

A PRELIMINARY STUDY OF THE REPRODUCTIVE ECOLOGY OF THE SEASTARS *ASTERIAS VULGARIS* AND *A. FORBESI* IN NEW ENGLAND

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ABSTRACT

Individuals of the carnivorous forcipulate asteroids *Asterias vulgaris* and *A. forbesi* occur in low intertidal and subtidal regions in New England. They occupy both hard- and soft-bottom habitats, but greatest densities occur around high concentrations of their preferred prey, mussels. Mean wet weight varied both among sites [from about 1 to 90 g (*A. vulgaris*) and 1.4 to 32 g (*A. forbesi*)], and within sites (e.g., mean wet weight declined from 90 to 6 g in 12 months at one site).

Both seastars broadcasted eggs and sperm in late spring and summer at various sites between 1973 and 1975. In Massachusetts, *A. vulgaris* spawned in June and *A. forbesi* spawned in July or August, while in Maine, *A. vulgaris* spawned in July. In Maine, gonad and pyloric caecum cycles were inversely correlated in *A. vulgaris*, with peak gonad size occurring in June 1973. In contrast, in Massachusetts, organ cycles were uncorrelated in either species. At sites with dense mussel populations, individuals of both seastars developed larger gonads than at sites with sparse mussel populations. Reproduction (and growth) in these species is thus flexible, and depends on prey abundance. Dissection of ripe seastars over a range of sizes indicates that both species reach reproductive maturity at small size, between about 1 and 10 g. These results contrast to those obtained for the west coast seastar, *Pisaster ochraceus*, in which reproductive maturity is not attained until a size of 70-90 g wet weight, and in which organ cycles seem consistently inversely related. I postulate that these differences in size of sexual maturation are due to higher mortality of larvae in the plankton on the west than on the east coast of North America. I further suggest that high larval mortality requires growth to large size before maturation because lifetime production of gametes needed for replacement of a female is high, while lower larval mortality permits reproduction at small size because lifetime production of gametes for replacement of a female is lower.

A major goal of evolutionary ecology is to delineate patterns in nature and determine the factors underlying their evolution. Reproductive patterns have received much attention, perhaps because they represent a crucial link between generations of organisms and are thereby one of the clearest adaptive responses to natural selection. Two general approaches are (1) theoretical examination of population models to discover how population parameters respond to different natural selective agents (MacArthur and Wilson, 1967; reviews by Stearns, 1976; 1977), and (2) an empirical focus on explaining the evolution of life histories among particular taxa (Grahame, 1975; Menge, 1975; Tuomi, 1980; Strathmann and Strathmann, 1982; Strathmann et al., 1984), the approach followed here. First, I examine reproductive patterns of two broadcasting forcipulate asteroids occurring in nearshore rocky habitats in New England. Reproduction in these seastars is variable, and is not a species- or site-specific characteristic. Second, I consider the influence of foraging, and distribution and abundance on reproduction. These data suggest that the variation in reproduction is due to flexible responses of energy allocation by the seastars to local variation in prey availability. Third, I compare these east coast species to a similar west coast species, and suggest the hypothesis that their contrasting reproductive ecologies are due to differences in larval mortality in the plankton, postulated to be greater on the

west than the east coast. This preliminary study indicates that a future focus coupling larval and adult ecology of these and similar species would be productive.

THE SPECIES

Asterias forbesi, the more southerly species, cooccurs with *A. vulgaris*, the more northerly species, along much of the east coast of North America from central Maine to Cape Hatteras (Gosner, 1971). Bathymetric spatial overlap is from the low intertidal to 49 m depth in the region of overlap (Gosner, 1971). When they cooccur, *A. forbesi* tends to be most abundant in shallower depths and *A. vulgaris* is more abundant in deeper water. Both are generally less common below 20 m (Menge, 1979). These predators have been studied extensively, with particular emphasis on their commercial importance (review by Sloan, 1980).

These asteroids are generalized consumers of sessile invertebrates and are a major determinant of patterns of distribution, abundance, and diversity in low intertidal and subtidal habitats (Lubchenco and Menge, 1978; K. P. Sebens, in prep.). Their abundance fluctuates seasonally, due to inshore migration in summer, presumably to feed on mussels, and offshore migrations in winter, presumably to avoid severe wave conditions in shallow water during storms (Menge, 1979). Population size structure can change dramatically, due to differential mortality of large individuals from severe storms occurring unexpectedly early (fall) or late (spring) in the season, epidemics, or other factors (Menge, 1979). Small individuals are always present, sometimes as the dominant size class.

These species probably evolved in allopatry during the mid to late Pleistocene, and may not yet have achieved reproductive isolation (Schopf and Murphy, 1973). Besides obvious morphological similarity, they share approximately 67% of electrophoretically active proteins (Schopf and Murphy, 1973), and "hybrids," or morphologically intermediate individuals are sometimes observed (e.g., 1.4%, $N = 295$ *Asterias* spp. collected from Long Island Bridge, Boston Harbor, Massachusetts; B. A. Menge, unpublished data). One aim of the present study, to determine periods of spawning, should provide insight into the specific status and likelihood of hybridization in the field by these asteroids.

Both species are broadcast spawners (Loosanoff, 1964), producing large numbers of small gametes. The bipinnaria are planktotrophic, spending two to six weeks feeding in the plankton before settling (Loosanoff, 1964). In Connecticut, recruitment in settling trays varied widely from year to year, producing large annual variation in density.

STUDY AREAS AND METHODS

The study sites, described in detail earlier (Menge, 1976; 1978a; 1978b; 1979; 1983; Lubchenco and Menge, 1978), were Diving Beach, Nahant and Outer Brewster Island, Boston Harbor, Massachusetts; and Grindstone Neck, Winter Harbor, Maine (see map in Menge, 1979). Data were obtained using standard methods (reviews in Sloan, 1980; Menge, 1982). Briefly, distribution and abundance of both seastars and prey were determined using a transect-quadrat method; feeding and size structure was determined by inspection and measurement (radius during underwater samples, radius and wet weight during low tide samples) of individuals collected haphazardly; and wet weights of gonad and pyloric caeca, sex, and state of gonad maturation were determined by dissecting 8 to 18 individuals of each species spanning a range of sizes per sample date. Gonad and pyloric caecum indices were obtained in the usual manner [(organ wet weight \div total individual wet weight) \times 100] (Giese and Pearse, 1974).

Gonads of ripe individuals were typically large, often completely filling the coelomic space in each ray. Sex was determined by inspecting ripe or partially spawned individuals; male gonads are white and female gonads are orange or yellow. Gonads of totally spawned-out and immature individuals were small, occupying little space in the coelomic cavity, and were usually tan. Size of sexual maturation was determined at the peak of gonad ripeness when the presence of gametes in the distended gonads

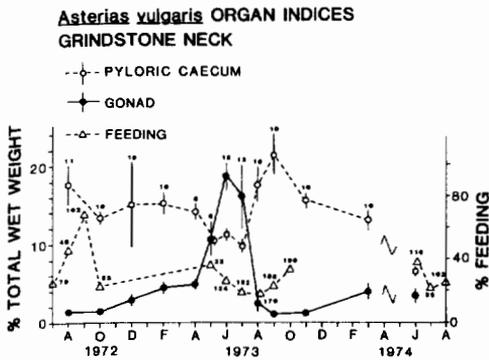


Figure 1. (Left) Gonad and pyloric caecum cycles, and percent feeding in the *Asterias vulgaris* population at Grindstone Neck, Winter Harbor, Maine from August 1972 to June 1974. Mean organ index (% of total wet weight) and 1 standard error are scaled on the left Y axis, percent feeding are scaled on the right Y axis. Sample sizes (organ indices: number of sexually mature individuals in each collection; percent feeding: number examined during each sample period) is given by each error bar or symbol. The zigzags in spring 1974 indicate the presumed period of peak gonad size for which no data were available.

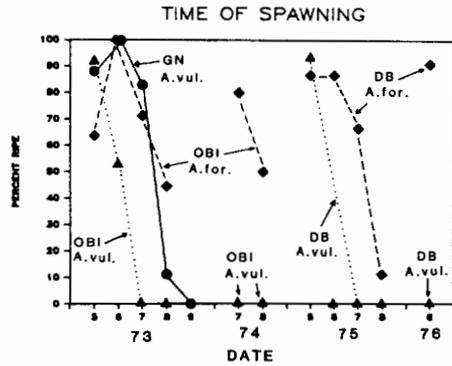


Figure 2. (Right) Percent of sexually mature individuals which had spawned in collections of seastars from Grindstone Neck, Outer Brewster Island, and Diving Beach.

of mature individuals was readily observed by eye. Individuals equal to and smaller than the size at which developed gonads were consistently lacking were assumed to be sexually immature.

Differences between means were tested with analysis of variance; data were transformed where appropriate before analysis (Sokal and Rohlf, 1981). Relationships among organ indices and feeding proportions, and seastar biomass and mussel abundance were determined with regression analysis and analysis of covariance. Variance is presented either as ± 1 standard error of the mean, or as 95% confidence intervals; sample sizes are included to permit estimation of standard deviation, if desired.

RESULTS

Changes in Gonad and Pyloric Caecum.—Organ cycles were determined for *Asterias vulgaris* for a 19-month period at Grindstone Neck, Maine (Fig. 1). Mean gonad size was small in August 1972, rose slowly until April 1973, after which it rose rapidly to a peak in June 1973. Individuals in this population spawned during July 1973, after which mean gonad size again began to slowly increase (Fig. 1). The pyloric caecae were relatively large ($>10\%$ of total wet weight) throughout the year, but were smallest when the gonads were largest (Fig. 1).

Organ indices were determined for populations of both *Asterias* spp. at the Massachusetts sites to permit intra- and interspecific comparisons of time of spawning. As indicated by both gonad indices (Table 1) and the percent of the sample with ripe gonads (Fig. 2), there was little interspecific overlap in time of spawning in Massachusetts; *A. vulgaris* spawned in June (at least in 1973 and 1975) while *A. forbesi* spawned in July and August (1973 to 1975). Hence, *A. vulgaris* spawned a full month later in Maine than in Massachusetts (Fig. 2). Whether or not the different spawning times of *A. vulgaris* in Maine and Massachusetts are due to natural selection to reduce the likelihood of hybridization, selection to release gametes coincidentally with phytoplankton blooms (which are progressively later in the season with increased latitude), or some other factor is unknown.

Gonad and pyloric caecum sizes are often inversely correlated in broadcasting seastars (Mauzey, 1966; Barker, 1979; Scheibling, 1981; Barker and Nichols,

Table 1. Organ indices of *Asterias vulgaris* and *A. forbesi* at Outer Brewster Island, Boston Harbor, and Diving Beach, Nahant, Massachusetts. Data are mean \pm 1 standard error of the mean; N = sample size; ND = no data available

Month, year	Site	<i>Asterias vulgaris</i>			<i>Asterias forbesi</i>			
		GI	PCI	N	GI	PCI	N	
May	73	OBI	10.5 \pm 1.9	8.6 \pm 1.0	12	6.3 \pm 1.3	8.2 \pm 1.1	14
June	73	OBI	7.6 \pm 2.2	14.4 \pm 0.6	18	17.3 \pm 1.9	10.6 \pm 0.6	17
July	73	OBI	0.8 \pm 0.1	17.6 \pm 1.7	13	15.7 \pm 3.1	7.8 \pm 0.7	14
August	73	OBI	1.0 \pm 0.1	20.4 \pm 0.7	10	15.5 \pm 5.1	12.7 \pm 1.7	9
July	74	OBI	0.7 \pm 0.1	14.3 \pm 1.4	10	20.4 \pm 3.4	7.6 \pm 0.9	10
August	74	OBI	0.6 \pm 0.2	14.8 \pm 0.9	10	7.1 \pm 1.4	9.2 \pm 1.1	10
December	74	DB	8.3 \pm 2.1	22.1 \pm 1.2	10	3.5 \pm 0.5	26.8 \pm 1.0	9
March	75	DB	ND	ND		5.9 \pm 0.8	17.8 \pm 0.8	9
May	75	DB	19.8 \pm 2.9	9.9 \pm 0.7	15	12.5 \pm 1.7	13.2 \pm 1.1	15
June	75	OBI	2.2 \pm 1.2	20.4 \pm 1.2	14	17.2 \pm 2.7	13.8 \pm 1.4	14
		DB	0.8 \pm 0.2	21.2 \pm 1.6	10	16.0 \pm 2.7	9.2 \pm 0.7	15
July	75	OBI	0.5 \pm 0.1	11.3 \pm 1.1	8	12.0 \pm 2.3	8.7 \pm 1.2	14
		DB	0.3 \pm 0.1	6.9 \pm 0.5	8	9.5 \pm 2.1	5.9 \pm 0.6	12
August	75	OBI	0.4 \pm 0.1	10.8 \pm 0.8	9	2.0 \pm 1.3	9.0 \pm 0.9	9
		DB	0.2 \pm 0.1	8.9 \pm 0.8	9	0.3 \pm 0.1	6.6 \pm 1.1	9
June	76	DB	0.6 \pm 0.2	7.7 \pm 1.0	9	10.8 \pm 3.0	7.0 \pm 0.6	11

1983), but this pattern is not universal (Harrold and Pearse, 1980). Organ sizes of *A. vulgaris* are inversely correlated in Maine, while organ sizes in both *Asterias* spp. are not correlated in Massachusetts populations (Fig. 3). Hence, there is both interspecific and intraspecific variation in the patterns of energy transfer from pyloric caecum to gonad in these, and probably other broadcasting asteroids.

Maturation Size.—Size at sexual maturation was determined by examining gonad size of individuals of different sizes just before spawning. Maturation size of *A. vulgaris* was between 2.6 and 9.1 g wet weight in Maine, and between 1.6 and 1.8 g wt weight in Massachusetts, while maturation size of *A. forbesi* was between 1.1 and 1.3 g wet weight (Fig. 4). In comparison, the brooding seastar *Leptasterias hexactis* matures at about 2 g and the broadcasting *Pisaster ochraceus* matures between 70 and 90 g wet weight (Menge, 1974; 1975).

Relation between Feeding and Organ Size.—Feeding activity and diet composition is dependent on local food availability (Menge, 1979). Although these seastars have broad diets, mussels, and sometimes barnacles, are by far the most frequently eaten prey (Fig. 5). As reported earlier (Menge, 1979), mussel availability was higher at Grindstone Neck and Outer Brewster Island than at Diving Beach. To determine whether or not this affected reproduction of either species, I examined the relationship between wet weight and gonad index in mature individuals just before spawning. Estimates from all dissected individuals which were either reproductively immature, or partially or totally spawned, were deleted from the data set. I then compared regressions between the natural logarithms of individual wet weight (X) and gonad index (Y) for each site and species combination using analysis of covariance. Although differences were detected among the species-by-site regressions (ANCOVA, $P < 0.0004$, 2,172 df), the regression lines did not differ significantly among the three sites (i.e., species lumped, $P = 0.075$) or the

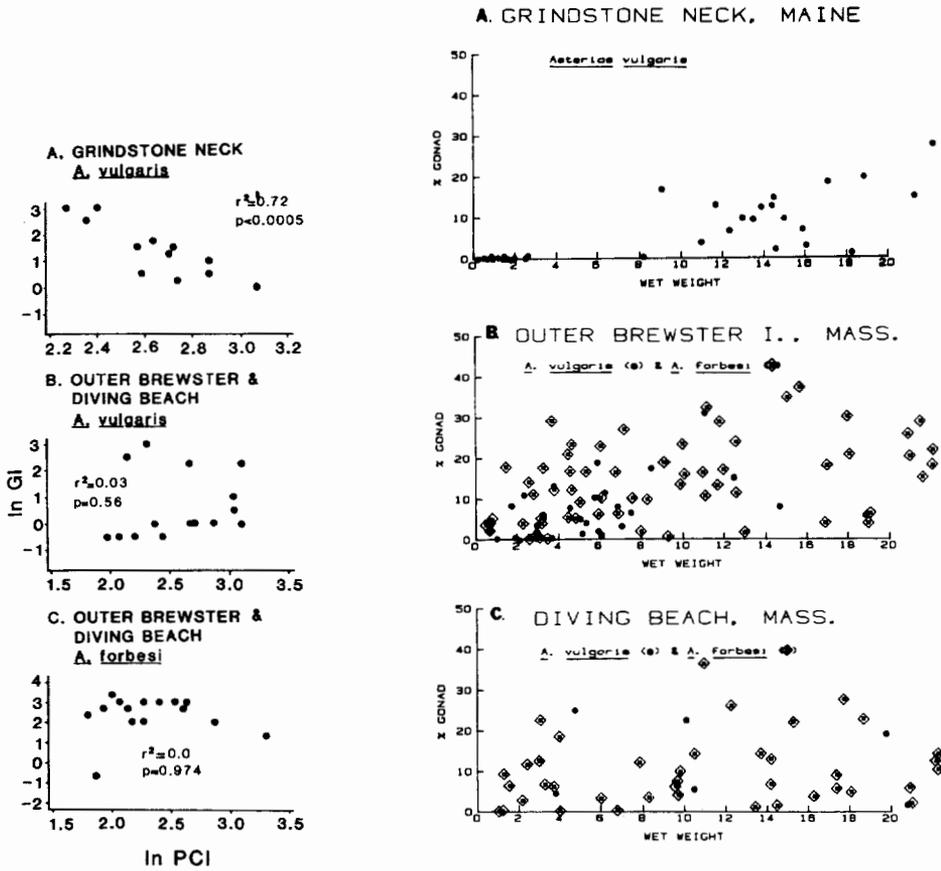


Figure 3. (Left) Relation between gonad and pyloric caecum indices prior to spawning. Shown are \ln pyloric caecum index (= \ln PCI; X) plotted against \ln gonad index (= \ln GI; Y) just before the occurrence of spawning. A. *A. vulgaris* at Grindstone Neck, B. *A. vulgaris* at Outer Brewster Island and Diving Beach, and C. *A. forbesi* at Outer Brewster Island and Diving Beach. Coefficient of determination (r^2) and the significance of the correlation (P) is shown in each panel.

Figure 4. (Right) Scatterplots of individual wet weight (g; X) against the gonad index (% gonad) for each species at each study site. Size of sexual maturation is indicated by the absence of non-zero gonad indices at small body sizes.

two species (i.e., sites lumped, $P = 0.435$). Examination of scatterplots suggested that the significance of the overall ANCOVA model was due to differences between two groups; with populations of *Asterias* spp. at Diving Beach constituting one group, and populations of *Asterias* spp. at both Outer Brewster Island and Grindstone Neck constituting the other. That is, size-specific reproduction differed among sites, but not between species. Reanalysis after lumping into these groups indicates that the regression of \ln (Gonad Index) = Constant + \ln (Wet Weight) for *Asterias* spp. at Grindstone Neck/Outer Brewster Island differs significantly from that at Diving Beach (ANCOVA, $P < 0.035$, 1,173 df). Slopes of both regressions are >0 ($P < 0.0004$), and the hypothesis of homogeneity of slopes cannot be rejected ($P = 0.772$), indicating that the regression lines are parallel. Gonad indices for individuals of a given size at Grindstone Neck/Outer Brewster

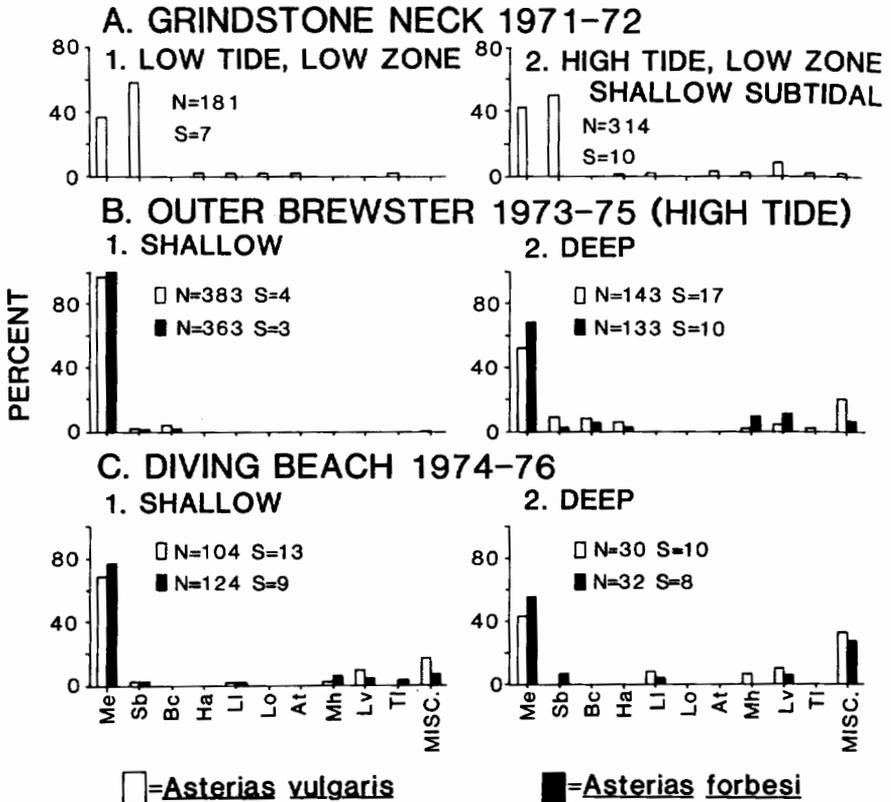


Figure 5. Diet composition of *Asterias* spp. at A. Grindstone Neck (LOW and HIGH tide data taken in the low intertidal and shallow subtidal), B. Outer Brewster Island (high tide data taken in low intertidal/shallow subtidal = SHALLOW, and a nearby kelp bed = DEEP), and C. Diving Beach (high tide data taken in the low intertidal/shallow subtidal = SHALLOW, and a nearby subtidal habitat = DEEP). N = total number of prey observed being eaten; S = number of species included in the diet. Data in B. and C. are taken from Tables 3 and 4 in Menge, 1979. Prey species codes: Me = *Mytilus edulis*, Sb = *Semibalanus balanoides*, Bc = *Balanus crenatus*, Ha = *Hyatella arctica*, Ll = *Liittorina littorea*, Lo = *L. obtusata*, At = *Acmaea testudinalis*, Mh = *Margarites helicina*, Lv = *Lacuna vincta*, Tl = *Thais lapillus*, MISC. = miscellaneous.

Island are larger than at Diving Beach. Hence, reproductive output is evidently not a species or site characteristic. Rather, gonad size seems most closely related to mussel availability, which was higher at Grindstone Neck and Outer Brewster Island, as noted above.

Feeding activity is inversely correlated to the gonad index of *A. vulgare* at Grindstone Neck and Outer Brewster Island ($r = -0.565$; $F = 8.3$, 1,14 df, $P = 0.023$). However, after adjustment for sample size, only 27% of the variance is explained by the regression between percent feeding and gonad index, and no such relationship occurs for *A. vulgare* at Diving Beach. Further, feeding activity of *A. forbesi* is unrelated to gonad index at any site, regardless of how the data are grouped ($P \geq 0.05$). Although further study is required, I tentatively conclude that feeding in *Asterias* spp. is variable in space and time, and is not consistently related to gonad or storage organ size.

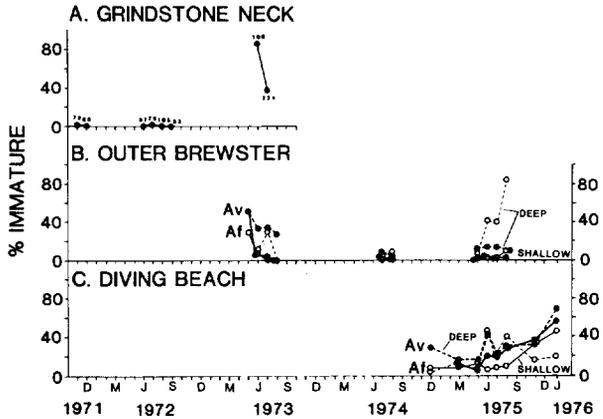
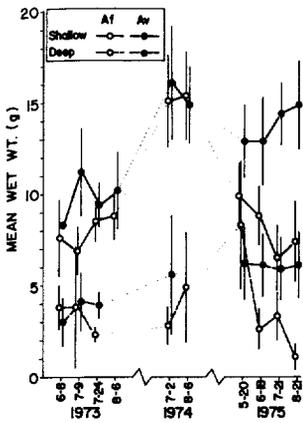


Figure 6. (Left) Average wet weight of *A. forbesi* and *A. vulgaris* in shallow and deep habitats at Outer Brewster Island. Data are mean wet weight and 95% confidence interval and are taken from figures 8 and 9 in Menge, 1979. Dotted connecting line and zigzags on x-axis indicate periods for which no data are available.

Figure 7. (Right) Proportion of sexually immature individuals of *Asterias* spp. at A. Grindstone Neck, B. Outer Brewster Island, and C. Diving Beach, at intervals from November 1971 to June 1976. Maturation sizes used were 2.6 g at Grindstone Neck, and 1.5 g (*A. vulgaris*) and 1.0 g (*A. forbesi*) at Outer Brewster Island and Diving Beach. "Shallow" and "deep" refer to low intertidal and subtidal subpopulations, respectively.

Variation in Body Size and Proportion of Immature Individuals.—Mean wet weight of both asteroids varies between sites, over time, and with depth (Fig. 6; see also figs. 4, 5, 8, 9, and 11 in Menge, 1979). In general, average size of both seastars is greatest when they have been feeding on mussel concentrations. Over the bathymetric range of these asteroids, mussel beds most typically occur at more wave-exposed rocky shores and are observed infrequently at wave-protected sites (Lubchenco and Menge, 1978). When dense patches of mussels develop at sites of moderate to low wave motion, *Asterias* spp. rapidly aggregate and decimate them (Menge, 1979). For example, *Asterias* biomass ($\sqrt{\text{g}/0.25 \text{ m}^2}$) is positively correlated to abundance of mussels (% cover, arcsin transformation; $F = 9.65$, $df = 10$, $P = 0.013$; summer data from 11 sites), explaining about 52% of the variance (data from last two columns of table 6 in Menge, 1979).

Proportion of immature individuals was calculated by combining estimates of size of sexual maturation with size frequencies in each population sample. As expected from the variation in means and 95% confidence intervals plotted in Figure 6, the proportion of immature individuals varies greatly from near 0 to 50–86% of the population for each species (Fig. 7).

The proportion of immature individuals also varied with depth and site. At Outer Brewster Island, where mussels were abundant in the low intertidal and shallow subtidal and scarce in deeper water, the proportion of immature individuals was always greater in deeper water ($N = 10$ samples). At Diving Beach, where mussel abundance was similar to that at Outer Brewster in deeper habitats, but less in low intertidal/shallow subtidal habitats, the proportion of immatures was greater in deep samples in seven (*A. vulgaris*) and four (*A. forbesi*) of eight cases. Although the pattern for *A. vulgaris* thus appears similar at the two sites, the differences in proportion immature in deep and shallow regions at Diving Beach

are small and the trends are similar (Fig. 7). I therefore conclude that proportions of immature individuals are similar in both deep and shallow populations of both asteroids at Diving Beach, but not at Outer Brewster Island. I suggest that this difference between the two sites is related to food availability; large, sexually mature individuals of this species are more likely to occur near mussel beds (e.g., Outer Brewster Island) where food is plentiful, and presumably, where high somatic and gonad growth rates can be maintained. Those individuals locating a mussel bed during their annual summer migration into shallow water are thus more likely to grow large and reach sexual maturity than are those that do not locate a mussel bed or remain in deeper water.

DISCUSSION

These seastars exhibit considerable flexibility in reproduction and growth. For example, time of spawning and size of sexual maturation varies with latitude in *A. vulgaris*. Among study sites, both asteroids differ in size-specific gonad weight just before spawning, the relationship between feeding activity and organ size, and the relationship between gonad and pyloric caecum size. Although inverse correlations between the latter are frequently observed in seastars, Harrold and Pearse (1980) question the universality of this relationship, noting that variation in food availability may cause the animal to alter patterns of energy allocation. Similarly, Barker and Nichols (1983) suggest that subtidal *A. rubens* and *Marthasterias glacialis* in southern England develop smaller gonads than do intertidal *A. rubens* because food in the subtidal is scarce.

These observations, with the variation among populations of *Asterias* spp. reported above, suggest that a more dynamic relationship between feeding, and gonad and pyloric caecum sizes may prevail in broadcasting asteroids than has been recognized. For example, when food is continuously abundant, gonad size may cycle but pyloric caecum size may not, remaining continuously high. Lower or more cyclic patterns of food abundance might lead to inversely correlated cycles of organ size, while food scarcity could require an iteroparous seastar to forego reproduction and channel all energy into maintenance and storage (Harrold and Pearse, 1980). If food availability is variable in space, time, or both, as it was during my New England study (Menge, 1979; Lubchenco and Menge, 1978), such flexibility should be readily observed both among and within populations of the same species. Further study of reproductive plasticity in seastars, its relation to food availability, and particularly, how individuals switch among these possibilities would be valuable.

In an earlier study, I found that *Pisaster ochraceus*, a west coast forcipulate asteroid, did not reach sexual maturity until it reached a size of 70–90 g wet weight (Menge, 1975). This contrasts strikingly with the maturation size range of 1–9 g wet weight of the east coast *Asterias* spp. Why does such a great difference exist? In the earlier report, I suggested that reproduction at a relatively large size in *P. ochraceus* was imposed by high mortality of larvae in the plankton, most likely due to predation or larval export or both. I suggested the hypothesis that, in order to grow large enough to produce sufficient offspring to ensure replacement during their lifespan, female *P. ochraceus* should delay sexual maturity in favor of growth and maintenance. Of course, large size could also enhance individual survival and greater success in obtaining food.

A corollary to this hypothesis is that if larval mortality in the plankton is low, then (assuming similar longevities) successful replacement by a female should be possible with fewer offspring, and annually broadcasting seastars should mature

at a smaller size. Even if longevities of *Asterias* spp. and *P. ochraceus* differ, *Asterias* would have to live longer than, or grow to sizes similar to those reached by *P. ochraceus* in order to equal the gamete production of the latter. Although growth rate and longevity in seastars is notoriously difficult to estimate, the evidence, and my experience with both species suggests that neither of these is true (Menge, 1974; 1975; 1979; Paine, 1976; Morris et al., 1980). Although *Asterias* spp. appear to recruit more densely, and grow faster than *P. ochraceus*, size structure of most populations I observed was dominated by small (<50 g wet weight) individuals and large (>100 g wet weight) individuals were almost never observed at sites lacking mussel beds. In contrast, *Pisaster* populations in Washington were typically dominated by large (>100 g wet weight) individuals, and small individuals were rare. *Pisaster* probably lives for ≥ 20 yr (Menge, 1975; Morris et al., 1980), while such longevity in *Asterias* spp. seems unlikely given the frequency with which I observed mass mortality of these seastars in New England (Menge, 1979). Although the evidence is consistent with my hypothesis, it is largely subjective; further work is needed. Studies coupling adult and larval ecology in these and similar species would be particularly valuable.

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LITERATURE CITED

- Barker, M. F. 1979. Breeding and recruitment in a population of the New Zealand starfish *Stichaster australis* (Verrill). *J. Exp. Mar. Biol. Ecol.* 41: 195-211.
- and D. Nichols. 1983. Reproduction, recruitment and juvenile ecology of the starfish *Asterias rubens* and *Marthasterias glacialis*. *J. Mar. Biol. Ass., U.K.* 63: 745-765.
- Giese, A. C. and J. S. Pearse, eds. 1974. Reproduction of marine invertebrates I. Academic Press, Inc., New York. 546 pp.
- Gosner, K. L. 1971. Guide to identification of marine and estuarine invertebrates: Cape Hatteras to the Bay of Fundy. Wiley-Interscience, New York. 693 pp.
- Grahame, J. 1975. Reproductive effort and r- and K-selection in two species of *Lacuna* (Gastropoda: Prosobranchia). *Mar. Biol.* 40: 217-224.
- Harrold, C. and J. S. Pearse. 1980. Allocation of pyloric caecum reserves in fed and starved sea stars, *Pisaster giganteus* (Stimpson); somatic maintenance comes before reproduction. *J. Exp. Mar. Biol. Ecol.* 48: 169-183.
- Loosanoff, V. L. 1964. Variations in time and intensity of setting of the starfish, *Asterias forbesi*, in Long Island Sound during a twenty-five year period. *Biol. Bull.* 126: 423-439.
- Lubchenco, J. and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48: 67-94.
- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Monogr. in Pop. Biol. 1, Princeton Univ. Press, Princeton, New Jersey. 203 pp.
- Mauzey, K. P. 1966. Feeding behavior and reproductive cycles in *Pisaster ochraceus*. *Biol. Bull.* 131: 127-144.
- Menge, B. A. 1974. Effect of wave action and competition on brooding and reproductive effort in the seastar *Leptasterias hexactis*. *Ecology* 55: 84-93.
- . 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal seastars *Leptasterias hexactis* and *Pisaster ochraceus*. *Mar. Biol.* 31: 87-100.
- . 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* 46: 355-393.
- . 1978a. Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia (Berl.)* 34: 1-16.

- . 1978b. Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia (Berl.)* 34: 17–35.
- . 1979. Coexistence between the seastars *Asterias vulgaris* and *A. forbesi* in a heterogeneous environment: a non-equilibrium explanation. *Oecologia (Berl.)* 41: 245–272.
- . 1982. Effects of feeding on the environment: Asteroidea. Ch. 25 in M. Jangoux and J. M. Lawrence, eds. Echinoderm nutrition. A. A. Balkema, Rotterdam, Holland. 654 pp.
- . 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia (Berl.)* 58: 141–155.
- Morris, R. H., D. P. Abbott and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford Univ. Press, Stanford, California. 690 pp.
- Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57: 858–873.
- Scheibling, R. E. 1981. The annual reproductive cycle of *Oreaster reticulatus* (L.) (Echinodermata: Asteroidea) and interpopulation differences in reproductive capacity. *J. Exp. Mar. Biol. Ecol.* 54: 39–54.
- Schopf, T. J. M. and L. S. Murphy. 1973. Protein polymorphism of the hybridizing seastars *Asterias forbesi* and *A. vulgaris* and implications for their evolution. *Biol. Bull.* 145: 589–597.
- Sloan, N. A. 1980. Aspects of the feeding biology of asteroids. *Oceanogr. Mar. Biol. Annu. Rev.* 18: 57–124.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*, 2nd ed. W. H. Freeman and Co., San Francisco. 859 pp.
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. *Q. Rev. Biol.* 15: 3–47.
- . 1977. The evolution of life history traits: a critique of the theory and a review of data. *Ann. Rev. Ecol. Syst.* 8: 145–171.
- Strathmann, R. R. and M. F. Strathmann. 1982. The relationship between adult size and brooding in marine invertebrates. *Amer. Nat.* 119: 91–101.
- , ——— and R. H. Emson. 1984. Does limited brood capacity link adult size, brooding and simultaneous hermaphroditism? A test with the starfish *Asterina phylactica*. *Amer. Nat.* 123: 796–818.
- Tuomi, J. 1980. Mammalian reproductive strategies: a generalized relation of litter size to body size. *Oecologia (Berl.)* 45: 39–44.

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