

Sexual Reproduction of Two Intertidal Sea Anemones (Coelenterata: Actiniaria) in Malaysia

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ABSTRACT

Sexual reproduction in the actinians *Anthopleura bandi* Dunn and *Haliplanella luciae* (Verrill) was studied through one year at Jeram, on the Malacca Straits. No evidence could be marshalled to support periodicity in gametogenesis of either species. The absence of cyclicity in prevalence and size of internally brooded young of *A. bandi* substantiates this finding for the species. Female, sterile, and hermaphroditic anemones brood. The sex ratio of smaller individuals is heavily biased toward females; that of larger anemones is more balanced, suggesting that some but not all individuals are protogynous. Sterile and hermaphroditic brooders are inferred to be transitional from female (when the young are produced) to male (by which time all young have been released). Only sterile and female individuals of *H. luciae* were found. Although as many as half the anemones may bear eggs at any time, the absence of males presumably precludes sexual reproduction. Asexual reproduction by pedal laceration appears to be the sole means of propagation.

THEORIES ABOUT ANNUAL REPRODUCTIVE PERIODICITY were developed from data on temperate species. Environmental cues triggering phases of cycles, or entraining endogenous rhythms, are those that vary conspicuously and include photoperiod and temperature (Welty 1962, Giese and Pearse 1974). Semper (1881: 135, 136) was apparently the first to propose that in the tropics, where such factors may vary little and unpredictably, "all periodicity, as regards summer and winter, must be entirely lost, and at last fully grown individuals and young ones, larvae and freshly laid eggs will all be found together at every season and in every month of the year." In the Philippines he noted "the total absence of all periodicity in the life of sea animals, particularly the Invertebrata; among these I could not detect a single species of which I could not at all seasons find fully grown specimens, young ones, and freshly deposited eggs," although he went on to remark that lack of periodicity is not unknown in cold seas.

Most early studies on reproductive periodicity of tropical marine invertebrates consisted of single samples of a species in various parts of its range (e.g., Pearse 1968), or sustained sampling in areas at the margins of the tropics (e.g., Pearse 1978). Recently, as data from prolonged research in the equatorial tropics have accumulated, it has become clear that tropical species, like temperate ones, engage in a variety of reproductive strategies, including annual cycling tied to environmental cues, local cycling that differs among populations, short-term cycling tied to factors such as tides and the moon, and lack of cycling altogether (e.g., Berry 1968, Vohra 1970, Lessios 1981).

This is the first long-term investigation to docu-

ment sexual reproduction in an equatorial actinian. The major subject of study, the actiniid *Anthopleura bandi* Dunn 1978, was of especial interest because it broods its young internally (Dunn 1978). Examined for comparison was the sympatric acontiate *Haliplanella luciae* (Verrill 1898), which is of interest because it is probably the most widely distributed sea anemone.

MATERIALS AND METHODS

The study site on the Malacca Straits, Jeram Beach, Selangor, Peninsular Malaysia (3°13'N, 101°19'E), type locality of *Anthopleura bandi*, was composed of mud and sand in variable proportions depending on the season, and apparently also on human activity. At the beginning of the study, the shoreline was receding, but by late in the study, attempts to stabilize it by planting mangrove tree seedlings appeared to be succeeding, and the sediment became noticeably muddier. Individuals of the two species of sea anemones were common at mid-tide level, generally attached to firm objects such as empty (but rarely living) mollusc shells, bricks, and mangrove tree roots.

Nineteen collections of from seven to nine specimens of each species were made from early February 1974 through late January 1975, on low tides. Each time, anemones of a variety of sizes were collected from throughout the study area, about 100 m seaward of the 1975 shoreline. The pedal disc diameter of each individual was measured *in situ* with plastic vernier calipers; pedal discs were usually circular but the mean of the longest and shortest diameters was recorded where they were not. Following measure-

ment, each anemone was removed from the substratum and placed in a numbered plastic bag containing a small amount of sea water.

Within three hours of collection the actinians were put into individual vessels in the laboratory at the University of Malaya School of Biological Sciences. Each anemone, along with any young that it might have released into the bag, was covered with fresh sea water, and relaxed with chloral hydrate. Fixation and preservation were in 10 percent sea water formalin (for procedural details see Dunn 1975b).

After at least one week in formalin, larger specimens were longitudinally bisected, often releasing young (individuals living independently are referred to as adults; those being brooded internally by adults as young or juveniles). One-half was dehydrated, cleared, and embedded in paraffin. Cross-sections 8 μ m thick, stained with hematoxylin and eosin, were made of the middle to lower third of each actinian for information on its gonadal state. Very small adults were not bisected, and juveniles were not sectioned. Anemones with sperm packets visible in section were scored as males, those with eggs as female, those with both as hermaphrodites, and those lacking gametes as steriles. In doubtful cases additional sections were cut and/or the other half of the anemone was studied.

RESULTS AND ANALYSIS

Anthopleura bandi.—A total of 148 specimens, ranging in pedal disc diameter from 3 to 39 mm, was collected. They were divided into seven 5 mm size classes (fig. 1). *Anthopleura bandi* appears to be gonochoristic. The two hermaphrodites (representing 1.4 percent of the total, or 1.8 percent of those with gonads) contained a few scattered eggs among dense, well-developed testes. All eight of the individuals less than 6 mm across were sexually sterile. The smallest male had a pedal disc 6 mm in diameter, and the smallest female 7 mm. No anemone exceeding 25 mm lacked gonads; the largest male was 30 mm and the largest female 39 mm. The overall sex ratio was 5:1 in favor of females, which represented 61.5 percent of the total sample. The discrepancy between the sexes diminished with size, being 8:1 (6-10 and 11-15 mm), 4:1 (16-20 mm), 3.3:1 (21-25 mm), and 2.3:1 (26-30 mm), although the three largest actinians (more than 30 mm) were all females. Table 1 provides data on size composition of the sample population. Average pedal disc diameter of the 111 fertile animals was 17.1 mm.

Figure 2 illustrates the changes in the sexual composition of the sample population during the study year. Females were present in all samples, but only one

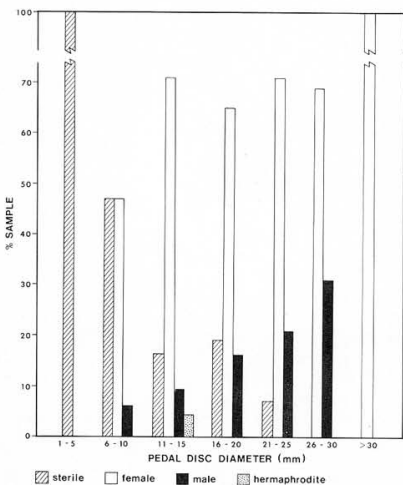


FIGURE 1. Sexual composition of *Anthopleura bandi* study population by size.

(late April; the fifth collection) comprised exclusively females. Males, females, and steriles were all present in eight collections, females and steriles constituted seven samples, two collections contained males and females, and the only two hermaphrodites found were in the third collection, which also had males and females.

Runs tests, to evaluate whether a sequence of events occurs in random order, can be performed only for two states (Sokal and Rohlf 1969). The null hypothesis, that presence/absence of males occurred in random order during the study year, could not be rejected. This was also true for steriles. Alternatively, the study year may be considered to reflect a repetitive annual pattern such that the last sample (taken in late January 1975) would be followed by a sample similar to the first (mid-February 1974). Males were

TABLE 1. Mean pedal disc diameter (mm) of *Anthopleura bandi*.

	All anemones (n)	Brooders only (n)
Males	18.8 (18)	—
Females	16.8 (91)	20.2 (26)
Hermaphrodites	15.0 (2)	15.0 (1)
Steriles	9.9 (37)	13.0 (5)
Total sample	15.3 (148)	18.9 (32)

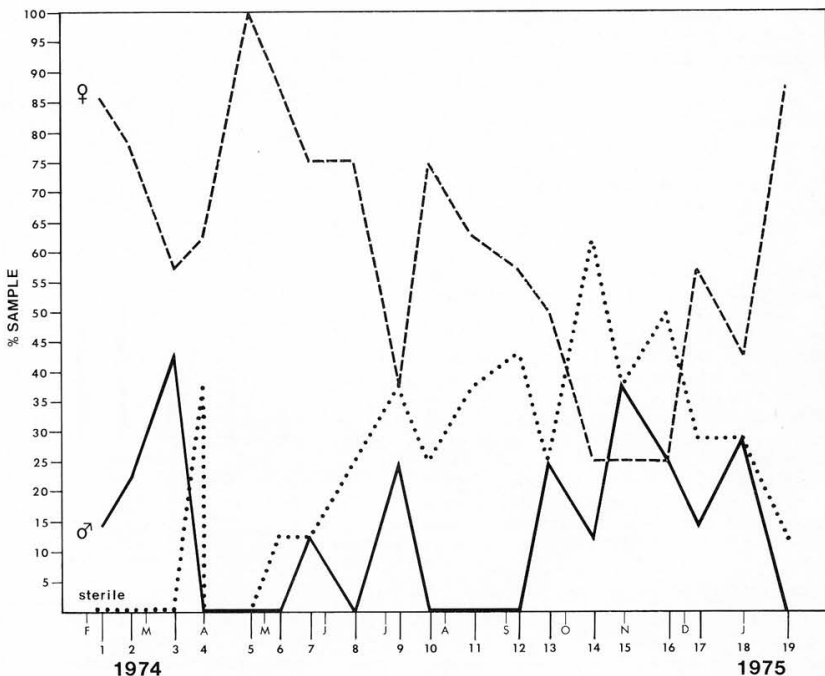


FIGURE 2. Sexual composition of *Anthopleura handi* study population through the year.

present in the first sample and absent in the last, whereas the reverse was true for steriles. Thus in both cases the number of runs is the same whether the 19 samples are considered linearly or circularly, and in neither case can randomness be rejected. Runs tests above and below the median were made separately for males (median prevalence 12.5%), steriles (median 25.0%), and females (median 62.5%). In no case could randomness be rejected for the data considered linearly. However, considering them cyclically diminishes the number of runs by one for steriles, resulting in the conclusion that there is a non-random pattern to their occurrence at the 0.05 level of significance.

Gametogenesis was typical of actiniid sea anemones, as described by Dunn (1975b) and Jennison (1979). Each egg had a trophonema, a channel between egg and edge of the enclosing mesentery, that

presumably functions in providing nutrients to the growing gamete (Dunn 1975b). Gametes of all stages were present in most fertile individuals. Even in cases of a preponderance of one developmental stage in one actinian, others collected at the same time contained gametes in other states of maturity. The largest eggs were 140 μm diameter in section, which would correspond to nearly 300 μm in the fresh state (Dunn 1975b).

Proportion of the sampled anemones brooding and average brood size through the study year are seen in figure 3. The rough positive correlation between these two parameters seems to be due to the fact that when the prevalence of brooders is zero, so is the average brood size. Both Kendall's and Spearman's coefficients of rank correlation (Sokal and Rohlf 1969) show significance beyond the 0.01 level when non-brooders are included in the analyses

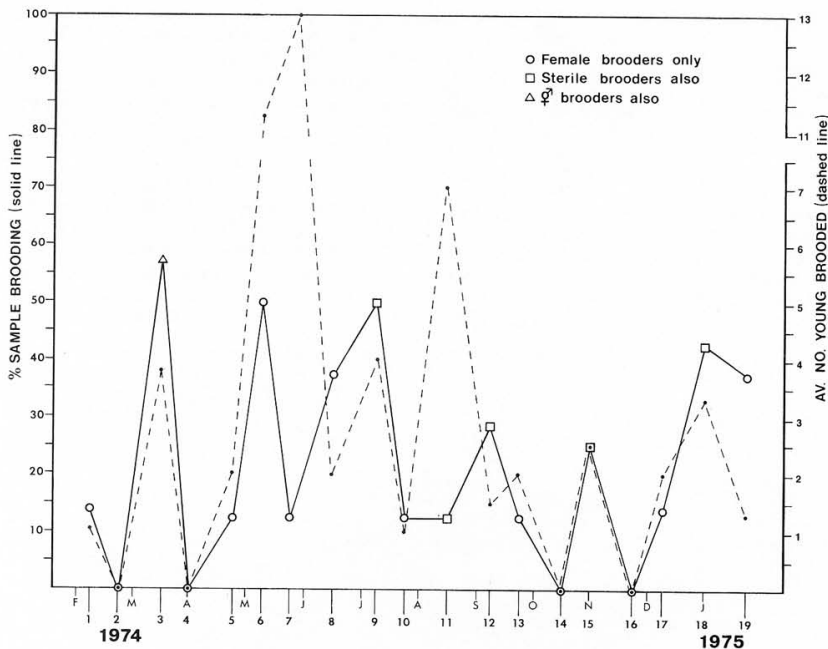


FIGURE 3. Proportion of brooding *Anthopleura bandi* and average brood size through the year.

(0.5937 and 0.6346, respectively) but neither is significant at 0.05 when they are excluded (0.3370 and 0.2563, respectively).

The 32 brooders, representing 22 percent of the sample, consisted of 26 females (81%), five steriles (16%), and one hermaphrodite (3%). All larger brooders were female, the hermaphrodite was 15 mm, and the steriles were 9 mm (two), 13 mm, and 17 mm (two). The proportion of brooders in the seven classes, ordered by increasing size, was 0, 14.7, 13.3, 29.0, 35.7, 46.2, and 33.3. The smallest brooders were 8 mm females, one collected in February, one in January; the largest brooder, a 33 mm female, was collected in June.

The average number of young brooded overall was 4.1 (range 1-23), being 3.8 for steriles, 4.0 for females, and 7.0 for the one hermaphrodite. The eight anemones containing a single young were females, ranging in basal diameter from 8 mm (both of the smallest brooders) to 26 mm (mean 16.4

mm); the individual with the largest brood was a 17 mm female. There was no correlation between brood size and size of brooder (Kendall coefficient 0.1514, Spearman coefficient 0.1562; $N = 32$). All young brooded by some actinians were of about the same size and stage of development, but many adults contained juveniles in a variety of stages. The largest brood consisted of four large young with 24 tentacles each, 13 medium-sized ones with 12 tentacles each, and six planuloids [ciliated, pre-tentacular, pear-shaped larvae about 1 mm long and with eight mesenteries, resembling figures 4 and 40 in Atoda (1954)]. Another brood was composed of three young with 12 tentacles each, two with eight each, and two planuloids. Commonly, two brooders collected at the same time contained young of different sizes (e.g., one with embryonic young and the other with a single 24-tentacle juvenile). The largest anemones being brooded had 24 tentacles and were up to 6 mm in diameter.

The symmetry of most specimens was regular, implying an absence of asexual reproduction.

Haliplanella luciae.—Basal diameter of the 153 specimens collected averaged 7.2 mm. The sampled population contained only female and sterile individuals. The size range of steriles was 3–15 mm and that of females was 4–15 mm, but only two of the 44 females were less than 5 mm in basal diameter whereas 31 of the 109 steriles were (12 were 3 mm and 19 were 4 mm). Mean size of females was 9.8 ± 2.8 mm, and of steriles 6.1 ± 2.3 mm. These figures are significantly different ($p < 0.001$; $t = 8.37$).

The proportion of fertile (=female) anemones averaged 27.3 percent with a range of 0–50 percent (fig. 4). A runs test above and below the median

(median prevalence of females was 25.0%) does not allow rejection of randomness, whether the data are considered linearly or cyclically.

Oögenesis appeared to conform to the typical actinian pattern, but no trophonemata were observed. Maximum diameter of eggs in section was about $125 \mu\text{m}$, corresponding to a fresh diameter of approximately $250 \mu\text{m}$. Although eggs in all stages of maturity occurred in some individuals, the gametes of most appeared to develop in synchrony. However, there was no agreement in size or abundance of eggs among fertile anemones from the same collection.

The animals were green with longitudinal orange stripes. Most of the 21 specimens in which they were counted had 10 or 11 single stripes, a few had 12,

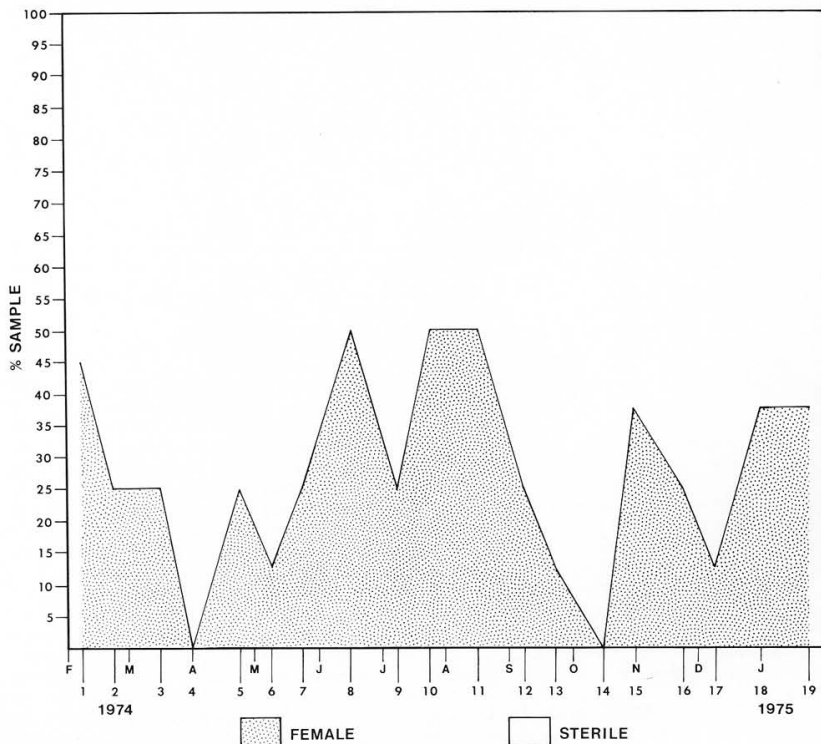


FIGURE 4. Sexual composition of *Haliplanella luciae* study population through the year.

and one each had 7, 9, and 22 stripes. This pattern corresponds to the first, and most widespread, of Uchida's (1932, 1936) four "races" of *Haliplanella* (= *Diadumene*) *luciae* (the other three morphs are not listed in the same sequence in the two papers). Three of the 153 anemones had catch tentacles, one each having one, two, and three in the innermost cycle. The internal symmetry of most specimens was irregular, implying that they were asexually produced. Pedal laceration was noted in the field.

DISCUSSION

Anthopleura handi.—The highly significant excess of females is not an uncommon phenomenon among the limited number of sea anemone species of known sexuality. Actinians with a preponderance of females include the external brooder *Epiactis prolifera* (see Dunn 1975a, b), and the internal brooders *Actinia equina* (see Chia and Rostron 1970, Gashout and Ormond 1979), *A. tenebrosa* (see Ottaway 1979), and the Roscoff population of *Cereus pedunculatus* (see Rossi 1975). For species in which only egg-producers brood young, maximization of the brood space would seem to be a significant selective force favoring more females than males and/or simultaneous hermaphroditism (Dunn 1975a). However, gynodioecy, known initially from *Epiactis prolifera* and *Cereus pedunculatus* (see Dunn 1975a and Rossi 1975, respectively), also occurs in the free-spawning *Bartholomea annulata* (see Jennison 1981). *Tealia lofotensis*, which exhibits the typical marine invertebrate pattern of dioecy and oviparity, nonetheless has a skewed sex ratio favoring females (Wedi 1978). Species with a 1:1 sex ratio include both free spawners (e.g., *Condylactis gigantea*) and brooders (e.g., *Phymanthus crucifer*) (Jennison 1981).

One factor confounding analysis of sexual pattern versus reproductive mode in actinians is sex change. All studies except for that by Carter and Funnell (1980) have been based on destructive sampling, so sex reversal has been inferred rather than being demonstrated by repetitive sampling of single individuals. A related issue hindering analysis of patterns, and one that has only recently been appreciated, is uncertainty about the origin of brooded young.

Brooding by males and steriles as well as by females is known for several actinians. Chia and Rostron (1970) explained it in British *Actinia equina* by positing that zygotes released by their mothers into the plankton develop there into planulae, then re-enter "foster parents" which can be in any sexual state. They implicitly assumed that the young were sexual in origin. Ottaway (1979: 284) explained

the same pattern for *A. tenebrosa* in New Zealand by sex change within one breeding season; thus "brooding adults would be the maternal parents of their brooded embryos." He dismissed the possibility of asexual production of the young, although he had earlier (Ottaway and Kirby 1975) demonstrated genotypic identity between a brooder and its young. Black and Johnson (1979), studying *A. tenebrosa* in Australia, confirmed that brooder and brood are genetically identical. They concluded that brooded young must be derived asexually, speculating that the apparently functional gonads might sexually produce young that are not brooded. Similar conclusions were reached for *A. equina* in Britain by Carter and Thorp (1979) and Gashout and Ormond (1979), although they postulated different mechanisms.

The proportion of females between 11 and 30 mm is rather constant in *Anthopleura handi* (fig. 1). Thus it might be argued that all females differentiate by 11 mm and all larger anemones attaining sexual maturity are males. This explanation fails to account for brooding sterile anemones. Moreover, the smallest male collected was smaller than the smallest female. Alternatively, very different growth and mortality rates of the two sexes could create the pattern of figure 1, but nothing in any study of actinian autecology suggests that anemones are so highly sexually divergent. Rather, the data on brooding, sex, and size suggest that the increasing proportion of males with size is due to protogyny in at least some individuals, operating as follows. The brooded young are produced by cross-fertilization within the gastrovascular cavity of the maternal parent. During the time that some anemones (about 20% annually) are brooding their young, they begin to undergo sex reversal. Commonly the ova have been fertilized and develop into juvenile anemones or are resorbed before spermatogenesis begins, resulting in transiently sterile individuals. Rarely, a few eggs remain after sperm have begun to develop. Sex change in *A. handi* is long relative to duration of brooding, so a complete switch in sexual states is never accomplished before the young are released; thus males never brood.

This hypothesis accounts for low numbers of sterile and hermaphroditic brooders. Sterile individuals include small anemones that have not differentiated sexually, and larger ones presumably in transition from female to male states. Probably most of those greater than 10 mm basal diameter fall into the latter category. The fact that the only two hermaphrodites collected were 15 mm suggests that sex change is most common at that size. The absence of sterile and hermaphroditic animals larger than 25 mm implies that that is an upper size limit for sex reversal.

Anthopleura bandi would thus actually be protogynous, with rare, transitory hermaphroditic individuals. Clearly only a minority of females change sex, however; perhaps there are two types of females, one with latent male potential and one without. The presence of males as small as and smaller than the smallest females suggests that there may be primary and secondary males as in fishes (Warner 1978).

This scenario assumes sexual production of the young. Electrophoretic comparisons of brooders and their broods could test this. However, the results might be equivocal because the individuals in each population, not to mention a parent and its brood, are likely to be genetically rather similar, even in the absence of asexual reproduction. This is because *Anthopleura bandi* apparently lacks a dispersal stage, and populations of the species are geographically isolated. Jeram's environment is unusual along the west coast of the Malay peninsula, and I have not found *A. bandi* elsewhere despite searches, although I have identified specimens of it collected by Soenarto Notosoedarmo from a similar environment in South Bais Bay, Negros Oriental, Philippines.

These two factors also suggest that inbreeding might be common in *Anthopleura bandi*, thereby accounting for the skewed sex ratio (Maynard Smith 1978). Dynamics of brood production argue against brood space being a limiting resource that necessitates excess females. Nearly three-quarters of the females sampled, including the largest individual, were not brooding. Moreover, large brooders did not harbor especially many nor predominantly small juveniles, and solitary young (brooded by very large as well as very small females) consisted of two planuloids, several intermediate-sized ones, and one anemone 6 mm in diameter. If the larger sterile individuals are transitional, their broods, having been produced while they were females, would be expected to consist of older and fewer young, compared with those of females. This expectation is belied by the data. In *Epiactis prolifera*, the young of which are known to be sexually produced (Bucklin, Hedgecock and Hand 1980), number of young brooded is related directly to parent size and inversely to juvenile size (Dunn 1977).

The data do not support an annual cycle of sexuality and reproduction. Figure 2 hints at a diminished prevalence of females and an increased prevalence of males during the latter half of the calendar year as compared with January-June, but randomness could not be rejected statistically. The situation in steriles is equivocal. Linear runs tests detected no pattern; the cyclical runs tests above and below the median, which requires assuming that the pattern of the

study year would be repeated, supported a non-random pattern. The higher prevalence of steriles in July-December than in the early half of the year suggests that either more newly released individuals that have not yet developed gonads enter the population late in the year, or that regression of gonads associated with sex change is more common then. The ratio of small (≤ 10 mm) to large (> 10 mm) steriles, which was 2.3:1 early in the year and 1.6:1 later, tends to support an early release of brooded young; and the two hermaphrodites were collected in March, suggesting that that might be a time of active sex change; but the five brooding steriles were collected in July, August, September, November, and January. The conflicting implications of the data are probably due to unrealistic assumptions for the cyclical runs tests, and to the fact that each collection included animals of a variety of sizes rather than being a random sample of the population, thereby over-representing rare-sized categories.

Likewise, brooding individuals were found throughout the year. Although several collections lacked them, they were not in sequence, and the absence of brooding individuals was probably attributable to small sample size. Brooding prevalence and mean brood size were, on average, higher during the first half of the year. If this situation were significant, more young would be expected to enter the adult population late in the year. Lacking quantitative sampling, it is impossible to know whether more small adults appear following a time of high brooding prevalence, but the smallest brooders were collected in January and February, and the three smallest adults (3 mm and presumably newly released) were found in April, July, and December, supporting the absence of a cycle. Broods composed of young of a variety of sizes are evidence against cohorts of simultaneously produced, synchronously growing juveniles, and thereby also against periodicity. The small number of young and the lack of cohorts preclude estimating juvenile growth rate and the duration of brooding. However, young are inferred to be brooded until they attain a minimum basal diameter of 3 mm, the size of the smallest adults collected. At that size, most sea anemones for which data are available grow about 1 mm in diameter per month (Dunn 1977). Young may be brooded much longer than the calculated three months, though, based on the finding of some as large as 6 mm (a size at which some adults have already developed gonads). While being brooded, juveniles presumably feed on food ingested by the parent, as is true for other internally brooding actinians (Chia and Rostrom 1970, Ottaway 1974). Feeding ability probably develops rather early because

A. bandi eggs are not particularly large and so contain little yolk, but it is possible that young could absorb dissolved organic molecules from the gastro-vascular fluid of the parent (Schlichter 1973).

Haliplanella luciae.—*Sagartia luciae* was described from southern New England by Verrill (1898), who provided compelling evidence that it had been introduced there. [Verrill's (1870) description of *S. lineata* from Hong Kong probably refers to the same species, which Williams (1980) now calls *Diadumene lineata* (Verrill).] Shick and Lamb (1977) summarized the distribution of this sea anemone in the northern hemisphere on both sides of the Atlantic and Pacific Oceans, and through the Mediterranean Sea to the Suez Canal. Since then, populations have been found in the southern hemisphere in Brazil (Belém and Monteiro 1977), at Dobo in the Aru Islands of eastern Indonesia (pers. obs., October 1977; anemones were dark green, up to 10 mm in diameter and with 12 single reddish orange stripes), and in Auckland Harbor, New Zealand (C. Hand, pers. comm., May 1981). Its success as a colonizer is attributable to its physiological tolerances, especially to extremes of salinity and temperature, which have made it a popular experimental subject (Shick and Lamb 1977), and to its ability to propagate asexually, permitting ready, if often ephemeral, establishment in suitable habitats.

The findings that most individuals of *Haliplanella* at Jeram are asymmetrical, and that gametes of only one sex are produced, correlate well with one another and with the observation of pedal laceration. In fact, they imply that asexual reproduction is the sole means of propagation, which has also been suggested for other populations of *H. luciae* (e.g., Shick and Lamb 1977). Indeed, aside from Verrill's (1898) initial observation of "ciliated embryos" in the gastrovascular space, no evidence of sexual reproduction has been documented for *H. luciae*, and populations of which the sex is known are invariably unisexual (Shick and Lamb 1977). Could the "embryos" observed by Verrill have been loose bits of acontia or mesenterial filaments?

Haliplanella often occurs in harbors and along shipping lanes, presumably because ships are important dispersal agents (Shick and Lamb 1977). The unisexual nature of the Jeram population and, to a lesser extent, the fact that all individuals are of a single morph, suggest that it consists of one clone. It is curious that multiple introductions should not have occurred, the Malacca Straits being one of the world's most heavily traveled waterways. Catch tentacles, first reported in *H. luciae* by Williams (1975)

who found one to three of them in 5 of 300 specimens taken at Plymouth, England (very similar to their rate of occurrence at Jeram), may provide contrary evidence. It was suggested by Williams (1975), then experimentally demonstrated by Purcell (1977), that catch tentacles in acontiate actinians function in aggression against nonclonemates. Much remains to be learned about their induction and function (Williams 1980); however, their presence suggests that more than one clone of *H. luciae* may be present at Jeram. On the other hand, catch tentacles can also act in interspecific aggression (Williams 1980), and that may explain their rare formation in the study population.

If the collected anemones were clonemates, this study would represent serial sampling of a single genetic individual. There is a size threshold for gametogenesis under identical environmental and perhaps genetic conditions. Even within a size class, there is no synchrony of gametogenesis; thus each individual, many, most, or all of which are genetically identical, appears to function independent of environment. There are three possible explanations for most of the small anemones being sterile: 1) asexual reproduction occurs only in sterile individuals; 2) lacerated pieces even from fertile animals contain no gonadal tissue and so the regenerates are initially sterile; or 3) any gonad included in a lacerated piece is resorbed to provide energy and material for somatic regeneration. In quantitative studies of asexual reproduction by longitudinal fission in *H. luciae*, Minasian (1979) noted that fission and gametogenesis are inversely related, as are temperature and individual size (1982). Regrettably, dynamics of asexual propagation were not evaluated for the Jeram population which reproduces by pedal laceration.

CONCLUSIONS

The Jeram population of the actinian *Anthopleura bandi* contains gravid individuals throughout the year. Brooded young of all sizes may be found at all times, substantiating the lack of reproductive periodicity. There may not be cyclicity even at the level of the individual: at least those more than 25 mm in basal diameter are continually fertile, with gametes in all stages of maturity, and therefore potentially reproductive year-round. Gametogenesis in the locally sympatric sea anemone *Haliplanella luciae* fluctuates in intensity, apparently without seasonal pattern. This may be irrelevant since the species is known to reproduce only asexually. Thus these species appear to exhibit the prolonged or continuous reproductive sea-

sons characteristic of many tropical and deep-sea marine invertebrates (Giese and Pearse 1974).

A close examination of the data shows for both species an increased prevalence of sterile individuals during the last quarter of the calendar year. This may reflect a subtle periodicity, controlled by equally subtle environmental factors. In his concluding remarks on the reproductive cycle of a pulmonate gastropod, studied in mangrove swamps within 10 km of Jeram, Berry (1968) eloquently identified some of the factors on which tropical marine species may key, factors that may escape those used to the conspicuous changes in temperate climates.

Beyond this coincidence in timing, *H. luciae* and *A. bandi* produce offspring with surprisingly similar origins and fates. In both species, progeny settle in the immediate vicinity of their parents, stocking a habitat that had proven suitable for their progenitors. In the former case, the young are genetically identical to the parents, in the latter, although presumably not identical, they are probably very similar. Sex change in *A. bandi* likely accounts for brooding by sterile individuals, as Ottaway (1979) and Jennison (1981)

explain males as well as steriles brooding in *Actinia tenebrosa* and *Phymanthus crucifer*, respectively. The low prevalence of female brooders in *A. bandi* argues against an abundance of females being uniquely required for producing and brooding young; inbreeding may be responsible for the skewed sex ratio. If, however unlikely it seems, the brooded young of *A. bandi* were asexually produced, the reproductive strategies of these two species would be virtually identical. It would be enlightening to find a bisexual population of *H. luciae* to evaluate the relative importance of sexual and asexual reproduction under conditions of genetic variability, where the possibility exists of recruitment by both sexual and asexual means.

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LITERATURE CITED

- ATODA, K. 1954. Postlarval development of the sea anemone, *Anthopleura* sp. Sci. Rep. Tohoku Univ., ser. 4 (biol.) 20 (3): 274-286.
- BELÉM, M. J. C., AND D. C. MONTEIRA. 1977. Contribuições ao conhecimento da fauna de cnidários do Rio de Janeiro II. *Haliphanella luciae* (Verrill, 1898) (Actiniaria, Acontinaria), uma nova ocorrência no Brasil. Univ. Fed. Rio de Janeiro Dept. Zool. 26: 1-19.
- BERRY, A. J. 1968. Fluctuations in the reproductive condition of *Cassidula auris-felis*, a Malayan mangrove ellobiid snail (Pulmonata:Gastropoda). J. Zool. 154(3): 377-390.
- BLACK, R., AND M. S. JOHNSON. 1979. Asexual viviparity and population genetics of *Actinia tenebrosa*. Mar. Biol. 53(1): 27-31.
- BUCKLIN, A., D. HEDGECOCK, AND C. HAND. 1980. Genetic evidence for self-fertilization in the sea anemone *Epiactis prolifera*. (Abs.) Am. Zool. 20(4): 818.
- CARTER, M. A., AND M. E. FUNNELL. 1980. Reproduction and brooding in *Actinia*. In, P. Tardent and R. Tardent. (Eds.). Developmental and Cellular Biology of Coelenterates. Pp. 17-22. Elsevier/North Holland, New York.
- , AND C. H. THORP. 1979. The reproduction of *Actinia equina* L. var. *mesembryanthemum*. J. mar. biol. Ass. U.K. 59(4): 989-1001.
- CHIA, F.-S., AND M. A. ROSTRON. 1970. Some aspects of the reproductive biology of *Actinia equina* (Cnidaria:Anthozoa). J. mar. biol. Ass. U.K. 50(1): 253-264.
- DUNN, D. F. 1975a. Gynodioecy in an animal. Nature, Lond. 253: 528-529.
- . 1975b. Reproduction of the externally brooding sea anemone *Epiactis prolifera* Verrill, 1869. Biol. Bull. 148(2): 199-218.
- . 1977. Dynamics of external brooding in the sea anemone *Epiactis prolifera*. Mar. Biol. 39(1): 41-49.
- . 1978. *Anthopleura bandi* n. sp. (Coelenterata, Actiniaria), an internally brooding, intertidal sea anemone from Malaysia. Wasmann J. Biol. 35(1): 54-64.
- GASHOUT, S. E., AND R. F. G. ORMOND. 1979. Evidence for parthenogenetic reproduction in the sea anemone *Actinia equina* L. J. mar. biol. Ass. U.K. 59(4): 975-987.
- GIESE, A. C. 1976. Reproductive cycles of marine invertebrates. Sem. Biol. Mar. 47 suppl.: 49-67.
- , AND J. S. PEARSE. 1974. Introduction: general principles. In, A. C. Giese and J. S. Pearse. (Eds.). Reproduction of Marine Invertebrates, vol. 1: 1-49. Academic Press, New York and London.
- JENNISON, B. L. 1979. Gametogenesis and reproductive cycles in the sea anemone *Anthopleura elegantissima* (Brandt, 1835). Can. J. Zool. 57(2): 403-411.
- . 1981. Reproduction in three species of sea anemones from Key West, Florida. Can. J. Zool. 59(9): 1708-1719.
- LESSIOS, H. A. 1981. Reproductive periodicity of the echinoids *Diadema* and *Echinometra* on the two coasts of Panama. J. Exp. Mar. Biol. Ecol. 50(1): 47-61.

- MAYNARD SMITH, J. 1978. The Evolution of Sex. Cambridge Univ. Press, Cambridge. 222 pp.
- MINASIAN, L. L., JR. 1979. The effect of exogenous factors on morphology and asexual reproduction in laboratory cultures of the intertidal sea anemone, *Haliplanella luciae* (Verrill) (Anthozoa: Actiniaria) from Delaware. J. Exp. Mar. Biol. Ecol. 40(3): 235-246.
- . 1982. The relationship of size and biomass to fission rate in a clone of the sea anemone, *Haliplanella luciae* (Verrill). J. Exp. mar. biol. Ecol. 58(2/3): 151-162.
- OTTAWAY, J. R. 1974. Resistance of juvenile *Actinia tenebrosa* (Cnidaria: Anthozoa) to digestive enzymes. Mauri Ora 2: 73-83.
- . 1979. Population ecology of the intertidal anemone *Actinia tenebrosa* II. Geographical distribution, synonymy, reproductive cycle and fecundity. Aust. J. Zool. 27(2): 273-290.
- , AND G. C. KIRBY. 1975. Genetic relationships between brooding and brooded *Actinia tenebrosa*. Nature, Lond. 255: 221-223.
- PEARSE, J. S. 1968. Patterns of reproductive periodicities in four species of Indo-Pacific echinoderms. Proc. Ind. Acad. Sci. 68B(6): 247-279.
- . 1978. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez. IV. The chitons *Acanthopleura haddoni* Winckworth and *Onitobochiton lyelli* (Sowerby), and the abalone *Haliotis pustulata* Reeve. Bull. Mar. Sci. 28(1): 92-101.
- PURCELL, J. E. 1977. Aggressive function and induced development of catch tentacles in the sea anemone *Metridium senile* (Coelenterata, Actiniaria). Biol. Bull. 153(2): 355-368.
- ROSSI, L. 1975. Sexual roles in *Cerereis pedunculatus* (Boad.). Pubbl. Staz. Zool. Napoli 39 suppl.: 462-470.
- SEMPER, K. 1881. Animal Life as Affected by the Natural Conditions of Existence. D. Appleton and Co., New York. 472 pp.
- SCHLICHTER, D. 1973. Ernährungsphysiologische und ökologische Aspekte der Aufnahme in Meerwasser gelöster Aminosäuren durch *Anemonia sulcata* (Coelenterata, Anthozoa). Oecologia 11(4): 315-350.
- SHICK, J. M., AND A. N. LAMB. 1977. Asexual reproduction and genetic population structure in the colonizing sea anemone *Haliplanella luciae*. Biol. Bull. 153(3): 604-617.
- SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry: the Principles and Practice of Statistics in Biological Research. W. J. Freeman and Co., San Francisco. 776 pp.
- THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Oresund). Meddr. Kommn. Danm. Fisk- og Havunders., ser. plankton, 4(1): 1-523.
- UCHIDA, T. 1932. Occurrence in Japan of *Diadumene Luciae*, a remarkable actinian of rapid dispersal. J. Fac. Sci. Hokkaido Imp. Univ., ser. 6, 2(2): 69-82.
- . 1936. Influence of the currents upon the distribution of races and frequency of asexual reproduction in the actinian, *Diadumene Luciae*. Zool. Mag. Tokyo 48: 895-906.
- VERRILL, A. E. 1870. Synopsis of the polyps and corals of the North Pacific Exploring Expedition. Part IV. Actinaria. Comm. Essex Inst. 6: 51-104.
- . 1898. Descriptions of new American actinians, with critical notes on other species, I. Am. J. Sci. ser. 4, 6(36): 493-498.
- VOHRA, F. C. 1970. Some studies on *Cerithiidea cingulata* (Gmelin 1790) on a Singapore sandy shore. Proc. malac. Soc. Lond. 39(2/3): 187-201.
- WARNER, R. B. 1978. The evolution of hermaphroditism and unisexuality in aquatic and terrestrial vertebrates. In, E. S. Reese and F. J. Lighter. (Eds.). Contrasts in Behavior. Pp. 77-101. John Wiley and Sons, New York.
- WEDI, S. E. 1978. Reproductive periodicity and gametogenesis in the sea anemone *Tealia lofotensis* (Danielssen, 1890). Unpubl. M. A. thesis, San Francisco State University. 88 pp.
- WELTY, J. C. 1962. The Life of Birds. W. B. Saunders Co., Philadelphia and London. 546 pp.
- WILLIAMS, R. B. 1975. Catch-tentacles in sea anemones: occurrence in *Haliplanella luciae* (Verrill) and a review of current knowledge. J. Nat. Hist. 9(5): 241-248.
- . 1980. A further note on catch-tentacles in sea anemones. Trans. Norfolk Norwich Nat. Soc. 25(2): 84-86.