3. THE REPRODUCTION OF SOME ECHINODERMS FROM MACQUARIE ISLAND

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SUMMARY

Three species of starfish, *Anasterias directa* (Koehler), *Anasterias mawsoni* (Koehler), and *Cycethra macquariensis* Koehler, and one species of holothuroid, *Pseudopsolus macquariensis* (Dendy) were collected over a period of one year from rocky sub-littoral shores at Macquarie Island. Study of preserved collections showed that both *Anasterias* species and the holothuroid have a brooding mode of reproduction and distinct reproductive cycles. For *Cycethra macauariensis* no cyclic reproductive pattern was evident. Ovarian condition in *Cycethra macquariensis* suggested a non-pelagic development; however the mode of this development was not observed. In addition, examination of some specimens of *Pseudocnus laevigatus* (Verrill), *Trachythyone macphersonae* Pawson (holothuroids) and *Pseudechinus novaezealandiae* (Mortensen) (echinoid) showed a brooding habit in *Pseudocnus* and ovarian conditions that suggested non-pelagic larval development for *Trachythyone* and pelagic larval development for *Pseudechinus*.

INTRODUCTION

Apart from prerequisite taxonomic studies, collections of marine invertebrates in the sub-Antarctic regions have been examined mainly for zoogeographical interpretation and reports on general ecology. Collections have usually been made in summer months and records of reproduction have been restricted to descriptions of non-pelagic development, especially via brooding or ovoviviparity. Simpson (1977) lists sources for the above studies.

At Macquarie Island, systematic collections were made each month for one year of some echinoderms from littoral and sub-littoral zones on rocky shores, in order to determine reproductive cycles and to categorise the mode of larval development as either pelagic or non-pelagic.

Apart from some nearby rocky outcrops, Macquarie Island (54° 38' S; 158° 53' E; Fig. 1) is isolated in the Southern Ocean. For studies of marine invertebrates, Macquarie Island is important in that (a) it marks the limit of southerly ice-free littoral zones and (b) its oceanic isolation bridges a geographic gap in any comparisons of littoral invertebrates over all southern latitudes in the Australian region.

MATERIALS AND METHODS

Specimens of the asteroids *Anasterias mawsoni* (Koehler) and *Anasterias directa* (Koehler), and the holothuroid *Pseudopsolus macquariensis* (Dendy) were collected at approximately monthly intervals between March, 1968 and March, 1969.

Another asteroid, *Cycethra macquariensis* Koehler, was collected monthly over the same period but collections were not obtained in the months of May, June and November. Within the size category designated for each species (see later), the first five specimens of each sex were examined from each monthly collection.

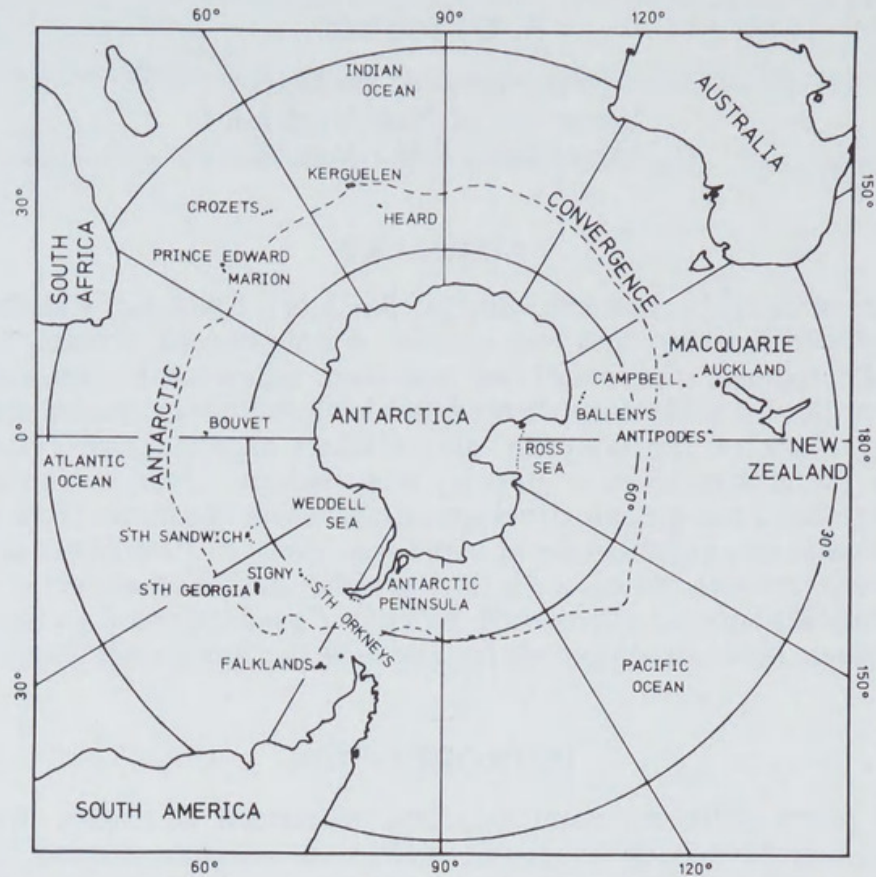Four specimens of the holothuroid *Pseudocnus laevigatus* (Verrill), ten specimens of

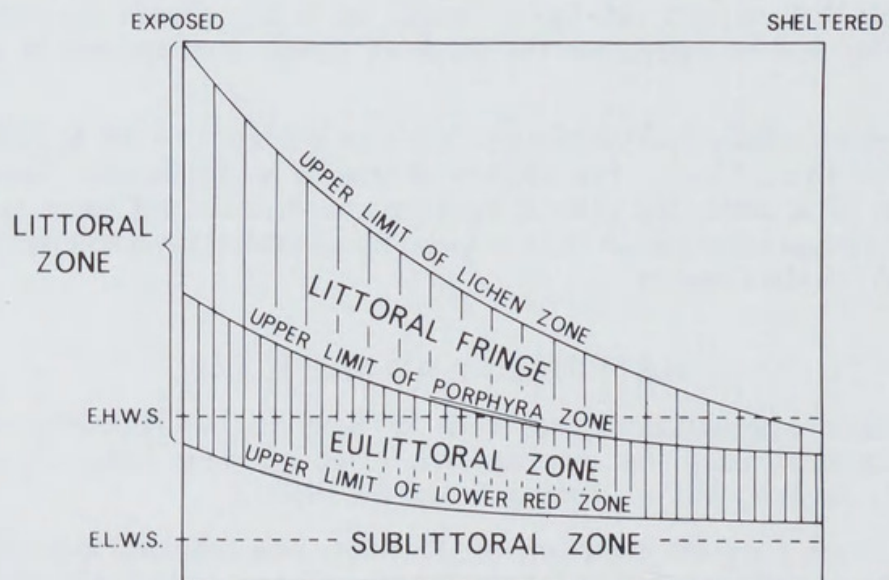Fig. 1. The sub-Antarctic and Antarctic regions.

Fig. 2. Zonation of Macquarie Island rocky shores correlated with a universal
scheme (from Simpson, 1976(a)). E.H.W.S.: extreme high-water spring tidal
mark; E.L.W.S.: extreme low-water spring tidal mark.

Trachythyone macphersonae Pawson and four specimens of the echinoid *Pseudechinus novaezealandiae* (Mortensen) were examined for mode of reproduction only.

All specimens were preserved immediately after collection and the material was examined approximately one year after collecting ceased. The methods of preservation were those described in Simpson (1977). That paper also outlines the rationale, method, and terms used in describing the reproductive condition of a large collection of preserved specimens. The same procedures were applied, as appropriate, to the echinoderms. Briefly, for those species collected over a period of one year, reproductive conditions of specimens are described by egg sizes, the state of gonads and of broods, and stages in spermatogenesis determined by microscopic examination of smears of testes. An individual was labelled as being in a particular reproductive stage which, in most cases, was clear. When there was overlap (e.g. for spermatogenesis) the most predominant state was assigned as the stage for that individual. For the brooding species, progression in a brood was described by classification into eggs, embryos, and juveniles: eggs — when no embryonic differentiation was evident; embryos — when eggs showed embryonic differentiation; juveniles — when embryos appeared as fully formed juveniles.

The position of collecting sites was maintained by reference to the shore zonation scheme, as defined by Simpson (1976a), (see fig. 2). *Anasterias mawsoni, Anasterias directa, Cycethra macquariensis*, and *Pseudopsolus macquariensis* had a vertical range from the kelp zone of *Durvillea antarctica* (Chamisso) Hariot holdfasts in the lower eulittoral zone, down to a depth of 10 metres — the maximum depth investigated. Extension of the range of the above echinoderms up into the kelp zone depends on the cover provided by the living kelp (Simpson 1976a). While *Durvillea antarctica* itself could be classed as a lower eulittoral species, the zone it creates justifies a biological classification into a "sublittoral fringe". Both *Anasterias* had average densities on rocky surfaces of one per m² in the upper sub-littoral zone and two per m² in deeper water (Simpson, 1976b). *Pseudopsolus macquariensis* was often found in patches of high density on rocky surfaces. These patches were more common in the sub-littoral zone, and immediately below it, than in deeper water. *Cycethra macquariensis* was not abundant in any of the areas investigated.

RESULTS

Anasterias mawsoni (Koehler)

Anasterias mawsoni is endemic to Macquarie Island. It is a six-armed starfish and has a number of colour forms, any one specimen having a single colour. Distinctive features of this species are outlined in Clark (1962).

A. mawsoni was found on solid, rocky substrata. Specimens were collected from channels, gutters and pools at the top of the sub-littoral zone. All animals used for reproductive investigations had a central disc diameter of at least 20 mm.

The sexes are separate; out of 157 specimens sexed, 61 were males and 96 were females. A pair of gonads was situated in each of the six interbrachial regions. In the males, the testes had a botryoidal appearance while in the females each ovary consisted of two compact, round sacs. When ripe, the testes greatly enlarged and extended down into the arms; in the females, the sacs expanded to accommodate the enlarging eggs.

Figure 3 shows the annual reproductive cycle of *A. mawsoni*. The female brooded the young from egg to juvenile stage, the brood forming a compact cluster overlying the oral region (see fig. 4). Females assumed a distinctively arched posture when carrying a brood. The central disc was raised, the proximal parts of the arms being at a steep angle to the substratum and the distal parts horizontal and still attached to the substratum. This created a protected cavity at the oral

Fig. 3. Reproductive cycles of *Anasterias mawsoni*. a. females, N = 5 each month; X = evidence of recent juvenile release, ▲ = juveniles in brood, △ = embryos in brood, O = eggs in brood, ■ = eggs in ovary; b. males, N = 5 each month; X = recent spawning, ● = ripe, O = abundance of spermatids, ■ = early spermatogenesis, □ = resting, ▲ = resorbing. (Each symbol represents one specimen, the gonad of which has been classified by its predominant reproductive state. The sets of each symbol are stratified on the figure for better visual interpretation.)
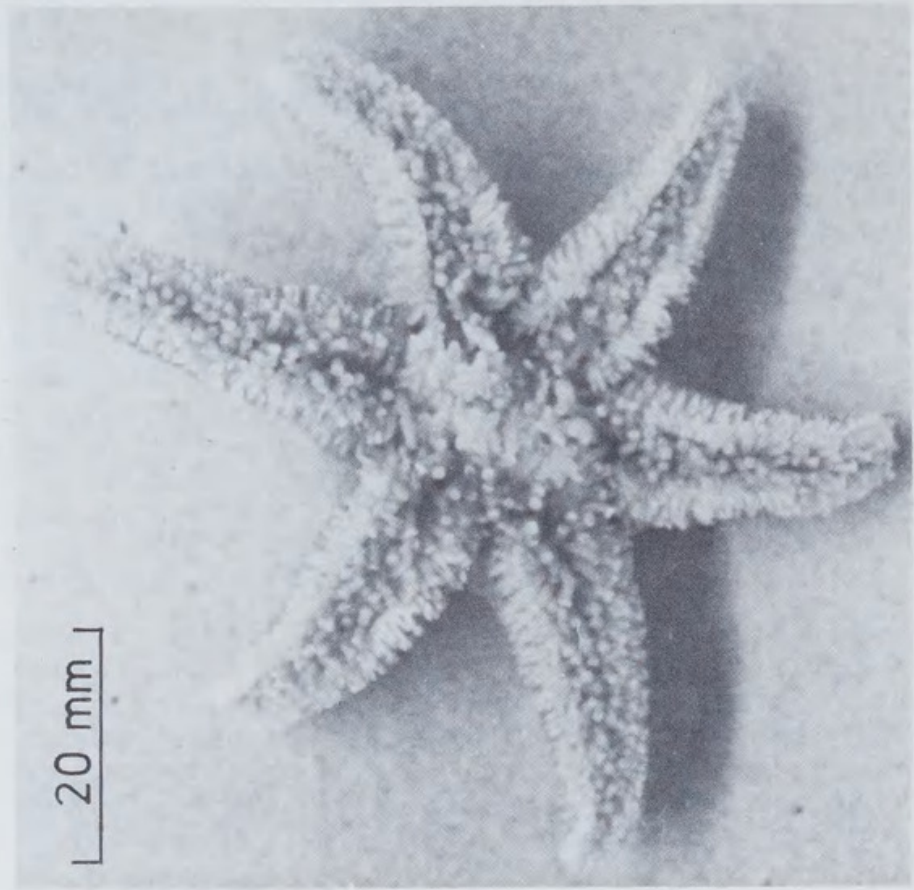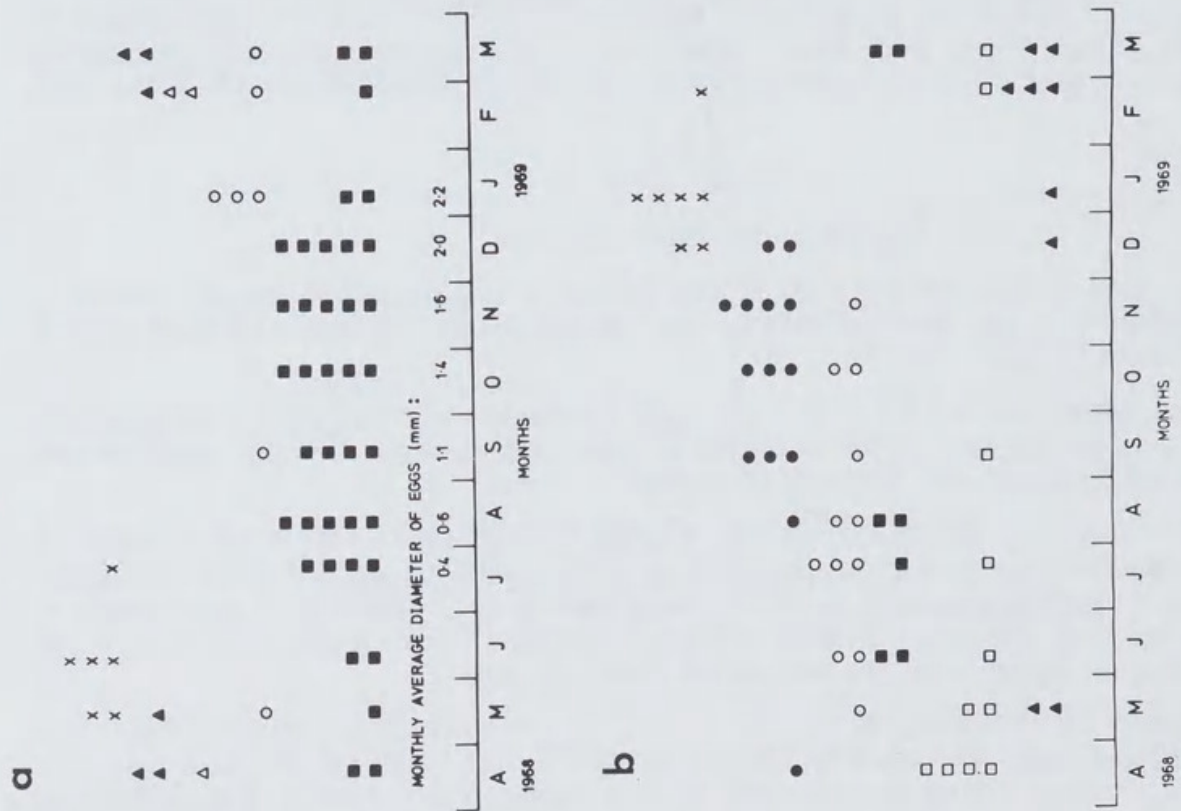

Fig. 4. *Anasterias mawsoni* with brood at juvenile stage.

region. Larger specimens could form a more spacious, protected cavity, and hence could presumably accommodate a larger brood. The number of eggs per brood varied from 168 to 296.

In July, the eggs in the ovaries averaged 0.4 mm in diameter. The eggs progressively increased in size, reaching 2.0 mm in December. They were transferred to the brood clusters in January-February at which time the diameter of eggs in a brood averaged 2.2 mm. Development proceeded in the brood to a juvenile stage in May and June when the juveniles were released. A female was classed in a "juvenile release" stage either when a very reduced brood was at the oral region or when there was no brood but there were membranous remnants of the brood sac around the oral region.

In males, the testes were generally reduced from February to May. There was some spermatogenic activity during this period, but occurrences were few. The testes then progressively increased in size and large, ripe testes were common from September to November. In December and January, they were reduced and mainly consisted of mature spermatozoa, indicating that spawning had recently occurred. The monthly reproductive conditions of the testes suggested that the breeding season occurred in early summer. During this period, the eggs were being transferred to the brood clusters.

Anasterias directa (Koehler)

Anasterias directa is endemic to Macquarie Island. It is a five-armed starfish and has a predominant dark olive colour form. Distinguishing features of the species are outlined in Clark (1962).

A. directa was found on solid, rocky substrata. Specimens were collected from channels, gutters, and pools at the top of the sub-littoral zone. All starfish used for reproductive investigations had a central disc diameter of at least 19 mm.

The sexes are separate. Out of 128 specimens sexed, 62 were females and 66 were males. A pair of gonads was situated in each of the five interbrachial regions. In the males, the testes had a botryoidal appearance, while in the females each ovary consisted of two compact round sacs. When ripe, the testes greatly enlarged and extended down into the arms. In the females, the sacs expanded to accommodate the enlarging eggs.

Figure 5 shows the annual reproductive cycle for *A. directa*. The female brooded the young from the egg to the juvenile stage, the brood forming a compact cluster overlying the oral region (see fig. 6). Small eggs were present in the ovaries in April and May, the average diameter in April being 0.5 mm. The diameter of the eggs increased to 1.1 mm in early June and progressively increased until they were transferred to a brood at the oral region in July, at which time diameter of the eggs ranged from 1.8 to 2.0 mm. Development of the embryos proceeded in the brood to a juvenile stage (October-November). The juveniles were released in the November-December period. Again, a female was classed in a "juvenile release" stage using the same criteria as for *A. mawsoni*. In January, the ovaries were small and the average egg size was 0.3 mm. The eggs progressively enlarged to an average diameter of 0.6 mm in mid-March.

In the specimens examined, the number of eggs per brood varied from 174 to 220, depending on the size of the starfish. Females exhibited a distinctively arched posture when carrying a brood (like that of *A. mawsoni*). Again, larger starfish were able to create a larger cavity and hence could accommodate a larger brood.

In males, during the corresponding period of brooding in the females, the testes were generally reduced in size and showed little signs of spermatogenic activity. Growth and spermatogenic activity were evident from November to February. Ripe testes were predominant in late February and March. They were present in April and May of the preceding year, but at

Fig. 5. Reproductive cycle of *Anasterias directa*. **a**. females, N = 5 each month; X = evidence of recent juvenile release, ◄ = juveniles in brood, △ = embryos in brood, O = eggs in brood, ■ = eggs in ovary; **b**. males, N = 5 each month; X = recent spawning, ● = ripe, O = abundance of spermatids, ■ = early spermatogenesis, □ = resting, ◄ = resorbing. (Each symbol represents one specimen, the gonad of which has been classified by its predominant reproductive state. The sets of each symbol are stratified on the figure for better visual interpretation).

Fig. 6. Brood, at juvenile stage, of *Anasterias directa*.

this time testes were mainly reduced and consisted of mature spermatozoa with little signs of spermatogenic activity, indicating that spawning had recently occurred. The monthly reproductive conditions of the testes suggested a breeding season in the autumn. Yet, in this period, the eggs were still mainly held in the ovaries. From this pattern it appears that male spawning was too early if the eggs were to be fertilized during the seemingly opportune time of transfer to the brood region. Fertilization may occur in some other way. However, it is more likely that the above is a discrepancy in the pattern owing to either (a) a bias resulting from the small number of specimens used or (b) an ecologically-induced difference, that is, males being taken from habitats different to those of females in the first part of the collecting period (April-June).

Cycethra macquariensis Koehler

The nomenclature for this species is not clear. The collected specimens were firstly identified as *Asterina hamiltoni* Koehler. However, on examination of type specimens held by The Australian Museum, Sydney, the specimens from Macquarie Island were then identified as *Cycethra macquariensis* in the family Ganeriidae. Yet, on the basis of the arrangement of plates and spines, the specimens could be identified as a genus in the family Asterinidae, in accordance with the key in Clark (1962). Clark (1962) remarked that the separation between *Cycethra* and *Asterina* is indistinct.

Cycethra macquariensis is endemic to Macquarie Island. It is a small, five-armed starfish. Specimens were collected from pools and channels in the sub-littoral zone. All animals used for reproductive studies were at least 22 mm in total body diameter.

The sexes are separate. Out of 141 specimens sexed, 96 were male and 45 were female. A pair of gonads was situated in each of the five interbrachial regions. The testes had a botryoidal appearance and when ripe, were large and extended into the arms. Each ovary consisted of a number of small sacs (typically seven) and each sac contained eggs of various sizes. The number of eggs per sac varied from 19 to 24, the average being 20. There were three distinct size categories (diameter): (a) less than 0.3 mm, (b) 0.3 to 0.49 mm, and (c) 0.5 to 0.8 mm. The smallest eggs were more plentiful than the largest. In grouping the figures from all specimens, the range of numbers in the three size categories was (a) 11 to 16 ($\bar{x}$ = 13), (b) 4 to 7 ($\bar{x}$ = 5), (c) 1 to 3 ($\bar{x}$ = 2).

The above condition of the ovaries was maintained throughout the collections. About 40% of the males had ripe testes in any one month. Thus *C. macquariensis* appeared to breed continuously throughout the year.

It is not clear whether females released ova to the sea for external fertilization. The average number of eggs per female is 20 x 7 x 10 = 1,400 (number of eggs per sac x number of sacs per gonad x number of gonads). However, from the size range of the eggs, it was apparent that only about 140 of these were mature ova. The release of such a number would hardly ensure successful fertilization or survival rate if eggs were released to the open sea. No brood was found either enclosed in the body cavity or on the surface of the starfish. From the above evidence, it appears reasonable to assume that *Cycethra macquariensis* lays egg cases.

Pseudopsolus macquariensis (Dendy)

Pseudopsolus macquariensis is endemic to Macquarie Island. A description of the species is given by Pawson (1968). Specimens were collected from channels and gutters encrusted with coralline algae at the top of the sub-littoral zone. Adult holothuroids were commonly 25 mm long from the base of the tentacles to the anus. For plotting the reproductive pattern, specimens of at least 15 mm were used.

The gonad consists of a cluster of unbranched caeca uniting at a common base in mid-dorsal mesentery, approximately one quarter body length from the anterior end of the animal. From the base, a single genital duct passes to an opening in the oral disc. Ludwig (1898) grouped the caeca into left and right tufts, presumably using the mesentery wall as the divider.

The species has previously been described as hermaphroditic (Ludwig, 1898; Mortensen, 1925) but this requires further examination. For a maturing gonad, there are a number of large caeca that contain the developing gametogenic material which, for each animal, is either male or female — not both. (Any further designation here of an individual as male or female has used the sexual status of the large caeca as the criterion). The contentious point is the role of the smaller genital caeca at the base of the cluster. Ludwig (1898) described one specimen, which was obviously a male with a ripe gonad, and noted much smaller caeca containing "small eggs" 0.23 to 0.28 mm in diameter. In a description of two specimens, Mortensen (1925) reported a condition similar to that found by Ludwig in one and, in the other (a small female), he observed ovarian caeca each with two eggs (1.5 mm diameter) and some smaller caeca which he classed into both male and female types.

In the present study, 181 specimens (measuring 15 mm or more from anus to the base of the tentacles) were sexed as 102 males and 79 females. This bias in sex ratio was greater in a collection of 29 smaller specimens that were 12 to 15 mm in length (20 males, 8 females, 1 immature). Further observations on the 181 larger specimens showed that the small genital caeca were divisible into two groups: (1) very small buds and (2) caeca 1 to 3 mm in length which nearly aways contained egg-like forms. Four male specimens had small non-differentiated caeca containing spermatogenic material. Three specimens had developing ovarian caeca and thin, male caeca that were in a regressed stage. Two females with broods had genital caeca containing egg-like forms in some and, in others, developing testes arranged in a bead-like pattern down the caeca. These last five specimens confirmed the occurrence of successive hermaphroditism as reported by Ludwig (1898) and Mortensen (1925). However, the deductions on this point by Ludwig and Mortensen were ill-founded in using the presence of smaller genital caeca with egg-like forms to indicate that the next sexual role would be female. Such caeca appear to contain precursor material for either male or female formation. Histological work on specimens in key reproductive stages is required for further elucidation of such a process.

It is unlikely that each individual would change sex each year with a resultant switch in the sexual bias. This was confirmed by a similar state of sexual bias showing at both the start and end of the period of collection, which covered two successive reproductive cycles (see later). Thus, some individuals must retain the same sex in successive cycles. If sex change is an option for an animal, there is the speculative hypothesis that the number of females increases in response to some form of feedback that favours a population increase, and vice versa.

In a description of 8 specimens (11 to 19 mm in length) of a new sub-species, *Pseudopsolus macquariensis gruai*, from the Kerguelen Islands, Cherbonnier (1974) found gonads with 4 to 5 thick, white, male caeca and "about ten" very fine, long tubules with a "few eggs" less than a micron in diameter. Such a gonadal condition was not found in specimens of *Pseudopsolus macquariensis* in the present study.

The number of large caeca varied from 12 to 24 in both males and females. The caeca were divided into two groups by mid-dorsal mesentery usually with half the number in each group. Smaller caeca and buds at the base of the gonadal cluster were more numerous. When sexually ripe, large male caeca were looped and the total length of some exceeded the body length of the animal. In females, the number of eggs in caeca varied from 73 to 154 and numbers of eggs/embryos in a brood varied from 61 to 130. These figures apply to specimens over 15 mm from anus to the base of the tentacles, and the number of eggs was related to the number of
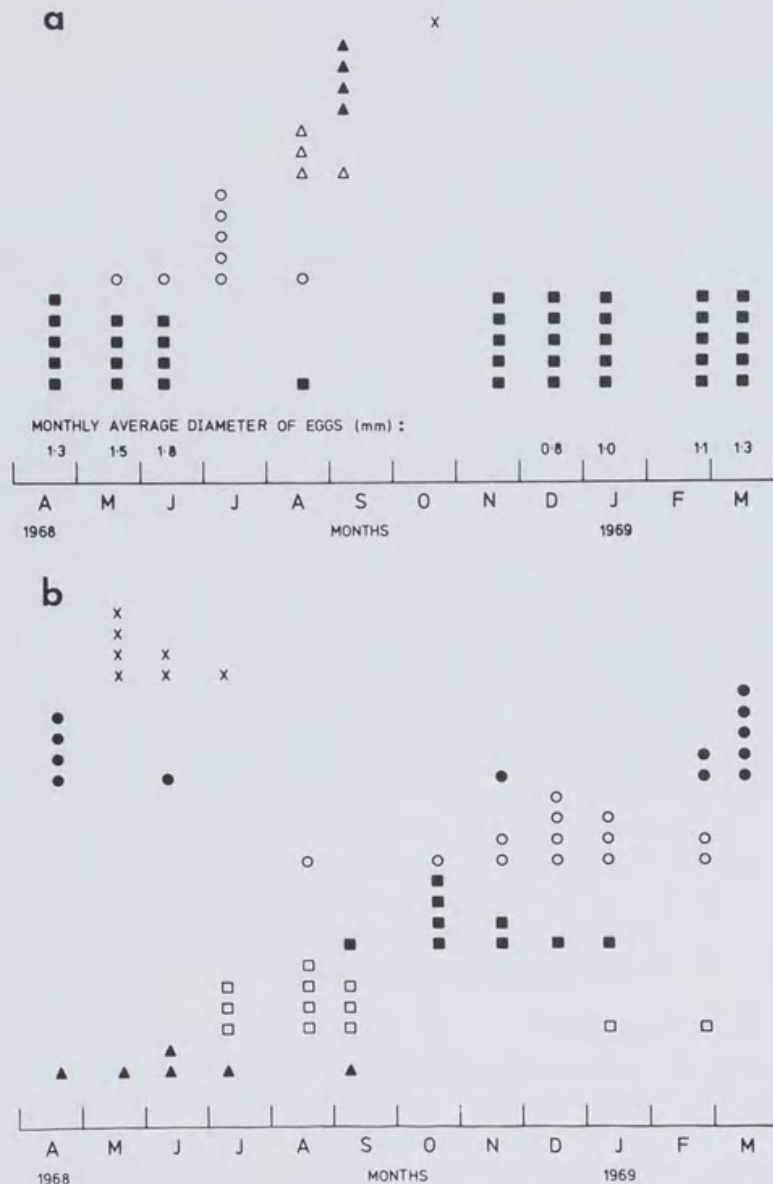
Fig. 7. Reproductive cycle of *Pseudopsolus macquariensis*. **a.** females, N = 5 each month (except October); X = no brood found in forty specimens — all juveniles released, ▲ = juveniles in brood, △ = embryos in brood, O = eggs in brood, ■ = eggs in ovary; **b.** males, N = 5 each month; X = recent spawning, ● = ripe, O = abundance of spermatids, ■ = early spermatogenesis, □ = regressed, ▲ = resorbing. (Each symbol represents one specimen (except for females in October), the gonad of which has been classified by its predominant reproductive state. The sets of each symbol are stratified on the figure for better visual interpretation.)

tubules and animal size; that is, the more tubules and/or the larger the animal, the more eggs. Eight females of 12 to 15 mm in length (in the above dimension) had egg numbers of 25 to 52 in the large caeca.

Figure 7 shows the annual reproductive cycle for *Pseudopsolus macquariensis*. Eggs were developing in the ovaries from November to June. In December, the eggs (averaging 0.8 mm diameter) were distinctly separate down the length of the caeca, resembling a string of beads. The size of the eggs progressively increased in the following months and in May, their diameter was 1.5 mm. In May and June, eggs appeared in internal brood sacs and at this stage were 1.8 mm in diameter. There was negligible variation in the size of eggs in an individual at any particular phase of the cycle. In the first week of July, all specimens assuming the female role had eggs in the internal brood sacs. There was no evidence of internal connection to these sacs. External transference was not observed nor did any specimen collected show an intermediate

phase, with some eggs in caeca and some in incubatory sacs. However, two females were found with a small stone in a brood sac that also housed eggs. This suggested insertion of eggs into the brood sacs from the outside.

Further development proceeded in the brood sacs, the September samples showing advanced embryos and juveniles. Release of juveniles occurred in late September-October. There was a high degree of synchronization during juvenile release. On 22nd October, juveniles were found underneath adults and large numbers of adults were collected on this date. Forty specimens from this collection were dissected and not one contained any juveniles.

The resting period of the testes was from July to September. Early spermatogenesis was predominant in October. Spermatogenesis and growth continued progressively with large, ripe testes predominating in March-April. In May and June, testes were in an obvious post-spawning condition, i.e. reduced, not firm, and full of mature spermatozoa with little spermatogenic activity. The cycle in the testes indicated that the breeding season occurred in May-June during the transfer period of the eggs from gonadal caeca to incubatory sacs. If the eggs are transferred externally, as findings here suggest, fertilization may depend on the coincidental timing of transfer and male spawning.

Two large, often convoluted, protuberances appeared on the ventral surface of many individuals, about half-way down the body (fig. 8). At first it was thought that these were "brood pockets" from which the young were released as the bulges coincided with the openings to the incubatory sacs. However, the protuberances were present in specimens assuming both male and female roles. The number of specimens with these growths increased during the juvenile-release phase of the cycle but with no bias to those acting as females. Histological sections of these areas showed that the extra growth was largely a result of increased connective tissue. The significance of these protuberances remains unexplained.

The incubatory sacs were deeply internal and not surface pockets. There were two sacs, divided into compartments, situated in the left and right ventral interambulacral areas. Each sac had a ventral opening via a single duct. Figure 9 shows a brood sac with eggs and a transverse section through the ventral duct. The opening was a simple hole, half-way down the ventral body wall and coinciding with the previously described protuberances (if they were present). Juveniles were released through these ventral pores and moved out from underneath the parent on to the surrounding rock surfaces. The walls of the sacs were transparent and of light texture.

Pseudocnus laevigatus (Verrill)

Only four specimens were collected from rock pools in the lower eulittoral zone. The largest individual (35 mm in length, from the base of the tentacles to the anus) contained 93 young in internal brood pouches. The brooding habit in this species has been previously reported by Pawson (1968).

Trachythyone macphersonae Pawson

Ten specimens of this species were collected from rock pools in the lower eulittoral zone. The sexes are separate. There were no small gonadal caeca opposite in sex to large caeca as in *Pseudopsolus macquariensis*. The females had a small number (110 to 130) of eggs in long, unbranched ovarian caeca; these eggs were large, diameters ranging from 0.2 to 0.8 mm with a fairly uniform size in any one specimen. The size of the egg appears to depend on the stage in the reproductive cycle. However, the small number and the 0.8 mm size eggs indicated that this species does not have a planktonic larval stage, most likely developing via a brooding habit.
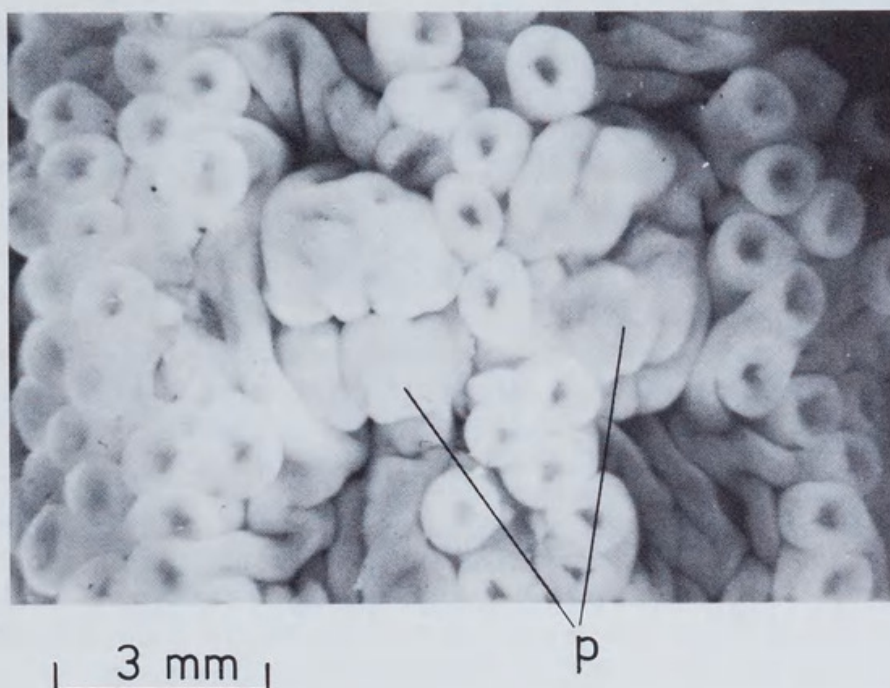
Fig. 8. Protuberances on the ventral surface of *Pseudopsolus macquariensis*, (p. = protuberances).
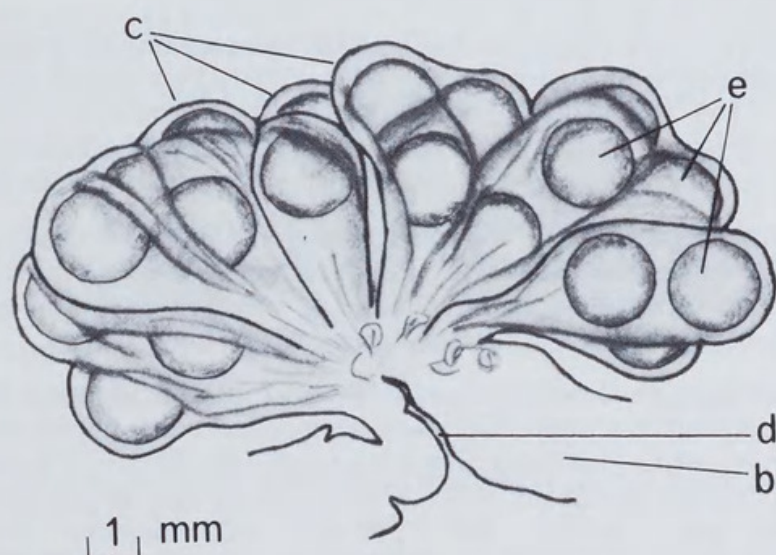

Fig. 9. Side view of brood sac and ventral duct of *Pseudopsolus macquariensis*. **b.** = ventral body wall, **c.** = compartments in the brood sac, **d.** = ventral duct, **e.** = eggs.

Pseudechinus novaezealandiae (Mortensen)

Four specimens of *P. novaezealandiae* were examined. Two were from collections during the present study (one from the sub-littoral zone, the other from a diving station at a depth of seven metres) and two were obtained from the National Museum of Victoria. As in other regular echinoids, there were five gonads suspended by mesenteries along the inner surface of the interambulacra. Three of the specimens were males, the other female. In the female, the ovaries were large and projected well down ventrally, filling a large part of the available space. The ovaries contained numerous eggs (diameter = 0.1 mm) suggesting that this echinoid has a planktonic larval stage.

DISCUSSION

For the seven species investigated, *Anasterias mawsoni*, *Anasterias directa*, *Pseudopsolus macquariensis* and *Pseudocnus laevigatus* were found to have a brooding habit. Ovarian conditions suggested non-pelagic development for *Trachythyone macphersonae* (most likely via brooding) and for *Cycethra macquariensis* (most likely via the laying of egg masses), and a pelagic larval development for *Pseudechinus novaezealandiae*. These predictions of larval development for the latter three species are based on the number and size of the ova. Invertebrate species with a non-pelagic larval development characteristically have a small number and large size of eggs (Thorson, 1950 and Mileikovsky, 1971.). The suitability of this type of prediction is discussed elsewhere (Simpson, 1977) as well as the less positive nature of the converse — that a large number of small eggs indicates a pelagic development.

For the four species collected at regular intervals, both *Anasterias* and *Pseudopsolus macquariensis* were found to have an annual reproductive cycle. *Cycethra macquariensis* appeared to breed continuously throughout the year. From the respective numbers examined, the sex ratios varied among the four species, that is female: male was approximately 1.5:1 (*Anasterias mawsoni*), 1:1 (*Anasterias directa*), 0.5:1 (*Cycethra macquariensis*), and 0.8:1 (*Pseudopsolus macquariensis*). However, no attempt was made to randomize collecting localities and hence the ratios may be affected by any sexual bias in distribution.

The reproductive condition found in *Cycethra macquariensis* is atypical for starfish. They generally have a well defined short breeding season, usually as part of an annual reproductive cycle (Boolootian, 1966). In a list of breeding seasons of asteroids compiled by Boolootian (1966), the two exceptions to this rule were in the family Asterinidae (*Patiria miniata* and *Asterina exigua*) which were reported as breeding continuously throughout the year.

Lawson-Kerr and Anderson (1978) confirmed that *Patiriella exigua* (named *Asterina exigua* by Mortensen (1921) in Boolootian's list) was potentially capable of breeding at any time of the year. A further species reported as being capable of breeding throughout the year is also in the family Asterinidae — *Patiriella vivipara* (Dartnall, 1969).

Although some species of asterinid starfish have limited breeding seasons, (Boolootian, 1966; Lawson-Kerr and Anderson, 1978; Komatsu, pers. comm.), it is curious that all starfish reported as capable of continuous breeding are in the Asterinidae. To elucidate the reasons for the reproductive strategies of marine invertebrates, many factors require examination. One of these factors is phylogenetic affinity for a particular reproductive type. It would seem that asterinid starfish present appropriate material for investigating such a factor.

Anasterias mawsoni and *Anasterias directa* had the same distributional range, occupied similar habitats and had very similar prey (Simpson, 1976b); yet their reproductive cycles were different in that there was a time difference of four months between the peak release of young

nd hence recruitment of the two species. This may be important in alleviating any competition
etween the recruitment of the two species into such similar ecological niches.

For the species collected, there is a predominance of a protective mode of larval
evelopment with a comparatively small number of offspring. This conforms with "Thorson's
ule" that there is an increase in frequency of non-pelagic development with increasing latitude.
he adaptive significance of this phenomenon has been the subject of much speculation and
nany hypotheses, which are linked to changing physical and biotic ecological conditions with
ncreasing latitude (Thorson, 1950; Mileikovsky, 1971; Menge, 1975).

The sub-Antarctic provides an important link in records of reproduction of marine
nvertebrates from tropical and temperate regions to the Antarctic. Gathering of data on the
node of reproduction of invertebrates from selected groups across the range of southern
atitudes should result in better interpretation of zoogeographical origins and lines of
listribution. This will provide a more complete historical background to possible investigations
)f adaptational advantages to be gained by animals with a protective mode of development in
ligher latitudes. Details of the timing of the events, when reproductive patterns of such animals
:an be obtained, will allow insight into key areas for such investigations.

ACKNOWLEDGEMENTS

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