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Divide or Broadcast: Interrelation of Asexual and Sexual Reproduction in a Population of the Fissiparous Hermaphroditic Seastar *Nepanthia belcheri* (Asteroidea: Asterinidae)

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Abstract

Asexual and sexual reproduction were studied in an intertidal population of *Nepanthia belcheri* (Perrier) at Townsville, Queensland, Australia, by regular sampling over a year (March 1976–March 1977) and by histological analysis of gonads. Fission reached a peak in early winter (April–June), when about 45% of the population showed evidence of recent fission. Propensity for fission was unrelated to longest arm length. Seven-armed seastars predominated in the population and these underwent fission in two stages to produce one 3-armed fragment and two 2-armed fragments. Fission planes were not related to numbers or positions of madreporites. Hermaphroditism was a normal sexual condition in the population. Almost all gonads contained oocytes, but some gonads functioned as ovaries (without spermatogenic tissue) while others functioned as testes. Seastars with mature ovaries were significantly larger than those with mature testes, indicating protandry, as in other hermaphroditic asteroids. However, fission complicates the pattern of gonad development by causing regression or retardation of gonads and by apparently having a masculinizing effect, so that ovaries may change to testes in fission products. There was a period of sexual reproduction in early summer (October–November). This followed the period of intense fission and regeneration, and a population change from predominately functional females to males. Consequently there was an extreme imbalance against mature females at sexual reproduction, further reducing potential fecundity. Thus, sexual reproduction was very subordinate to fission as the means of recruitment. The 450 μm diam eggs probably give rise to pelagic lecithotrophic development and, if this is the case, *N. belcheri* retains the advantage of complementing reliable recruitment from fission with a dispersive phase. The combination of fission and hermaphroditism is particularly advantageous for a very sparse dispersal of larvae, as a functionally dioecious population may develop from one larva settling in a new locality.

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Introduction

Emson and Wilkie (1980) reviewed the literature on the processes of fission and autotomy whereby echinoderms reproduce asexually. In asteroids, fission takes the form of a spontaneous division of the seastar through its disc, while reproductive autotomy occurs by spontaneous shedding of individual arms or sections of arms. Neither process is widespread among asteroids. Autotomy was thought to be peculiar to the genus *Linckia* (Hyman, 1955), but it has been reported more recently for several other species. Observations of fission are restricted to 6 genera in the families Asterinidae and Asteriidae (Clark, 1967; Emson and Wilkie, 1980). Gonads have been reported in most of the fissiparous species and it has not been established that an asexual process completely replaces sexual reproduction in any asteroid.

Sexual reproduction in asteroids ranges from stable gonochorism, through labile gonochorism, to functional hermaphroditism (Delavault, 1966, 1975). Labile gonochorism generally is in the form of aberrant gonads within some individuals of a species. Species in which hermaphroditism is the normal sexual condition have been reported from 3 genera, *Asterina, Asterias* and *Fromia,* and most work has been done on one species, *Asterina gibbosa* Pennant (Delavault, 1975).

Almost all seastars reproducing asexually and all hermaphrodites are from 3 unrelated families: the spinulosid Asterinidae, the forcipulatid Asteridae and the valvatid Ophidiasteridae. Therefore, it is not surprising to discover the combination of fission and hermaphroditism in a population of an asterinid, *Nephanthia belcheri* (Perrier).

Nepanthia belcheri is a small cryptic seastar found on hard substrates in muddy conditions from the intertidal zone to a recorded depth of 46 m (Rowe and Marsh, in

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press). In intertidal zones it is found on the undersurfaces of and beneath, rock fragments and boulders. It is morphologically variable over its geographical range from northern and eastern Australia to the S.E. Asian continent (Rowe and Marsh, in press). Fission has been reported for *N. belcheri* at various localities (Clark, 1938, 1946; Kenny, 1969; Rowe and Marsh, in press) and hermaphroditism was first reported by Dartnall (1971), who examined some specimens from Moreton Bay, Queensland.

This study establishes that hermaphroditism is a normal condition in a population of *Nepanthia belcheri* at Rowes Bay, Townsville, North Queensland (19°15′S; 146°7′E), and it considers the interrelation of concurrent asexual and sexual processes in the population.

Materials and Methods

The intertidal zone of Rowes Bay, Townsville, consists of muddy sand with rock fragments and other rubble. Inshore water temperatures range from 21.8 °C in July to 31.2 °C in January (monthly mean values) (Kenny, 1974). *Nepanthia belcheri* (Perrier) occurs with another asterinid, *Patiriella obscura* Dartnall, in the lower part of the intertidal zone, but not in the sublittoral where there are insufficient hard substrates. Between March 1976 and March 1977, the *N. belcheri* population was sampled at low water of spring tides on 10 occasions, recording arm number and measuring all arm lengths (*R*), to 1 mm accuracy, for a total of 613 individuals. Some seastars were kept for histological examination and all others were returned.

On 6 occasions during the year, a sample of seastars (16 to 28 individuals) was dissected for analyses of organ index and reproductive condition. The longest arm and representative portion of the disc were cut off and the pyloric caeca and gonads excised. The organs and eviscerated arm and disc were dried of surface moisture and weighed to 0.1 mg. Twenty-two specimens, 3 collected in September 1976 and 19 collected in March 1980, were totally eviscerated to compare gonads in different-sized arms of the same individual. Organ indices were calculated according to Pearse (1965), but the organ and eviscerated body weights of only the longest arm were used.

Dissected gonads were fixed in marine Bouin's fluid (85% saturated picric acid in seawater, 10% unneutralised formalin and 5% glacial acetic acid) and embedded in paraffin. Sections were cut at 6 μm and stained with Mayer's haemalum and an eosin-erythrosin counterstain. Sections were examined by light microscope for sexuality and reproductive stage.

Some large specimens were treated with 1-methyladenine (1-MeAde) in an attempt to induce oocyte maturation and spawning (Kanatani, 1969; Stevens, 1970). Two treatments were used: small volumes of 1×10^{-5} *M* or 1×10^{-3} *M* 1-MeAde were injected into the coelomic cavities of whole seastars; excised gonads were placed in filtered seawater with 1 or 2×10^{-5} *M* 1-MeAde.

Results

Asexual Reproduction

Seven-armed individuals predominated in the Rowes Bay population of *Nepanthia belcheri* and overall this condition was almost twice as frequent as the next most common condition, 6 arms (Table 1). Fission was a frequent occurrence and most seastars showed variation in arm size, reflecting two or three generations of arms in each individual. Those seastars with 5 mm or less variation between longest and shortest arms were considered to be "regular"; they constituted only 6.4% of the total sample.

The pattern of fission and regrowth was observed in 7-armed seastars kept in the laboratory in seawater at ca. 25 °C (Fig. 1). The first indication of splitting was the formation of a shallow furrow across the centre of the disc. This furrow subsequently became the line of fission. The parts of the seastar on either side of the furrow began to pull in opposite directions. Often, projections and irregu-

Table 1. *Nepanthia belcheri.* Frequency distributions of number of arms per seastar in samples from Rowes Bay, Townsville, Queensland, Australia, from March 1976 to March 1977. No data collected in November, January, February

Month	Sample size	Percent frequency of seastars with arm number:								
		1	2	3	4	5	6	7	8	9
March	92	0	5.4	6.5	0	3.3	42.4	37.0	4.3	1.1
April	63	4.8	15.9	17.5	3.2	3.2	19.0	31.7	3.2	1.6
May	119	0.8	17.6	8.4	4.2	2.5	25.2	37.8	3.4	0
June	80	0	13.7	10.0	5.0	1.3	17.5	50.0	2.5	0
July	82	0	14.6	0	0	1.2	25.6	47.6	11.0	0
August	45	2.2	4.4	11.1	0	0	17.8	57.8	6.7	0
September	62	0	6.4	3.2	1.6	1.6	29.0	48.4	9.7	0
October	29	0	13.8	6.9	0	0	13.8	55.2	10.3	0
December	25	0	0	0	0	0	12.0	68.0	20.0	0
March	16	0	18.8	18.8	6.3	0	18.8	37.4	0	0
Total	613	0.8	11.7	7.7	2.1	1.8	24.8	44.5	6.2	0.3

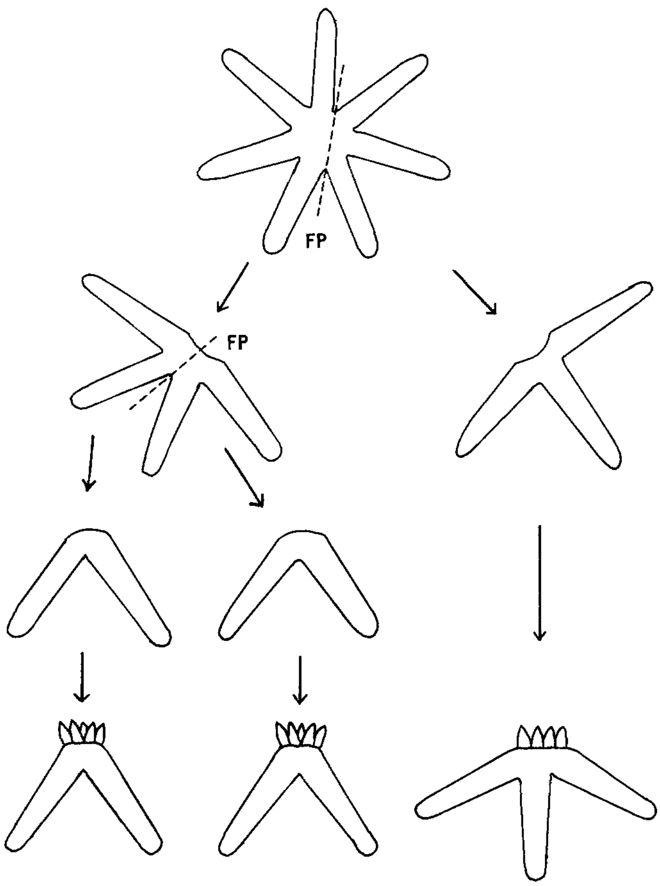

Fig. 1. *Nepanthia belcheri.* Sequence of fission and budding of new arms in 7-armed seastars. FP: fission plane

larities of the substrate were used as physical aids in separation. After several hours of pulling, during which time the seastar might rest and then move to find a new surface or adopt a new orientation that aided splitting, separation into a 4-armed individual and a 3-armed individual occurred. The 4-armed state was not favoured and further fission commenced immediately in the 4-armed individual, subsequently producing a pair of 2-armed individuals. The damaged tissue infolded after separation and scar tissue was evident after several days. Primordial arm buds developed within 2 wk. Three-armed seastars regenerated 4 new arms, while the 2-armed seastars regenerated initially 4 and then a 5th arm in the middle of the developing 4.

The field data of Table 1 support these laboratory observations in that 2- and 3-arm conditions predominated among recently split individuals, comprising 11.7 and 7.7% of the total sample, respectively. As expected, assuming that fission follows the pattern described above, 2-armed seastars were more common than 3-armed. However, this interpretation is complicated by the significant proportion of 6-armed seastars, which must undergo division into two 3-armed or three 2-armed individuals. The very small percentage of single-armed seastars presumably arose by fission of 2- or 3-armed individuals rather than by autotomy, as there were no signs of autotomy, i.e., seastars with scars from shedding single arms or segments of arms.

No relationship between lines of fission and numbers or positions of madreporites was discerned. Madreporite number, counted on 240 seastars between June and October 1976, was found to be highly variable, even in individuals with the same number of arms (Fig. 2).

There were pronounced temporal changes in the frequency of fission in the *Nepanthia belcheri* population. The percent frequency of seastars showing evidence of recent fission (i.e., scar tissue or developing arms 3 mm and less in length) was at a peak of approximately 45% of the population from April to June, then it declined to zero in December and rose again the next year (Fig. 3).

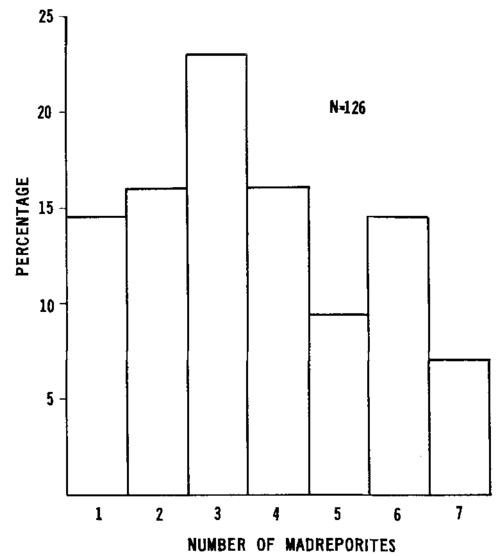

Fig. 2. *Nepanthia belcheri.* Histograms showing percentages of 7-armed seastars with 1 to 7 madreporites, in samples from June to October 1976

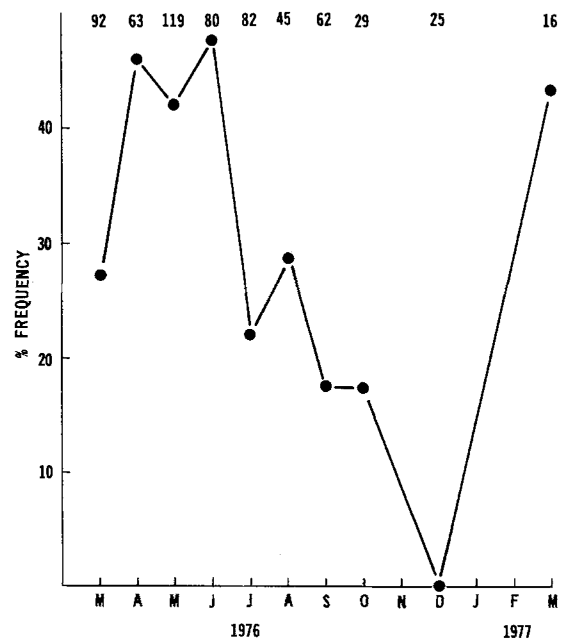

Fig. 3. *Nepanthia belcheri.* Percent frequency of individuals showing evidence of recent fission (i.e., scar tissue or developing arms 3 mm and less in length). Monthly sample sizes are included

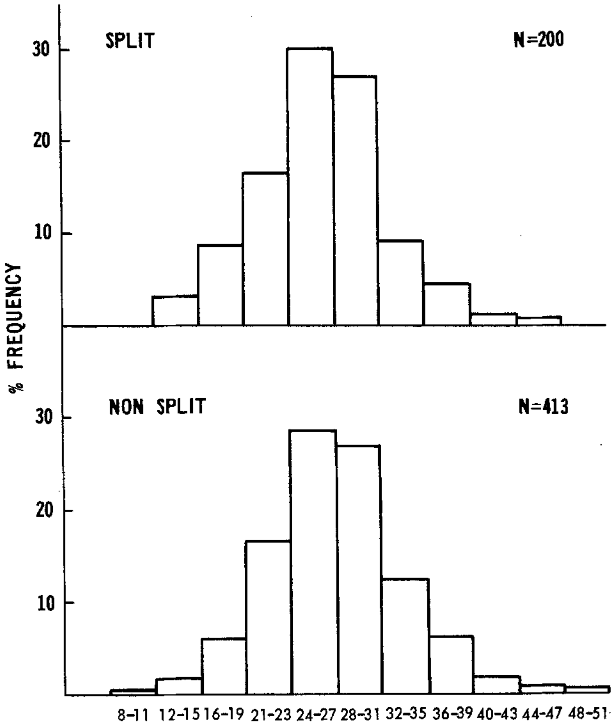

Fig. 4. *Nepanthia belcheri.* Size-frequency histograms showing percentages of individuals with evidence of recent fission (SPLIT) and those which have not recently divided (NON SPLIT) versus longest arm length, in samples from March 1976 to March 1977

It is probable that the majority of seastars underwent fission at least once, because (i) almost 50% of the population showed evidence of recent fission for 3 mo of winter (Fig. 3); (ii) each seastar usually divides into 3 individuals and thus about one-quarter of the population must have undergone fission to result in half the population (including the fission products) showing evidence of recent fission; (iii) arm buds develop about 2 wk after fission and seastars probably only remain in the recent-fission category (arm buds 3 mm) for about 1 mo. Thus, during the period April to June, about one-quarter of the population underwent fission each month.

Over the considerable size range of *Nepanthia belcheri* collected in this study, the probability of fission was not related to longest arm length. Largest arm-length frequencies of individuals showing evidence of recent fission (criterion above) and of those showing no such evidence are compared in Fig. 4. These data were analysed using a Kolmogorov-Smirnov two-sample test (Siegel, 1956) and no significant difference was found between the distributions with respect to central tendency, dispersion or skewness ($D_{\text{calculated}} = 0.056$; $D_{0.01\ \text{significance}} = 0.140$). Therefore, there is no longest arm size at which fission occurs significantly more frequently.

Sexual Reproduction

Paired lobulate gonads occur in the lateral regions of each arm proximal to the disc. Each gonad is attached to the wall near the interbrachial septum by a short gonoduct which opens abactinally. Gonad colour varies from olive green in ovaries with developed eggs to creamy white in testes filling with spermatozoa, while very small gonads are translucent. Gonad condition varies between arms in irregular seastars and longest arms tend to have the largest gonads. Even the two gonads in an arm may differ in size and maturity, with a smaller gonad on the side next to a fission scar or arm buds. This suggests that gonad development in large arms is retarded or reversed by the tissue demands of adjacent developing arms. Although a gonad may be functionally male or female at different times (see below), all developing gonads within one individual were found to be the same functional sex. The smallest developing arm in which gonads were found was 10 mm long, while no gonads were found in some regenerating arms up to 15 mm.

The paired gonads in the largest arm of 155 seastars were examined histologically. Almost all gonads contained oocytes. The exceptions were some very small gonads which were regressing and filled with phagocytic cells. Other small gonads contained previtellogenic oocytes or remnants of oocytes. The large gonads either contained developing oocytes (i.e., they were functional ovaries), or oocytes among spermatogenic tissue, with the latter dominating and leading to large accumulations of spermatozoa in the lumen (i.e., gonads functioning essentially as testes).

To follow the patterns of gonad development through the year, a series of 7 arbitrary stages was recognised, based on sexuality and state of maturity:

Stage i. Small and very small gonads (lobule diameter < 100 to $300\,\mu$m) containing previtellogenic and immature oocytes usually attached to the gonad wall (Fig. 5: *1*). The lumen is usually filled with interstitial tissue. In some gonads the oocytes are degenerating and there may be associated phagocytic cells.

Stage ii. Maturing ovaries, larger than Stage i (lobule diameter 300 to $700\,\mu$m), containing a range of oocytes from previtellogenic to mature (Fig. 5: *2*). The smaller oocytes tend to be imbedded in a matrix of interstitial tissue.

Stage iii. Large ovaries (lobule diameter $550\,\mu$m to 1.1 mm), filled with regular-shaped mature and maturing oocytes (lobule diameter 350 to $500\,\mu$m) (Fig. 5: *3*). Some small oocytes persist near the gonad wall.

Stage iv. Small gonads, immature testes, similar to Stage i (lobule diameter < 100 to $350\,\mu$m), but with spermatic columns and, in some, a small accumulation of spermatozoa (Fig. 5: *4*)

Stage v. Maturing, functional testes (lobule diameter 200 to $400\,\mu$m), dominated by spermatogenic activity (Fig. 5: *5*). There are large concentrations of spermatids distal to the

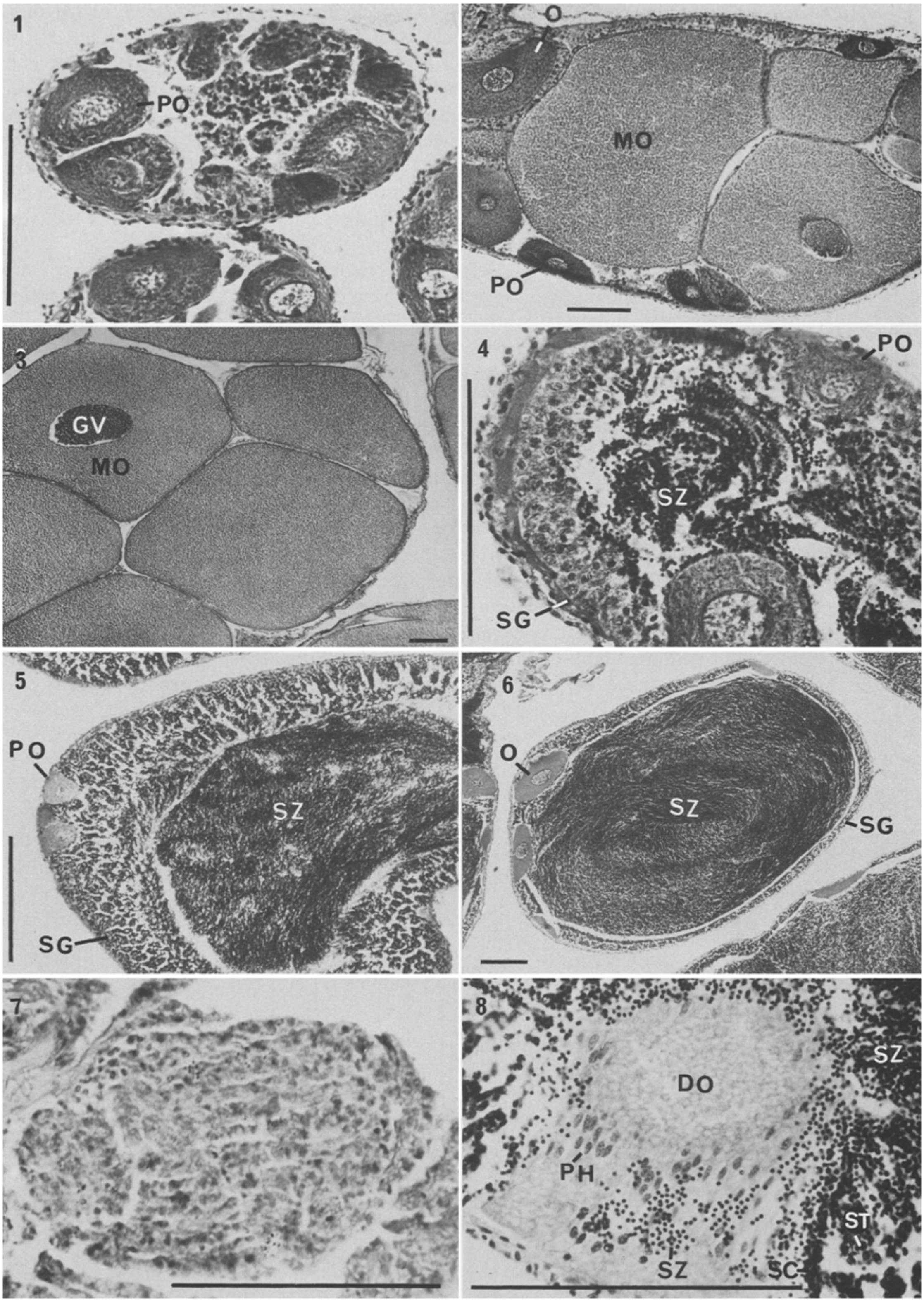

Fig. 5. *Nepanthia belcheri.* Sections of gonads. *1:* Immature gonad (Stage i); *2:* developing ovary (Stage ii); *3:* mature ovary (Stage iii); *4:* immature testis (Stage iv); *5:* maturing testis (Stage v); *6:* mature testis (Stage vi); *7:* spent gonad (Stage vii); *8:* oocyte degeneration in Stage v gonad. DO: degenerating oocyte; GV: germinal vesicle; MO: mature oocyte; O: oocyte (immature); PH: phagocytic cells; PO: previtellogenic oocyte; SC: spermatic column; SG: spermatogenic layer; ST: spermatids; SZ: spermatozoa. Scale bars = 100 μm

spermatic columns and spermatozoa are beginning to fill the lumen. Previtellogenic and immature oocytes are attached to the gonad wall, embedded in spermatogenic tissue, and in some gonads oocytes may be degenerating and being absorbed by phagocytic cells (Fig. 5: *8*).

Stage vi. Large, functional testes (lobule diameter 400 to 800 μm) with lumen packed with spermatozoa (Fig. 5: *6*). In some gonads the spermatogenic layer has thinned. Oocytes are still present and some may be degenerating.

Stage vii. Spent gonads, small and very small gonads (lobule diameter <100 to 350 μm), usually containing previtellogenic and young oocytes (Fig. 5: *7*), and distinguished from other stages by the presence of large numbers of phagocytic cells in the lumen (Fig. 5: *8*).

There were marked temporal changes in the proportions of seastars with the different gonad stages (Fig. 6). In March and May 1976, individuals with ovaries (especially Stage ii gonads) were common, and the only seastars with gonads showing spermatogenesis were in an early condition (Stage iv). By July, gametogenesis in the population had shifted strongly to spermatogenesis, with a marked decline in the proportion of seastars with ovaries. Individuals with well developed testes (Stages v and vi) were now present. The trend to spermatogenesis continued into September, with further increase in the proportion of seastars with well developed testes (Stage vi). Then there was a marked change by December, when seastars with testes were no longer present, being replaced by a high proportion of individuals with spent gonads (Stage vii) and some with developing ovaries (Stage ii). Thus, many seastars spawned in the period between September and December. The March 1977 sample suggests another general shift from oogenesis to early spermatogenesis (Stage iv), occurring somewhat earlier during the year than in 1976.

Despite the changing proportions of seastars with ovaries and testes, individuals with mature or near-mature ovaries (Stage iii) were present in all except the December sample (which was dominated by seastars with spent gonads). These Stage iii seastars were always the largest or near-largest individuals in each sample.

The relationship between seastar size and gonad condition (of largest arm) is shown in Fig. 7, using both longest arm and mean arm length as the criterion of size. Despite the large ranges within each gonad category, statistical comparisons (Student's *t*-tests) reveal some very significant differences between the mean sizes of seastars in different gonad categories. In the longest arm data, individuals with functional ovaries (Stages ii and iii) are significantly larger ($P<0.025$ to <0.001) than all other groups. Seastars with spent gonads (Stage vii) are significantly larger ($P<0.025$) than individuals with immature gonads and

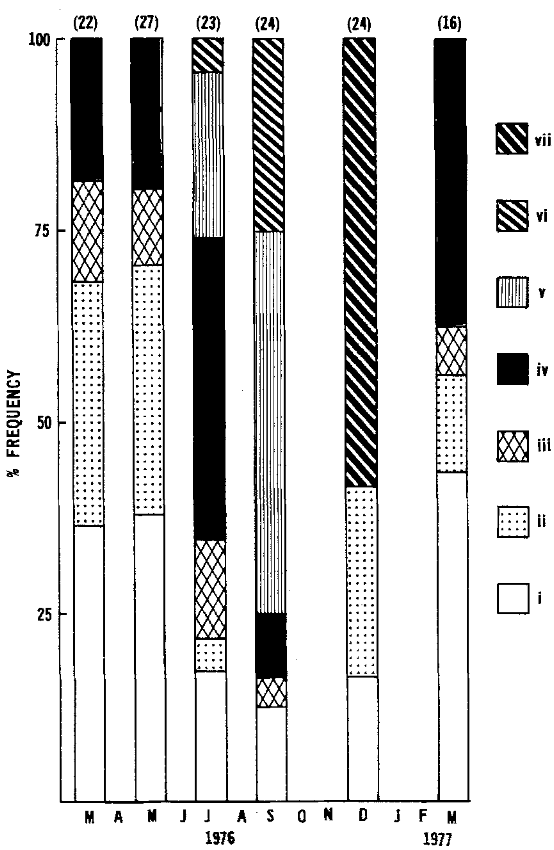

Fig. 6. *Nepanthia belcheri.* Percent frequencies of gonad stages in each sample for the longest arm of seastars. Sample sizes in parentheses

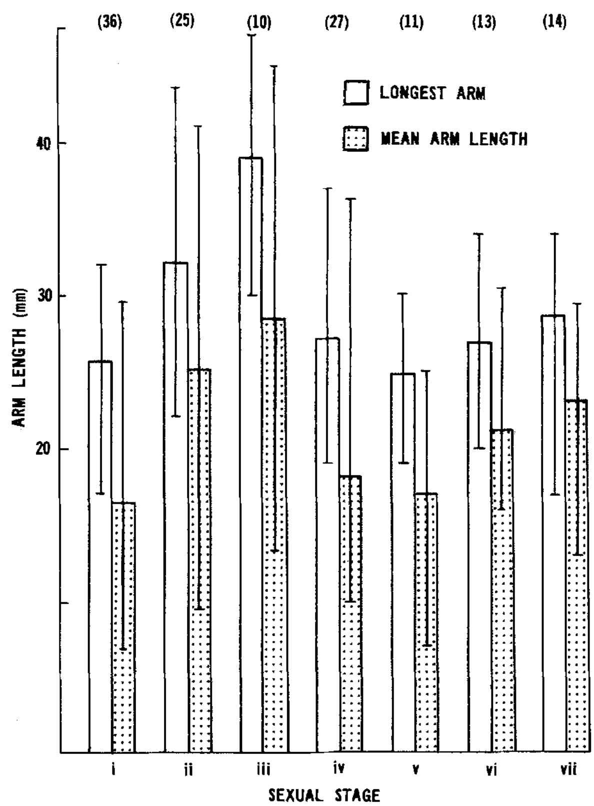

Fig. 7. *Nepanthia belcheri.* Seastar size (longest arm length and mean arm length) versus gonad condition of longest arm. Histograms are mean values, vertical bars are ranges. Number of individuals in parentheses

developing testes (Stages i and v, respectively). Seastars with immature gonads and functional testes (Stages i and iv–vi, respectively) are not significantly different.

In the data for mean arm sizes in each gonad category (Fig. 7), some ranges are very large. This is because the appearance of tiny arm buds on a recent fission product abruptly reduces the value of mean arm size without necessarily affecting gonad category; *a priori,* one would not expect a precise relationship between mean arm size and gonad condition of the longest arm. Nevertheless, the mean arm-size data show a similar pattern to the longest arm data. Mean arm sizes of seastars with functional ovaries (Stages ii and iii) are significantly larger ($P < 0.05$ to < 0.001) than values for those with immature gonads and functional testes (Stages i, and iv–vi, respectively). Individuals with spent gonads (Stage vii) are not significantly different from those at Stages ii and iii or at Stage vi (mature testes). Mean arm sizes of seastars with immature gonads and developing testes (Stages i and iv and v, respectively) do not differ significantly, but they are significantly smaller than individuals with mature testes and spent gonads (Stages vi and vii, respectively) ($P < 0.05$ to < 0.001).

It is apparent that seastars with functional ovaries are generally larger than individuals with functional testes and that those with spent gonads (previously ovaries and testes – predominantly the latter in these data, see Fig. 6) are intermediate in size. There is little difference in size between individuals with functional testes and those with immature gonads. While the size range for longest arms of seastars with mature testes is 20 to 34 mm, this range for individuals with mature ovaries is 30 to 47 mm, i.e., the longest arm does not contain mature ovaries until it reaches at least 30 mm.

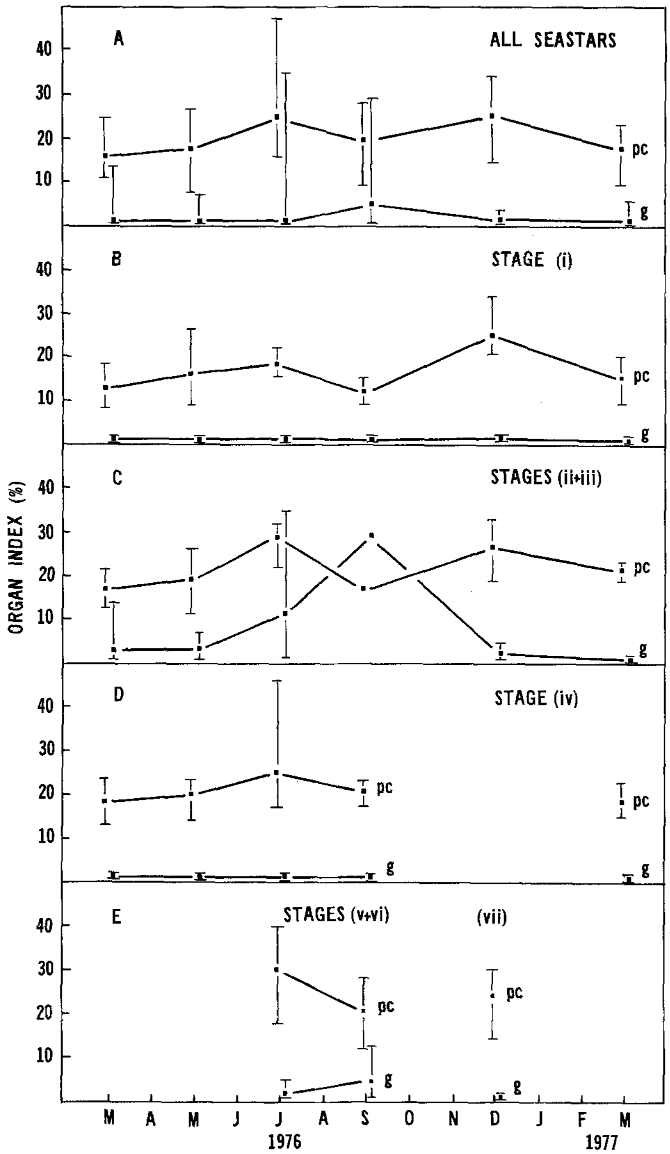

Fig. 8. *Nepanthia belcheri.* Temporal variation in mean pyloric caecum index (pc) and gonad index (g) (data for longest arm of each individual). (A) All seastars combined. (B) individuals with immature, Stage i gonads; (C) individuals with functional ovaries, Stages ii plus iii; (D) individuals with immature testes, Stage iv. (E) individuals with developed testes, Stages v plus vi, and with spent gonads, Stage vii. Vertical bars are ranges

Further Population Parameters

Seasonal changes in organ indices for all seastars and for those at the various gonad stages are shown in Fig. 8. In the combined data (Fig. 8A), there are 2 peaks in the pyloric caecum index: one in July, after the period when fission was common, and the other in December, after general spawning. The decline in this index between July and December corresponds to the peak in the gonad index. Similar declines in pyloric caecum index and increases in gonad index are evident in the data for individuals with maturing and mature ovaries (Fig. 8C) and testes (Fig. 8E). As expected, seastars with immature gonads (Stages i and iv) have consistently lower gonad indices (Fig. 8B, D), than individuals with spent gonads (Fig. 8E).

Size-frequency histograms of arm length are presented in Fig. 9 to show the changes in population structure from March 1976 to March 1977. Arms are recorded individually in the data of Fig. 9, i.e., the seastar population is treated as a population of arms. Plotting mean arm length per seastar would obscure the large discrepancies in arm length in some individuals and introduce biases due to variability in arm number. In each month's data there is a wide range of arm lengths. Modes are evident in the histograms, but they are generally not prominent nor clearly traceable through successive samples. In most months there is a mode of short arms which includes the smallest size category, and this reflects regeneration of arms after fission. This mode was present from March to September 1976, peaking in June after the period of highest fission frequency (Fig. 3). It was lost progressively from October to December, corresponding to the period of no fission (Fig. 3) and reappeared in March 1977. Changes in mean arm length values of the population were also related to fission frequency: the lowest value was in June

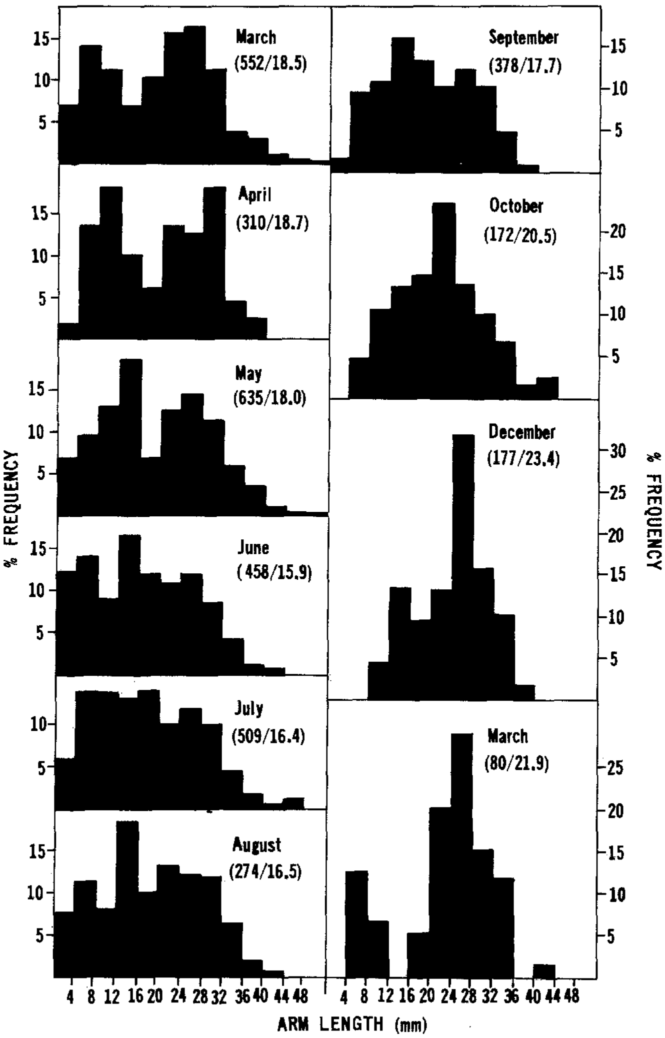

Fig. 9. *Nepanthia belcheri.* Size-frequency histograms of arm lengths in population samples from March 1976 to March 1977. Numbers in parentheses are number of arms/mean arm length (mm)

(after the period of intense fission) and the highest in December (period of no fission). Mean arm size was substantially larger in March 1977 than in March 1976. Although no data are available on changes in population density, seastars became increasingly scarce from December 1976 to March 1977, suggesting a marked decline in population numbers during that summer period.

Virtually all the data for small arms in Fig. 9 are from regenerating arms. Only one regular seastar with mean arm length less than 12 mm was collected during the year of sampling. This was an individual with 4×9 mm and 3×7 mm arms (and one madreporite), collected in September. It is the only seastar identified as a juvenile recruited from larval development.

Eggs

Attempts to obtain fertilizable eggs from ovaries and whole seastars, using 1-MeAde, were unsuccessful. The processes mediated by 1-MeAde, ovulation and germinal vesicle breakdown, were not observed. Eggs dissected from Stage iii gonads were large (ca. 450 μm diam), olive green in colour, buoyant and adhesive.

Discussion

Fission

The findings on fission contrast with those for a temperate population of *Nepanthia belcheri* at Moreton Bay, Southern Queensland (Kenny, 1969). In the latter population, the 6-armed condition predominated (approximately twice as common as 7 arms); the general incidence of fission was lower; fission peaked during the spring months, September-November; and the frequency of fission was size-related, i.e., a histogram of frequency of recent fission versus largest arm size was bimodal, with modes at 15 and 22 mm arm length. Kenny (1969) interpreted these modes of fission frequency as the approximate sizes of 2- and 3-yr old seastars during the spring period of rapid growth and frequent fission.

Data for *Nepanthia belcheri* from other parts of Australia show further geographical variation in the pattern of fission. Five-armed starfish greatly predominate in collections from Torres Strait to North Western Australia, with the size of specimens increasing and evidence of fission decreasing westwards (Rowe and Marsh, in press).

Emson and Wilkie (1980), in reviewing data on fissiparous seastars, discuss several species in which a large 5-armed, non-fissiparous form and a small multi-armed, fissiparous form have been described from the same population. They acknowledge the possibility that in each case the two forms may be sympatric species. These two forms are also present in *Nepanthia belcheri*, but they are known as geographically separated populations.

In relation to asexual reproduction through autotomy, Emson and Wilkie (1980) listed *Nepanthia belcheri* among the small group of asteroids which can generate whole individuals from single arms or segments of arms. This was on the basis of our reports of single-armed seastars and "comets" (regenerates from a single arm) in the Rowes Bay population. However, there is no evidence that *N. belcheri* spontaneously sheds single arms or segments of arms. Single-armed individuals probably arise as a further division of a 2- or 3-armed fragment during the fission process (Fig. 1).

Hermaphroditism

The complex interrelations between gonad stages in *Nepanthia belcheri* resulting from hermaphroditism and other influences (considered later in this discussion), are postulated in Fig. 10.

The other 3 hermaphroditic asteroids (*Asterina gibbosa, A. pancerii* Gasco and *Fromia ghardagana* Mortensen) which have been extensively studied are protandric

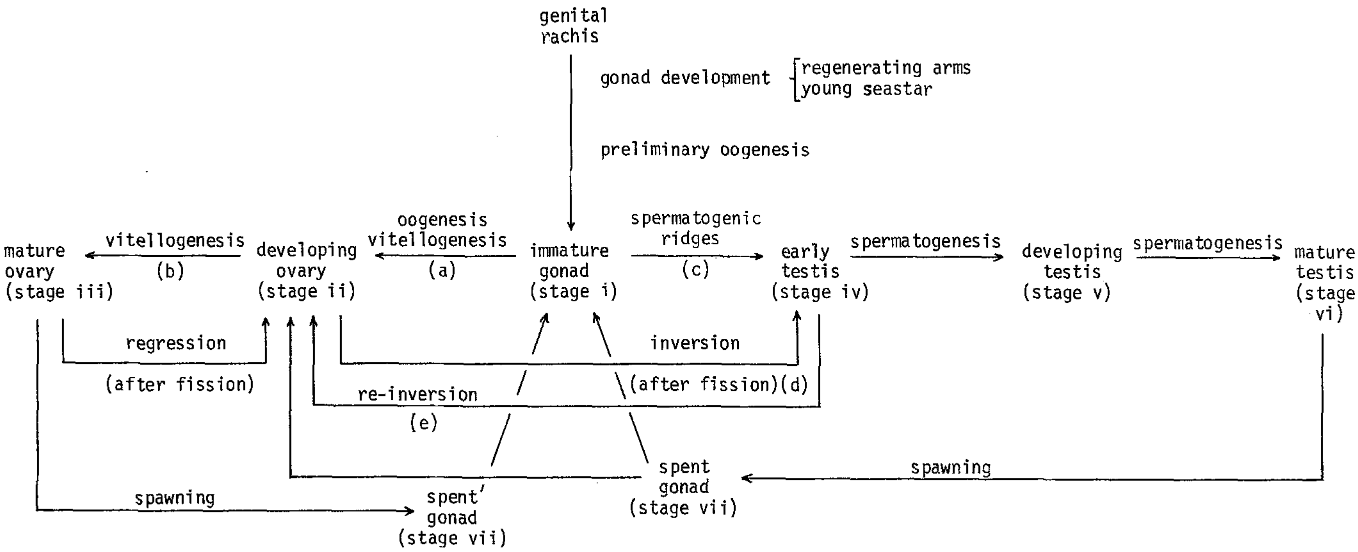

Fig. 10. *Nepanthia belcheri.* Postulated interrelations between various gonad stages (see Fig. 5) based on gonad histology and changes in reproductive condition of the population. (a) – (e) are steps specifically described in "Discussion"

hermaphrodites, although, in some populations, a "resurgence" of spermatogenesis within the mature ovaries results in the presence of both kinds of mature gametes and the possibility of self-fertilization (Delavault, 1975). During the spermatogenic phase of *Nepanthia belcheri,* the gonad condition is like that of other hermaphroditic seastars (e.g. compare Fig. 5: *4* with the functional testis of *A. pancerii* figured by Delavault, 1975, his Fig. 1a). However, in *N. belcheri,* spermatogenesis was completely suppressed during the phase of oocyte maturation (Steps a and b in Fig. 10) and there was no opportunity for self-fertilization. Thus, *N. belcheri* would not be classed as a "functional hermaphrodite" according to the criterion of Delavault (1975).

The course of gonad development in *Nepanthia belcheri* is complicated by the processes of fission and regeneration, and it is only protandric in the sense that the first maturation of gonads is as testes. In the data of longest arm size versus gonad condition (Fig. 7), the size range of seastars with mature testes only overlaps with the size range of those with mature ovaries in the 30 to 34 mm size range. The gonads in the longest arm are testes at their first maturation and there is a subsequent inversion of sex, related to size. However, seastars with developing ovaries (Stage ii) range from a minimum of 22 mm longest arm size, i.e., some seastars have functional ovaries, without achieving ovary maturation, in the size range typical of seastars with functional testes. These data raise the possibility that the first development of gonads is not always as testes.

The factor complicating protandric sexual development in *Nepanthia belcheri* is that most gonads develop in regenerating arms rather than in the arms of young seastars first reaching sexual maturity. These gonads in regenerating arms assume the same functional sex as the associated continuing arms, as is the case in fissiparous gonochoric species, e.g. *Sclerasterias richardi* (Falconetti *et al.,* 1976). Consequently, even if the young *N. belcheri* is protandrous at its first gonad maturation, the initial gonad development in regenerating arms (Steps a and c in Fig. 10) will not necessarily be protandrous because this is determined by internal factors from the current sexual phase of the continuing arms.

Some gonads in regenerating arms will develop initially as ovaries, from their association with female-phase continuing arms. Thus, small functional female seastars (Stage ii, Fig. 7) will arise when these gonads continue as ovaries to the point where the seastar divides and they are in the longest arm of a resultant fragment.

Asexual versus Sexual Reproduction

There is considerable interaction between the asexual and sexual processes of *Nepanthia belcheri,* with the latter subordinate to the former. In seastars regenerating after fission, the gonads proximal to the new arms were regressed or retarded by the demands of regeneration. During the peak period of fission, April–June, there was no decline in the pyloric caecum index, although this index declined during the period July–September when most gonad development occurred. Thus, regeneration was not at the expense of reserves in the pyloric caeca, but rather at the expense of gonads.

Another way in which fission appears to affect sexual reproduction is by causing gonads to change from functional ovaries to functional testes in the fission products. During and after the period of intense fission there was a progressive increase in the proportion of males in the population (Fig. 6). Many of these males had substantially developed oocytes in their gonads, indicating that these gonads functioned as ovaries prior to spermatogenesis, i.e., that these testes were derived from maturing ovaries (Stage ii) rather than from immature gonads (Stage i), confirming the switch from ovary to testis (Step d, Fig. 10). It is unlikely that this switch was purely a seasonal phenomenon, unrelated to fission, considering the profound effects that fission and the subsequent regenerative processes must have on these seastars.

We suggest that the reduction in body size with fission has a masculinizing effect on the gonads. Both kinds of germinal cells are continuously present in the gonads of hermaphroditic asteroids, and which kind of germinal cell develops at any stage depends on internal factors that have yet to be elucidated (Delavault, 1975). At this stage we cannot postulate how this size-related sex-determination is mediated.

Fission, however, does not always result in a masculinizing of gonads. Some fission products with large continuing arms apparently resisted the influence and persisted with ovaries (Stages ii and iii). These are evident in the low mean arm lengths of some Stage ii and iii individuals in Fig. 7, i.e. individuals with new regenerating arms. Also, in Fig. 7, the largest Stage iv (early spermatogenesis) individuals are bigger than the largest Stage v (accumulating spermatozoa) individuals. Some of these large Stage iv seastars were recent fission products (before arm regeneration), and these observations suggest that, although spermatogenic ridges initially appeared after fission, the gonads reverted to ovaries before spermatogenesis proceeded to Stage v gonads (Steps d and e, Fig. 10).

While a discrete period of sexual reproduction in October–November 1976 was observed, fission led to an extreme imbalance against females in the population approaching spawning. The effect of size-related sex-determination and fission was to greatly decrease the fecundity of the population, which, due to large egg size and small seastar size, was necessarily low.

Reproductive Strategy

Among asteroids, the main exceptions to planktotrophic development are Arctic, Antarctic and deep-sea species, as in other marine invertebrate groups (Thorson, 1950). Exceptions also occur among the smaller, short-lived asteroids, and Chia (1968) and Menge (1975) have suggested that the very high mortality associated with planktotrophic development has caused selection against this mode of development in these small species with necessarily small resources for reproduction.

The alternatives to pelagic planktotrophic development have all been adopted by various small asteroids: (1) pelagic lecithotrophic development, e.g. *Gomophia egyptiaca* Gray (Yamaguchi, 1974); (2) direct development, e.g. *Patiriella exigua* (Lamarck) (Lawson-Kerr and Anderson, 1978); (3) direct-development and brooding, e.g. *Leptasterias hexactis* (Chia, 1966); (4) viviparity, e.g. *Patiriella vivipara* Dartnall (Dartnall, 1969); (5) asexual reproduction by fission or autotomy. In the order given, they represent a sequence of increasing expenditure of energy per reproductive unit and increasing protection during the early development of the reproductive units to facilitate their entry into the parental population.

The eggs of *Nepanthia belcheri* are larger than the size range of egg diameters in echinoderms with planktotrophic larvae (Strathmann, 1974), and it is very likely that they lead to pelagic lecithotrophic development. The possibility of direct development, with eggs attached to the substrate, cannot be completely precluded; but, the abactinal position of the gonopores militates in favour of release into the water column and pelagic dispersal.

Assuming that *Nepanthia belcheri* has a pelagic lecithotrophic phase, this gives it a means of dispersal to complement the fission process which has no dispersive function. Thus, *N. belcheri* probably has adopted two of the reproductive strategies outlined above, giving it a means of dispersal and a means of reliable recruitment. Other fissiparous asteroids are known to complement their asexual process with a dispersive larval stage, and these "seem to produce normal planktotrophic larvae" (Emson and Wilkie, 1980). That *N. belcheri* produces a lecithotrophic egg, however, further reduces its fecundity, which is low due to both small size and the effects of fission and regeneration discussed previously. Only one juvenile resulting from sexual reproduction the previous year was collected during the year of population sampling in Rowes Bay. Thus, in this population, reliable asexual reproduction completely dominates sexual reproduction as the means of recruitment.

Larvae or embryos must nonetheless be produced, and the combination of hermaphroditism with fission is particularly favourable for dispersal at very low densities of larvae. If even one larva reaches a new favourable locality and metamorphoses, it may populate the new locality by its successive fission products which, in turn, may reproduce sexually, i.e., a functionally dioecious population may develop from a single larva. This is an advantageous reproductive strategy for *Nepanthia belcheri* in the North Queensland region, where most of the mainland coast is sandy beaches or fine sediments associated with mangroves. Rock-fragment habitats, such as Rowes Bay, are very localised and sparsely distributed along the coast.

Menge (1975) addressed the question of whether small asteroids should brood or broadcast. The alternatives for *Nepanthia belcheri* are whether to divide or broadcast. In the Rowes Bay population the balance is strongly towards fission. In other populations fission is not as important (Kenny, 1969; Row and Marsh, in press). Thus, this initial study of *N. belcheri* reveals its potential for reproductive and ecological studies including the factors that determine a reproductive strategy.

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