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The Reproductive Biology of *Hymenaster membranaceus* from the Rockall Trough, North-East Atlantic Ocean, with Notes on *H. gennaeus*

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Abstract

Samples of the deep-sea spinulosan asteroid *Hymenaster membranaceus* Wyville Thomson were collected in a time-series of 19 bottom trawls spanning the period April 1978 to October 1981 from a 2 200 m-deep station in the northern Rockall Trough. The reproductive biology of this species was studied from histological sections of the gonad, and compared with that of *H. gennaeus* H. L. Clark which was collected in the same hauls. At first sexual development, oogonia develop in nests surrounded by small accessory cells. Previtellogenic oocytes remain in the periphery but, at maturity, oocytes ranging up to 1 100 μm fill the ovary. A variety of accessory cells pack the lumen and may be nutritive or degenerative. It appears that a small number of oocytes are spawned intermittently, but there is no evidence of overproduction and break-down of superfluous oocytes. A few large oocytes become senescent and undergo internal break-down, releasing periodic acid Schiff-positive material into the lumen. Size-frequencies of oocytes indicate that eggs may be spawned as a continuous slow release, and there is no evidence of reproductive synchrony between or within samples. On reaching maturity, males appear always to be ready to release spermatozoa. Spawning is probably stimulated by egg release during chance encounters with mature females. There is no evidence for brooding, and from the large size and yolky nature of the egg direct lecithotrophic development at or near the seabed is inferred. A limited histological study of *H. gennaeus* indicates that egg production is very similar, but the two species differ in the nature of the accessory cells and amorphous material filling the lumen.

Introduction

Hymenaster membranaceus [1] is a spinulosan asteroid, with a restricted bathymetric range, found throughout the North-East Atlantic Ocean (Sibuet, 1976a; Gage *et al.*, personal communication, 1982). We have studied previously the life histories of a number of deep-sea phanerozoan seastars in trawl samples from the Rockall Trough (N.E. Atlantic) (Tyler and Pain, 1982; Tyler *et al.*, 1982a, b). *H. membranaceus* is the first spinulosan seastar to be examined from these deep-sea hauls. Shallow-water seastars, particularly the hermaphroditic *Asterina gibbosa*, have received considerable attention in the past and show a variety of gametogenic strategies (Cognetti and Delavault, 1960; Delavault, 1960a, b; Achituv, 1969; Bruslé, 1969; Chia, 1970). Fisher (1940) predicted that all species of the pterasterid genera would be brooders and Thorson (1952) illustrates a juvenile being brooded in the supradorsal chamber of *H. pellucidus* Wyville Thomson. Preliminary observations of the egg size of *H. membranaceus*, as well as a number of other deep-sea asteroids (Tyler *et al.*, 1982b) would suggest direct development, but as yet no evidence of brooding has been observed.

Adult *Hymenaster membranaceus* probably live partially buried in bottom sediments, with only the valves of the central opening protruding above the sediment. The dorsal surface is ventilated internally by the flow of water through this opening to the supradorsal cavity (Mortensen,

[1] Some confusion in taxonomy and synonomy surrounds the genus *Hymenaster* in the North Atlantic Ocean. We believe that *H. pellucidus* Wyville Thomson is restricted to the Norwegian Sea to the north of the Wyville Thomson ridge, whilst the common deep-sea form of the North-East Atlantic is *H. membranaceus* Wyville Thomson. Taxonomic separation of the large forms ($R >$ ca. 70 mm) *H. giganteus* Sladen, 1891, *H. gennaeus* H. L. Clark, 1923 and *H. rex* Perrier, 1894, depends mainly on the number of adambulacral spines, the number of oral spines and the thickness of the tegument (Sibuet, 1976b). Our specimens conform to the description of *H. gennaeus* H. L. Clark, especially in the shape of the oral shield (Sibuet, 1976b). However, this feature may be variable, as is the number of adambulacral spines (Miss A. M. Clark, personal communication), and thus these three nominal species of *H. giganteus, H. gennaeus* and *H. rex* may prove to be synonymous, with *H. giganteus* Sladen taking precedence.

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1927). This species would appear to feed on bottom deposits and small benthic invertebrates (Mortensen, 1927; Madsen, 1956; present authors' personal observations, 1981).

This paper presents the results of an analysis of the reproductive biology and population-size structure of *Hymenaster membranaceus* and compares the reproductive biology with that of other deep-sea asteroids.

Materials and Methods

Material was collected in the course of the Scottish Marine Biological Association's deep-sea benthic sampling programme on Station 'M' at 2 200 m depth near the base of the Hebridean slope, northern Rockall Trough (Gage and Tyler, 1982). Nineteen bottom hauls were made between April 1978 and October 1981 using either a 3 m wide Agassiz trawl or an epibenthic sledge. Details of these hauls are given in Table 1. Sufficient numbers of *Hymenaster membranaceus* Wyville Thomson were collected to permit analysis of both reproductive biology and population-size structure.

Specimens were fixed in 8% seawater formalin and subsequently transferred to 70% alcohol. Sub-samples of 20 individuals from each sampling period were examined for the reproductive study.

The whole individual was damp-dried and weighed and the distance from the centre of the disk to the arm tip (R) was measured. This measurement was difficult to make with great accuracy owing to the morphology of the seastar, which has no distinct centre to the disk, and the thin and rather membranous nature of the arms that are frequently curled up at the tip of fixed specimens. Hence, an accurate measurement from the centre of the disk to the interradius (r) was deemed impossible. Each specimen was examined carefully for signs of brooding.

Table 1. Details of bottom hauls on Station 'M' (northern Rockall Trough). AT: Agassiz trawl; ES: epibenthic sledge

Gear and Station No.	Date	Mean depth (m)	No. of individuals
AT 144	19. IV. 1978	2 240	287
AT 151	6. VI. 1978	2 175	30
AT 153	15. I. 1979	2 200	203
AT 154	21. V. 1979	2 264	111
AT 161	8. VIII. 1979	2 055	3
AT 167	13. VIII. 1979	2 300	137
AT 171	3. III. 1980	2 225	556
AT 175	28. V. 1980	2 210	180
ES 176	28. V. 1980	2 245	60
AT 177	29. V. 1980	2 200	319
AT 181	16. IX. 1980	2 220	354
ES 182	16. IX. 1980	2 170	16
ES 184	17. IX. 1980	2 260	79
AT 186	12. IV. 1981	2 170	423
AT 191	17. VIII. 1981	2 190	46 (juveniles)
AT 192	18. VIII. 1981	1 862	409
AT 195	18. VIII. 1981	2 190	359
ES 197	19. VIII. 1981	2 200	37
AT 198	15. X. 1981	2 215	125

The gonads and gut caeca of one arm were dissected-out from each specimen and damp-dried and weighed separately. Dissection of these organs required care, since the caeca had often penetrated the fine membranous skin covering the dorsal surface of the arm. The gonads also were held tightly by the thin membranous skin, which had to be removed with some care before extracting the gonad.

The gonad index ($GW/TW \times 100$) and caecum index ($CW/TW \times 100$) were calculated for each individual from total body and organ weight. These data were summed for each sample and the mean and 95% confidence limits calculated.

The gonads and caeca were embedded in paraffin wax, sectioned at 7 μm, and stained with Ehrlich's haematoxylin and eosin. Sections were examined microscopically and at least 80 oocytes sized and grouped in 50 μm increments. Only oocytes having a visible nucleus were measured. For each individual, an oocyte size-frequency diagram was constructed in order to ascertain whether there was within-sample synchrony of gametogenesis. The individuals from each sample were then combined to determine whether or not there was between-sample synchrony.

After this initial histological examination, a number of gonad sections at different stages of development were stained with periodic acid Schiff (PAS), alcoholic toluidine blue, and Sudan black B in acetone.

For analysis of population structure, body size (R) of all specimens ($N = 3\,143$) collected over the 4 yr period was measured to the nearest millimetre.

During the same sampling period, 7 specimens of the larger and much rarer spinulosan *Hymenaster gennaeus* H. L. Clark were collected. One male and three females were examined histologically, and notes on the histological and histochemical features of the gonads are presented here as a comparison with *H. membranaceus*.

Results

Hymenaster membranaceus is a gonochoric asteroid and not one of the 200 individuals examined was found to be hermaphrodite (Table 2). The ratio of males to females did not differ significantly from the expectation of equality ($\chi^2 = 8.49$; DF = 10; $P > 0.05$; $N = 200$).

Gonad Morphology

Gonads were distinguishable in every specimen examined and sex in all but one. The gonad lies immediately distal to the interradius and opens dorsally by a short gonoduct to release eggs or sperm into the chamber formed by the supradorsal and actinolateral membranes. Both ovary and testis are very compact, held tightly in place (in preserved specimens) by the thin membranous skin of the arm. The

Table 2. *Hymenaster membranaceus.* Sex ratios of seastars in samples collected at Station 'M'

Gear and Station No.	Date	Male	Female	(Immature, indeterminate)
AT 144	19. IV. 1978	10	10	0
AT 151	6. VI. 1978	9	11	0
AT 153	15. I. 1979	8	12	0
AT 154	21. V. 1979	8	11	0
AT 167	13. VIII. 1979	13	7	0
AT 171	3. III. 1980	9	11	0
AT 175/177	28. V. 1980	7	12	1
AT 181	16. IX. 1980	13	7	0
AT 186	12. IV. 1981	11	9	0
AT 195	18. VIII. 1981	6	14	0
AT 198	15. X. 1981	10	10	0

morphology of the arm is such that the organs are held tightly together, there being no stiff supporting skeleton dorsally. The ovary, bright orange when fresh, consists of a large mass of very short lobulate tubules, packed closely together. The testis is paler in colour and is a similarly compact organ, consisting of a large mass of short (a few mm long), but fine tubules.

Gonad Histology

Hymenaster membranaceus

Ovary. From light microscope examination, the ovary wall appears to conform to the three-layered structure described for *Asterias vulgaris* by Walker (1974) and for *Bathybiaster vexillifer* by Tyler *et al.* (1982 a), but differs in having a relatively wide perihaemal sinus (Fig. 1 A, B, C). The outer sac of the gonad wall is comparatively thick and has a distinct PAS-positive layer within it. The inner sac is thin, with a narrow haemal sinus that shows a positive reaction with PAS. The great width of the perihaemal sinus may be an artefact of fixation. In contrast to other species examined, there may be several separate lobes of germinal tissue surrounded by separate layers of inner wall tissue within the outer sac of the ovary.

Oogenesis. The oogenic cycle closely resembles that of the phanerozoans *Bethopecten simplex* and *Pectinaster filholi,* taken from the Rockall Trough (Pain and Tyler, personal observation). Small oocytes ($< 50\,\mu$m) have a single nucleolus and are surrounded by a layer of small accessory cells (Fig. 1 C). In some sections there appear to be large "nests" of small oogenic cells surrounded by a deep layer of small accessory cells. Most, but by no means all, oocytes remain at the periphery of the tubule but this may be caused by physical constraints imposed by the narrow lumen. Some small oocytes do occur in the lumen, so the "position effect" (*sensu* Worley *et al.,* 1977) is not critical.

In well developed ovaries there is a range of sizes from very small ($< 50\,\mu$m) to large vitellogenic oocytes, reaching a maximum of 1 100 μm. The larger oocytes are packed with PAS-positive cortical granules. Cortical granules begin to appear in oocytes of about 250 μm in a broad, diffuse peripheral band, later filling the entire cytoplasm and becoming most dense in the extreme periphery. There is very little space within the tubule: a "packing" of small cells and some PAS-positive material fills much of the tubule between oocytes (Fig. 1 C). These cells are similar to those surrounding nests of developing oocytes and to the accessory cell layer surrounding larger individual oocytes and may have some nutritive function.

In each tubule of well developed ovaries, there is generally only one, or perhaps two, large yolky oocytes, together with a range of smaller-sized oocytes. Once the oocytes are ripe they are presumably spawned, allowing a smaller oocyte to develop to maximum size in the tubule. The narrow ductules and gonoduct have thick, much-folded walls that can expand to accommodate the passage of a very large oocyte (Fig. 1 A, B), and are lined by ciliated columnar epithelial cells.

Oocyte Degeneration. Evidence for internal break-down of large vitellogenic oocytes has been observed in some sections but occurs less commonly than noted for *Bathybiaster vexillifer* by Tyler *et al.* (1982 a), for *Psilaster andromeda* and *Plutonaster bifrons* by Tyler and Pain (1982) and for *Ctenodiscus crispatus* by Shick *et al.* (1981). Staining with PAS shows that the spherical cortical granules begin to break-down, forming amorphous clumps of very PAS-positive substance within the oocyte. This type of degeneration does not occur in smaller oocytes. There is no obvious evidence for phagocytic break-down of small or large oocytes as commonly occurs in other species, but there are large amounts of what appears to be break-down products within the lumen of the ovary in many sections (Fig. 1 C, D).

Brooding. In none of the specimens examined was there any evidence of brooding. The Arctic species *Hymenaster pellucidus* broods its young attached to the actinolateral membrane (Thorson, 1952). Fisher (1940) suggested that probably all species of *Hymenaster* would brood. The large egg size and small number of eggs that appear to be spawned at any one time would indicate that *H. membranaceus* might be a brooding species but, despite close inspection of the supradorsal cavity and of the supradorsal and actinolateral membranes, no larvae or embryos were found.

Testes. The testis wall has the same construction as that of the ovary, with the same very large perihaemal sinus (Fig. 1 E). The haemal sinus is often very wide and the inner sac forms a very thin layer around the germinal tissue. The structure within the testis tubule differs from that of the deep-sea phanerozoans studied previously (Tyler and Pain, 1982; Tyler *et al.,* 1982 a, b). In many

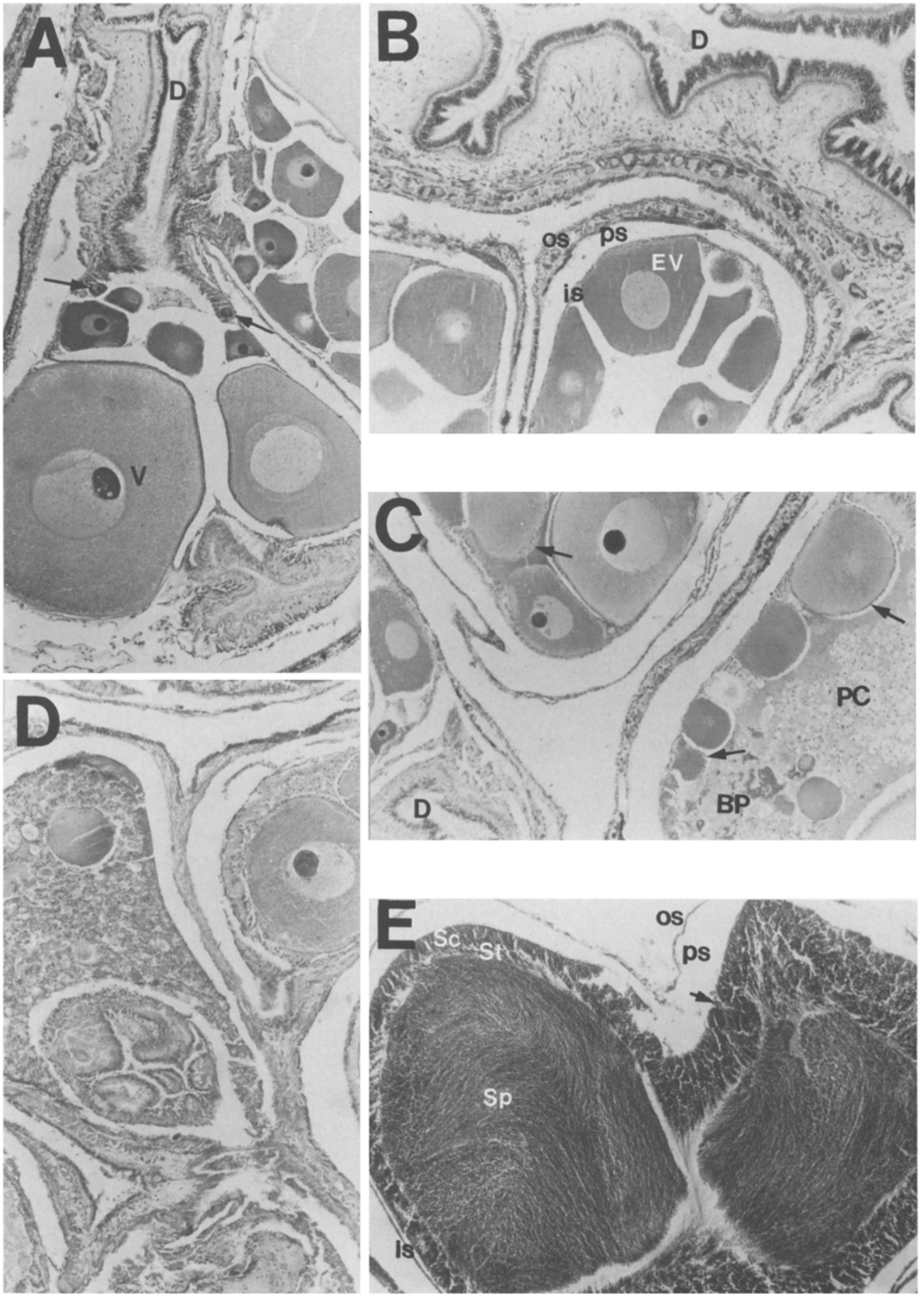

Fig. 1

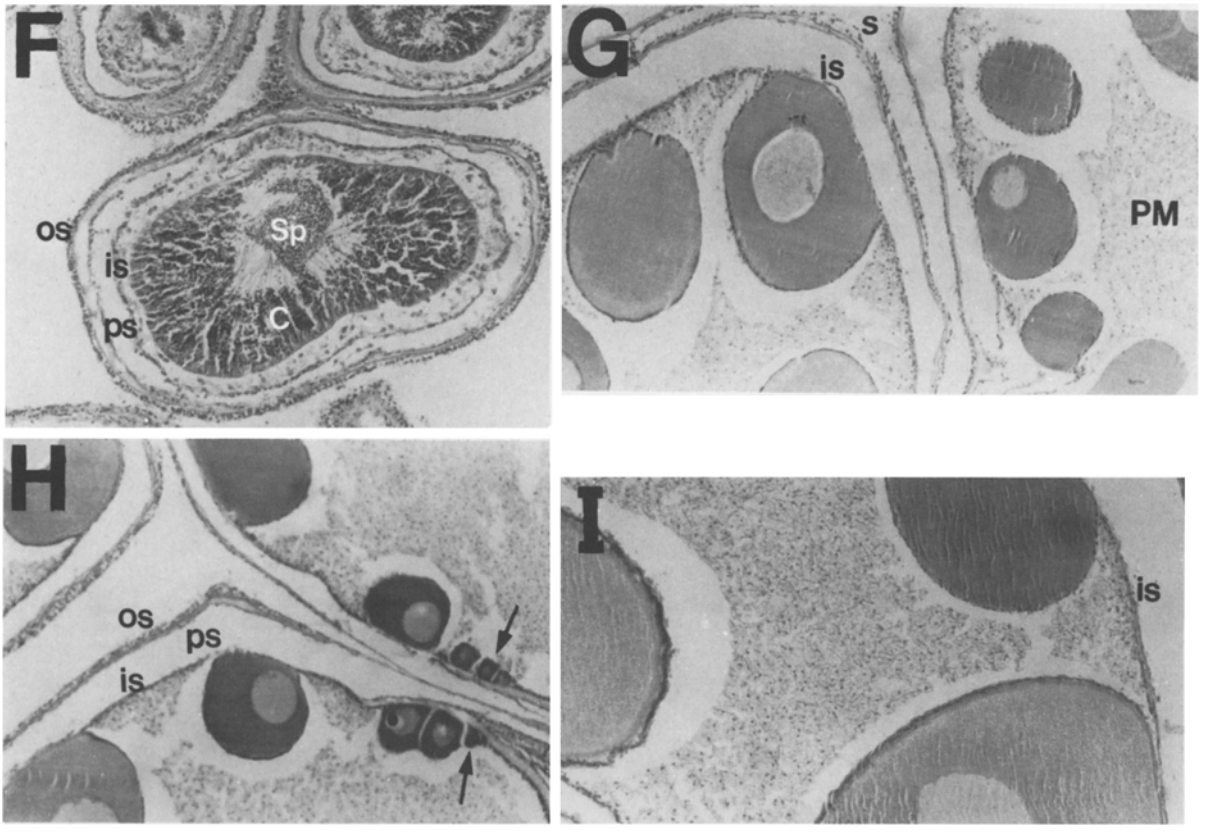

Fig. 1 (A)–(I). *Hymenaster membranaceus:* (A) Well developed ovary showing single lobe with duct (D) leading to gonoduct, developing oocytes (arrows) and vitellogenic oocytes (V); ×133. (B) Ovary showing early vitellogenic oocytes (EV) attached to ovary wall; wall consists of an outer sac (os), wide perihaemal sinus (ps) and thin inner sac (is); wall of gonoduct is multilayered and much infolded; ×132. (C) Ovary showing range of oocyte sizes and thick layer of accessory cells (arrows) surrounding oocytes; lumen of ovary is filled with packing material of small cells (PC) and apparent products of oocyte breakdown (BP); ×125. (D) Section through a lobe of an ovary in which break-down products fill almost an entire lobe; ×125. (E) Transverse section of mature testis showing outer and inner sacs, spermatocytes (Sc), spermatids (St) and spermatozoa (Sp) whorled in the lumen; there is some infolding of the germinal epithelium (arrow); ps: perihaemal sinus; ×124. (F) – (I) *Hymenaster gennaeus:* (F) Transverse section of developing testis showing very thick outer and inner sacs separated by a wide perihaemal sinus; colonettes (C) of spermatocytes are quite well developed, but spermatocytes are few; ×125. (G) Ovary showing wall structure and oocytes arranged at periphery, surrounded by a matrix of packing material (PM) consisting of small cells and "spicules"; ×108. (H) Ovary showing arrangement of oocytes at wall and size-ranges of oocytes from small developing (arrows) to early vitellogenic; ×95. (I) Higher magnification of ovary to show packing material; ×123. All sections were stained with haematoxylin and eosin

tubules the germinal tissue is separated into several distinct lobes. Within each lobe the germinal epithelium may be folded inwards, stretching to accommodate large numbers of spermatozoa as the testis ripens.

Spermatogenesis is very similar to that described for other asteroid species (Walker, 1974; Worley *et al.,* 1977; Shick *et al.,* 1981; Tyler *et al.,* 1982 a, b). Spermatogonia line the germinal epithelium, forming a dense layer of several cells thick in places. Spermatogonia are 5 μm in diameter, with a large nucleus and pale cytoplasm. Spermatocytes develop in colonettes (Cognetti and Delavault, 1960) and have a diameter of about 3 μm. Spermatids arise from the apex of the colonette and differentiate into spermatozoa with a head diameter of about 1.5 μm. In ripe testes, the spermatozoa appear to form long "strings" within the lumen and become whorled when the testis is crammed tightly with spermatozoa.

Hymenaster gennaeus

Compared to *Hymenaster membranaceus, H. gennaeus* is a much more robust animal. The arm skeleton is fairly rigid, with heavy spines supporting the supradorsal membrane. The actinolateral membranes are thick and fleshy and the chamber formed between the two is a more rigid structure. In the females examined (largest $R = 70$ mm) the ovaries were very similar to those of *H. membranaceus* but larger, with very large lobes. The male ($R = 53$ mm) had small unripe testes with fine, short tubules resembling those of *H. membranaceus.*

Ovary. The ovary wall resembles closely that of *Hymenaster membranaceus,* although the two sacs, inner and outer, are thicker. Both haemal and perihaemal sinuses are strongly PAS-positive.

The internal structure of the ovary presents a marked contrast to that of other asteroids studied. Although the tubules are of wide diameter they contain few oocytes, which are of varying size and remain attached to the germinal epithelium at all stages. These oocytes do not form a continuous layer around the periphery of the ovary, but are scattered around it (Fig. 1 G, H). The tubule between the oocytes is filled with material that appears to consist of large numbers of small cells, possibly nutritive cells and long "spicule-like" particles (Fig. 1 I). This central mass contains small, strongly PAS-positive granules scattered throughout, resembling closely the cortical granules in the cytoplasm of yolky cells. The oocytes occur in a range of sizes up to 1 200 μm. All oocytes are surrounded by accessory cells, which form a layer several cells deep, around the smaller oocytes. The accessory cells are densely packed and are rather spherical with dark staining nuclei. In the largest eggs, the accessory cell layer is stretched to a covering 1-cell thick. The larger yolky oocytes have a thick vitelline membrane that is metachromatic when stained with toluidine blue. The accessory cell layer remains intact outside the vitelline membrane.

The largest oocytes are packed with PAS-positive cortical granules which, in several medium-sized oocytes, appear initially around the nucleus, spreading to fill the entire cytoplasm as the egg develops.

No indication of phagocytic break-down was observed, but one large yolky oocyte showed evidence of internal break-down beginning in the outer regions of the cell, where clumps and patches of PAS-positive material occur.

Testes. The testes of the *Hymenaster gennaeus* specimen examined were not fully developed (Fig. 1 F), although the specimen was of considerable size ($R = 57$ mm). The wall structure was consistent with that described for the ovary, both sacs being very thick and separated by a wide space. The wall was strongly metachromatic. Both haemal and perihaemal sinuses were strongly PAS-positive. Most of

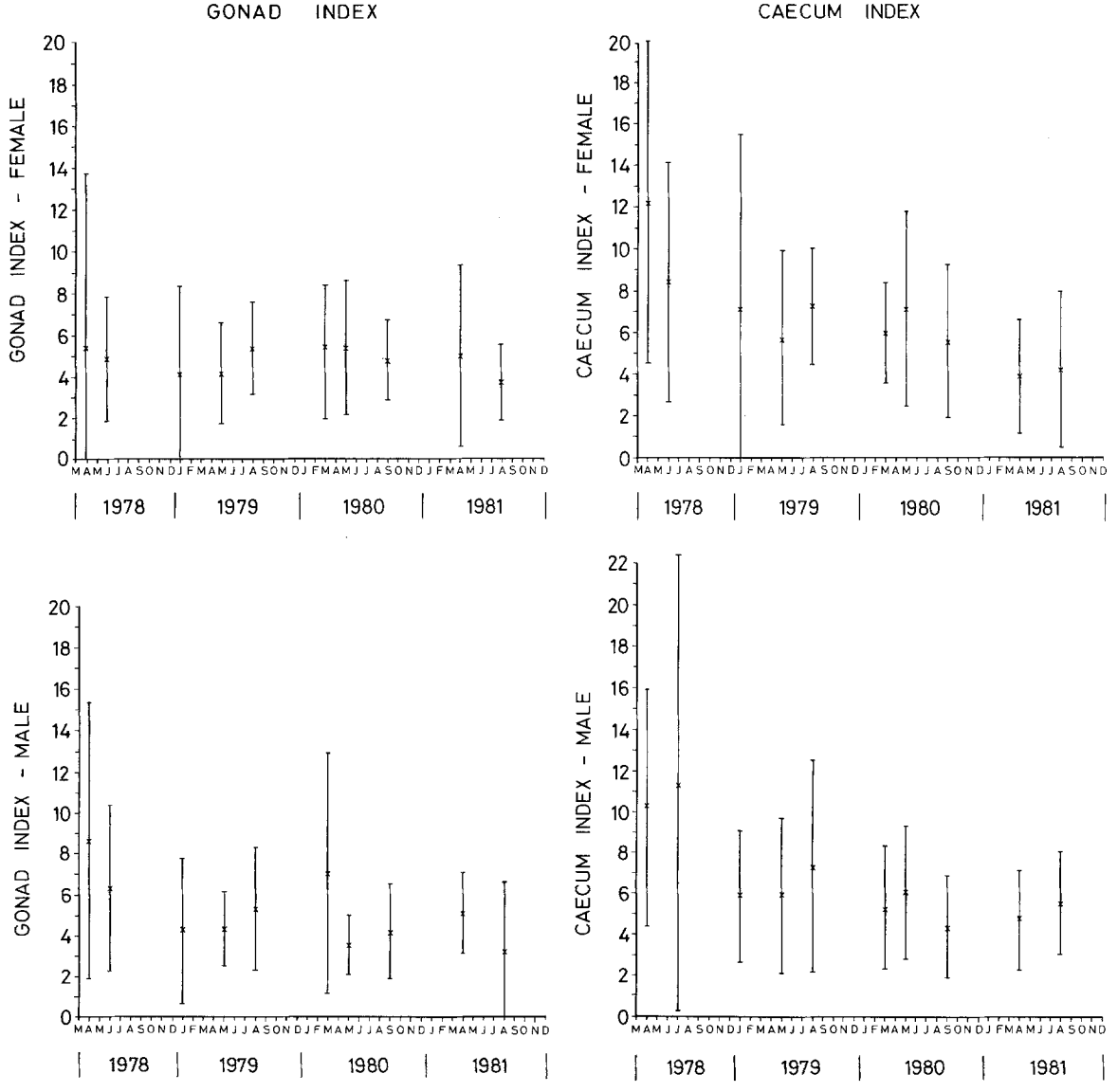

Fig. 2. *Hymenaster membranaceus.* Seasonal variation of gonad index and caecum index

the cells within the testis were spermatogonia, lining the germinal epithelium and about 7 μm in diameter. Spermatocytes of about 3.5 to 4 μm diam formed colonettes, but these were not as distinct as in most species examined. In this species they have a broad base and are packed closely, tending to merge in places. It may be that their structure is more distinct in better developed specimens. The few spermatids were 2.5 μm in diameter and very few spermatozoa were present in the section.

The Seasonal Reproductive Cycle

Organ Indices

The female gonad indices (GI) for *Hymenaster membranaceus* range from 1.8 to 16.7, although the mean GI for each sample shows little variation (Fig. 2).

The male gonad indices range from 1.1 to 12.72, but again these are rather extreme values. In all samples, the 95% confidence limits of the mean GI value overlap considerably, suggesting that there is no reproductive seasonality.

The values for the caecum index likewise show no seasonal variation, and there was no correlation between gonad index and caecum index in females or males.

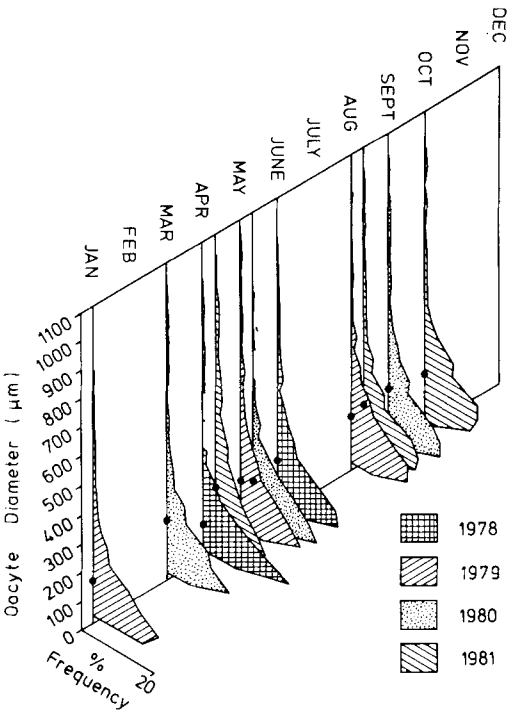

Fig. 3. *Hymenaster membranaceus.* Summated oocyte-size/frequency distribution for all samples, showing intersample asynchrony

Oocyte Size Frequency

Histograms of oocyte size-frequencies for each sample in the time-series are very similar and therefore provide no evidence of seasonal reproduction (Fig. 3).

When oocyte size-frequencies from each individual are compared within each sample (Fig. 4), there is again a close similarity and no obvious indication of intra-sample synchrony.

Most oocytes are smaller than 400 μm in diameter, with small numbers reaching a larger size ranging from 400 to over 1 000 μm. In most specimens it seems that only one or two oocytes per tubule develop fully at any one time, and after release perhaps a few of the small oocytes begin to develop further. Thus, it seems that there is continuous production of eggs, only a small number being released at a time and some of the remaining oocytes undergoing vitellogenesis to be spawned after an interval of growth.

Population Size-Structure

Histograms of frequencies of R are difficult to interpret (Fig. 5). Although showing a varying pattern between samples, a trend towards a unimodal distribution is evident that peaks between 30 and 45 mm. Many distributions also show one or two secondary modes that appear identifiable in consecutive samples of the series.

Ripe gonads were not found in individuals smaller than $R=21$ mm, although the size at first maturity may vary a little as the gonads of two females of $R=24$ mm were small and developing while another specimen of $R=25$ mm was well developed. Hence, the small left-hand modes visible in Samples AT 144 (19 April, 1978); ES 176 and AT 177 (28 May, 1980); AT 181 (16 September, 1980); AT 186 (12 April, 1981); AT 195 (18 August, 1981); and AT 198 (15 October, 1980) (Fig. 5) are probably composed of immature individuals.

As fecundity is evidently low and no periodicity has been detected in oogenesis, a continual, low-level recruitment of juveniles to the adult population would seem reasonable.

The large size (1 100 μm) of ripe oocytes suggests to us that the smallest free-living juveniles may be caught in epibenthic sledge hauls (0.5 mm meshes), but not in the Agassiz trawl employed (1 cm meshes when fishing). In view of the low numbers of individuals <20 mm recovered from the epibenthic sledge hauls taken on 28 May (ES 176) and 16 September (ES 184) 1980 (Fig. 5), it also seems reasonable to conclude that juvenile sizes in the Agassiz samples also provide evidence for the occurrence of such low-level recruitment, and also indicates that this was variable over the period of sampling. It is tempting to infer that the large mode of adult frequencies results from the slowing of growth of individuals on becoming reproductively mature. However, the modes appearing in the right-hand frequencies in Samples AT 153, AT 154, AT 161 and the pooled sample from AT 181, ES 182 and ES 184, are more difficult to explain.

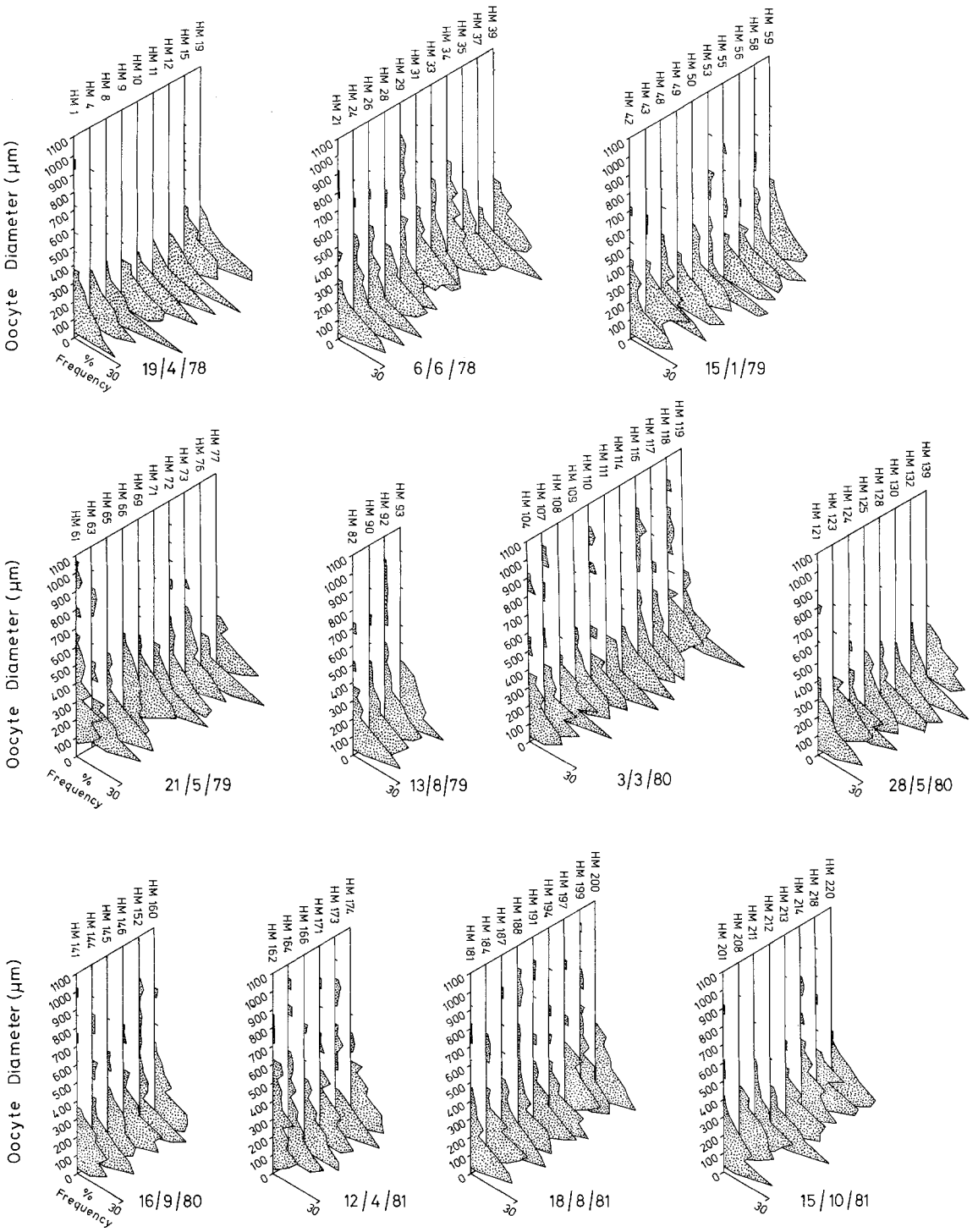

Fig. 4. *Hymenaster membranaceus* (HM). Oocyte-size/frequency of individuals, showing within-sample asynchrony

We suggest that the appearance of these modes in consecutive samples of the time-series reflects their derivation in periods of enhanced recruitment. In addition, the very variable overall pattern of adult frequencies would seem inconsistent with the expectation for a slowly growing, long-lived population. However, we cannot rule out the possibility that the demographic composition of the population in the vicinity of Station 'M' is spatially heterogeneous, as the bottom tracks of the trawls made on this station cover a considerable area. Hence, the samples obtained of *Hymenaster membranaceus* may reflect spatial variation in age composition resulting from local differences in spawning frequency in the population, although we have no data to support this hypothesis.

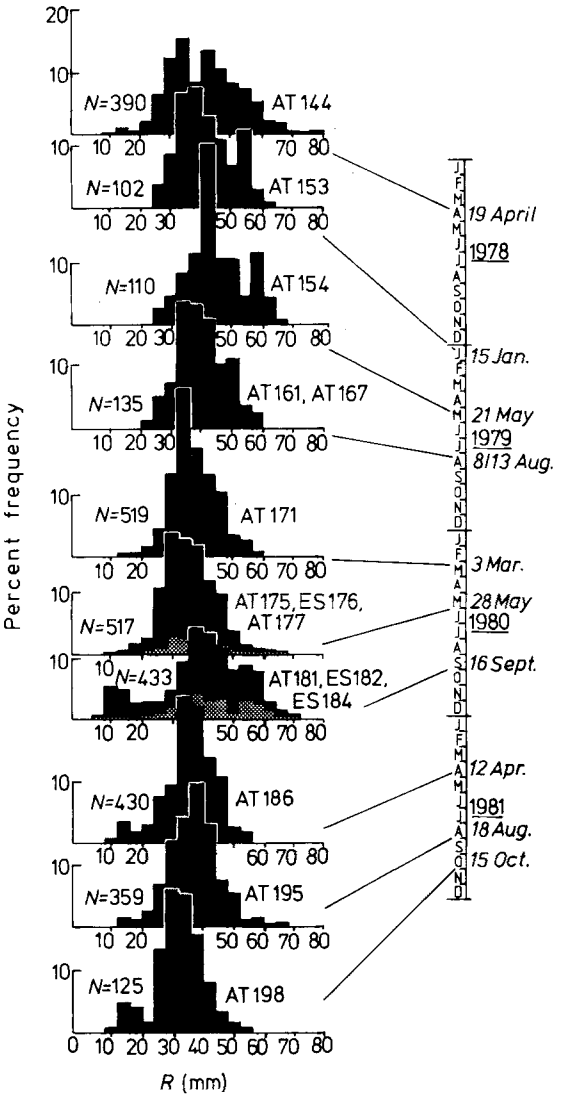

Fig. 5. *Hymenaster membranaceus.* Histograms of body size (*R*) in samples from Station 'M' time-series. Stippled areas show frequencies obtained from epibenthic sled (ES) hauls

Discussion

The gametogenic cycle of *Hymenaster membranaceus* resembles that of the phanerozoan seastars *Benthopecten simplex* and *Pectinaster filholi* in many of its characteristics, but also displays a number of features not found in asteroids previously studied (Tyler *et al.*, 1982 b). *H. membranaceus* also exhibits a number of significant differences when compared with the congeneric *H. gennaeus.*

The oogenic cycle begins when the arm radius reaches about 25 mm. The oogonia develop in "nests", surrounded by many small accessory cells. In developing ovaries all the oocytes are small and exhibit the "position effect" (Worley *et al.*, 1977), but once reproductive maturity is reached the ovary contains oocytes of all sizes up to 1 100 μm. The ovary is packed with a variety of accessory cells, whose function is possibly nutritive.

It appears that only a small number of oocytes reach maximum size at any one time; these few are probably spawned intermittently, making room in the tubule for the further development of other oocytes. Evidence for the break-down of superfluous oocytes and recycling of nutrients is limited. There are a few instances of internal break-down within senescent oocytes that have not been spawned, but there is no obvious indication of phagocytic break-down of oocytes of any size. There does not appear to be any overproduction of oocytes that might subsequently be broken down to supply nutrients to developing oocytes in the manner of "nurse cells", as observed by Tyler *et al.* (1982 a) in *Bathybiaster vexillifer* and in other seastars with large eggs (Cognetti and Delavault, 1960; Pearse, 1965). It seems more probable that in *Hymenaster membranaceus* nutrients are provided by the abundant accessory cells.

Spawned oocytes are released through the ducts of the tubules, where their passage is facilitated by the ciliated epithelial cells lining the walls. The walls of the ducts and the main gonoduct are folded considerably and can expand to accommodate the large eggs.

On release, the eggs pass into the cavity formed by the supradorsal and actinolateral membranes, where they may be retained for fertilization and brooding of the larvae as suggested by Fisher (1940) and Thorson (1952). However, there is no evidence of brooding, and it may be that the eggs have an abbreviated demersal development, as might be expected from the large amounts of yolk in the egg (Thorson, 1936). If the larvae are not brooded, then the eggs on release from the gonoducts may pass into the supradorsal chamber and pass out through the central opening in the ventilatory flow of water to be fertilized externally. Alternatively, sperm may be drawn into the chamber in the inflow of water and fertilized eggs released from the chamber.

As with most of the asteroids studied from the Rockall Trough, *Hymenaster membranaceus* shows no indication of synchronous reproduction between the individuals in one sample or between samples. This suggests that some individuals of the population are ready to spawn throughout the year.

Growth of the testis follows a pattern similar to that of the astropectinid seastar *Bathybiaster vexillifer* and the benthopectinids *Benthopecten simplex, Pectinaster filholi* and *Pontaster tenuispinus,* although there are some slight differences in general morphology. Spermatogonia form a dense layer lining the very thin germinal epithelium of newly developing testes, and divide to produce spermatocytes that form colonettes (Cognetti and Delavault, 1960).

After reaching maturity, the testes appear always to contain abundant spermatozoa, suggesting that the testes are always in a condition of readiness to release sperm when a female releases ripe eggs. A few specimens appeared to have undergone a complete spawn-out but this may have occurred in response to trawling.

The population structure of *Hymenaster membranaceus* is difficult to analyze, but it would seem that there is a

very low level recruitment of juveniles to the population. This might be expected in a species with such low fecundity. The absence of any obvious synchrony in reproduction would mean that any polymodal size-structure corresponding to identifiable year-classes is unlikely to be present. Growth rate of individuals is likely to decrease when individuals reach reproductive maturity and channel their resources to reproductive rather than somatic growth.

Although detailed analysis of the reproductive cycle of the sympatric species *Hymenaster gennaeus* awaits more available specimens, the evidence available suggests definite differences in details of gametogenesis. Egg production would appear to be similar in both species, but it is in the accessory cell meshwork filling the lumen of the ovaries in each species that the main differences exist. In *H. membranaceus* this material consists of small cells and a mass of amorphous PAS-positive material. In addition to these components, the material in *H. gennaeus* contains a large number of spicule-like structures. As yet we have only been able to speculate on the nature of this material, which may be nutritive or result from a degenerative process.

At this stage, it is not possible to comment on the adaptive significance of these minor variations in gametogenic strategy. All other evidence of the reproductive biology of these two species suggests the formation of a large egg, with fertilization in the supradorsal chamber. As there is no evidence of brooding, it is believed that both species undergo lecithotrophic development at, or very close to, the sea bed.

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