A Note on the Evolution of Gamete Dimorphism in Algae

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Several authors have hypothesized that anisogamy would evolve from isogamy by disruptive selection if larger zygotes were selectively favored over smaller zygotes (Parker et al. 1972; Bell 1978, 1982; Maynard Smith 1978). These authors assumed that the fitness of a parent would be proportional to both the number of successful gametes produced and the fitness of the zygotes produced from those gametes. In these models, the fitness of a zygote is assumed to be an increasing function of its volume, and a necessary condition for the evolution of anisogamy is that this relation be steeper than linear. Schuster and Sigmund (1982) have instead suggested that Brownian motion alone is enough to favor the evolution of gamete dimorphism by increasing the rate of encounters between the two types of gametes.

Although such theories and their predictions are straightforward, tests of the predictions have been indirect and plagued by ambiguity. Because there is no direct evidence available of how zygote fitness depends on zygote size, Knowlton (1974) and Bell (1978) instead sought out comparative data on adult size in a number of algal groups to provide indirect evidence in support of the theory. They reasoned that unless zygotes also increased in size, increasing adult size would require greater time and energy for development, thereby exposing the zygote to increased hazards and reduced survivorship. This could produce the required disruptive selective pressure for the appearance and maintenance of a macrogamete with cytoplasmic reserves and a microgamete with greater dispersability. We will refer to this as the "adult size" hypothesis.

Knowlton (1974) compared gametic condition to colonial cell number at maturity in genera of the family Volvocaceae and found an association between colonies with large numbers of cells and anisogamy. However, Bell (1978) noted several exceptions to this trend. Furthermore, cell number may not be an accurate measure of adult volume, so data on adult cell number are only an indirect test of the adult size hypothesis. In particular, this approach obviously cannot account for patterns observed among the unicellular algae.

Bell (1978, 1982) has also argued that increased zygote size facilitates differentiation in those groups with a variety of tissues: "optimal zygote size should increase with vegetative size and complexity" (Bell 1982, p. 491). We refer to this latter idea as the "morphological complexity" hypothesis. Increased cytoplasmic storage does usually accompany morphological complexity, but there are also many exceptions to the expected pattern of increased gamete dimorphism in groups characterized by more cell types. For example, members of the Oedogoniales are all simple filaments yet exhibit oogamy, while *Fritschiella* and *Chaetophora* are morphologically complex yet exhibit isogamy. Bell (1978) admits these inconsistencies and suggests that in such cases other factors, such as colony

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volume or internal fertilization, could play a role. Even in cases of apparent agreement with this hypothesis, however, it is impossible to determine whether large zygote size is favored for development into diverse cell types or simply growth to a large size. This is because large adult size generally accompanies increased complexity. Moreover, measures of vegetative complexity usually include cells specialized for producing dimorphic gametes, biasing any comparison with the incidence of anisogamy.

Sexual reproduction in many algae is triggered by deteriorating environmental conditions and involves the production of a dormant zygospore. This association between sex and dormancy could favor anisogamy or oogamy in any group in which large zygospore size is favored directly, irrespective of adult size. Large zygospore size could provide several advantages: (1) reduced predation by zooplankton; (2) rapid settling to the sediment (which would both limit dispersion and exposure to predation); (3) large energy reserves which would permit an extended period of dormant respiration; or (4) a reserve for rapid growth immediately after germination. Thus, situations that favor pronounced dormancy could also favor anisogamy. Such situations include seasonal changes (e.g., overwintering) or nonseasonal responses to temporal instability, such as drought.

To provide a more direct test of the importance of size at maturity, we compared gametic condition to colony volume in 130 species of algae distributed among 17 orders. To consider the alternate hypothetical advantages for anisogamy (the defense and storage requirements of dormancy and the need for a fast start), we also compared gametic condition to each species' characteristic habitat.

We obtained information on gametic condition (asexuality, isogamy, anisogamy, or oogamy), adult sizes, and ecological habitat for species in the Chlorophycophyta and Chrysophycophyta (excluding the Bacillariophyceae) from Bold and Wynne (1978) and Smith (1950). We used all species in these groups for which gametic condition and at least one other variable was available. Oogamy is defined as occurring when the egg lacks a flagellum and is correspondingly nonmotile. The egg is usually larger in these species than in species defined only as anisogamous. We estimated cell volumes from photomicrographs or scale drawings using either the equation for a sphere ($4/3\pi r^3$) or the equation for a cylinder ($\pi r^2 h$) for those species whose shape was definitely elongated (e.g., *Chlorogonium elongatum*). Total adult volumes were only computed for species that exhibit a deterministic growth form, such as the coenobia of the Volvocaceae.

Species were classified ecologically by whether they occurred in: (1) pools, ponds, ditches, or some other temporary body of water; (2) larger lakes, which presumably provide a more stable environment; or (3) soil, tree bark, leaves, or other terrestrial habit. Although limited in extent, this ecological information is valuable for suggesting how unstable the habitat of each species is. Of the 130 species described in some detail, we obtained habitat information for 116 and volume data for 65.

Algae with a large volume at maturity usually displayed anisogamy or oogamy, as expected if larger zygotes permit more rapid growth to these sizes (fig. 1). However, ecological circumstances also appear to influence gametic condition. A contingency table (table 1) shows a significant tendency for oogamy to occur in

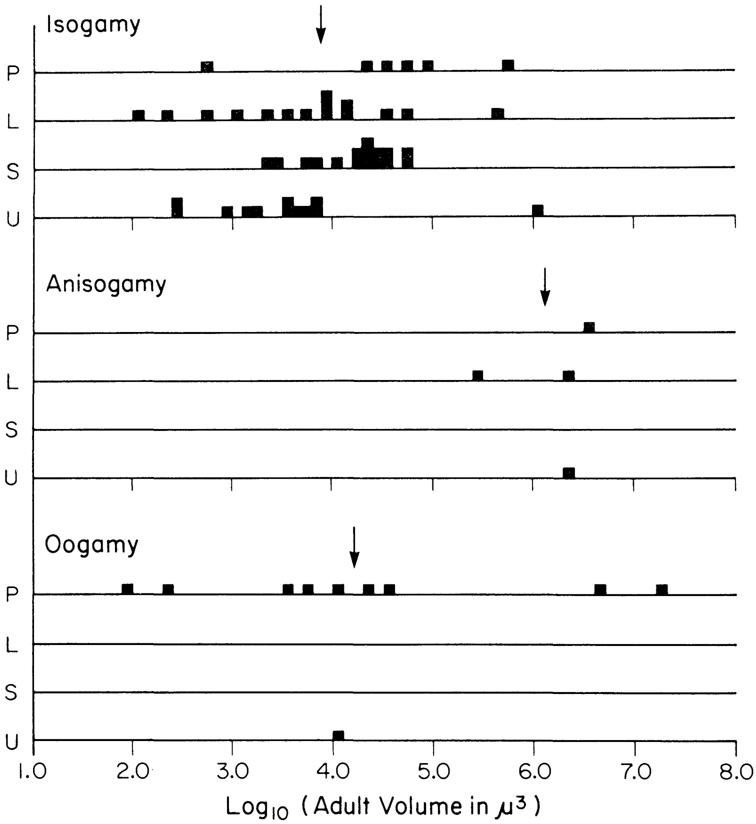

FIG. 1.—Distribution of adult cell volumes and habitat for 65 species of algae. Data derived from Bold and Wynne (1978) and Smith (1950) (see text). Habitats: P = Pools, L = Lakes, S = Soil, U = Unclassified. Arrow indicates mean adult cell volume.

pools or stressful environments rather than lakes. A discriminant analysis (not shown) confirmed this association and its statistical significance.

The correlation between the degree of gamete dimorphism and adult size includes effects resulting from increased adult volume in unicellular algae, such as *Eremosphaera viridis*, as well as increases in cell number, as in *Eudorina elegans* and *Volvox aureus*. Thus, the adult size hypothesis appears to be substantiated, especially for those algae whose zygote undergoes a genetically predetermined number of postmeiotic divisions. In such "coenobia," growth only occurs by cell enlargement after the initial cell divisions. A much larger zygote is obviously required for the 50,000 cell coenobium of *Volvox aureus* than for the four-celled coenobium of *Gonium sacculiferum*. The coenobic condition probably explains the regular agreement with the adult size hypothesis in the Volvocales. Algae which continue to divide after zygospore germination (e.g., *Cladophora*) rely more on photosynthesis than stored reserves to increase their cell number and may, therefore, not fit this hypothesis so well.

Two exceptions to the adult size hypothesis are *Chlamydomonas pseudo-*

TABLE 1

INCIDENCE OF GAMETIC CONDITION IN CONTRASTING ENVIRONMENTS

GAMETIC CONDITION	ENVIRONMENT	
	Pools	Lakes
Isogamy	10* *11.0*†	45 *49.5*
Anisogamy	4 *4.4*	13 *14.3*
Oogamy	15 *16.5*	4 *4.4*
Overall $\chi^2_{(2)} = 24.69$; $P < .001$		

* Count.
† Percent.

gigantea and *Golenkinia minutissima*. Both of these unicellular algae exhibit oogamy despite small total cell volume at maturity. Because they inhabit temporary pools or ponds, these species may reflect the demands of dormancy or a fast start.

The fast start hypothesis views the larger zygospore as a competitive adaptation to allow early germination and rapid growth through several cell divisions, traits that may improve the ability of a species to colonize new areas or outcompete other algae. This hypothesis, however, also applies to the coenobic and large unialgal species since a larger reserve in the zygote allows for faster growth or cell division in these species, too. A large zygote is also capable of producing a large number of swarm cells able to disperse and establish themselves, as in *Coleochaeta* which competes for epiphytic space in early spring by producing more than four meiospores upon zygote germination (Hopkins and McBride 1973; they also suggest that the zygote's elevated DNA levels may be an adaptation for the rapid production of many meiospores). Unfortunately, it is difficult to distinguish between the immediate needs of dormancy and the subsequent needs for a fast start or large adult size.

Just as habitat conditions and not adult stature have been found to be most predictive of seed size in higher plants (Salisbury 1942), ecological circumstances appear to exert a strong influence on the evolution of zygote, hence gamete, size. Large mature size most often accompanies anisogamy and oogamy in the unicellular and coenobic algae. For algae with other growth forms, and also in perhaps these first two groups, the unstable or harsh conditions may favor large zygotes capable of withstanding the rigors of dormancy and providing rapid, early growth. Although morphological complexity often accompanies increased gamete dimorphism, it does not reliably predict whether a species will display gamete dimorphism. Studies of zygospore survivorship and the speed of development in species with contrasting zygotic size, or of the energetic contribution of the zygote to the developing adult compared to energy inputs by photosynthesis, may illuminate the role of zygotic cytoplasmic supplies in dormancy and development. This would help determine whether a large zygote is an evolutionary adaptation to the immediate demands of dormancy or a fast start in a transient habitat rather than an alga's ultimate size.

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