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Life cycles and evolution of clonal (modular) animals

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Life cycles of clonal benthic animals are more complicated than those of aclonal species because there are more parameters to vary, and because an individual clone can grow in disconnected bits and pieces and widely different shapes. Consequently, the schedule of life-history events in clonal animals is as closely tied to their size as to their age. The bigger the animal the more likely it is to survive, and there is usually no limit to this advantage. Senescence is typically absent, or unmeasurable. Reproduction and recruitment of new individuals into local populations occurs by both sexually and asexually produced larvae, and by fragmentation. In general, asexual recruitment is more frequent. Larvae of clonal species are strongly philopatric whereas those of aclonal species are dispersed over considerable distances. These differences, and the high incidence of asexual reproduction, mean that parents, siblings, and clonemates may become mixed together within a small area. Under these conditions inbreeding is likely, and there is even evidence of selection for inbreeding in several clonal phyla. Nevertheless, clonal species tend to persist as long in the fossil record as do aclonal species. Thus the relative frequency of sexual reproduction among benthic animals, if not its incidence *per se*, would appear to have little or no macroevolutionary significance.

INTRODUCTION

Most animals are modular at one or more levels of organization (Beklemishev 1969). Cells are universal modules of multicellular animals. Likewise, the segments of tapeworms and polychaetes are modular organ systems, and the polyps of corals and zooids of bryozoan colonies are modular 'individuals'. A fundamental characteristic of such modular individuals, and one that distinguishes them from modules at lower levels of organization, is their usual ability to function, survive, and reproduce sexually alone or in small groups if separated from each other by injury or fission. Common examples are the fragmentation of staghorn corals (Tunncliffe 1981; Highsmith 1982), budding of hydras, or fission in sea anemones. This *clonal* replication of totipotent individuals has considerable ecological and evolutionary significance, as reflected in the striking differences that exist between the life histories of clonal and aclonal species.

In this paper we review four of the most important of these distinctions in life histories between clonal and aclonal animals, using as examples bottom-dwelling, aquatic animals such as sponges, hydroids, corals, bryozoans, and ascidians. These factors are: (i) complication and multidimensionality of life cycles; (ii) confounding of the relation between individual size and individual age; (iii) variations in the relative contributions of asexual and sexual reproduction of individuals in populations; and (iv) the tendency towards philopatric dispersal of sexual and asexual propagules. We then consider the implications of these factors for the genetic structure of clonal populations, and some of their evolutionary consequences. We have excluded

planktonic and terrestrial animals because we know less about them, and because we suspect that their clonal behaviour may have different evolutionary bases (cf. Bell 1982).

Terminology for clonal organisms is not standardized, so we will define ours briefly. We use the term individual to refer to one or more physically and physiologically interconnected modules, regardless of their genetic identity, which is usually unknown and is often unknowable in natural populations of clonal organisms. Thus an individual is an organism that can be counted. These are often called ramets or colonies and usually, but not always, the terms are synonymous. In contrast, a genetic individual, or genet, is the sum of all the individuals, usually but not always genetically identical, that are produced clonally from the same zygote. A genetic individual may be uniquely located in space, or spread out as many individuals over a considerable distance. Thus, operationally, genets are difficult things to study or count, and border on abstractions in our present ignorance of the population structure of most clonal animals. Notwithstanding these difficulties, however, and excepting potentially important somatic mutations within clonal individuals (Buss 1982, 1983), genets are the fundamental units of populations upon which natural selection acts. Compilation of accurate demographics of genets is essential to eventual understanding of the evolutionary bases of life-history variations in clonal animals.

MULTIDIMENSIONALITY OF LIFE CYCLES

Life cycles of benthic clonal animals are more complex than those of comparable aclonal animals because there are more kinds of features to vary, and thus more possible patterns of life history (Jackson 1977, 1979, 1985; Buss 1979; Hughes 1984; Caswell 1985; Jackson & Hughes 1985).

Numbers of individuals in a population can increase by asexual as well as sexual reproduction, either by injury or fission, and decrease by fusion of previously separated individuals as well as by death. Individual size can decrease markedly over time by fission or injury, stay constant, or increase by fusion or growth. This greatly complicates demographic studies of clonal organisms, although standard techniques, such as the population projection matrices of Leslie (1945), can be generalized to include them (Sarukhán & Gadgil 1974; Hughes 1984; Caswell 1985).

The shape or 'growth form' of a clonal animal depends on the spatial arrangement of its tissues or modular components just as in aclonal animals. The flexibility of these arrangements, however, is much greater in clonal animals. Different species in the same genus, different individuals of the same species, or sometimes even different individuals of the same genet can grow in arborescent, plating, massive, encrusting, or linear forms, depending on a variety of both intrinsic and extrinsic factors (Dustan 1979; Foster 1980; Willis & Ayre 1985).

Life histories of clonal animals vary in relation to their growth form, and the dynamics of their 'mobility' over the substratum due to growth, partial mortality, and passive dispersal of fragments (Buss 1979; Jackson 1979; Coates & Jackson 1985; Jackson & Hughes 1985). Clonal animals may be attached or free-living, the former usually on hard substrate and the latter on sediments or up in the water column. Among attached forms, animals differ in the ways modules (or masses of tissue in organisms like sponges that lack distinct modules) are arranged relative to each other (uniserial or multiserial) and in their primary directions of growth, which can be encrusting, massive, or erect.

Uniserial animals grow as single or loosely branching runners or vines that are highly directional forms adapted primarily for location of spatial refuges (Buss 1979; Jackson 1979). The probability that any module will die is high, but so also is the probability that some other modules will find a refuge and survive. In contrast, multiserial animals grow laterally as well as distally to form more or less continuous surfaces more likely to be able to persist on a given bit of substratum. Their survival is more dependent on maintenance of the genet as fewer, more highly integrated individuals occur than in uniserial forms. The probability that any module will die is relatively low, but so also are the chances of locating different habitats (refuges) by growth.

Encrusting growth on a stable substratum sets no special mechanical constraints for support, and so is potentially infinite, but at a cost of all the potentially harmful processes more likely to occur on the surface of the substratum than above it (Jackson 1979). Erect growth places stringent mechanical demands for support and attachment, but with the potential advantages of greater access to resources in the water, escape from risks on the substratum, and increase in surface area, feeding, and reproductive capacity beyond that possible on the bottom surface (Cheetham 1971; Cheetham & Thomsen 1981). Costs and benefits of massive growth are intermediate between encrusting and erect habits in all respects.

Quantitative relationships between growth forms and growth, maintenance, and reproduction have not been well established, but circumstantial evidence suggests different patterns of investment consistent with the above interpretations. For example, growth rate and larval recruitment both decrease with increasing massiveness of colonies of cheilostome bryozoans on Caribbean reefs. The growing tip of uniserial cheilostomes like *Aetea* sp. advances over the substratum as fast as 72 cm per year compared with about 3–11 cm per year for multiserial encrusters like *Steginoporella* and *Reptadeonella*, and only 1 or 2 cm per year for multilaminate encrusters like *Trematooecia* (Jackson & Hughes 1985; M. Gleason, unpublished data; J. B. C. Jackson and K. Kaufmann, unpublished data). Similarly, in Gleason's recent study of larval recruitment onto fouling panels placed on Venezuelan reefs, 590 *Aetea* settled onto six different sets of fouling panels within six weeks of submergence, as opposed to a total of only five recruits of the three multiserial genera combined.

Growth rate and recruitment also vary within and between growth forms of Caribbean reef corals (Hughes & Jackson 1985; Jackson & Hughes 1985; Hughes 1985). Massive encrusting corals like *Montastrea annularis* and brain corals extend their boundaries at about 1 cm per year and show very little larval recruitment (Bak & Engel 1979; Rylaarsdam 1983). Branching erect species like staghorn and elkhorn *Acropora* grow extremely fast, up to 20 cm per year, but unlike rapidly growing bryozoans they also show little larval recruitment (Adey 1978; Tunnicliffe 1981). Exclusively plating species, which represent a kind of intermediate morphology, have intermediate growth rates, and depending on the species, high or low rates of larval recruitment (Hughes & Jackson 1985). Of course, recruitment rates are not equivalent to reproductive effort, and many corals that show negligible recruitment produce enormous numbers of gametes, including *Montastrea annularis*, brain corals, and other large, massive species (Szmant-Froelich 1985a). What the cost of reproduction of these broadcasting species might be, compared with those with high recruitment, which typically brood large planula larvae, is unknown. In contrast, bryozoans that are common on reefs brood larvae that apparently recruit in numbers roughly proportional to their standing crop and production in the local population (Jackson & Wertheimer 1986; J. B. C. Jackson, unpublished data).

The relative 'mobility' of clones across and above the substratum is another important component of their life histories which varies considerably both within and between growth forms (Jackson & Hughes 1985). This is because mobility depends not only on growth rate, but also the continuous persistence of a clone in a particular place. Uniserial species like *Aetea* commonly fail to regenerate after injuries and grow extremely fast, so that they may appear in and disappear from an area within a month or less. *Steginoporella* is another highly mobile encrusting bryozoan. It grows fast and regenerates only within the younger regions of colonies, whereas older zooids senesce, so that the location of encrusted substratum changes entirely from one year to the next (Palumbi & Jackson 1982, 1983; Jackson & Hughes 1985). In contrast, slower growing encrusting species like *Reptadeonella* and *Trematoeocia* regenerate over their entire surfaces at rates at least as fast as they extend their margins. Erect branching staghorn coral *Acropora cervicornis* and plate-like *Leptoseris cucullata* also combine extremely rapid distal growth with failure to regenerate proximal tissues as in *Steginoporella*, whereas massive and plating *Montastrea annularis* regenerate rapidly everywhere on the colony (Hughes 1985).

Despite such striking differences in mobility and persistence, genets of all of the above species (except perhaps uniserial forms like *Aetea*) may live very long, up to decades or centuries for the bryozoans and for centuries to millenia for the corals as calculated from population projection matrices (cf. Hughes 1984). Over time they may come to dominate large areas of their habitats at the apparent expense of other bryozoans or corals. Furthermore, because of their potentially large size, these spatially dominant species may also invest more in reproduction than more ephemeral species, despite relatively late reproductive maturity and poor recruitment. On the other hand, the bryozoan *Membranipora membranacea*, which lives on ephemeral substrata like kelp in the temperate zone, combines the potential for early reproductive maturity and high recruitment rates with exceptionally rapid growth and strong ability to compete for space and ward off predators (Lutaud 1961; Bernstein & Jung 1979; Yoshioka 1982*a, b*; Harvell 1984). Concepts of *r*- and *K*-selected species, tenuous at best for asexual animals (Wilbur *et al.* 1974), tend to break down completely for clonal species which typically include in the same animal characteristics attributed to both opportunistic and specialist species.

This extensive variability does not mean, however, that all conceivable combinations of life-history traits exist among clonal animals, any more than they do among asexual forms. For example, we do not know of any uniserial species that can persist long in any one place through a combination of slow growth and strong resistance to competitors and predators. It is likely that the recognition of theoretical patterns that do not exist in Nature may eventually tell us more about the constraints acting on the evolution of clonal life histories than those that do.

SIZE, AGE AND SENESCENCE

Decrease in size due to injury, fragmentation, and fission, confound relationships between the size and age of individual clonal animals (Hughes & Jackson 1980, 1985; Highsmith 1982; Hughes 1984; Jackson & Hughes 1985). Chances of these events vary with time, size, and location of the animal. They also vary greatly between species, so that size is probably a good predictor of individual age in some clonal species, individuals of which are unlikely to regress or divide, and an extremely poor predictor for others. This is the basis for the confused relationship between individuals and genets; among species likely to undergo frequent division,

the genetic age of newly formed, small individuals in a population may vary by thousands of years.

As a result of such differences in positive and negative growth of individuals, their schedule of life-history events are often more closely tied to their size than to their age (Connell 1973; Hughes & Jackson 1980, 1985; Highsmith 1982; Jackson 1985; Jackson & Hughes 1985). Competitive ability; regenerative capacity; fecundity; and resistance to predators, catastrophic storms, and many diseases; all increase with individual size. The bigger the animal, the more likely it is to survive. Moreover, except for some forms of epidemic disease or geological catastrophes such as changes in sea level, there appears to be no real limit to this benefit of increasing size. Although we live in a period of exceptional environmental instability due to rapid fluctuations in sea level, there are still many examples of scleractinian reef corals 5–10 m in extent and almost certainly thousands of years old (Potts 1984; Potts *et al.* 1985; Hughes & Jackson 1985). In more stable times in the Earth's history, the potential for increase and dominance of local populations by a few genets of extraordinary age must have been far greater.

These observations suggest that reef corals do not senesce, and there is now much evidence to this effect for many other clonal animals (Palumbi & Jackson 1983; Jackson 1985). Individual modular elements of colonies such as hydrozoan polyps and polypides of bryozoans may degenerate permanently or undergo cycles of degeneration and regeneration that are often referred to as modular senescence, but the colonies typically persist. Likewise, the seasonal degeneration of individual sponges, hydrozoans, and bryozoans is usually accompanied by the production of some form of resistant mass that regenerates under more favourable conditions (Crowell 1953; Hartman 1958; Gordon 1977; Ryland 1979; Dyrinda & Ryland 1982; Frost *et al.* 1982). Although there are proven examples of semelparous species, especially among colonial ascidians (Grosberg 1982), few clonal individuals or genets seem to degenerate irreversibly with age, at least not to any measurable degree.

Two sorts of quantitative evidence support this view. First, there is no age-related decrease in physiological capacity among most clonal animals. Fecundity or the standing crop of reproductive products increases proportionally to surface area or numbers of polyps or zooids (Davis 1971; Hayward 1973; Sugimoto & Nakauchi 1974; Babcock 1984; Jackson & Wertheimer 1986; Szmant-Froelich 1985*b*). Similarly, growth rate as measured by the rate of linear extension, does not appear to vary with size or age except among very small individuals. This has been suggested for all clonal groups, and has been measured in the field for foliaceous corals (Hughes & Jackson 1985). In addition, although not specifically tested for, we know of no reports of decreased rates of regeneration of injured tissues as a function of size, except among small 'juvenile' individuals, from any of the myriad experimental investigations of regeneration by corals, gorgonians, bryozoans, sponges, and ascidians (see, for example, Bak *et al.* 1977; Palumbi & Jackson 1982, 1983; Wahle 1983*b*).

The second kind of evidence for lack of senescence comes from induced juvenilization of individuals by experimentally decreasing their size below threshold levels sufficient for reproduction (Wahle 1983*a*; Kojis & Quinn 1985; Szmant-Froelich 1985*b*). Small portions of large, reproductively mature colonies cease reproduction after isolation from the original 'parent' colonies which themselves continue to reproduce, as do isolates above the threshold size. In Szmant-Froelich's experiments, the parent colonies exceeded 2 m diameter and thus were minimally a century old, and probably much older (cf. Hughes & Jackson 1985). The small isolates from these retain their parental genetic age, but they came to behave reproductively like colonies less than three or four years old.

It would appear that reproductive value, in the sense of Fisher (1930), can increase indefinitely with increasing individual and genet size in clonal animals (Caswell 1985). The apparent absence of senescence in these organisms supports the idea that senescence evolves in response to age-specific rates of reproduction and mortality, rather than being an inevitable physiological necessity (Williams 1957; Bell 1984).

SEXUAL VERSUS ASEXUAL REPRODUCTION AND RECRUITMENT

Reproduction and recruitment, defined simply as the appearance of new individuals in a population, occur sexually via larvae, the only means available to asexual species. Asexually, they result from localized death of tissues, fragmentation, fission or budding, and asexual production of larvae. The relative contribution of these sexual versus asexual modes to recruitment of new individuals into populations of clonal animals ranges widely. In general, asexual processes appear to be far more successful.

Larval production and recruitment rates of clonal species vary from non-existent to very high values, especially among broadcasting species, but rarely approach those of asexual species (Jackson 1983, 1985). Recruits derived from larvae are so rare among many abundant clonal species as to be undetectable, even in quite intensive searches (Bak & Engel 1979; Tunnicliffe 1981, 1983; Rylaarsdam 1983; Szmant-Froelich 1985*a*). In some cases, as for *Pocillopora damicornis* in the eastern Pacific, reproduction involving larvae may not normally occur (Richmond 1985).

In contrast, recruitment of asexually derived colonies is common among most clonal species, although their origin tends to vary with growth form, material, design, and habitat (Glynn *et al.* 1972; Hughes & Jackson 1980, 1985; Jackson & Winston 1981; Woodley *et al.* 1981; Bothwell 1982; Highsmith 1982; Winston 1983; Lasker 1984; Benayahu & Loya 1984; Farrant 1985; Heyward & Collins 1985; Jackson 1985). This has been true throughout the Phanerozoic (Jackson 1983; McKinney 1983). Among sessile species, fragmentation is the most common mechanism of propagation among branching species, whereas more massive organisms are more likely to divide through localized partial mortality (Highsmith 1982; Done & Fisk 1986; Hughes & Jackson 1985). Asexual production is typically most prolific for branching species, but even among encrusting and massive forms it commonly exceeds input from larvae. Budding and fission are most common among free-living animals like sea anemones, fungiid corals, and lunulitiform bryozoans (Marcus & Marcus 1962; Goreau & Yonge 1968; Francis 1973, 1979; Sebens 1982; Cook & Chimonides 1983).

Electrophoretic analysis suggests that asexual production of larvae is common among anthozoan cnidarians (Black & Johnson 1979; Stoddart 1983; Ayre 1984; Ayre & Resing 1986; Stoddart & Black 1985). This conclusion is based on studies of several species whose larvae are consistently genetically identical to their brood-parents, even at polymorphic loci. In contrast, larvae of other species regularly show non-parental genotypes consistent with expectations of sexual reproduction. These results raise questions of interpretation concerning gametogenesis and sexuality based solely on descriptive histological techniques in all other invertebrates for which fertilization has not actually been observed. Asexual production of larval-like individuals also commonly results from production of buds and gemmules in sponges, hibernaculæ in bryozoans, and 'polyp bail-out' in corals (Ryland 1970; Bergquist 1978; Ayling 1970; Sammarco 1982; Richmond 1986).

DISPERSAL AND GENETIC COMPOSITION OF LOCAL POPULATIONS

One of the most striking features of clonal benthic animals is their characteristically short-distance (that is, philopatric) dispersal of both sexual and asexual propagules compared with aclonal species (Ryland 1981; Jackson 1985, 1986).

Both clonal and aclonal sea anemones may be transported tens to hundreds of metres by currents (Mackie 1974; Shick *et al.* 1979; Ayre 1984), and passive dispersal of sponges and corals or their fragments may take place over distances of 10–50 m during storms. Such dispersal has actually been observed for *Acropora cervicornis* and labelled rope-like sponges (Woodley *et al.* 1981; Wulff 1985). Comparable dispersal has also been inferred by mapping clonal boundaries by using tissue grafting (Bothwell 1982; Neigel & Avise 1983*a,b*; Hunter 1986) and by electrophoresis (Ayre 1984; Stoddart 1984*a, b*; Willis & Ayre 1985). Grafting is not entirely reliable in distinguishing genetically different clones (Curtis *et al.* 1982; Ayre & Resing 1986; Stoddart *et al.* 1985). Nevertheless, considerable evidence suggests that clonal dispersal of fragments up to 50 m or more is common on reefs over a few years time. The only limits to the process are inhospitable areas too broad for fragments to traverse in a single episode of dispersal (Ayre 1984).

All clonal ascidians, all but about 30 species of bryozoan, most sponges, hydrozoans, and octocorals, and an appreciable minority of clonal corals produce brooded, short-lived larvae that disperse much shorter distances than larvae of aclonal animals (Knight-Jones & Moyses 1961; Kott 1974; Ryland 1981; Jackson 1985, 1986). Many, perhaps most, of these brooded larvae are capable of settlement within minutes or seconds of their release from their parents, even though they commonly swim for much longer periods when confined in containers in the laboratory. The best data are Olson's (1985) for the clonal ascidian *Didemnum molle*. He managed to follow 14 larvae *in situ*, from release to settlement, all of which settled within 40–370 s of their release and within 2–12 m of their parents.

In addition to this general pattern, the great majority of species with *extremely* short-distance dispersal, often by benthic larvae that crawl less than 1 m from their brood parent, are clonal. Examples include demosponges (Ayling 1980), hydroids (Pyefinch & Downing 1949; Nishihira 1967; Williams 1965, 1976; Hughes 1977), hydrocorals (Ostarello 1970), scleractinians (Lewis 1974), alcyonaceans (Sebens 1983; Benayahu & Loya 1984; Benayahu 1986, personal communication; Farrant 1985), cyclostome bryozoans (C. McFadden, personal communication), and ascidians (van Duyl *et al.* 1981; R. Grosberg, personal communication). Brooded larvae of many aclonal species also disperse very short distances, but these are mostly very small or free-living animals (Gerodette 1981; Fadlallah & Pearse 1982*a*; Strathmann & Strathmann 1982). In contrast, the great majority of species with extremely long-lived (teleplanic) larvae are aclonal (Eckelbarger 1978; Scheltema 1971; Fadlallah & Pearse 1982*b*; Tranter *et al.* 1982; Scheltema & Williams 1983).

The most glaring exception to the pattern of philopatric larval dispersal by clonal animals is that of scleractinian reef-building corals, particularly in Australia where about two-thirds of all the species on the Great Barrier Reef synchronously broadcast gametes during one to three nights per year (Harrison *et al.* 1984). Even there, however, the proportion of brooding species with potentially short-distance dispersal is much higher than for major groups of associated aclonal animals like bivalves, barnacles, or echinoderms.

Frequent asexual reproduction by fragmentation and injury, asexual production of larvae,

and the retention of the products of sexual and asexual reproduction near their site of origin should all promote a high degree of genetic relatedness in many clonal populations. Thus parents, siblings, and clonemates may all be mixed together within small areas. Patterns consistent with this view have been demonstrated by electrophoretic analyses of populations of an anemone (Ayre 1984), coral (Stoddart 1984*a, b*), bryozoan (Gooch & Schopf 1971), and ascidian (Sabbadin 1978). Moreover, to the extent that fertilization occurs among neighbouring individuals that have a high probability of being clonemates or relatives, considerable inbreeding must also occur. The fact that their progeny are likely to settle nearby will contribute to the process even more with every passing generation.

Various observations suggest that high levels of relatedness in clonal populations, and perhaps also the occurrence of inbreeding, are not just an accidental consequence of short-distance dispersal, but the result of natural selection for these characteristics (Jackson 1986). The evidence, most of which is circumstantial and equivocal, includes: evolution of decreased potential for larval dispersal among hydroids (Hyman 1940; Ryland 1981; Boero 1984), gymnolaemate bryozoans (Zimmer & Woollacott 1977), and clonal ascidians (Kott 1974); polyembryony in cyclostomes (Harmer 1893); spontaneous tissue degeneration and localized constrictions in the branches of gorgonians that suggest they are 'designed' to fragment (Lasker 1984), and sibling gregariousness of larvae at settlement (Keough 1984; R. Grosberg, personal communication). Of these, sibling gregariousness is the most important because it is a specific behaviour that has evolved polyphyletically (bryozoans and ascidians) and independently of the distance of larval dispersal, or of any simple predisposition for asexual reproduction.

EVOLUTIONARY BASIS FOR SHORT-DISTANCE DISPERSAL

There are at least three possible kinds of evolutionary explanations for widespread philopatry among clonal animals, none of which are mutually exclusive. These concern theories of sexuality as an individual adaptation (Williams 1975; Maynard-Smith 1978), costs and benefits of forming chimeras (L. Buss and R. Grosberg, personal communication), and consequences of inbreeding (Shields 1982).

According to the strawberry-coral model, the cost of meiosis is offset by sexual production of very large numbers of genetically diverse propagules that are widely dispersed, thereby maximizing chances that some offspring will find and succeed in some other location (Williams 1975). These predictions describe well the characteristics of most aclonal animals like oysters and barnacles. They do not, however, describe most clonal animals which, on the contrary, tend to produce relatively few sexually derived propagules that commonly disperse quite short distances.

It is important to note, however, that among these contradictions to the strawberry-coral model, the probable-proximity of siblings due to philopatry actually increases the probability that one of the most important assumptions in all of Williams' models for the explanation of sex as an individual adaptation is met, namely that of intense competition among sibling recruits to a local population (Williams & Mitton 1973). Moreover, among clonal animals living on hard substrata, environments change greatly over short distances due to heterogeneities in distributions of potential competitors for space, as well as other factors (Jackson 1977, 1979; Sebens & Thorne 1985), so that wide dispersal should not be necessary to encounter 'new' environments where the parental genotype is no longer optimal. There is, however, little

evidence for sibling competition among postlarvae of clonal species which usually settle in low densities, and are more likely to suffer in conflicts with preexisting adults (Jackson 1977, 1979). On the other hand, the evidence I have presented here suggests that these adults could also be siblings. In short, Williams' arguments may be right for clonal animals, but only because their life histories differ in every important respect from those he assumed in the strawberry-coral model.

The most interesting aspect of the life histories of clonal animals is unquestionably the widespread retention of sexuality, with its potential 50% loss in fitness due to the 'cost of meiosis', when the sexual propagules are dispersed over such short distances. Moreover, the evolutionary trend has been to decrease the dispersal distance of sexual propagules, even though similar propagules can be produced asexually that disperse comparably short distances. This pattern is not a taxonomic artefact; it has evolved many times in many clonal clades, and thus must be adaptive. Exceptions like the majority of reef corals do not change this, but simply require an alternative explanation. Indeed, Australian corals seem to fit certain aspects of the strawberry-coral model quite nicely. Catastrophic mortality due to epidemic outbreaks of the coralivorous starfish *Acanthaster planci* or bleaching of tissues (possibly due to epidemic disease?) occur in a complex mosaic pattern all along the Great Barrier Reef every decade or so (Bradbury *et al.* 1985; Done & Fisk 1986). Production of vast numbers of gametes and larvae allows exploitation of distant refuges, although contrary to Williams' view, this could occur as easily by larvae derived from parthenogenetic as from fertilized eggs. The proportion of investment in sexual versus asexual dispersal should depend on the commonness or rarity of the parental habitat elsewhere (Hamilton & May 1977); if it is predictably and commonly distributed, asexual dispersal may be favoured.

An entirely different kind of explanation for philopatric sexual dispersal by clonal animals is related to postlarval fusion, a process that results in sudden size increase, and thus may increase survival at this vulnerable stage. Philopatry could decrease the potential genetic costs of fusion by helping to keep siblings together (Buss 1982, 1983; Buss *et al.* 1985). Fusion by postlarvae of most clonal groups has been observed in the laboratory (Duerden 1902; Boschma 1929; Stephenson 1931; Schijffsma 1935, 1939; Edmundson 1946; Knight-Jones & Moyses 1961; Harrigan 1972; Sabbadin 1978), often in cases where the participants were known to be siblings, or as we now realize, perhaps, clonemates (Stoddart 1983). The fusion hypothesis needs support from observations of postlarval fusion in the field. If this is common, it may also help to explain widespread fusion of allografts in grafting studies.

Another hypothesis is that philopatry is an adaptation to promote inbreeding as the means of reproduction that best duplicates genotypes over many generations, minimizing as it does the negative effects of both Muller's ratchet and the cost of meiosis (Shields 1982). Shields predicted that the advantages of inbreeding should be greatest for long-lived organisms with low fecundity living in stable environments, all characteristics of most clonal animals (Jackson 1977, 1985). The fit seems good and deserves investigation.

BIOGEOGRAPHY AND EVOLUTION

Philopatry, inbreeding, and asexual reproduction should severely restrict gene flow between local populations, and thus increase chances of evolutionary adaptation to local environmental conditions and of speciation among clonal animals. Genetic and morphological differentiation consistent with this prediction have been observed for the cheilostome bryozoan *Schizoporella*

errata sampled over a distance of 102 km along the southern shore of Cape Cod (Schopf & Dutton 1976). Significant morphological and genetic changes occur over distances as little as 11–13 km, a result consistent with the very short larval life of this species. In contrast to this pattern, however, between 80 and 89% of the electrophoretically sampled genome in this species is identical over a distance of 1000 km along the eastern coast of North America, including the Cape Cod region (Gooch & Schopf 1971). This relative homogeneity on a broad regional scale, in the face of marked local differentiation of populations, suggests some mode of dispersal must be acting other than the larval stage.

The sea anemone *Actinia tenebrosa* and coral *Pocillopora damicornis* also exhibit significant genetic differentiation of local populations consistent both with clonal proliferation and short-distance dispersal by larvae (Ayre 1984; Stoddart 1984*a, b*). However, these species of anemone presumably differ from *Schizoporella* in their asexual production of larvae, despite routine production of sperm and eggs (we say presumably because *Schizoporella* has not been examined for this). Although sexually produced larvae have not been observed in either species, their existence was inferred from high levels of variation observed by pooling local populations, existence of unique heterozygous genotypes, and the concordance of pooled clonal populations to Hardy–Weinberg expectations. Moreover, both authors have assumed that these presumed sexual propagules are the agents of long-distance dispersal and gene flow in these species. However, as pointed out by Ayre (1984), this latter assumption would be invalid if asexual propagules were found to disperse between local populations, and at least for *Pocillopora damicornis* there is strong evidence that this is true.

There is no evidence for or against intense local selection in any of these three species.

What is called *Pocillopora damicornis* is almost certainly a complex of species (Richmond 1986, personal communication). Local populations in southwestern Australia differ considerably in allelic frequencies over distances of a few kilometres (Stoddart 1984*b*), and populations in Enewetak, Hawaii and Panama differ strikingly in all life-history characteristics measured (Richmond 1986). These differences suggest considerable potential for allopatric speciation, as is supported by existence of reproductively isolated ‘morphs’ in the eastern Pacific (Richmond 1985, personal communication). On the other hand, this species is the most commonly rafted coral in the Pacific, occurring commonly on drifting pumice (Jokiel 1984), and it possesses a larva that is at least theoretically competent to survive the journey across the eastern Pacific barrier (Richmond 1982, 1986).

The examples of *Schizoporella* and *Pocillopora* are instructive for calling into question the kinds of assumptions that are commonly made regarding larval life and species distributions. In fact, there is no correlation between the presumed length of larval life and the geographic ranges of clonal species, including corals, bryozoans, and colonial ascidians (Kott 1974; Jackson *et al.* 1985; Jackson 1986). Species of clonal animals are, on average, distributed at least as widely as asexual animals with long-lived planktonic larvae like barnacles and molluscs. The only explanation is dispersal of the normally sessile stage by some process such as rafting, as observed for *Pocillopora damicornis* (Jokiel 1984). Indeed, the primary role of larvae in promoting long-distance dispersal of clonal animals may be to get them onto and off rafts, although this might also occur simply by growth and fragmentation (many potential rafts like kelps and mats of sea grasses break away from the bottom after they have been colonized (Gerodette 1981; R. C. Highsmith, unpublished). In such cases, or in those in which larvae are produced asexually, the distributions of single clones may be enormous. Many genets of *Pocillopora damicornis* are probably alive today on both sides of the Pacific Ocean.

MACROEVOLUTION

Two theories predict that the chances of speciation should be different for clonal and aclonal animals. The first derives from Stanley's (1975) observation that speciation is more likely to occur in sexual clades than in asexual clones, and Chapman's (1981) prediction that the probability of evolutionary divergence and speciation should increase with increasing potential for genetic recombination. The second theory relates the probability of speciation to generation time (Potts 1984). By this model, generation times of clonal animals like corals are so long as to approach the average intervals between catastrophic environmental change, so that processes leading to speciation and extinction cannot go to completion.

Species durations are, on average, a function of the probability of speciation and the probability of extinction. If the standing crop of species stays constant, high probability of speciation implies high probability of extinction, and thus short average durations of species. Likewise, if the standing crop of species is constant, low probability of speciation implies low probability of extinction, and thus long species durations. Thus both the Stanley–Chapman and Potts theories suggest that species durations should be longer for clonal species than for aclonal species.

We tested these predictions by examining the durations of 1381 species of scleractinian corals as compiled from 128 monographic publications of faunas ranging in age from mid-Triassic to Pleistocene. Holocene and Recent faunas were excluded to avoid biases due to presumably artificially short durations of unpreserved modern taxa (cf. Stanley 1979). (References to sources are available from A.G.C.) They cover a wide range of places and times, but inevitably over-represent American and Indo-European faunas compared with other less studied regions. Many published data were checked by reference to major museum collections, and obvious duplications were eliminated by using available synonymies, but no taxonomic revisions were attempted. There seems no reason to believe that the inevitable biases inherent in such a data set should be different for clonal or aclonal species.

All corals were classified as clonal if there was any evidence for budding or fragmentation of polyps, and as aclonal if there was not. Both species diversity and the relative proportions of clonal and aclonal corals have varied considerably since the Triassic, but without any consistent long-term trends (Coates & Jackson 1985). Data are present in table 1. The mean duration of clonal species is slightly but not significantly greater than that of aclonal species ($t = 2.00$, $p = 0.16$), despite the enormous sample size for both groups.

TABLE 1. MEAN SPECIES DURATIONS IN MILLIONS OF YEARS FOR CLONAL AND ACLONAL SCLERACTINIAN CORALS

	number of species	mean duration	standard deviation
aclonal corals	376	9.06	5.51
clonal corals	1005	9.57	6.06

The corals were also classified by growth form (Coates & Jackson 1985), and their mean species duration compared by analysis of variance (table 2). Differences are highly significant ($F = 3.34$, $p = 0.001$); erect clonal species have evolved faster than all other growth forms, especially massive clonal species. Thus, to the extent that erect growth forms are more specialized than others (cf. Cheetham 1971; Cheetham & Thomsen 1981), table 2 suggests that

TABLE 2. MEAN SPECIES DURATIONS IN MILLIONS OF YEARS FOR DIFFERENT GROWTH FORMS OF SCLERACTINIAN CORALS

growth form	number of species	mean duration	standard deviation
solitary aclonal	376	9.06	5.51
solitary clonal	15	9.53	5.15
pseudocolonial	157	9.21	5.40
massive	645	10.00	6.02
erect	188	8.40	6.63

more specialized species evolve more rapidly than less specialized species, whether clonal or not.

These data do not exclude the possibility that clonality influences evolutionary durations of coral species. However, they do demonstrate that should such an effect occur, it is of much smaller extent than those due to variations in life-history features or some other factors related to growth form. This should not be surprising, because the relative proportions of clonal and aclonal taxa have not obviously changed on the sea floor throughout the Phanerozoic (Jackson 1983).

N. Knowlton showed us that G. Williams was more likely to be right about clonal animals because the strawberry-coral model was wrong, and helped in many other ways. Discussions with L. W. Buss, T. P. Hughes, and S. Lidgard were important to the development of many of the ideas presented here.

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