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Gynodioecy in an animal

GYNODIOECY, a breeding system in which the population consists of hermaphrodites and females only, is a well known botanical phenomenon with a literature dating back at least to Darwin[1]. It has never previously been reported in an animal.

A population of the sea anemone *Epiactis prolifera* Verrill, 1869, living in the rocky intertidal zone near Bodega Marine Laboratory, Sonoma County, California, was studied from April 1970 to March 1972. Of 269 animals from monthly collections examined histologically, 31 were sterile, 138 were female, and 100 were hermaphroditic (Fig. 1). This pattern of gynodioecy persisted all year round. Fertile anemones ranged from 5.8 to 35.7 mm in basal diameter. As an effort was made to include individuals of all sizes in each collection, the largest and smallest animals were represented in excess of their relative proportions in the population.

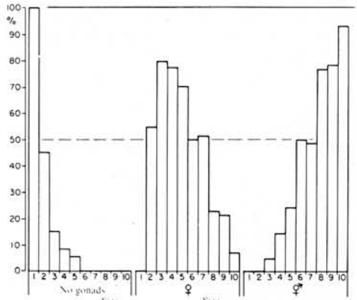
E. prolifera broods its young externally, one of 16 actinian species known to do so[2]. Females and hermaphrodites spawn relatively few large yolky eggs which soon adhere to the parent's ectoderm, where they develop directly into juvenile anemones. When sufficiently large, juveniles move from the parent on to the surrounding substrate (D.F.D., unpublished).

Some ideas from the botanical literature are relevant to an analysis of the breeding system of *E. prolifera*, but that part consisting of genetic analyses and models[1,3–8] is not. Among gynodioecious plants which have been examined, individuals are genetically either hermaphroditic or female. In *E. prolifera* it seems that sex determination is virtually identical in all individuals so that animals begin their reproductive lives as females, and most that survive sufficiently long become hermaphrodites. Thus gynodioecy in *E. prolifera* is serial and developmental, whereas in plants it is fixed and genetic.

A major advantage of gynodioecy—its ability to adjust the degree of heterozygosity in a population[3,4,9]—obtains only if the species is at least potentially self fertile. There is no reason to dismiss this possibility in *E. prolifera*, where ripe ova and spermatozoa frequently occur in the same animal simultaneously (D.F.D., unpublished). If hermaphroditic individuals were facultatively self fertile, advantageous characters, including those which enabled them to survive sufficiently long to develop testes, could be fixed in the genome of the population by homozygosity. Under favourable environmental conditions, longevity would increase, raising the proportion of hermaphrodites in the population and thereby the potential for inbreeding. When conditions were such that few anemones survived long enough to develop testes, inbreeding would decline, thus increasing the proportion of heterozygous offspring with greater genetic flexibility to meet the stressful conditions.

Genetic factors allowing animals to survive long enough to develop testes and producing gynodioecy in *E. prolifera* are favoured numerically, even if selfing is impossible. Offspring of females receive half their genes from hermaphrodites: those of hermaphrodites receive all of theirs from hermaphroditic parents, one if by selfing and two if by crossing. Thus the genetic contribution to the next generation from hermaphrodites, no matter how few, cannot be less than 50%. It is usually greater because hermaphrodites will have already produced offspring as females, and because larger anemones brood more young (D.F.D., unpublished).

It is crucial to the species' success that the prevalence of egg-producing individuals in the population be as great as possible, for fecundity of *E. prolifera* is restricted by brood



Size class	Range (mm)	n	Size class	Range (mm)	n
1	→ 5.5	9	6	15.6 - 18.0	44
2	5.6 - 8.0	31	7	18.1 - 20.5	39
3	8.1 - 10.5	20	8	20.6 - 23.0	26
4	10.6 - 13.0	35	9	23.1 - 25.5	14
5	13.1 - 15.5	37	10	25.6 →	14

Fig. 1 The relationship between size and gonadal state of 269 *E. prolifera* collected approximately monthly over a period of 2 yr. Size classes are based on pedal disk diameter at the time of collection.

space. The strategy of having barely enough males to fertilise the ova produced by a population consisting largely of females might be genetically too inflexible. The extreme in maximisation of brood space would be for all members of the population to produce eggs, some or all of them producing sperm also. (Carlquist[10] reasons similarly regarding gynodioecious plants.)

This last possibility, simultaneous hermaphroditism, occurs in the only other species of externally-brooding actinian to have been studied[11], called *E. prolifera* at that time, this species is now identified as *E. japonica* (T. Uchida, personal communication). Selection against sperm production beyond what is necessary to fertilise sufficient ova to fill the brood space by restricting it to certain members of the population is a possible evolutionary pathway from simultaneous to gynodioecious hermaphroditism. The larger anemones might have been favoured as sperm-producers since they had proved best adapted by virtue of their longevity, and because proportionately less of the energy and material budgeted for gametes could be used by them for sperm than by smaller animals.

Developmental gynodioecy in self fertile species would favour reproduction by only the fittest colonists of new habitats, maximising the chances of survival of succeeding generations. If a hermaphrodite were the founder, it could begin to establish a population immediately. If the animal had not yet attained hermaphroditism, it could begin to reproduce successfully only after having proved its fitness for the new circumstances by surviving in them. Even assuming *E. prolifera* can self, however, it must rarely survive being swept into a new site, so this advantage probably had little to do with the evolution of gynodioecy in this species.

Developmental gynodioecy is an adaptable breeding system. Theoretically, the genetic diversity of gametes is as great as in simultaneous hermaphrodites because virtually all individuals eventually produce sperm as well as ova. Excessive sperm production can be prevented by evolutionary adjustment of the time of onset and extent of testicular development to optimise the sperm : egg ratio of the population. At any one time, the same ratio can be attained as in dioecious species but with greater genetic diversity of sperm because more hermaphrodites are required to produce as many sperm as can be produced by a given number of purely male individuals of the same size.

The genetically-fixed gynodioecy of plants apparently evolved as a mechanism for enhancing outbreeding among normally self fertile hermaphrodites. The developmental gynodioecy of *Epiactis prolifera* probably evolved as a means of increasing the number of brooders (egg-producers) in a population with limited fecundity to a maximum, and possibly also of enhancing inbreeding among normally cross fertile individuals.

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