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## Why Life Histories Evolve Differently in the Sea<sup>1</sup>

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**SYNOPSIS.** Marine life histories differ from terrestrial life histories because seawater is denser and more viscous than air, because desiccation is not a problem for organisms in water, and because food is abundant in suspension and solution. (1) Mating and competition for paternity in the sea often differs. Female gametes are often spawned freely. Passively dispersed spermatophores could in some cases provide single paternity to an entire clutch of offspring. Penises of sessile animals reach far for copulation. There are no pollinators. (2) In many clades of benthic marine animals, greater dispersal of offspring is associated with large adult size, and greater parental care of offspring and reduced planktonic larval periods are associated with small adult size. (3) Many benthic marine animals are colonies with modular construction, and these also commonly brood embryos and have short-lived larvae, in contrast to related solitary forms. (4) Unlike dispersal of terrestrial animals, larval dispersal of marine animals is often obligate with sexual reproduction and often includes a precompetent period during which larvae cannot settle at good sites. Unlike terrestrial seeds, marine larvae have no clear adaptations for dispersal, often grow during dispersal, and often leave bad sites. Feeding planktonic larvae are common among marine animals and rare among other aquatic animals, perhaps because of persistent aquatic routes between habitable sites for marine animals. Peculiarities in marine life histories may influence many aspects of evolution in the sea. Closely related sedentary marine animals can differ greatly in larval dispersal with consequences for recruitment to populations, genetic exchange between benthic populations, adaptation to local conditions, sex allocation, interaction with kin, speciation, and extinction.

### INTRODUCTION

Do life history traits of aquatic animals differ from those of terrestrial animals or plants? Do the differences result from physical differences between water and air? Do the differences have interesting evolutionary consequences? I will argue that the answer to all three questions is yes. For this purpose I will consider traits common among marine animals with benthic adults in contrast to traits common among terrestrial animals or terrestrial plants. I will ignore parasites and unicellular organisms. Non-marine aquatic environments present some special features that will be briefly mentioned separately.

Contrasting benthic marine animals with both terrestrial animals and terrestrial plants is not arbitrary. Predictions on life histories often arise from research on terrestrial animals and plants and are then applied to benthic marine animals. Results

of research on terrestrial animals (usually mobile) and terrestrial plants (usually sessile) often do apply to benthic marine animals, but we can be misled when we ignore differences between land and sea. This essay explores some life history traits that are common among marine animals with benthic adults but are rare or absent among the closest terrestrial analogues, whether animal or plant.

I hope my generalizations will be read critically. Because of my limited knowledge of life on land, I may have exaggerated or overlooked differences between marine and terrestrial life histories. There may be terrestrial life history traits that closely resemble traits that I believed to be peculiarly aquatic, and I expect there to be important differences between terrestrial and aquatic life histories that I have missed.

### PHYSICAL DIFFERENCES BETWEEN AIR AND WATER

A few physical differences between water and air underly several differences between aquatic and terrestrial organisms. The density of sea water is more than 800 times the density of air, a difference resulting in

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<sup>1</sup> From the Symposium on *Concepts of Adaptation in Aquatic Animals: Deviations from the Terrestrial Paradigm* presented at the Annual Meeting of the American Society of Zoologists, 27-30 December 1988, at San Francisco, California.

TABLE 1. Comparison of approximate values for air (at 1 atm) and sea water at 20°C.\*

	Density g·cm <sup>-3</sup>	Viscosity g·cm <sup>-1</sup> ·sec <sup>-1</sup>	Diffusion constant for O <sub>2</sub> cm <sup>2</sup> ·sec <sup>-1</sup>
Sea water	1.02	$1.1 \times 10^{-2}$	$2 \times 10^{-5}$
Air	$1.20 \times 10^{-3}$	$1.8 \times 10^{-4}$	$2 \times 10^{-1}$
Water/air	850	60	1/10,000

\* The values are approximate and are from Sverdrup *et al.* (1942), Gray (1957), and Prosser and Brown (1961).

greater buoyancy for aquatic organisms. The viscosity of sea water is about 60 times the viscosity of air (Table 1), a difference resulting in much slower sinking rates for organisms. Desiccation is not a problem in water but often a problem in air. Water carries an abundance of dissolved and particulate materials in solution and suspension, so that abundant nutrients are accessible to small suspended organisms in water. Small suspended organisms in air do not have this access to nutrients.

#### SOME CONSEQUENCES OF DIFFERENCES IN PHYSICAL PROPERTIES

The differences in physical properties make water a much more favorable medium than air for small planktonic organisms, and this has caused several peculiarities of aquatic animals that affect life history evolution.

Small stages in the life histories of aquatic animals are often planktonic. This includes gametes, embryos, and larvae of otherwise benthic animals. Sinking and desiccation are not problems in water and are problems in air.

Planktonic larval stages have the evolutionary option of feeding on smaller planktonic organisms. This is not an option in air, where suspended organic material is less concentrated.

Abundant suspended food in water has also affected postlarval traits. Large stages in the life histories of aquatic animals are often sessile suspension feeders, a rare condition for animals on land. Many suspension feeders are colonial forms that consist of many joined repeats of a body plan; this modular form of construction is unusual

among terrestrial animals though common for terrestrial plants.

Thus water directly and indirectly favors both planktonic and sessile habits to a much greater extent than does air and thereby produces different conditions for mating and dispersal.

There is another physical difference between water and air that may encourage the scattering of small aquatic offspring. The diffusion constant of oxygen and many other molecules in air is about 10,000 times the diffusion constant in water (Table 1). Although desiccation of a mass of embryos can be a problem in air, diffusive supply of oxygen into a mass of embryos should be much more rapid in air. Interstitial flow through a mass of embryos is also retarded in water because of higher viscosity. The lower diffusion constant in water and higher viscosity of water may limit parental protection of benthic clutches of embryos and thereby reinforce the evolution of planktonic embryos and larvae.

These differences in physical properties of air and water are not the only differences that might underly different evolution of life histories, but they are major ones. The following discussion examines effects of these differences on mating, parental protection, dispersal, and their evolutionary consequences.

#### MATING

The most striking difference between aquatic and terrestrial mating is that aquatic organisms commonly shed female gametes as well as male gametes. Terrestrial organisms retain female gametes on or in their bodies. However, the evolutionary consequences of shedding female gametes are not so striking. When female gametes are shed, sexual dimorphism is minimal and male and female gonads are nearly equal in size, but many terrestrial animals also show little sexual dimorphism despite copulation or transfer of spermatophores. Multiple paternity is another likely consequence of shedding female gametes, but wind-pollinated plants must be at least as open to multiple paternity (for example, Schoen and Stewart, 1986). Although

shedding of female gametes is distinctively aquatic, distinctively aquatic evolutionary consequences are not yet proven.

Dilution of gametes may have consequences that are not yet recognized. Though water is a benign medium for gametes, external fertilization is by no means easy. There is no evidence that dispersal of gametes in the sea exceeds dispersal of pollen on land. Fertilization by distant males and females is limited by the life span of active sperm, predation on gametes, and dilution of gametes with dilution probably the greatest obstacle. Pennington (1985) found rapid decreases in capacity for fertilization downstream from spawning male sea urchins. In his assay, percent fertilization decreased to about 20% at 1 m downstream from a single spawning male even in a slow current. His simple field experiment suggests that time and place of free spawning is important in achieving paternity. Denny (1988) reached similar conclusions with a diffusion model and laboratory data. Levitan (1988) argues that for some free-spawners the high fertilization success in crowded populations offsets the reduced fecundity from resource limitation. Under Levitan's hypothesis, it seems possible that a female that sought crowded conditions that limited her size and fecundity could leave more offspring. Even in less extreme circumstances, a female would do well to wait until there is much sperm in the water, and this confronts males with strategic problems that are not well understood. In many species, females are induced to spawn by spawning males; a male that spawns with other males may therefore be more likely to put his sperm where the ova are, but he also encounters greater competition from other sperm. Though the situation resembles some group mating displays by terrestrial males, one would expect there to be less female choice, more opportunity for multiple paternity of a clutch, and less pre-mating competition among males.

Given the difficulties of ensuring contact between sperm and ovum in suspension, it is not surprising that a number of devices for bringing sperm to ova have evolved.

Paired mating by copulation, spermatophores, or simply paired free-spawning has evolved many times in marine animals. Some aquatic sperm transfer resembles terrestrial sperm transfer, but many aquatic animals are sedentary or completely sessile, and for these sperm transfer presents unusual problems that have been met with curious solutions, not fully analogous with either pollen transfer in terrestrial plants or sperm transfer by terrestrial animals.

One solution to the problem of sperm transfer is the water born spermatophore. Water born spermatophores are common among sessile suspension feeders, presumably because suspension feeding sessile animals cannot move to mate but are well equipped to intercept objects from a large volume of water (Hadfield and Hopper, 1980). Examples of the independent evolution of spermatophores in animals of this type include some oysters (Coe, 1931), pogonophorans (Webb, 1963), phoronids (Zimmer, 1967), vermetid gastropods (Hadfield and Hopper, 1980), and spionid polychaetes (Rice, 1980).

Terrestrial organisms have spermatophores, but methods of transfer are different even in the closest analogues to water dispersed spermatophores. Some plants, such as milkweeds (Bookman, 1981), package many pollen grains into pollinia, but these are transferred by insects. To my knowledge, windborn pollen grains are not combined in large packets. Some arachnids (Thomas and Zeh, 1984) and amphibians (Halliday and Verrell, 1984) deposit spermatophores on the ground, but transfer depends on motility of females, and this mode of transfer depends on moist habitats.

Water born spermatophores of solitary benthic animals potentially could combine passive dispersal of spermatophores with single paternity for a clutch of eggs. Single paternity of clutches fertilized by water born spermatophores is not inevitable, however. In the vermetid gastropod *Serpulorbis squamigerus*, the males produce sperm over a longer period than the females produce eggs; the females store sperm; and the females might therefore store sperm

TABLE 2. *Some distinctively aquatic types of mating.*

Type of mating	Aquatic	Terrestrial
Female gametes shed	common	absent
Passively dispersed spermatophores with potential for single paternity	common	absent?
Sessile copulators	common	rare
By pollinators	absent	common

from several spermatophores (Hadfield, 1967). Nevertheless, single paternity appears to be likely in some other benthic marine animals with spermatophores, and the combination of single paternity for an entire clutch and passive dispersal of male gametes by the ambient fluid may be common in water for animals though rare or absent on land for both animals and plants.

Most thoracican barnacles are outcrossing hermaphrodites whose penises can reach farther than their body length. Optimal male allocation involves not only density of neighbors (Charnov, 1987) but potentially such factors as risk of losing a penis to a predator. What is unusual in barnacles is the combination of a plant-like sessile habit with the active copulation of animals.

Given the sessile habit of many marine animals and plants and the difficulties in mating with distant neighbors, it is surprising that there are no known marine analogues of pollinators. There are two obvious hypotheses for the absence of marine pollinators but neither has been investigated. (1) For a given added investment in energy or materials, passive dispersal of more gametes may provide more fertilizations than a reward for pollinators that carry male gametes. Water is a more favorable medium than air for passive transport of male gametes. Also if prospective pollinators have access to better alternative sources of food in aquatic habitats than in terrestrial habitats, higher rewards to pollinators might be required in aquatic habitats (as suggested by L. Hickey, personal communication). (2) Costs to pollinators might be greater in water so that the necessary rewards might be greater in water than in air. Costs of locomotion or risks during a search may not be espe-

cially severe in water, but visibility is poor in many waters and may limit the effectiveness of offering advertised rewards to pollinators.

In summary, release of female gametes before fertilization, passive dispersal of spermatophores capable of fertilizing all ova of a female, and copulation between sessile organisms are common traits for aquatic animals but rare among terrestrial animals and plants (Table 2). Transfer of male gametes by an animal that receives a reward is common among terrestrial plants but absent among marine organisms.

#### PARENTAL INVESTMENT PER OFFSPRING

To my knowledge, minimal parental investment per offspring is generally lower for free-living aquatic animals than for free-living terrestrial animals or terrestrial plants with seeds. Propagule sizes between 50 and 100  $\mu\text{m}$  occur among bivalves, opisthobranchs, polychaetes, ectoprocts, phoronids, and echinoids that begin feeding as larvae (Silén, 1954; Strathmann and Vedder, 1977; Emler *et al.*, 1987; McEdward and Strathmann, 1987). The energy content of eggs less than 100  $\mu\text{m}$  in diameter has been estimated to be about 0.003 joules of energy or less for some of these animals. The data tabulated by Anderson (1972) suggest that free-living terrestrial insects have eggs larger than 100  $\mu\text{m}$  in smallest dimension, and this seems to be the rule for most externally deposited eggs of free-living terrestrial animals whose adults are several millimeters or more in length. (Minute metazoans tend to have small eggs wherever they live.) When minimum parental investment per offspring is lower, maximum fecundity per reproductive allocation is higher. Fecundities exceeding  $10^7$  are common among free-living aquatic animals but uncommon for terrestrial animals.

When we include plants, however, the aquatic-terrestrial contrast is not so great. Plant spores, whether terrestrial or aquatic, can be much smaller than propagules of free-living animals. Fungi release propagules to the air that are on the order of 10  $\mu\text{m}$  diameter (Ingold, 1971) and thus orders of magnitude smaller in volume or weight

TABLE 3. *Differences between marine and terrestrial dispersal.*

Characteristics of dispersal	Marine larvae	Terrestrial animals
Obligate with reproduction	common	rare
Fortuitous consequence of feeding larvae or shed ova	common	absent or rare
Must pass good sites without settling	common	rare?
Characteristics of dispersal	Marine larvae	Terrestrial seeds
Propagule adapted for dispersal	no?	common
Growth during dispersal	common	no
Actively leaves bad substrata	common	no

than any propagules released into the water by aquatic animals. Seeds of vascular plants tend to be larger than freely spawned eggs of aquatic animals, though the smallest seeds of orchids and some other vascular plants with saprophytic germlings are reduced to a little more than 100  $\mu\text{m}$  in size (Salisbury, 1942; Ingold, 1971; Harper, 1977).

Several factors could contribute to the generally larger sizes of propagules for free-living animals in air. The abundance of small food in water permits initiation of feeding at minute sizes and desiccation is not a problem. However, the problem of desiccation is avoided by many aerial propagules that remain in a dry and inactive phase until they encounter a moist site. The advantages of minimizing parental investment per offspring are obvious; more offspring can be produced. The limits on low parental investment per offspring are less obvious because they are affected by numerous factors: risks from predators, competitors, and the physical environment on the one hand and methods of nutrient uptake and rates of growth of offspring on the other.

#### ADULT SIZE AND BROODING

For many taxa of aquatic animals, species with small adults are commonly brooders with embryos held on or in the adult body, but in species with larger adults, there is no care for offspring or offspring are released at an earlier stage (Table 4). The trend can be found within a class or even within a genus. Not all taxa of aquatic animals show this trend. It is unreported and unapparent in crustaceans. I know of only one report of the opposite trend: among

gastropods of the genus *Margarites* in the North Pacific a species with the largest adults is an umbilical brooder (Lindberg and Dobertein, 1981). Thus brooding is size dependent in many taxa of aquatic animals, and the smaller adults provide protection to more advanced stages. A result of size-dependent brooding is that dispersal of embryos and larvae of closely related aquatic animals can range from none to tens of kilometers. I have found no reference to decreased parental care by larger adults in terrestrial organisms and provisionally conclude that this pattern is rare or absent in air. I also know of no analogy to this trend in either terrestrial or aquatic plants.

There are several possible reasons for the association of large adult size with less brooding in aquatic animals (Strathmann and Strathmann, 1982). Only one of these hypotheses directly involves the physical properties of water. In comparisons both within and between species, larger individuals usually have larger clutches. The low diffusion constant and high viscosity of water (Table 1) may limit gas exchange for embryos near the center of large clutches (Strathmann and Chaffee, 1984). However, all the hypotheses for less brooding by larger adults indirectly involve the physical properties of water; it is because water is a benign medium for small planktonic animals that large aquatic adults can release embryos or larvae into the surrounding fluid. The common inverse correlation between adult size and brooding in many aquatic animals appears to result from an alternative to brooding in aquatic habitats. This alternative is more costly or absent in air.

TABLE 4. *The association of small adult size with brooding in marine animals.\**

Taxon	Source
Polychaeta, Sabellida	Knight-Jones and Bowden (1984)
Bivalvia	Sastry (1979)
Veneridae	Sellmer (1967)
Ostracidae	Sellmer (1967)
Gastropoda, <i>Crepidula</i>	Gallardo (1977), Hoagland (1977)
Polyplacophora	Pearse (1979), Creese and O'Neill (1987)
<i>Lepidochitona</i>	D. J. Eernisse (1988)
Cephalopoda, <i>Octopus</i>	Green (1973)
Brachiopoda, <i>Articulata</i>	Reed (1987), C. Thayer (personal communication)
Ophiuroidea	Hendler and Littman (1986)
Asteroidea	Chia (1968)
Asteroiidae	Menge (1975)
Asterinidae	Dartnall (1968, 1971) Emson and Crump (1979)
Holothuroidea	
Cucumariidae	Menge (1975)
Synaptidae	unpublished review of literature
Fishes of coral reefs	Barlow (1981)

\* Crustaceans are notable by their absence.

#### MODULAR CONSTRUCTION AND BROODING

Brooding is common among colonial animals that are composed of many small modules (Strathmann and Strathmann, 1982; Jackson, 1986). Animals with modular construction include bryozoans, pterobranch hemichordates, compound ascidians, and several kinds of hard corals and soft corals. The ascidians provide the strongest correlation between brooding and modular construction because almost all colonial ascidians brood and most solitary ascidians spawn gametes into the surrounding water. The scleractinian corals provide the most vexing exception to this correlation because many do not brood, and there is no apparent relation between polyp size and brooding (for example, Szmant, 1986). Larval offspring of brooding colonies typically disperse for very short distances (van Duyl *et al.*, 1981; Olson, 1985; Jackson, 1986; Grosberg, 1987), though there can be exceptions as in the coral *Pocillopora damicornis*, which broods

but releases potentially long-lived larvae (Richmond, 1987). Thus for aquatic animals, modular construction is associated with increased brooding after fertilization and decreased dispersal of planktonic propagules.

The example of ascidians is instructive because the module size is smaller in the colonial than in the solitary forms, but the amount of tissue of one genotype and its longevity can be at least as great in colonial forms as in solitary forms. Thus the correlation between adult size and genet size that occurs among solitary forms of benthic animals breaks down in comparisons that include both solitary and colonial ascidians. Several causes for the association of modular construction and brooding have been suggested (Strathmann and Strathmann, 1982; Jackson, 1986; Grosberg, 1987). A general hypothesis for the relation between module size and brooding is that smaller modules provide more surface for brooded clutches of embryos. Some hypotheses are peculiar to coloniality: colonies might commonly allocate more to growth and less to dispersing propagules than do solitary forms, and thus have more space for brooding; or colonies might benefit more from settling and growing in proximity to kin. Whatever the causes, this is another association of life history traits that appears to be peculiar to aquatic animals in contrast to terrestrial animals or terrestrial plants. Also, the degree to which terrestrial plants are modular does not appear to be correlated with the distances over which seeds are dispersed, whether modular construction is defined in terms of branches or ramets.

#### LARVAL DISPERSAL

Dispersal of terrestrial animals and plants contrasts with dispersal of benthic marine animals with planktonic feeding larvae. It makes sense for mobile organisms to disperse when cues indicate that conditions are likely to be better elsewhere and stop moving when they reach a place where conditions are likely to be better than they are elsewhere. This pattern of dispersal is very common for mobile animals on land or in the sea but is not the pattern for a

great many sedentary benthic marine animals (Table 3). (1) Dispersal of marine larvae is obligate with sexual reproduction. For many marine animals this is the only form of reproduction and not a response to poor conditions. (2) Passive transport of planktonic feeding larvae can carry offspring far beyond any advantageous dispersal distances or favorable habitats. Such extensive transport is common because with most feeding larvae there is an obligate period of growth before the larvae become competent to settle. Though marine dispersal can be over enormous distances, with some feeding larvae crossing oceans (Scheltema, 1977), models of spreading risk by dispersal indicate diminishing returns or increasing costs from dispersal in environments with plausible patterns of variation (Palmer and Strathmann, 1981). Even without a feeding larva there can be an obligate dispersal period; when ova are shed into the plankton, there is typically more than a day of planktonic development before competence for settlement. (3) Dispersal of marine larvae may be a byproduct of putting propagules in the plankton for feeding or safety. Most feeding larval stages of benthic marine animals develop in the plankton rather than on the bottom, possibly because a small unprotected animal is safer in the plankton than on the bottom (Strathmann, 1982). In marine species in which embryos are protected in benthic broods or egg masses, larvae are not released into the plankton until they are capable of feeding or nearly competent to settle. In the latter case, planktonic periods are short and dispersal usually quite limited. Thus the obligate dispersal occurring during the precompetent larval period may be an accidental byproduct of a migration of offspring into the plankton for safety or acquisition of food (Strathmann, 1982, 1985).

It is tempting to compare dispersal of seeds of terrestrial plants and dispersal of larvae of sessile marine animals because both are sessile as adults and both have passively dispersed propagules, but the analogy between seed dispersal and larval dispersal fails in at least three ways (Table 3). (1) Among benthic marine species in

similar conditions, duration of the larval phase is correlated with the amount of larval growth so that in general the larvae that grow the most also disperse the most. Seeds in air do not grow during dispersal. To my knowledge, the seeds that germinate and grow during dispersal are aquatic seeds, as in mangroves. (2) In contrast to many widely dispersed seeds of terrestrial plants, the marine larvae that disperse the most (feeding forms) have no structures that are specifically for dispersal. The larval structures consist mostly of devices for feeding, defense, and (in competent stages) habitat selection. Other than initial upward swimming, special adaptations for larval dispersal are not apparent, and many marine species with planktonic adults have larvae similar to the dispersing larvae in species with sedentary benthic adults (Strathmann, 1985). In contrast, terrestrial fruits or seeds commonly have special devices whose only known function is to enhance dispersal (Harper, 1977). (3) Marine larvae possess some capacity to move from a poor habitat. Seeds can abstain from germination but movement to a new position is beyond their control.

#### DISPERSAL OF AQUATIC ANIMALS THAT ARE NOT MARINE

Feeding planktonic larvae have been eliminated from the life histories of most marine animals that have invaded freshwater. Non-marine aquatic animals commonly have a dispersal or resting phase in their life history that is adapted to dry conditions; such a desiccation resistant phase is rare among marine animals. Desiccation resistant phases include many types of cysts, unhatched embryos, and other inactive stages (Hutchinson, 1967; Pennak, 1978) as well as the flying adults of many insects with aquatic larvae (Usinger, 1956; Cheng, 1976).

Possession of a stage that can withstand a period in air suggests that an aerial dispersal route is advantageous for many non-marine aquatic organisms. Lakes and ponds are isolated and ephemeral (Hutchinson, 1957), whereas marine habitats are permanently connected by large expanses of water (Schopf, 1980; Tchernia, 1980). In

TABLE 5. *Potential consequences of decreased planktonic larval period for benthic animals.*

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More regular recruitment, less irregular year classes
Decreased dispersal
Less genetic variation within populations
More genetic variation between populations
Adaptation to more local conditions
More inbreeding
More simultaneous hermaphrodites
More interaction among kin
More speciation
More extinctions
Shorter geographic ranges

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persistent systems of streams passive dispersal is overwhelmingly downstream, whereas marine habitats are better connected by multi-directional water routes. It appears that marine organisms can be more fully aquatic than many other aquatic organisms and that this affects the way they disperse.

#### EVOLUTIONARY CONSEQUENCES AND CORRELATIONS OF MODE OF DEVELOPMENT

Do aquatic life history traits have interesting and peculiarly aquatic evolutionary consequences? Evolutionary correlates of larval dispersal suggest that the answer is yes. We should expect some peculiarly marine evolutionary patterns that arise from peculiarly marine patterns of life history traits.

For species with sedentary adults, larval dispersal is reported to have numerous and partly related evolutionary consequences (Table 5). Duration of the planktonic larval period potentially affects regularity of recruitment to the adult population (Thorson, 1946; Ebert, 1983), genetic variation within and among sites (Berger, 1973; Burton, 1983; Eernisse, 1984; Buroker, 1985; Waples and Rosenblatt, 1987), adaptation to local conditions (Crisp, 1978; Strathmann, 1982; Vermeij, 1982; Ayre, 1985), inbreeding and interaction with kin (Jackson, 1986; Grosberg and Quinn, 1986; Grosberg, 1987), inbreeding or outbreeding depression (Grosberg, 1987); the evolution of hermaphrodites (Heath, 1977;

Strathmann *et al.*, 1984), geographic range, speciation, and extinction (Powell, 1942; Shuto, 1974; Scheltema, 1977; Hansen, 1980; Perron and Kohn, 1985; Jablonski,

At this stage of marine evolutionary studies some qualifications must be added. Good comparative data are few. Larval dispersal is not the only mode of dispersal. Some animals are frequently rafted to other sites (Jokiel, 1984; Highsmith, 1985; Jackson, 1986), and dispersal of sperm may contribute to gene flow (R. Grosberg, personal communication). Dispersal is not the only determinant of gene flow, and gene flow is not the only determinant of cohesion or divergence of populations (Berger, 1977; Burton, 1983; Hedgecock, 1986). Obligate dispersal is not favorable to colonization because descendants cannot be retained at favorable sites once they have been reached (Strathmann, 1974). Geographic range is not correlated with extent of larval dispersal in all faunas (D. Lindberg and M. Russell, personal communication), and species durations are confounded with species geographic ranges (Russell and Lindberg, 1988). Nevertheless, duration of the planktonic larval stage is the primary determinant of dispersal for many sedentary marine animals. Extensive larval dispersal is common among marine animals and unusual elsewhere, and even more peculiar to marine animals is the extreme variation in scale of dispersal of closely related animals with its varied evolutionary consequences. Winged and wingless insects could be considered a terrestrial analogue, but wings do not appear to have such a large effect on dispersal and gene flow in carabids (Liebherr, 1988), and I do not know what patterns have been found for other families that include winged and wingless species. Modes of development of benthic marine animals and their evolutionary consequences appear to differ from those common among terrestrial or freshwater organisms.

A peculiarly marine evolutionary pattern may arise from the correlation between adult size and brooding. Brooding and a shorter planktonic larval period are associated with small adult size (Table 4) within a number of taxa of marine animals.

This association may connect otherwise unrelated traits. Among closely related species, larger adult size is commonly correlated with greater age at maturation, greater longevity, more bouts of reproduction, and greater fecundity (Strathmann and Strathmann, 1982). Adult size also affects interspecies interactions (Menge, 1975). All the consequences listed in Table 5 have not followed every time that small adult size has evolved, but small adult size and its correlates are connected to evolutionary trends in a manner that appears to be peculiar to marine animals.

A very short planktonic period is also common among colonial benthic animals with modular construction and here also there are consequences for gene flow, inbreeding, and interactions among kin. Coloniality can also result in indefinite growth and longevity and in reduced allocation to reproduction (Jackson *et al.*, 1985; Harvell and Grosberg, 1988). Here again, a peculiarly marine correlation between adult and larval traits may connect traits that would otherwise be unassociated or related in quite different ways.

Available evidence suggests that there are peculiarly marine evolutionary patterns that arise from peculiarly marine life history traits, and that these life history traits have resulted in large part from the different physical properties of air and water.

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