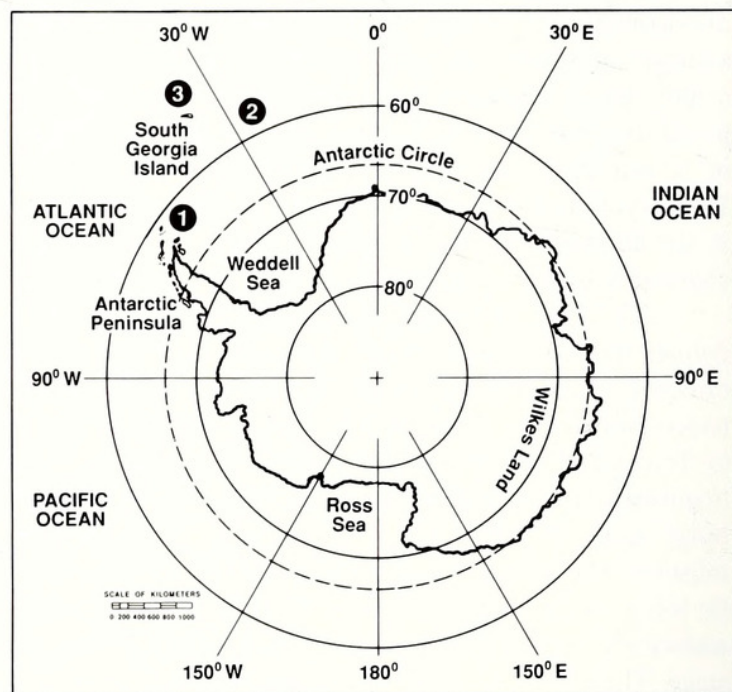


Fig. 2. Antarctic station map. Exact locations are noted in the text. Site 1, 3 January 1972 collection; Site 2, 31 May and 2 June 1975 collections; Site 3, 12 May 1975 collection.

alcohol within two weeks of collection (B. Burch, pers. comm.). They were transferred to 70% ethanol in February 1986.

To obtain specific data on sex ratios, stages of development, and reproductive and brood capacity, clams from the 3 January 1972, 31 May and 2 June 1975 samples were divided into six size classes based upon maximum height (<1.0mm, 1.0-1.99mm, 2.00-2.99mm, 3.00-3.99mm, 4.00-4.99mm, and >5.00mm). A further breakdown of size classes at the 0.5mm level was also instituted in order to resolve more finely the possibility of an ontogenetic shift in sex ratio. Fifty specimens from each size class had their length, height and breadth measured to the nearest 0.1mm. Each specimen was then opened and examined under a dissecting scope to determine sex, number of mature ova, number of nonshelled embryos, and number of shelled juveniles in brood. Maturity of ova was determined by size, mature ova being much larger than immature. Histological subsamples were taken to confirm maturity of ova. There was a clear distinction between shelled and nonshelled embryos with, in our samples, very few intermediates.

To determine if there was any segregation of stages or sex along individual echinoid spines, 15 spines from 12 May 1975, and 34 spines from 31 May 1975 were photographed carefully from two angles to expose all attached clams. These two collections were used because of their sampling time proximity. Only spines containing five or more byssally attached clams were examined. Each individual clam was numbered and the numbers keyed into similarly numbered photographs. Each numbered clam was then removed from the spine, measured to the nearest 0.01 mm and examined for sex, mature ova, nonshelled and shelled brood. Each clam was placed into one of three spine sectors determined in two ways. First, the entire spine from base to tip was divided into thirds. The distance of each specimen was measured from the base of the spine to the point of byssal attachment on the spine. These clams were then placed in categories of top, middle or bottom third of a total spine. To account for segregation *within* a population on a spine, clams were also measured in terms of their position within a particular spine population. Thus, the lowest attached clam represents the position of the lowest measurement; the highest clam on a spine represents the top measurement. With these two demarcations, the individual spine populations were again divided into thirds and clams were denoted as being in one of the three intrapopulation sectors.

Statistical evidence for our conclusions are given along with the collation of data in the results section. All statistical decisions were made at the $\alpha = 0.05$ level, however the actual probabilities in each case are also given. One way analyses of variance (ANOVA) were conducted to test for possible differences among the four specified groupings (i.e. male, female with ova, female with nonshelled embryo, female with shelled

juveniles) with respect to length, height and breadth of the clams. Tukey's Test was also conducted as a follow-up specific comparison test to determine pairwise differences among the four groups. Strength of Association measures were also calculated. One-way ANOVAs were also conducted to test for differences among sample dates with respect to the number of nonshelled embryos and number of shelled juveniles in brooding females. Since the data consisted of counts, square-root transformations were used.

Combining the data from all spines examined, chi-square tests were done to compare the groupings within populations along the bottom, middle, and top thirds of the *entire* spine and also the populations demarcated by the uppermost and lowest clam (i.e. *within* spines). Pairwise specific comparisons were conducted when the initial analysis showed significance. Further chi-square tests were performed to examine the relative abundance of each grouping within a segment of the spine.

Chi-square tests and pair-wise specific comparisons were also used to determine if different *patterns* existed between any specific grouping with respect to the distribution of clams along the bottom, middle and top third of the entire spine (and also within a population on a spine).

RESULTS

Sexes typically appear separate in *Lissarca notorcadensis* although a small percent (less than 5%) of the population examined, especially in the 3.5 - 4.0 mm size range, possess both testes and ovaries. Another indication of protandric hermaphroditism includes proportionally more males than females of smaller size. A compilation of total number of males versus females in the combined 31 May 1975 and 2 June 1975 samples reveals that approximately 73% of the mature population for the size class between 3.00 and 3.99 mm were males ($n = 159$); between 4.00 and 4.50 mm 55% were males ($n = 166$); between 4.51 and 4.99 mm 35% were males ($n = 101$); and over 5.00 mm 39% were males ($n = 31$) (Fig. 3). These numbers do not change substantially when specimens from 3 January 1972 are incorporated into the calculations (respectively males then compose 66%, 54%, 33%, no specimens in the largest size range were collected on this date). Thus there is an inversion from approximately 70% of the total population being male at sizes under 4.00 mm to about the same percent being female at sizes above 4.50 mm. About equal numbers are diagnosed as male or female in the 4.00 - 4.50 mm range. Recall it is also in this size range where we find most specimens possessing both gamete types.

An examination of mean lengths, heights and breadths for each grouping reveals a clear trend (Table 1). For all three size variables measured, the males are the smallest, the

Protandry

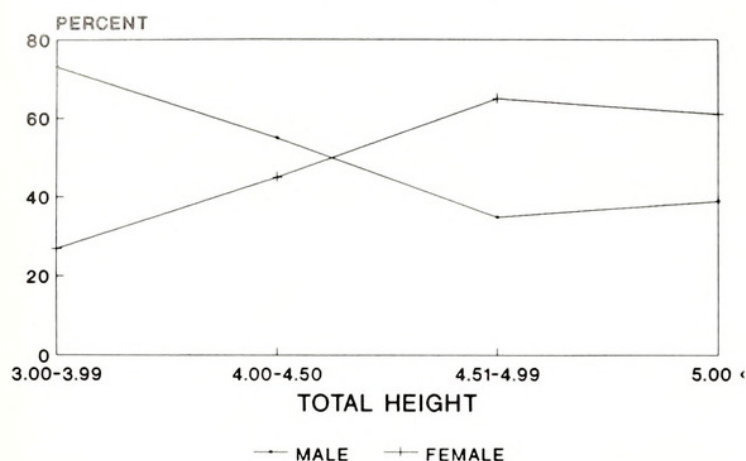


Fig. 3. Total percent male versus female in incremental size classes. The graph represents cumulative totals in each size class from 31 May and 2 June 1975. The cross-over point also represents the approximate size class that has shown the greatest number of simultaneous hermaphrodites.

females with ova are next to the smallest, brooding females with nonshelled embryos are next to the largest and brooding females with shelled juveniles are the largest. Statistically, for all three variables, males were significantly smaller than both brooding female groups, while females with ova were significantly smaller than females with shelled juveniles. Although males were not significantly smaller than females with ova and females with ova were not significantly smaller than females with embryos, the trend remains intact. As would be expected, the correlation between the three measurement variables is strong. For example, the correlation coefficient in a sample of males ($n = 110$) is 0.95 for length and height.

Strength of Association measures for length, height, and breadth respectively are 0.105, 0.125 and 0.113. This means, for example, that 10.5% of the variation observed in the length data can be accounted for by differences in the specific groupings identified, whereas 89.5% of the variation is due to the combination of the influence of other factors (e.g. environment) on length not accounted for in this analysis.

A mature female *Lissarca notorcadensis* generates relatively few (approximately 25-35) large eggs packed with

yolk. Mature eggs average 140 μm in diameter. There is little variation in number of ova produced with adult growth as most clams examined containing mature ova, contained the same approximate number. Eggs are most likely fertilized in the pallial cavity immediately after release through the paired oviducts.

Lissarca notorcadensis broods its young in the infrabranchial chamber, showing several adaptations that could enhance brooding capabilities. The filibranch ctenidium, with firm but few ciliary junctions, allows spacious volume for development of a brood of few but large embryos and juveniles. Additionally the absence of an anterior adductor produces a spacious pallial cavity for the developing brood. We suspect that the pallial current, flowing from anterior to posterior, also support brood maintenance. There are no indications of any material tissue connections to the developing brood. A preshelled embryo and shelled juvenile are the most common brood stages found in our samples (although very rarely we found partially shelled embryos with merely incipient shell formation). The two stages commonly found in our samples are found independently and do not overlap in a single brood. Both stages contain large quantities of yolk droplets. In the shelled juvenile these yolk droplets surround the developing digestive diverticula.

TEMPORAL ASPECTS. Males form about 60% of the total population of specimens collected on 31 May and 2 June 1975 but only 40% on 3 January 1972 in geographically closely situated samplings. The sample from near South Georgia had 45% males on 12 May 1975 (Fig. 4).

Taking into account the disparate years of sampling, there appears to be a decline in females brooding nonshelled young from January to June. Numbers are quite low for total females with shelled brood in January 1972 but reach a higher plateau in the May-June 1975 samples (Fig. 4). Females with mature ova in January 1972 and 12 May 1975 compose 40% of the total female population rising to over 60% in late May and early June 1975 (Fig. 4). Over 50% of the total female population in January 1972 were collected with early broods. Only 22% of the females on 2 June 1975 contained early broods. In all these data there is the problem of temporal gaps and various sampling sites that can confound the results. Nevertheless, the trends appear in our limited sample set.

DISTRIBUTION ON SPINES

Size Distribution. Size class distributions of specimens from 12 and 31 May 1975 and 2 January 1972, still attached to spines are displayed on the percentage polygon in figure 5. Clams between 2.1 - 4.0 mm in height dominate collections from 12 May 1975 ($N = 208$). The collection from 31 May 1975 ($N = 414$) shows a slight bimodal distribution with peaks in size classes between 1.6 - 3.0 and 3.6 - 5.0 mm. The

Table 1. Average (\pm S.D.) lengths, heights, and breadths (in mm) of the four groupings in cumulative samples of *Lissarca notorcadensis* ($n = 195$) from May, June 1975 and January 1972.

Grouping	Length	Height	Breadth
Males	3.98 \pm .57	4.75 \pm .89	2.64 \pm .56
Females with ova	4.14 \pm .50	5.00 \pm .87	2.81 \pm .53
Females with embryos	4.43 \pm .36	5.56 \pm .60	3.09 \pm .35
Females with shelled juveniles	4.59 \pm .40	5.81 \pm .64	3.27 \pm .39

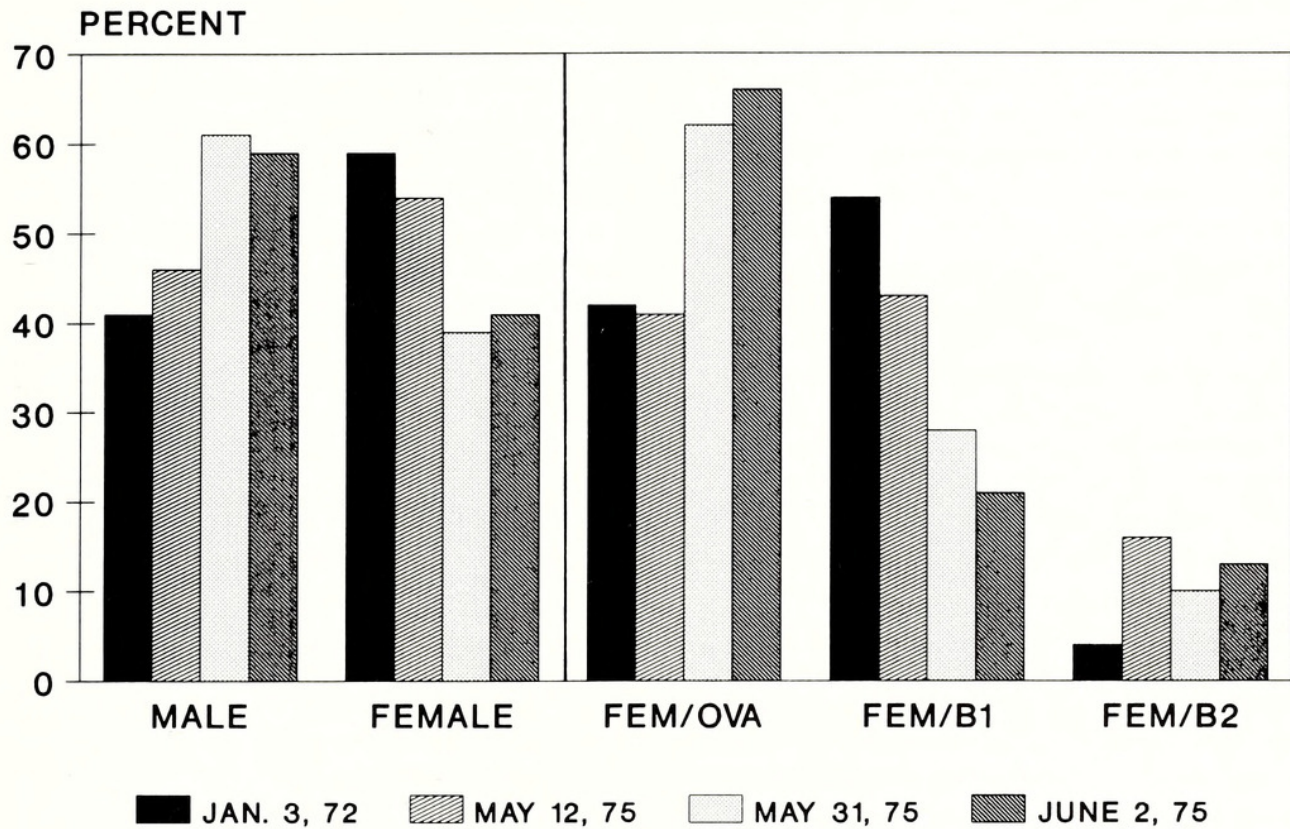


Fig. 4. Proportion of male versus female clams from the four collection dates. The two groups of bars to the left of the vertical line compare total male and female. To the right of the vertical line, the bars represent the break-down of stages of females only. Thus, for 3 January 1972, about 42% of all females had mature ova. FEM/OVA = females with mature ova; FEM/B1 = females with nonshelled brood; FEM/B2 = females with shelled brood. 3 January 1972, N = 85; 12 May 1975, N = 348; 31 May 1975, N = 575; 2 June 1975, N = 187.

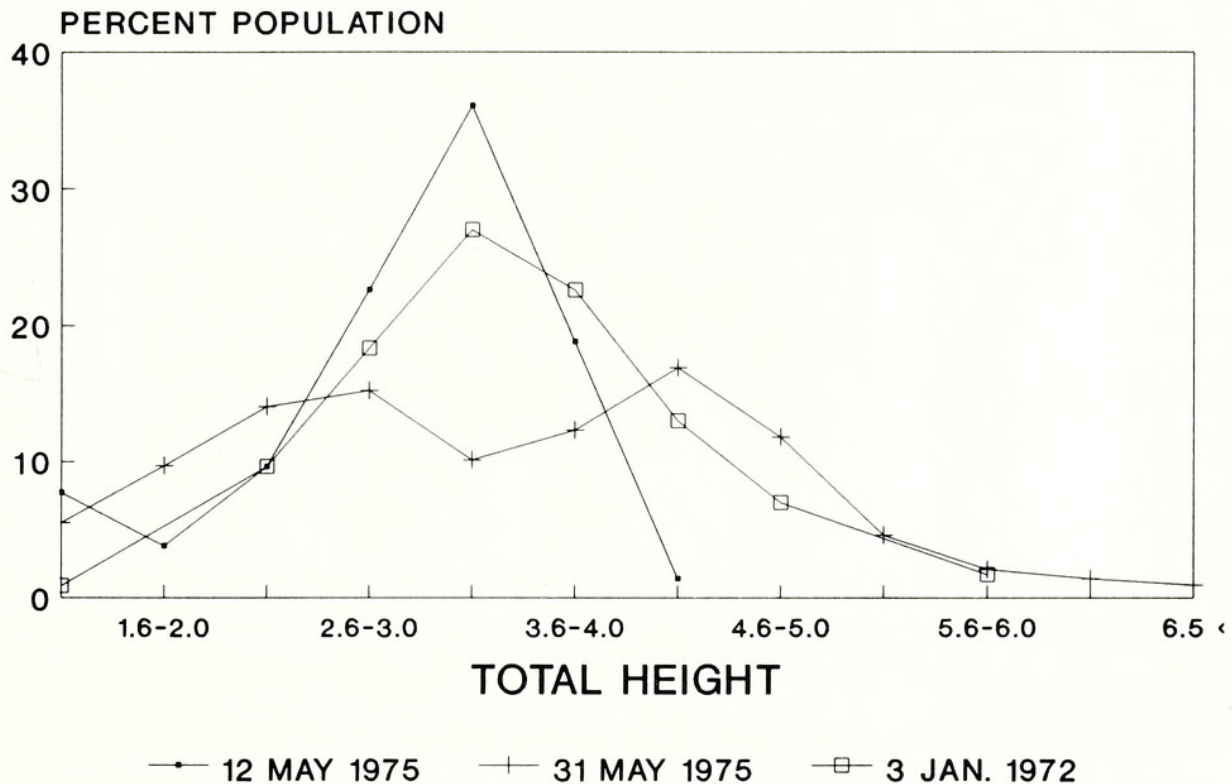


Fig. 5. Length percentage polygon for populations occurring on spines only at three collection dates. The x-axis represents total height in mm; y-axis percent of total population from specific collection date.

size distribution of the January 1972 collection ($N = 115$) is similar to that of 12 May 1975 in that 77.5% of the 12 May 1975 population examined falls between 2.6 and 4.0 mm length and 67.9% of the January 1972 collection falls into the same size range. Only 37.6% of the 31 May 1975 population falls into this size range and it is only this population, as well, that has adults forming a substantial component above the 5.1 mm length.

Sex and Stage Distribution. For the 49 spines analyzed (Fig. 6), a trend for the *entire* spine distribution of decreasing numbers of clams from bottom to top third of the spines was detected for all groupings. Indeed, except for immature clams, more clams are found on the bottom third of the spines than the upper two thirds combined. In general, few clams were found on the upper third of the spines. Figure 7 diagrammatically shows the distribution and significance of all groupings analyzed along the entire spine. A similar representation is seen in figure 8 for *within* spine population distribution.

Even though all groupings exhibited the same general trend of decreasing numbers from bottom to top third, the data were examined further for possible differences between groupings in the relative "steepness" of the overall decreas-

ing pattern. No significant difference was found in the distribution pattern of clams among the bottom, middle and top third of the entire spine between males and total females ($p > .18$), males and females with ova ($p > .87$), females with nonshelled embryos and females with shelled juveniles ($p > .93$), total females and immature clams ($p > .05$), females with embryos and immature clams ($p > .50$), females with shelled juveniles and immature clams ($p > .66$), females with ova and all brooding females ($p > .23$) and all brooding females and immature clams ($p > .39$). A significant difference, however, in the pattern was found between males and all brooding females ($p < .04$), males and immature clams ($p < .001$) and females with ova and immature clams ($p < .03$). A significantly greater proportion of males than brooding females was found on the bottom third compared to the top third of the spines ($p < .01$) and also on the middle third when compared to the top third ($p < .05$). No difference in distribution pattern was significant for these two groupings when comparing the middle with the bottom third of the spines ($p > .49$). A significantly greater proportion of males than immatures was found on the bottom third compared to the middle ($p < .004$), on the bottom compared to the top ($p < .001$) and on the middle compared to the top ($p < .03$). A significantly greater proportion of females with

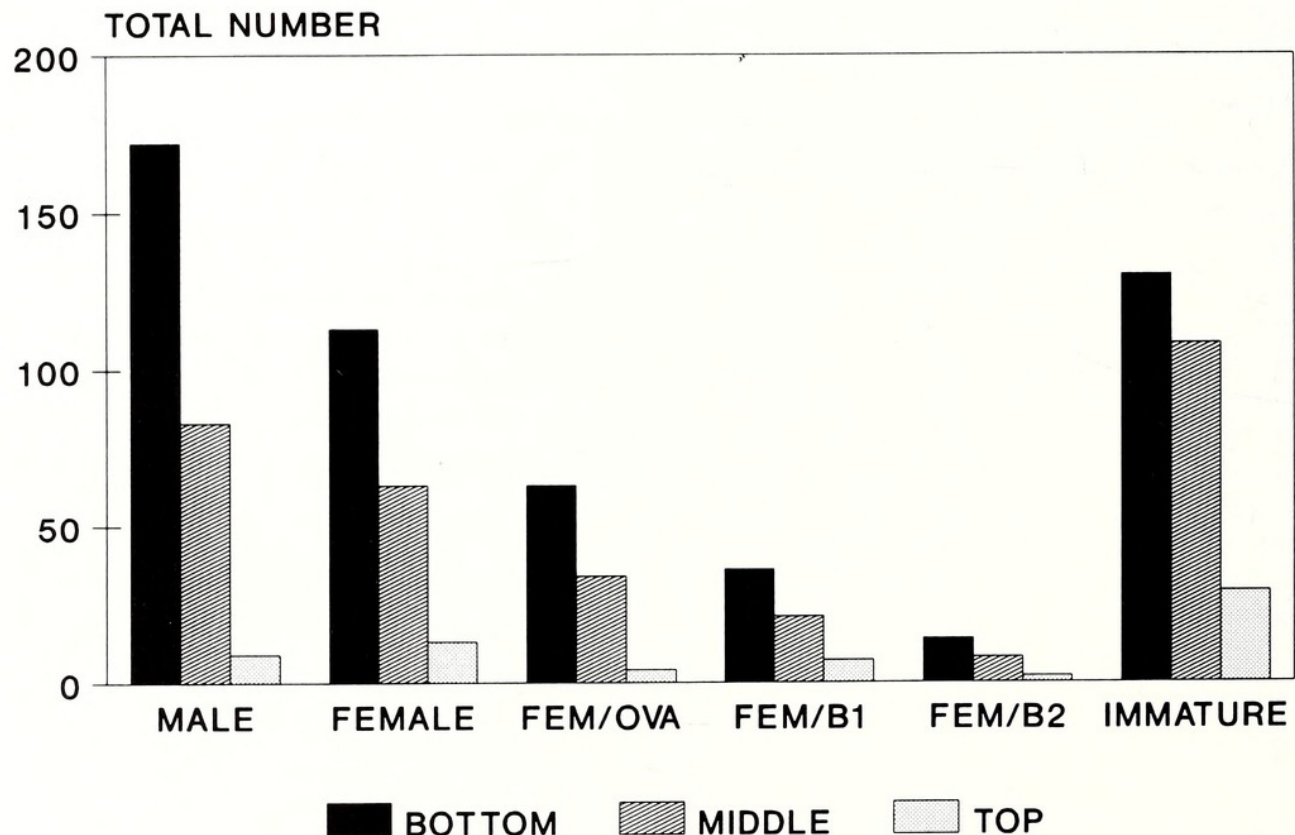


Fig. 6. The distribution of clams along total spine sectors. Bottom = bottom third of total spine; Middle = middle third of total spine; Top = top third of total spine. y-axis is total number of clams of specific stage or sex. FEM/OVA = females with mature ova; FEM/B1 = females with nonshelled brood; FEM/B2 = females with shelled brood; Immature = clams, usually less than 3.0 mm in height, with nondifferentiated gametes. 49 spines analyzed from 12 and 31 May 1975.

ova than immatures were found on the bottom third compared to the top ($p < .02$), however the distribution patterns of these two groupings were not significantly different when comparing the bottom with the middle ($p > .08$) and comparing the middle with the top ($p > .13$).

Examining the bottom third of the spines, the region with the greatest concentration of clams, reveals that there is a progressive decline in total number from male to total female ($p < .05$) and, within females, from mature females with ova to females brooding nonshelled embryos ($p < .05$) and shelled juveniles ($p < .05$) (Fig. 6).

Because spines only infrequently have clams attached along their entire length, separate measurements of abundance were taken by dividing the length of spine that did contain clams into thirds. This accounts for what we have termed *within* population distributions. Figure 9 denotes the cumulative distribution of clams on 49 spines for 12 and 31

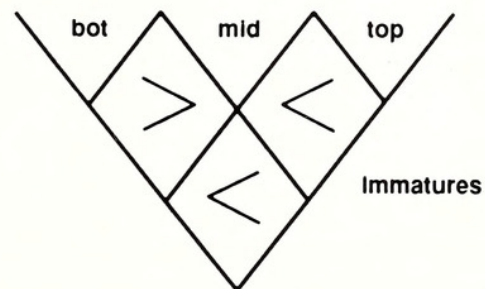
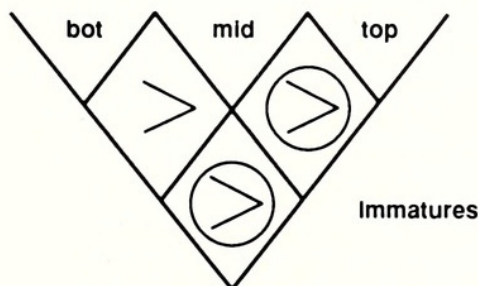
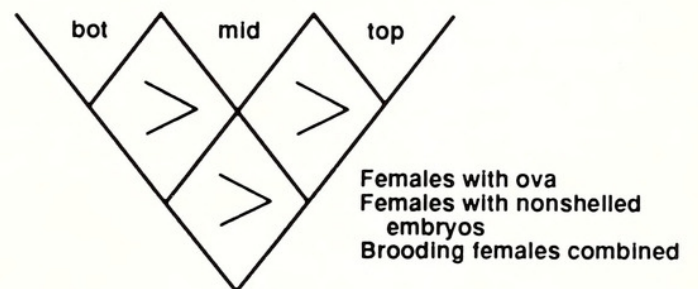
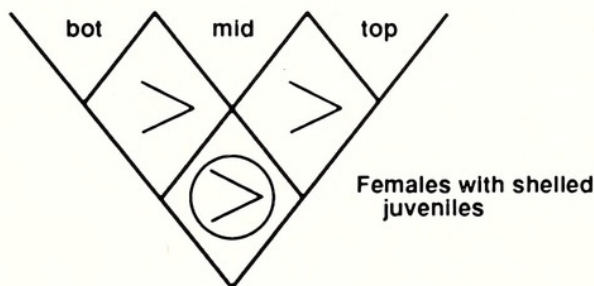
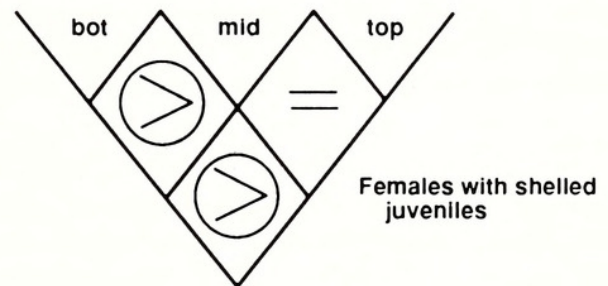
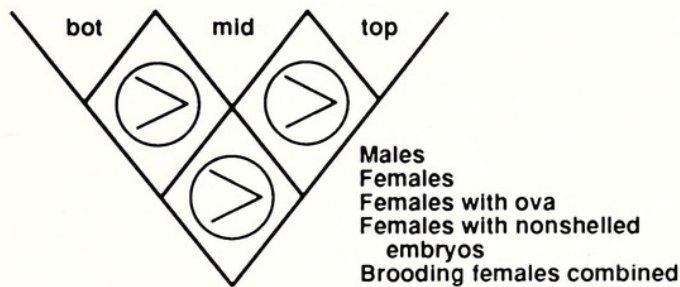
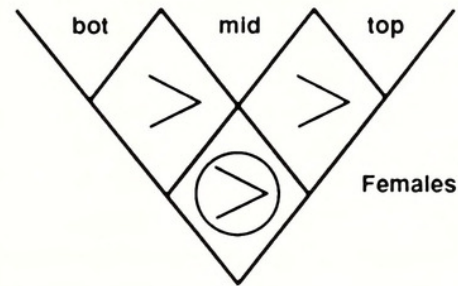
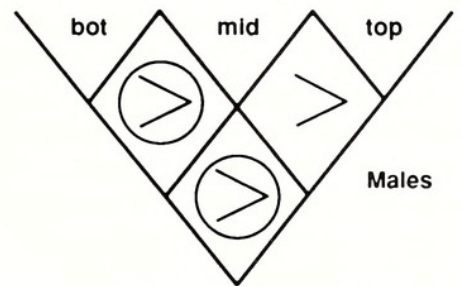


Fig. 7. A diagrammatic representation of clam grouping distributions along entire spine length. Bot = bottom third of spine, Mid = middle third, Top = top third; > = greater than, < = less than, circled symbols are statistically significant.

Fig. 8. A diagrammatic representation of clam groupings distributed *within* a given spine population. Symbols and abbreviations as in figure 7.

May 1975. The trend seen on the *entire* spine of decreasing numbers of clams from bottom to top is not exactly seen in the *within* spine populations (compare Figs. 7 and 8). Some of the groupings were more evenly distributed within the spine. Figure 10 shows distribution of each grouping on the spines compared against themselves, with the exception of juveniles, again demonstrating the reduction in numbers with ascent on the spine.

Possible differences between groupings in distribution patterns of clams among the bottom, middle and top thirds within the spine population were also checked. No significant differences were found in the distribution patterns between males and females ($p > .34$), females with ova and all brooding females ($p > .64$), males and all brooding females ($p > .84$), females with nonshelled embryos and females with shelled juveniles ($p > .24$), males and females with ova ($p > .23$), females with ova and immature clams ($p > .15$) and females with embryos and immatures ($p > .16$). A significant difference in pattern was found between males and immatures ($p < .05$), brooding females and immatures ($p < .05$) and females with shelled juveniles and immatures ($p < .05$). Except for the comparison between males and immatures, all of these significant pairings are different than those found to be significant for the *entire* spine. Similar to the earlier test for the entire spine, a significantly greater proportion of males than immatures was found in the

bottom third compared to the top third ($p < .001$) however no statistical difference was exhibited between the middle and top ($p > .09$). A greater proportion of females than immatures was found in the bottom third compared to the top ($p < .01$) and more in the middle than the top ($p < .05$). No significant difference was observed between the bottom and middle ($p > .45$). A greater proportion of all brooding females than immatures was observed in the bottom third of the population than the top ($p < .01$) but no difference in pattern was detected for these two groups between the bottom and middle ($p > .27$) and between the middle and the top ($p > .14$). This same result is exhibited when comparing females with juveniles and immatures. Since females with shelled juveniles are a part of the grouping of all brooding females, the previous result could be due to the overriding influence of the females with juveniles in this grouping. In particular, a greater proportion of females with juveniles than immatures was observed in the bottom third than the top ($p < .05$), however no differences were detected between the bottom and middle ($p > .05$) and middle and top ($p > .77$).

Brood Distribution. Table 2 shows the average number of nonshelled embryos and shelled juveniles found in broods from each collection. The average number of nonshelled embryos within a brooding female was significantly higher in the 31 May 1975 sample (avg. = 14.4) than in either

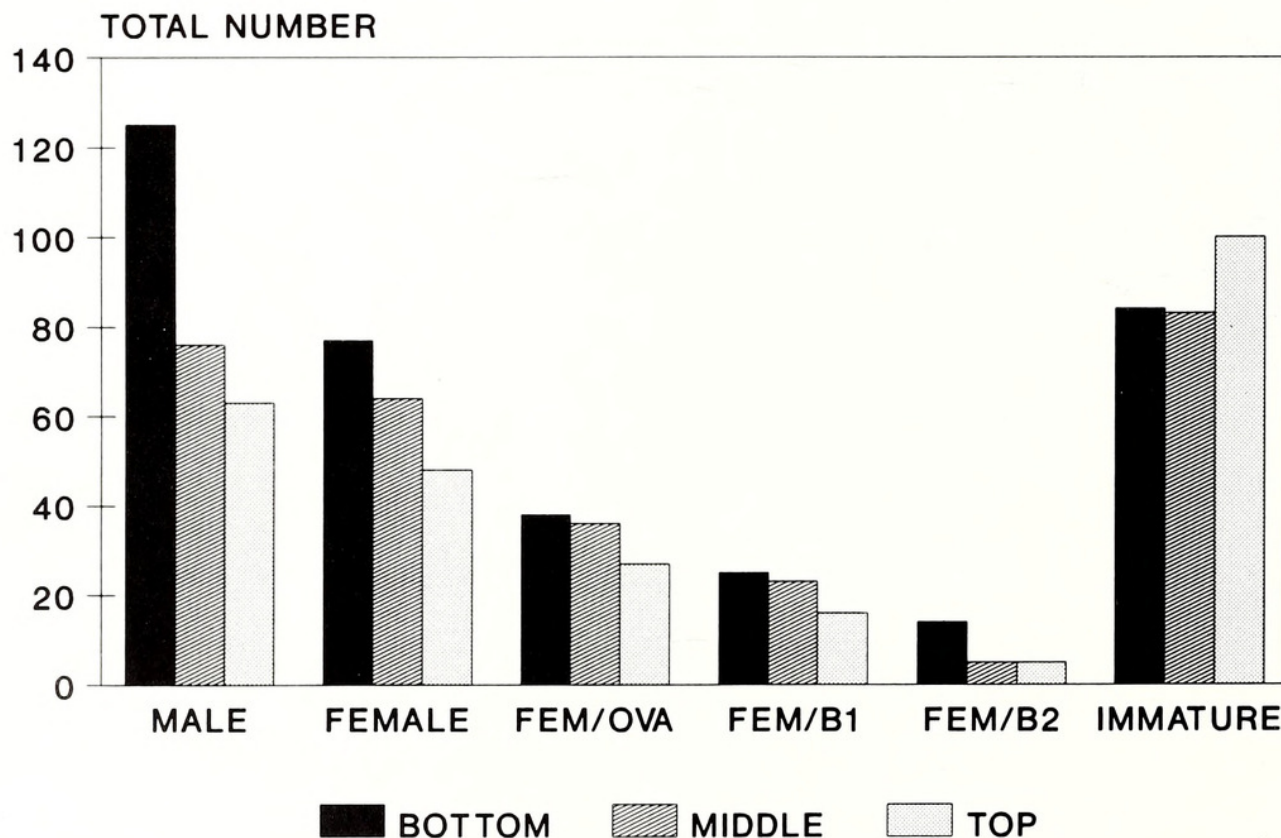


Fig. 9. Total number of clams in each sector from each sex and stage within population on echinoid spines. 49 spines analyzed from 12 and 31 May 1975.

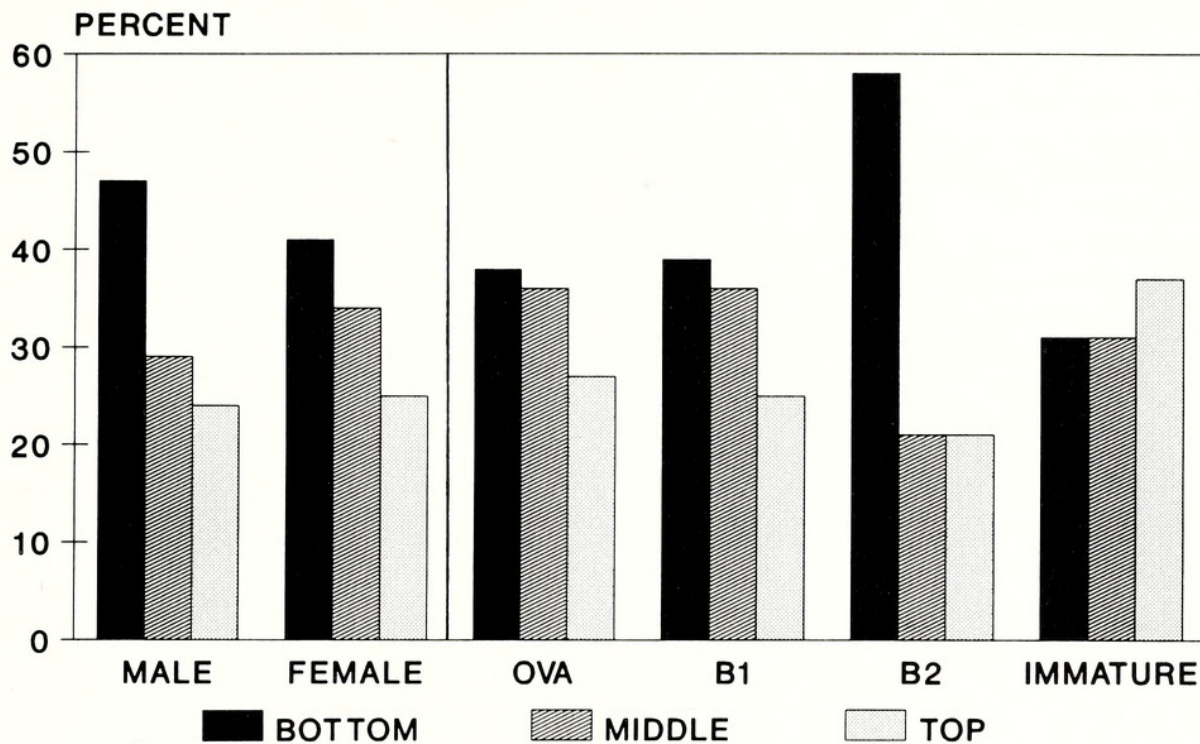


Fig. 10. Percent of total sex and stage in each sector of echinoid spine. Bars for females with ova, nonshelled and shelled brood, represent percent of total female population, not total population. Population as per figure 6.

the 2 June 1975 (avg. = 10.9, $p < .05$) or 12 May 1975 (avg. = 9.5, $p < .05$) samples. Furthermore, the 3 January 1972 sample (avg. = 12.9) is significantly higher than the 12 May 1975 sample. There are no statistically significant differences between the 31 May 1975 and 3 January 1972 samples, between the 2 June 1975 and 3 January 1973 samples, or between the 2 June 1975 and 12 May 1975 samples.

In contrast, when comparing the number of shelled juveniles within a brooding female among the sample dates, no significant differences were found ($p > .05$). The 3 January 1972 sample was not included in the analysis since it contained only a single adult brooding shelled juvenile.

PROPOSED LIFE CYCLES

Based on samples from 3 January 1972, 31 May and 3 June 1975, the following life cycle is proposed for *Lissarca notorcadensis* (see Fig. 11). Fertilization occurs in the mantle cavity after release of mature eggs in the early austral summer or late spring. During the summer, when females dominate in total numbers over males, many females are brooding early stage, nonshelled embryos. Shell development begins during the late summer and early autumn with simultaneous redevelopment of mature ova. Many females brooding late stage young also possess mature ova. In late autumn and early winter, males dominate females in abundance and ova are fully developed. Among females, those with mature ova dominate at a time when males dominate the total population. Shelled juveniles are released in late winter to early summer. Only a single adult was found

brooding shelled juveniles in the January 1972 sample.

This basic cyclic trend (Fig. 11) is superimposed on populations where each stage can be found at some level in the population year round and is characteristic for stations sampled in January 1972, and 31 May and 2 June 1975. That for the 12 May 1975 sample is slightly offset, possibly reflecting the proximity to South Georgia. It is possible that the conversion of some portion of the population from males to females also occurs at a specific season, perhaps just after austral summer, accounting for some of the differences in sex and stage noted. Some of the basic features of this life cycle are noted in Table 3 along with a comparison of the same features for *L. miliaris*.

DISCUSSION

The Antarctic Ocean benthos, below the 33 meter limit of anchor ice formation, offers a rich and diverse assemblage including close to 900 species of molluscs (Moss, 1988). Most of our knowledge of the benthos reflects research that has occurred over the past three decades. Many collected materials have been deposited in various museums and much remains to be discerned from these stored collections that essentially remain untouched.

The Smithsonian Institution Oceanographic Sorting Center represents a rich repository of historical collections of Antarctic molluscs. Many of these collections were obtained during expeditions of the early to mid-1970s. The present research examined specimens available from those

Table 2. Average number (\pm S.D.) of nonshelled embryos and shelled juveniles retained in brood of females from various sampling times and sites. The collection for 12 May 1975 is adjacent to South Georgia Island. The other collections are closer to the Antarctic Peninsula. Note that the 3 January 1972 sample had only a single female brooding shelled juvenile.

Date	N	Average number of nonshelled embryos	N	Average number of shelled juveniles
3 Jan 1972	24	12.9 \pm 4.1	1	10.0
12 May 1975	32	9.5 \pm 2.7	15	8.9 \pm 2.5
31 May 1975	35	15.1 \pm 4.2	27	10.4 \pm 4.9
2 June 1975	17	10.9 \pm 3.2	10	9.0 \pm 3.1

collections and as such was limited to samples outlined in the methodology. Before discussing the results per se, we must ask, can we lend confidence to interpretations based on a rather disparate set of Antarctic collections? The tentative answer is yes, at least until we have a more complete set of data with more closely set samples over a much longer period of time and from more defined benthic sites. Additionally, the clear clues offered in the analyzed data set in conjunction with data from the work of Richardson (1979) on *Lissarca miliaris*, lends additional credence to our speculation. *L. notorcadensis* offers a classic example of a polar brooder leaning heavily towards the "k-selection" side of an r-K continuum [as designed by Pianka (1970)]. K-selected species vie for maximum competitive ability in a "saturated" environment (as outlined by Southwood, 1977) with slow growth, delayed maturation, iteroparity, low fecundity and large yolky eggs. It is recognized, however, that an examination of living populations through time is called for to refine our concept of reproductive ecology of this philobryid.

Berkman *et al.* (1991) examined recently the planktotrophic development of the Antarctic scallop *Adamussium colbecki* (Smith) and suggest that various anatomical features prohibit brooding. Included in these restraints are a filibranch gill without "strong tissue connections", an open mantle cavity without mantle edge connections, and a lack of siphons. Considering these same characters in *Lissarca notorcadensis*, it is doubtful that these inhibit internal pallial brooding. *L. notorcadensis* brood their young in their relatively spacious infrabranchial chamber. Increased volume for brooding results from a lack of anterior adductor muscle and a reduced outer ctenidial demibranch. We suggest that flexibility of the filibranch ctenidial filaments allows the growing brood to essentially impinge upon the gills without disruption of function. The ctenidial filaments are relatively short but "stout". Burne (1920; p. 238), in fact, suggests that the gills "present a somewhat embryonic appearance." The anterior flow of pallial water across the gills, as discerned for other philobryids by Tevesz (1977) and Morton (1978), can serve to efficiently aerate the developing young, which presumably

are retained in brood for an extended period of time.

Large yolky eggs, as found in *Lissarca notorcadensis*, are typical of direct developing bivalves (Matveva, 1978). Similarly large eggs are found in other brooding philobryids (eg. *L. miliaris*; Richardson, 1979) as well as several other brooding bivalves including species of *Lasaea* Beauchamp, 1986; McGrath and Ó Foighil, 1986), *Transennella tantilla* (Gould) (Asson-Batres, 1988) and *Kellia suborbicularis* (Montague). Thorson (1950) suggested that eggs of many polar marine invertebrates are large and have dense concentrations of yolk. This suggests that reproduction in polar habitats is expensive energetically and would require large energy stores (Clarke, 1979). Vance (1973a, b) suggested that it is more efficient to produce fewer but larger eggs in a uniform, stable environment as opposed to a variable or unstable environment. The large and yolky eggs of the philobryids, once fertilized, give rise to slowly developing young that are retained in the pallial cavity past prodissoconch stages and into an early dissoconch stage. When released, the young of *L. notorcadensis* have a full complement of organs including a nearly complete digestive system. They retain, however, a quantity of yolk that surrounds the developing digestive diverticula. It is not certain whether the newly released brood actively feed but it is unlikely. Similar stores of apparent nutrients (yolk) in released young are also found in direct developing *Lasaea* (Ó Foighil, pers. comm.) and in another Antarctic bivalve, *Kidderia subquadratum* Pelseneer (Shabica, 1974). In the latter, Shabica (1974:59) also found that "digestive diverticula of the embryos remain nondifferentiated until approximately two months post-liberation suggesting that no active uptake of particulate nutrients occurs while the embryos are developing within the maternal organism or even immediately after liberation." Additionally Shabica found that "large amounts of yolk" were widely distributed in the early

Table 3. Comparative data for *Lissarca notorcadensis* and *L. miliaris*. Data for *L. miliaris* is adapted from Richardson (1979). Sex size ratio signifies comparative sizes of males and females at various stages. Sex ratio indicates total number of male versus female. ¹See text for clarification.

	<i>L. miliaris</i>	<i>L. notorcadensis</i>
Depth	5-9 m (to 121 m)	100-400 m (to 1000 m)
Maximum height	6.0 mm	7.0 mm
Height at maturity	2.5 mm	2.9 mm
Brooding height	3.1 mm	3.6 mm
Average brood	60	9
Brood range	54-70	6-16
Pre-release size	0.57 mm	1.1 mm
Sex size ratio	1:1	female > male ¹
Preshelled brood	Feb. - July	Summer (Jan.; some year round)
Partial shelled	Aug. - July	
Shelled brood	Nov. - Dec.	By May
Recruitment	Dec. - Feb.	June - Dec. ¹

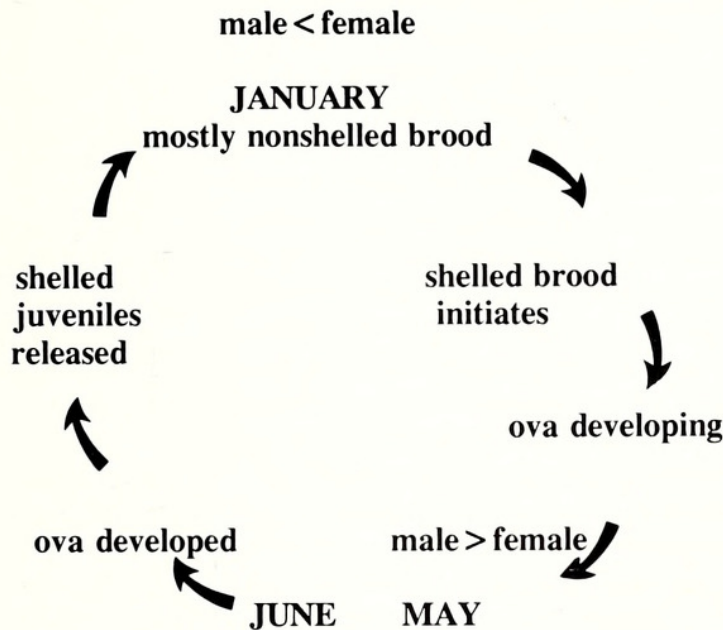


Fig. 11. Proposed life cycle for *Lissarca notorcadensis*.

embryo of *K. subquadratum* but later surrounded developing organs. In fact, as noted by Shabica (1974:iii), yolk was still present in newly released embryos, which can continue development "...at least for short periods, outside the maternal organism." We have predicted that *L. notorcadensis* release shelled brood in late winter to early summer. In cases where the brood is released in later winter, these presumed nutrients may well serve to satisfy nutrient requirements prior to the end of the austral winter and up to a time when primary production increases in the Southern Sea. It is also possible that the final stages of development occur post-release as they do in *K. subquadratum*. On the other hand, Ralph and Everson (1972) speculate that the brooded young of another Antarctic bivalve, *K. bicolor* (Martens), could remain in the parental mantle cavity for "their first winter" prior to release. This is certainly possible for *L. notorcadensis* as well and in fact the dissoconch shell deposited prior to release could indicate this extended brood. There is, however, no way of knowing with certainty until monthly samples are available.

The brood of *Lissarca notorcadensis* develops synchronously, as in the intertidal Galeommatoidean *Lasaea rubra* (McGrath and Ó Foighil, 1986). Prior to brood release, the developing young have all deposited significant dissoconch shell material and young are released as juveniles. Numerous females examined that contained developing broods were also well into a renewed oogenesis cycle (unpub. data). There appears to be a decrease in number of mature ova to early nonshelled brood and finally shelled juveniles. Unlike *L. rubra* (McGrath and Ó Foighil, 1986) and *L. miliaris* (Richardson, 1979), ultimate brood size in *L. notorcadensis* is very small and is independent of adult size. The smallest as well as the largest specimens averaged 9.4 shelled young. Similarly, there was an average of 12.1 nonshelled young in broods of com-

parable sized animals and these in turn were generated from a potential field of at least 25 eggs. The decline is specifically unaccounted for but we assume a loss once eggs are released into the infrabranchial chamber which is essentially open to the environment since the adult mantle edges remain unfused. Decline in the potential number of recruits was noted by Shabica (1974) who discussed "sloughing-off of eggs" in the brooding Antarctic bivalve *Kidderia subquadratum*.

Young of *Lissarca notorcadensis* are released presumably from the pallial brood chamber directly into their parent's microhabitat. At time of release the byssal gland is fully functional and young can attach immediately to either the home spine or the shell of another member of the population. In either case, the young are released into the immediate vicinity of the adult and hence obtain whatever benefits are derived from this microhabitat. An association between bivalve and sea urchin is not unique to this philobryid. *Axinodon symmetros* (Jeggrens) is, for instance, associated with deep water echinoids (Ockelmann, 1965). The symbiosis for *L. notorcadensis* appears to be commensalistic with the bivalve being held above the sediment and in the water column where filtration efficiency could be increased due to lack of sedimentary interference. Additionally, the bivalves obtain a ready dispersal agent while nestled among protective spines. Dell (1965) suggests that the epifaunal habits of some small Antarctic organisms on motile hosts is related to the "lack of motile larval stages" (Dell, 1965). The lack of other hard substrata must also be a factor in deeper waters.

According to Fretter and Graham (1964), dioecious species of molluscs often have more females than males. They suggest this is related to males dying at a younger age or size. This could be the case in *Lissarca notorcadensis* but, like several other small brooding bivalves, such as *Transenella tantilla* (Kabat, 1985; Asson-Batres, 1988), *L. notorcadensis* could be a protandric hermaphrodite. Evidence for this includes the comparatively larger females found in the populations examined and the cross-over at around 4.0 mm height (probably more than coincidentally also the size range where we located several simultaneous hermaphrodites) from male to female dominated populations. *T. tantilla* show male dominance up to a size of 3.5 mm with females ranging from 3.5 - 7.0 mm in length (Kabat, 1985). It is possible that all specimens found on a single spine are members of the same family line. This, of course, could limit outbreeding. Protandry would, on the other hand, increase reproductive success by insuring availability of members of both sexes.

Ockelmann and Muus (1978) found that several species of the Montacutidae show reverse geotactic responses just prior to release of their larval brood. Thus, for example, *Mysella bidentata* (Montagu), a normally infaunal bivalve, becomes negatively geotactic and will emerge from the sediment and crawl upward upon available vertically oriented objects. Upon reaching the highest point available, the veliger

brood is released. Ockelmann and Muus (1978) suggest this behavior is stimulated by a "specific substance released by the young when they become ready to begin life on their own." Most specimens of *Lissarca notorcadensis*, including reproductively active adults, occur on the lower portions of the host spines. There are two likely explanations for this relationship. First, there could be an inherent or external stimulus that attracts males and females to the lower third of the spine. Extrinsically there could be a stimulus released by the surface of the urchin that attracts males and mature females or perhaps these specific bivalves are positively geotactic. On the other hand, there could be an intrinsic stimulus, such as endocrine or hormonal shifts, that are activated when either males or females reach maturity and these chemical shifts stimulate a downward migration. Similarly, one sex or stage could preferentially react to stimuli indicated above and in turn "attract" the other sex through an allelochemic interaction.

A second possible explanation is that males preferentially remain near the spine's bottom third and, being protandric hermaphrodites, a conversion of sex would result in a preferential appearance of more mature females along the spine base as well. The positioning of mature males and females along the basal third of the spine would, of course, promote successful fertilization. Brooding females are not preferentially clumped along any region of the spine. This could be indicative that brood are released along the length of the spine as a result of an upward migration of many of the brooding females after fertilization near the spine's base.

There is also an apparent seasonal influence in terms of sex dominance. As noted in the results, there is a transition of dominance from close to 60% male in May and June 1975 to about 40% in January 1975 and 45% on 12 May 1975 at a very different site. By eliminating the 12 May 1975 sample, which is situated close to the north side of South Georgia Islands (see Fig. 2) thus strongly influenced by this land mass, certain trends relegated to an austral summer and spring become clearer (Fig. 12). According to Dell (1972) the South Georgia area represents a distinct biogeographic subdivision of the Antarctic Region. This site is north of the Antarctic convergence and represents a milder climate (see Simpson, 1976). In fact, South Georgia is the northernmost distribution limit for many Antarctic species (Dell, 1965) and the northern side of the island is especially productive (DeWitt *et al.*, 1976). Thus this single site of the four sampled is placed in the South Georgian District (Dell, 1972) and results of a reproductive ecology study might be expected to differ from the other three. Another interesting difference between the two May samples is in size class distribution. The 12 May sample, again from South Georgia, contained no specimens larger than 4.5 mm in length. All other samples had larger bivalves and that from 31 May 1975, in fact, had about 20% of its population longer than 4.5 mm. It is again possible that the less stable and more seasonal South Georgia site could yield bivalves that grow slower. What is more likely is that this population is on the distributional fringe for this species and thus is subject to an earlier demise. The other three sample sites are placed in the Continental Antarctic Division

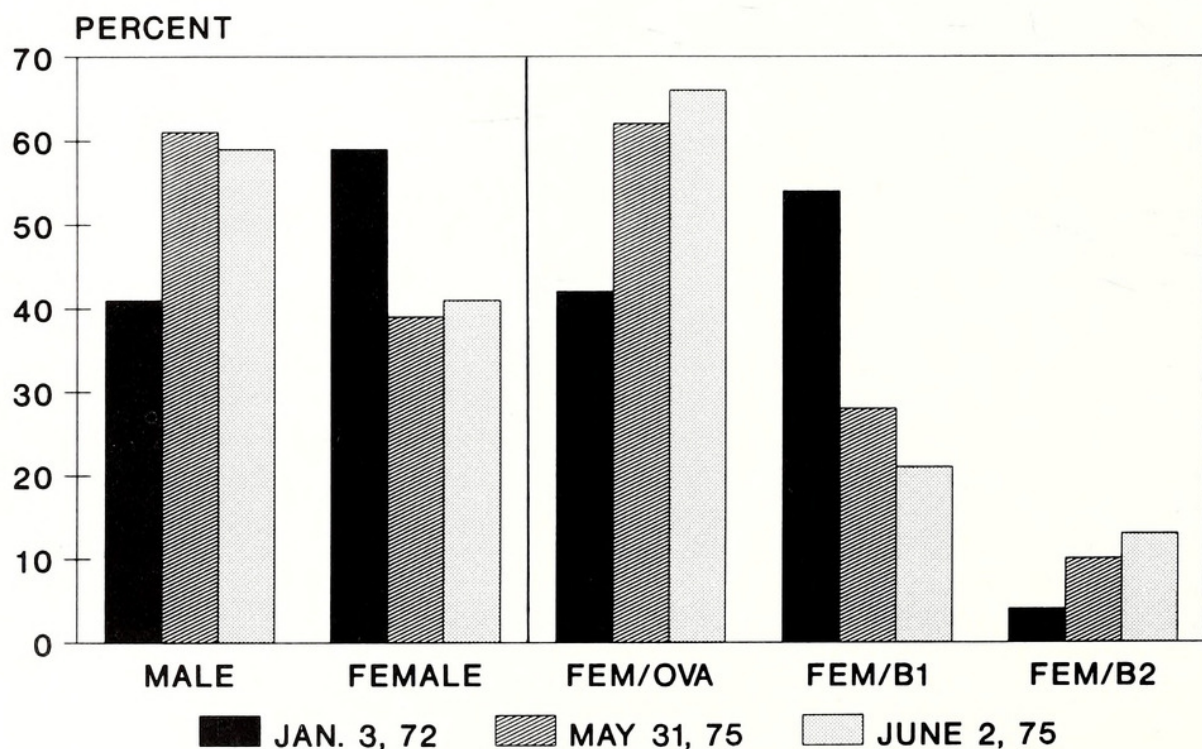


Fig. 12. Removing the 12 May 1975 (South Georgia Island) sample, more easily shows specific trends outlined in text. Again, female stages to right of vertical line represent percent of total female population only. Population numbers as per figure 4.

(Dell, 1972). The 31 May and 2 June 1975 samples are very similar to each other and clearly different from January 1972. This holds true for all stages sampled (Fig. 4).

An additional difference of some note is that of total size class distribution between 12 and 31 May 1975 and 3 January 1972. Specimens sampled on 12 May 1975 show a unimodal distribution with most specimens being between 2.6 and 4.0 mm in height. The January 1972 sample shows a similar distribution. The sample from 31 May 1975, however, has a more uniform distribution with a strong indication of bimodality (see Fig. 5). We have little information on growth rates for any philobryid. Extrapolating from commarginal lines and incremental growth measurements, Richardson (1979) suggested that *Lissarca miliaris* deposited growth rings slowly, with only one ring deposited in 3 - 15 month old clams. Indeed, Nicol (1966) suggested that, along with small size of Antarctic bivalves, these organisms are slow growing and this is indicated by numerous, narrowly spaced growth rings. Although *L. notorcadensis* is almost certainly slow growing, with growth rings already deposited in its dissoconch shell prior to release from the brood, it is difficult to extend the measurements suggested by Richardson to this philobryid. A recent review by Bourget *et al.* (1991), in fact, casts doubt on many reports that use shell growth marks to determine or substantiate bivalve age.

The differences and similarities in population size classes between *Lissarca notorcadensis* and *L. miliaris* are perhaps reflective of temporal and environmental differences as discussed elsewhere in this paper. At this point it is uncertain if the bimodal distribution represents a failed reproductive event or a natural depression in seasonal reproduction in an iteroparous bivalve reproducing more than once per year.

The philobryids are a relatively speciose and common component of the Antarctic malacofauna and yet there is very little information available on their reproductive ecology aside from Richardson's (1979). Data have been extracted from that paper for comparative purposes and are outlined on Table 2. Most importantly, any comparison drawn between these two species must be done in light of the fact that Richardson used a population of philobryids attached to a brown alga from waters less than 10 m in depth (although this species can reach depths to 121 m). Specimens of *L. notorcadensis* examined here are from waters no shallower than 110 m (this philobryid has been collected from depths as deep as 1000 m). Ice scouring is an important factor controlling shallow water fauna of Antarctica down to depths of 15 m (Moss, 1988). *L. miliaris* is restricted to protected embayments of the near sublittoral zone. Additionally, Richardson's samples of *L. miliaris* were obtained from within the bounds of the Weddell Drift, a highly productive zone of the Southern Ocean (Moss, 1988).

The two philobryids attain approximately the same maximum size although *Lissarca miliaris* reaches sexual

maturity at a slightly smaller size than *L. notorcadensis*. Additionally, *L. notorcadensis* is larger when it reaches brooding size. In the more heterogeneous shallow waters inhabited by *L. miliaris*, it might be predicted that fecundity would be higher. *L. miliaris* broods 54 to 70 juveniles, directly increasing in number with adult size. *L. notorcadensis*, on the other hand, broods a consistently smaller number regardless of adult size. Size of juveniles at release reflects the differences in brood number. Pre-release size for juveniles of *L. miliaris* is half that of *L. notorcadensis*. This of course reflects specifically the volume available for brood in the two species and the number of young able to be packed into the infrabranchial chamber.

There appears to be no size difference between males and females of *Lissarca miliaris* while this varies in *L. notorcadensis*. In the latter, females reach a larger size than males, perhaps reflecting protandry as discussed above. It is clear that brooding females in *L. notorcadensis* are larger than males as well as sexually mature but nonbrooding females.

The general life cycles of the two species have some basic similarities in terms of development but there are important temporal differences noted in the populations examined. Preshelled young are evident from February to July in *L. miliaris* but likely dominate in the austral summer for *L. notorcadensis*. In the latter species, however, some preshelled brood are evident in all samples examined. Fully shelled juveniles dominate from November to December in *L. miliaris* and can be found at some level in all our samples of *L. notorcadensis* but are presumed dominant in May and almost absent in January. Recruitment for *L. miliaris* and *L. notorcadensis* is from December to February and likely June through December respectively. The latter significant time shift again seems to reflect habitat differences in populations studied. Pearse *et al.* (1991) review the contrast in the "physically unstable shallow benthos" and the "physically stable deeper benthos". In oligotrophic waters deeper than 20 - 30 m many benthic invertebrates produce pelagic lecithotrophic larvae that yield larger juveniles more resistant to predation pressures. *L. notorcadensis* extends this to release of brooded juveniles that are not only large but protected by the host urchin. As *L. notorcadensis* is one of the most common molluscs of the antarctic region, the success of this mode of development seems apparent. Grahame and Branch (1985) review different modes of reproduction in marine invertebrates and recognize that Antarctica represents an intriguing case where primary production and potential paucity of food could regulate reproductive strategies. They suggest that more information on these south polar organisms is needed to fully appreciate their modes of reproduction. While we are able to discern much information through the use of museum material, to fully appreciate the unique evolutionary game plans developed by these small brooding molluscs, we must promote longer term studies of the living organisms.

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