THE NATURAL HISTORY OF INBREEDING AND OUTBREEDING

Theoretical and Empirical Perspectives

EDITED BY
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Inbreeding and Outbreeding in Marine Invertebrates

Nancy Knowlton and Jeremy B. C. Jackson

Of the approximately thirty-one phyla of multicellular animals, twenty-five are primarily or exclusively marine or have important marine representatives (Parker 1982). Thus marine invertebrates exhibit an enormous diversity of lifestyles, even when only the major free-living groups are considered. Some, such as corals and sponges, resemble plants, with typically sessile adults, passively dispersed young, and often the capacity for clonal propagation. Others, like most snails and crabs, have freely moving adults with modes of life superficially similar to those of *Drosophila* or mice. Permutations and combinations abound. All, however, live in a medium where floating, and thereby dispersing, is easier relative to comparable situations on land, particularly for preadult stages.

In this chapter, we attempt to address four questions. First, what features of the biology of marine invertebrates influence the potential for inbreeding and outbreeding? We review major theoretical issues in the context of life histories of marine invertebrates, and illustrate important points using a few well-studied model systems. Second, to what extent are natural populations of marine invertebrates in different taxa inbred or outbred? We focus our discussion on twelve major groups belonging to nine phyla. Much of our assessment depends on inference from life history traits related to dispersal and mode of reproduction. Information on the genetic structure of populations and on the extent of inbreeding and outbreeding depression is limited. Third, what characteristics are shared by inbreeding species? We review the taxonomic, morphological, and ecological patterns revealed by our survey. Finally, what processes generate these patterns? Most of the traits involved have important ecological, functional, and genetic consequences that are difficult to disentangle. Consequently, comparisons

between sessile marine invertebrates and plants prove particularly instructive. Marine invertebrate zoologists and students of inbreeding in other groups are our intended audience for this first major review of the scattered literature in this area.

General Features of Life Histories and Mating Systems

Inbreeding has been well studied by theoreticians, and a number of models with a variety of parameters have been examined (e.g., Wright 1969: 169–172; Kimura and Ohta 1971: 117–140; Pollak 1987, 1988; Slatkin 1985; D. Charlesworth and B. Charlesworth 1987). Leaving aside much of the detail, inbreeding depends on (1) the extent to which a species is reproductively divided into populations and subpopulations, especially the size of these units and the probability and pattern of migration among them, and (2) the potential for and direction of nonrandom mating within these breeding units.

These two features are sometimes referred to as the random and nonrandom components of inbreeding, respectively (Kimura and Ohta 1971), and similar concepts may be applied to outbreeding. The less technical literature sometimes ignores random (or "background") inbreeding, but both kinds result in a loss of genetic heterozygosity. Nonrandom inbreeding causes a more rapid drop in heterozygosity than does random inbreeding (Futuyma 1986: 123) unless the deviation from randomness in the former case is slight and the population size in the latter case is very small (Pollak 1987, 1988). Levels of random and nonrandom inbreeding can in theory be inferred from Wright's F statistics (F_{IS} and F_{ST} respectively), but to do so without independent evidence of population boundaries and nonrandom mating is problematic.

Below we consider the features of the natural history of marine invertebrates that are most likely to influence inbreeding or outbreeding potential through their effects on population structure and nonrandom mating.

Dispersal

Many models of population structure assume discrete but interconnected breeding units. In such models, routine dispersal distances define the geographic limits of breeding units, while extraordinary dispersal events are responsible for the connections between them (figure 10.1). Connections may occur between all units (island models, figure 10.1C) or be limited to spatially adjacent breeding units (stepping-stone models, figure 10.1D) (Slatkin 1985). Such models can be hierar-

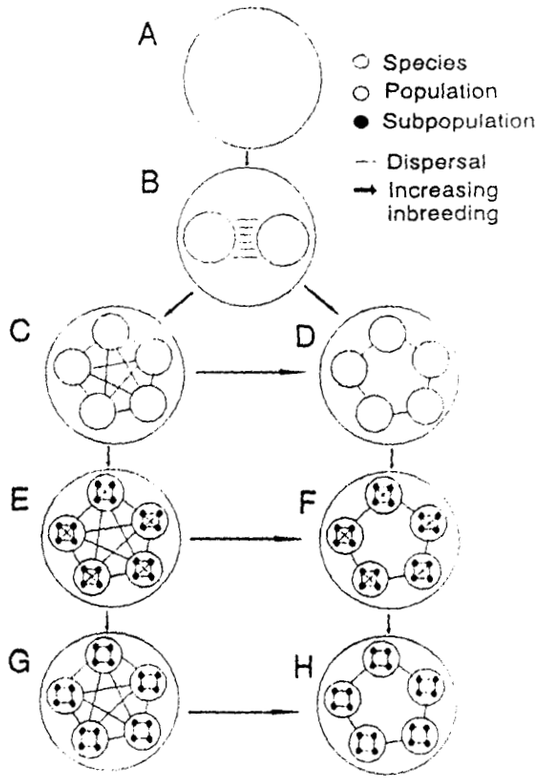

FIGURE 10.1 Symbolic representation of the effect of population structure on random inbreeding. Illustrated are varying degrees of population subdivision combined with island and stepping-stone models of gene flow (see text) among populations and subpopulations.

chically organized (Wright 1969; Chakraborty 1980), with subpopulations within populations (figure 10.1E–H). A hierarchy of stepping stones (figure 10.1H) is probably a good approximation to the more problematic (Felsenstein 1975; Slatkin 1985) isolation by distance model. In any model with discrete populations, dispersal influences both the size of the breeding units, by determining their spatial extent, and the magnitude and pattern of connections between them. In general, the more limited the dispersal, the greater the potential for inbreeding.

Individual dispersal may be defined as movement from the point of conception of an individual to the point of conception of its offspring. In marine invertebrates this movement can take place at various stages in the life cycle and by various means (table 10.1, figure 10.2). Adults may be sessile, sedentary, or highly mobile. Mobility of adults may be active, by walking or swimming, or passive, by floating or rafting

TABLE 10.1 Characters Influencing Dispersal, Their Combined Influence on Overall Dispersal Potential, and Examples

Larval Development	Adult Mobility	Gamete Spawning	Total Dispersal	Examples
Direct/abbreviated	Sessile/sedentary	None	Low	Crustacean symbionts
Direct/abbreviated	Sessile/sedentary	Sperm	Low	Some corals, ascidians
Direct/abbreviated	Sessile/sedentary	Egg + sperm	Low	Some sponges, anemones
Direct/abbreviated	Mobile	None	Moderate/high	Some snails
Direct/abbreviated	Mobile	Sperm	Moderate/high	None?
Direct/abbreviated	Mobile	Egg + sperm	Moderate/high	Some echinoderms
Extended	Sessile/sedentary	None	High	Barnacles
Extended	Sessile/sedentary	Sperm	High	*Membranipora*
Extended	Sessile/sedentary	Egg + sperm	High	Mass-spawning corals
Extended	Mobile	None	High	Many decapod crustaceans
Extended	Mobile	Sperm	High	None?
Extended	Mobile	Egg + sperm	High	Most echinoderms

Note: The combination of direct development and spawned eggs implies that eggs are released prior to fertilization, but that they are nonmobile, and that adult existence begins shortly after hatching. The apparent lack of mobile species with retained eggs and spawned sperm probably reflects past sexual selection favoring males that placed sperm on or in the female.

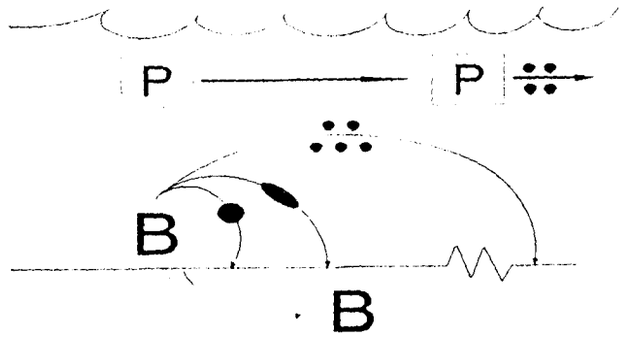

FIGURE 10.2 Mobility in the life cycle of marine invertebrates. P, planktonic (free-floating) adult; B, benthic (bottom-dwelling) adult; solid dots, larvae of different sizes; arrows, movement.

(Highsmith 1985). Male and female gametes may both be spawned into the water column, females may retain eggs until they are fertilized by spawned sperm, or copulation may occur. The embryo may be brooded by the female, attached to the substratum, or free-floating to varying degrees and for varying periods of time. The larva, if it exists, may float, swim actively, or remain near or on the bottom, with time before metamorphosis ranging from seconds to months. Alternatively, a juvenile may emerge from the egg case or parent to begin an adultlike existence.

An extended larval phase is generally capable of greater dispersal than a mobile adult phase (Crisp 1978), although exceptions occur in particular taxa. This is because nearly neutrally buoyant larvae disperse with little expenditure of energy, while most movement by adults is accomplished by more energetically expensive, active locomotion (species that spend their entire lives drifting in the plankton being an obvious exception).

In contrast, maximum dispersal of ultimately successful gametes is typically much lower than either maximum larval or adult dispersal unless adults are entirely sessile. Sperm once spawned have relatively limited life spans (e.g., less than 5 minutes in the ascidian *Botryllus schlosseri* [Grosberg 1987]; less than 4 hours in the hydroid *Hydractinia echinata* [Yund 1990]). Sperm spawned in packages (spermatophores) may have longer lifetimes, however. Although not common in spawning marine invertebrates, spermatophores have been reported in several sessile groups (M. F. Strathmann 1987; R. R. Strathmann 1990). In phoronids they are equipped with sails or filaments (Zimmer 1987)

which might aid dispersal. Unfertilized, spawned eggs also have short life spans, although they are often somewhat longer than those reported for sperm (e.g., more than 90 versus less than 20 minutes for eggs and sperm of *Strongylocentrotus droebachiensis* [Pennington 1985], and 4–6 versus 1–2 hours for eggs and sperm of the mussel *Mytilus edulis* [Bayne 1976]).

Short gametic life spans limit matings to relatively nearby individuals, and dilution further narrows the distances that successful gametes travel prior to fertilization. In wave-swept environments, the role of turbulence in limiting typical effective distances between spawning individuals is marked (Denny 1988: 147–151; Denny and Shibata 1989). For example, at distances greater than 20 cm from the sperm source, less than 15% of eggs were fertilized in the sea urchin *S. droebachiensis* (Pennington 1985). Studies of *Hydractinia echinata* (Yund 1990) and the sea urchin *Diadema antillarum* (Levitan 1991) done in calmer waters showed a similar pattern on a slightly greater scale, with low probabilities of fertilization at distances of 7 and 3 m respectively.

Diversity of dispersal modes within a single species' life history can generate complex and hierarchical breeding structures. For example, small species often brood young, which disperse relatively short distances after release (Strathmann and Strathmann 1982), and small species are also more likely to be transported long distances by rafting (Highsmith 1985). This pattern might generate subpopulations defined by larval crawling, connections among subpopulations via occasional storm-mediated longer-distance dispersal of larvae or adults, and rare connections among the populations through rafting. These variable dispersal modes can also create situations where the pattern of connection between breeding units is not the same at all levels of the hierarchy (Stoddart 1988). For the case described above, stepping-stone models are most appropriate for dispersal by larval crawling and storm-mediated dispersal, while island models better describe rafting (e.g., figure 10.1G).

In contrast, other common life histories generate comparatively simple population structures. Some marine invertebrates have larvae that spend months in the plankton and are routinely capable of traveling great distances (Scheltema 1971, 1986a, 1986b). Although the concept of a panmictic planktonic soup is overly simplistic, it nevertheless remains clear that some species with planktonic larvae have much more limited partitioning of the gene pool (as in figure 10.1B) than do species lacking a dispersal phase (Burton and Feldman 1982; Burton 1983; Hedgecock 1986).

Even in the simplest cases, accurate measurements of dispersal pat-

terns are difficult to make. Indirect and direct methods each have their own weaknesses; the former are based on numerous theoretical assumptions, while the latter cannot adequately quantify rare events (Slatkin 1985). Their combined use can be particularly informative, however (e.g., Grosberg 1991, see below).

Effective Population Size

The effective size of a breeding unit, as defined spatially by routine dispersal, is limited by the number of genetically distinct breeding individuals (N) it contains. The effective population size is maximally $2N - 1$ for hermaphrodites or $2N - 2$ for gonochores, but it is generally less because of population fluctuations, unequal contributions of individuals to reproduction, overlapping generations, and biases in sex ratio (Wright 1969; Kimura and Ohta 1971; Crawford 1984b). The smaller the effective population size, the greater the degree of random inbreeding.

The number of genetically distinct individuals in an area necessarily depends on population density, which varies enormously among marine invertebrates. Differences in densities are most critical for species that are highly philopatric at all life stages. In cases where total lifetime dispersal is such that most offspring are found within 1–10 m of the parent, the potential for inbreeding is much higher for low-density species (less than 10 individuals per m^2) than for high-density species (more than 1,000 individuals per m^2). Once dispersal is widespread, however, most species will have effective population sizes too large for random inbreeding to be important. Among sessile species generally, unitary forms often have much higher densities of genetically distinct individuals than modular or clonal forms (e.g., we crudely estimate densities of 10^0–$10^2/m^2$ for sponges, hydrocorals, and corals; and 10^1–$10^3/m^2$ for hydroids, bryozoans, and colonial ascidians; compared with 10^3–10^6 for solitary ascidians, vermetids, barnacles, and polychaetes).

Prevailing abundances will generate overestimates of effective population size, however, if population bottlenecks have occurred in the past. Population bottlenecks may arise from catastrophic declines in generally abundant species or from chance colonizations by one or a few individuals. Theoretical studies of such events (Nei, Maruyama, and Chakraborty 1975; Chakraborty and Nei 1977) have shown that loss of heterozygosity depends very sensitively on the severity of the bottleneck (e.g., two versus ten individuals) and the rate of recovery as measured by reproductive potential ($r = 0.1$ versus $r = 1.0$). The initial loss occurs comparatively rapidly, the bulk of it within 10 generations (although with larger founding groups and a slower recovery, hetero-

zygosity continues to drop through 100 generations). Most importantly, heterozygosity typically does not begin to recover before 10^5–10^6 generations. This is far more than enough time for populations to return to carrying capacity, even assuming the smaller of the two founding sizes and rates of increase (exponential growth would yield a population of $2e^{100,000}$!). Thus one cannot rule out the effects of random inbreeding simply on the basis of currently large population sizes.

The most dramatic and best-studied catastrophic decline in a marine invertebrate was caused by an epidemic disease in the once very abundant sea urchin *Diadema antillarum*. Between January 1983 and February 1984, the urchin was reduced to between 0.01% and 7% of its original density throughout its neotropical range (Lessios 1988). This catastrophic reduction has produced as yet no measurable genetic changes, however. Persistent low densities may eventually result in loss of genetic variability (Lessios 1988); alternatively, even this bottleneck may not have been sufficiently extreme to produce detectable genetic effects.

Bottlenecks stemming from chance colonizations by one or a very few individuals are probably more common, particularly in groups where routine dispersal is limited. Many large, isolated populations of brooding species may be derived from only a single, accidently transported individual that has the potential to rapidly increase over a relatively short period of time. The best-studied cases involve the snail *Littorina saxatilis*. In South Africa, two populations apparently started by a few introduced individuals had heterozygosities much lower than those of thirteen North Atlantic populations (0.05 versus 0.18 respectively) (Knight, Hughes, and Ward 1987). Reduction in heterozygosity was much less marked, however, for populations on minute, recently emerged islands off the Swedish coast (0.13 on the islets versus 0.16 on the mainland [Janson 1987b]). Janson suggested that this was due to the rapid potential for increase shown by these snails (she estimated the intrinsic rate of increase at $r = 2.0$). However, results in South Africa for the same species (Knight, Hughes, and Ward 1987) and the sensitivity of models to the size of the founding group (Nei, Maruyama, and Chakraborty 1975; Chakraborty and Nei 1977) make it difficult to eliminate slightly larger founding populations as the source of the difference between the two studies. Unfortunately, we entirely lack information on the frequency and severity of bottlenecks for almost all marine invertebrates.

The potential for clonal reproduction also complicates estimates of effective population size, because physiologically separate "individuals" are not necessarily genetically distinct. The two major methods of

clonal reproduction are agametic division of the adult body (by fission, budding, etc.) and parthenogenetic production of diploid eggs or larvae (Hughes 1987, 1989). In general, the former is more common among marine invertebrates, and taxa that practice one form tend not to practice the other (Hughes 1989). Clonal division of embryos (polyembryony) and larvae has also been recorded in bryozoans and echinoderms (Ström 1977; Bosch, Rivkin, and Alexander 1989). Clonal reproduction at the expense of sexual reproduction strongly influences effective population size by reducing the number of genetically distinct individuals within the breeding unit.

Another important source of reduction in effective population size is uneven contributions to reproduction. This may occur through differences among genets in size, life span, or ability to acquire mates, whatever their origin. Stoddart's (1984) study of genetic structure of the coral *Pocillopora damicornis* provides a clear example of the first mechanism. On average, each individual genotype was represented by 4.3 colonies, but the two most abundant genotypes of the fourteen detected represented 66% of all colonies in one population, and 95% of the colonies in the largest size category. Wulff (1986) documented similar inequality in abundances of clones in three sponges. In many marine invertebrates, reproductive output is correlated with size (Jackson 1985). Size can vary enormously, particularly when modular construction or cloning results in a body plan with no intrinsic limits on the maximum amount of tissue associated with a single genotype. Clonal organisms also have at most weak tendencies towards senescence (Caswell 1985; Hughes 1989), and survivorship may increase with increasing size, further increasing inequalities in lifetime reproduction between long-lived and short-lived genets. Lack of senescence additionally increases the potential for overlap among generations, which also reduces effective population size (Felsenstein 1971). The potential variation in reproduction is less in unitary (nonmodular) organisms, even when the latter have very steep or exponential size-fecundity relationships, because of their much more limited ranges in body size and life span. In aclonal, behaviorally sophisticated marine invertebrates, there is some evidence for polygyny (e.g., Upton 1987; Christy 1987), but it is not as extreme as that reported for some vertebrates (e.g., Emlen and Oring 1977; Alexander et al. 1979).

Finally, biased sex ratios are not uncommon in species known to reproduce sexually (e.g., male:female ratios of 1:8 for a tetractinomorph sponge [Ayling 1980] and up to 1:20 for an isopod [Carvalho 1989]). Some of these biases may reflect differential rare recruitment and subsequent asexual proliferation of dioecious colonists, however, as re-

ported for starfish (Achituv and Sher 1991) and brittle stars (Mladenov and Emson 1988).

Nonrandom Mating

Nonrandom mating occurs when all members of a breeding unit, as delimited by routine dispersal, are not equally likely to mate. More specifically, nonrandom inbreeding or outbreeding is enhanced when the probability of two individuals mating is a function of their degree of relatedness. The former occurs through higher than expected probability of kin mating and selfing, the latter via behavioral avoidance of kin as mates and genetic or physiological incompatibility systems. Many of the mechanisms that have received much attention in vertebrates (patterns of mate preference and sex-specific dispersal [Bateson 1983; Pusey 1987; Forster Blouin and Blouin 1988]) are largely unstudied in marine invertebrates.

A major component of nonrandom inbreeding for the phyla considered here is the greater probability of fertilization between gametes originating from nearby sources. Copulating partners are necessarily adjacent. In many species females retain eggs until fertilization occurs, and most gametes spawned into the sea probably travel relatively short distances before they are fertilized (see above). This will not lead to inbreeding, however, unless neighbors are close relatives due to cloning, extreme larval philopatry, or kin recognition at settlement.

In contrast, among the best potential candidates for random mating within a population are mass-spawning species, such as epitokous polychaetes (Schroeder and Hermans 1975) and the majority of corals on the Great Barrier Reef. In the latter, synchronous spawning of buoyant egg and sperm packets by the entire population produces enormous egg and embryo slicks visible from the air (Harrison et al. 1984; Oliver and Willis 1987). In typical *Acropora*, which represent a majority of the mass spawners, gametic packets break up when they reach the surface, but a delay in fertilization of 10–20 minutes probably enhances cross-fertilization (Richmond 1990).

Many invertebrates, however, show nonrandom mating patterns such as self-fertilization and sib mating that probably contribute to inbreeding. In the absence of genetic blocks, synchronous hermaphrodites should be particularly susceptible to selfing, especially if they are isolated or large (Maynard Smith 1978: 136), as is frequently true of some clones. Sequential hermaphrodites in which physiological isolation by budding or fragmentation leads to asynchrony in sexual stages may also self-fertilize beyond random expectation, provided the clonemates remain nearby. If clonemates are dispersed, however, only the

random component of selfing will increase through reduction in effective population size.

Aggregations of kin in excess of that predicted by dispersal distance alone will increase the probability of sib matings in both hermaphrodites and gonochores. This phenomenon is not well studied in marine invertebrates, but has been reported in two phyla (Keough 1984; Grosberg and Quinn 1986). The bryozoan *Bugula neritina*, for example, is a protandrous hermaphrodite and therefore cannot self-fertilize. However, aggregation of kin at settlement combined with probably synchronized release of eggs and sperm in neighboring colonies (Keough 1984) makes inbreeding probable.

Genetic blocks to self-fertilization, on the other hand, promote nonrandom outbreeding. In the absence of such a block, random mating among N synchronous hermaphrodites would be expected to yield selfed progeny in the proportion $1/N$. Genetically based gametic incompatibility systems are common in plants (D. Charlesworth and B. Charlesworth 1987) but are less well known in marine invertebrates. Heyward and Babcock (1986) provide evidence for gametic incompatibility blocking selfing in the coral *Montipora digitata*, a species which also propagates clonally through fragmentation. The genetics of gametic incompatibility are best understood for ascidians (Oka 1970; Scofield, Schlumpberger, and Weissman 1982). Selfing is probably more commonly prevented by a kind of hermaphroditism which is broadly synchronous, but in which the times of sperm and egg release are slightly offset, thereby preventing fertilization between gametes from the same individual (alternating sequential hermaphroditism of Ghiselin [1974: 109]).

Genetic and temporal systems differ in the extent to which they favor outbreeding. Gametic incompatibility prevents all selfing as well as varying proportions of sib matings, depending on the extent of relationship between the parents. In some ascidians, for example, fertilization is blocked for sperm that share an allele with the maternally derived, diploid egg envelope. Thus 50% of matings between siblings should be blocked, assuming no alleles in common between their parents (Grosberg 1987). In contrast, alternating sequential hermaphroditism will not necessarily prevent sib matings, and will not even block selfing when clonal reproduction produces genetically identical individuals that are physiologically separate and reproductively out of synchrony.

Finally, Hoagland (1978) reported an intriguing comparison of postsettlement behavior among species of *Crepidula* with differing larval dispersal abilities. Species with planktonic larvae have juveniles that

are immediately attracted to conspecific adults upon settlement. The resulting clusters function as long-term mating groups. In species in which the females brood the young to metamorphosis, however, juveniles are not immediately attracted to conspecific adults, and breeding attachments are relatively transient. Hoagland (1978) suggested that delayed and transient aggregations in species without planktonic young are the result of selection to avoid inbreeding.

Inbreeding and Outbreeding Depression

Offspring fitness has long been known to vary as a function of the degree of relatedness of the parents. The traditional perspective has two components: inbreeding depression, which occurs when mates are closely related, and outbreeding depression, which occurs at or around the point of interspecific hybridization (figure 10.3). This pattern is undisputed for many species (i.e., Stebbins 1950; Dobzhansky 1951; Wright 1977; D. Charlesworth and B. Charlesworth 1987). Inbreeding depression is thought to result from the unmasking of deleterious recessives and the loss of heterozygote advantage at individual loci (partial dominance and overdominance, respectively) while interspecific outbreeding depression is believed to be due to the combination of incompatible genetic systems (D. Charlesworth and B. Charlesworth 1987).

Others, however, have stressed that in species where inbreeding is common, the theoretical predictions and data are not consistent with the traditional view (e.g., Shields 1982, chapter 8, this volume; Bateson 1983; Schemske and Lande 1985; Waser, chapter 9, this volume). They argue that in the face of persistent inbreeding for whatever reason, the costs of inbreeding are likely to be low or nonexistent (figure 10.3), particularly due to the elimination of unfavorable recessives. At the same time, inbreeding results in linkage disequilibrium and the assemblage of intrinsically well-coordinated gene complexes, while limited dispersal often associated with inbreeding permits the buildup of locally favorable genetic combinations (Endler 1977; Templeton 1986). As a consequence, mating of conspecific individuals from unrelated populations leads to loss of fitness (figure 10.3). The empirical demonstration of intraspecific outbreeding depression (Price and Waser 1979; Willson and Burley 1983: 31, 35) provides particularly compelling evidence for this perspective. Inappropriate experimental design may complicate interpretation of results, however. For example, the mere absence of inbreeding depression may be misleading if the entire area studied represents one inbred population so that no comparisons with truly outbred crosses are made (D. Charlesworth and B. Charlesworth

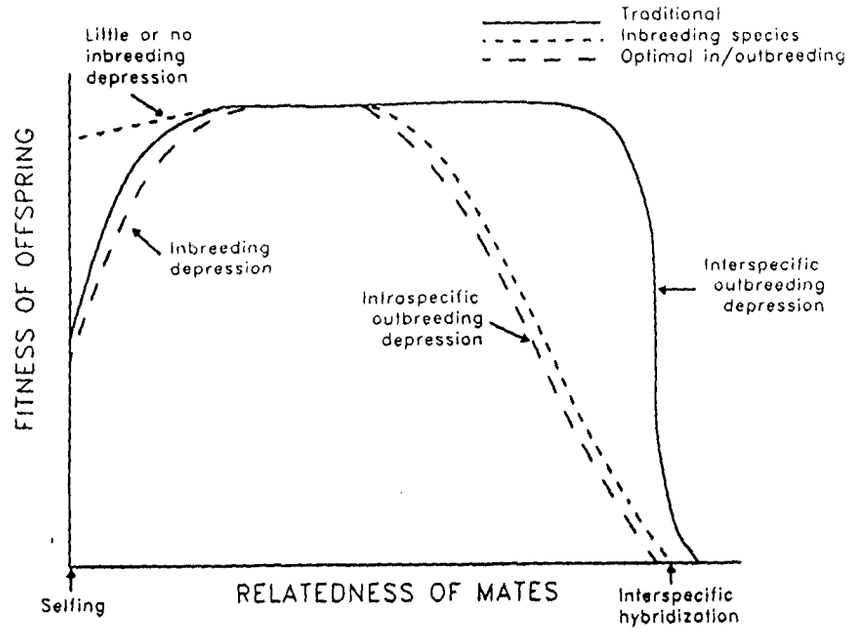

FIGURE 10.3 Proposed relationship between the degree of relatedness between mates and the fitness of their offspring. Three commonly discussed patterns (see text) are illustrated.

1987). Studies of outbreeding that consider only the first generation of crosses may also be deceptive, because initial increases in fitness are likely to be replaced by declines in subsequent generations (Lynch 1991).

In marine invertebrates, studies of the relationship between parental relatedness and offspring fitness are far more limited than in many other groups, due to frequent difficulties with breeding and rearing of offspring. Loss of viability may occur with hybridization of closely related species (e.g., Longwell 1976; Lucas, Nash, and Nishida 1985; Ward, Warwick, and Knight 1986; but see Strathmann 1981), and inbreeding depression has also been reported (Barnes and Crisp 1956; Potswald 1968; Sabbadin 1971; Longwell and Stiles 1973; Longwell 1976; Beckwitt 1982; Beaumont and Budd 1983). Even in species that are almost certainly outbred, however, unambiguous evidence for strong inbreeding depression is not always found (e.g., see Mallet and Haley [1983] for a review of studies on the oyster *Crassostrea virginica*). The evidence for inbreeding depression is particularly scanty for spe-

cies in which inbreeding is likely (Strathmann, Strathmann, and Emson 1984). Moreover, intraspecific outbreeding depression on scales consistent with dispersal abilities has been reported for the ascidian *Botryllus schlosseri* (Grosberg 1987) and the copepod *Tigriopus californicus* (Burton 1986, 1987). Thus marine invertebrates tend to support the pluralistic view more recently expounded for other taxa.

Model Systems

The diversity of life histories and mating systems reviewed above suggests that marine invertebrates are likely to contain many examples at both ends of the inbreeding-outbreeding continuum. Here we review in greater detail the relevant evidence in four particularly well-studied species. They were chosen because they are representative of several common patterns and because they illustrate the strengths and weaknesses, as discussed by Hedgecock (1982, 1986), of the data available.

The Colonial Ascidian *Botryllus schlosseri*

This widely distributed species often dominates hard substrata in shallow, protected waters. In Eel Pond at Woods Hole, Massachusetts, maximum densities reach 2,000–7,000 colonies per m^2 (R. Grosberg, personal communication, 1989). Adults are sessile, and although of modular construction, they do not regularly fragment, so that physiologically separate individuals are usually genetically distinct (Grosberg 1987). Some colonies even represent more than one genotype, due to the fusion of adjacent colonies that share a histocompatibility allele. Persistent chimeras usually contain very close relatives, however, due to the high diversity of the histocompatibility system (Grosberg and Quinn 1986) and the long-term instability of fusions between individuals that are not identical at loci governing histocompatibility and resorption (Rinkevich and Weissman 1989). The species is hermaphroditic, but selfing is generally prevented by asynchrony in the release of eggs and sperm within a colony (Sabbadin 1971). All these characters are compatible with outbreeding.

Other aspects of the life history and the data on proximity-dependent mating success strongly suggest, however, that *B. schlosseri* is inbred. Gamete and larval dispersal are generally extremely limited. Fertilization of the eggs takes place in the mother colony. The life span of sperm is less than 5 minutes (Grosberg 1987), and the average distance of sperm dispersal, based on studies using rare electromorphs, is less than 17 cm (Grosberg 1991). Larvae are capable of settlement and metamorphosis immediately upon release. Grosberg (1987) found that

over 80% of the larvae settled within 25 cm of their place of birth (although estimates of larval dispersal may be biased due to the use of empty settlement panels when natural substrata are crowded). Other evidence for limited dispersal of larvae comes from spatial patterns in field populations of a number of genetically controlled characters (histocompatibility type [Grosberg 1987]; enzymes and color [Sabbadin 1978]). Larvae also tend to settle next to histocompatible individuals, which are typically siblings, resulting in even tighter associations among close relatives than would be predicted by limited dispersal alone (Grosberg and Quinn 1986). The effect of this behavior on inbreeding is difficult to judge, however, because these individuals may then fuse and form stable chimeras, thus reducing inbreeding by synchronizing the sexual cycle and preventing fertilization between close relatives (Grosberg and Quinn 1986).

The strongest evidence for routine inbreeding in this species comes from Grosberg's (1987) studies of proximity-dependent mating success. He found that the success of fertilization, embryogenesis, and larval metamorphosis all declined significantly with increasing distance between mates. Success rates through larval metamorphosis were 89% for crosses between neighbors, 70% for crosses between individuals separated by 1.5 m, and 58% for crosses between individuals separated by 4.5 m. This pattern is consistent with predictions based on larval dispersal distance. None of the colonies mated were genetically identical, so inbreeding depression with selfing cannot be entirely ruled out from the published data. Indeed, strong inbreeding depression has been reported in other populations of this species (Sabbadin 1971, 1982), and R. Grosberg (personal communication, 1989) has observed sporadic failures of selfed lines in the F_1 generation. Inbreeding depression for matings between close relatives does not occur, however, and intraspecific outbreeding depression over very small spatial scales is striking. These data provide compelling evidence that inbreeding is high in this species.

Grosberg (1991) has also calculated Wright's F statistics for the random and nonrandom components of inbreeding for the Eel Pond population. At three independently segregating loci, F_{IS} and F_{IT} were comparable and ranged from 0.25 to 0.50, while population subdivision (F_{ST}) made a small contribution to the overall F values at spatial scales ranging from 6 m down to 0.5 m. Grosberg's earlier (1987) report of proximity-dependent mating success, which documented intraspecific outbreeding depression over a scale of 3 m, is somewhat puzzling in light of the absence of population subdivision over a 6-m scale.

The absence of differentiation does suggest that gene flow greater

than that shown by Grosberg's larval dispersal experiments must occasionally occur, and seasonal or episodic variation in dispersal is to be expected. The calculations of Pollak (1987, 1988) predict the pattern of *F* statistics found by Grosberg (1991) whenever the probability of matings with close relatives is substantially greater than the reciprocal of the population size. This is because heterozygosity is lost much more rapidly from nonrandom matings than from genetic drift in all but the smallest populations. As a crude approximation for population size, one can use Crawford's (1984a) methods, coupled with Grosberg's (1987) larval dispersal measurements, to estimate a minimum neighborhood area of approximately 0.2 m^2 (assuming that 86% of larvae settle within 25 cm of their mother, and that this is equivalent to Crawford's formulation of an 86% expectation that a central individual's parents lie within 25 cm). If there were on average 1,000 colonies per m^2 (yielding a minimum population of 200), then Pollak's criterion would hold when the probability of sib or parent-offspring mating was substantially higher than .005. These conditions seem quite likely for *B. schlosseri*.

The Mussel *Mytilus edulis*

Mytilus edulis and two taxonomically controversial sibling species, *M. galloprovincialis* and *M. trossulus* (Varvio, Koehn, and Väinölä 1988; McDonald and Koehn 1988; Gosling 1984), are the most widely distributed members of the Mytilidae, a family renowned for its dominance of rocky shores (Suchanek 1986). Some of the characters described below come from sources predating the recognition of the species distinctions, but except as noted, the characters are shared by all.

Edulis-like mussels are found in a variety of temperate habitats; they dominate portions of many intertidal zones and may attain very high densities (e.g., nearly 8,000/m^2) (Suchanek 1978). Almost all individuals are either males or females for their entire life span (Seed 1976), asexual reproduction is unknown, and there are no reports of strongly biased sex ratios. Eggs and sperm remain viable for several hours (Bayne 1976), and are spawned directly into the water, where fertilization occurs. The larvae spend 3 to 7 weeks in the plankton (Bayne 1976; Strathmann 1987: 325), which is the period of maximum dispersal potential. Levinton and Koehn (1976) estimated a minimum net dispersal distance of nearly 175 km, and Koehn, Newell, and Immermann (1980) documented dispersal by oceanic larvae of over 25 km into Long Island Sound. The juveniles and adults are also capable of some movement (Levinton and Koehn 1976). In sum, due to high dispersal, high densi-

ties, and the impossibility of selfing, inbreeding in this species is inconceivable.

Electrophoretic variation in *Mytilus edulis* has been intensively studied, and the data illustrate well the dangers of assessing inbreeding from genetic data alone. Populations from widely separated regions differ electrophoretically (Levinton and Koehn 1976), even when the sibling species are analyzed separately (Varvio, Koehn, and Väinölä 1988). Genetically uniform populations spread over large areas also occur, as in nonestuarine environments south of Cape Cod (Koehn 1983). These patterns are consistent with expectations based on larval dispersal (Slatkin 1981). There are, however, sharp clines over distances as short as a few kilometers (Koehn 1983), and heterozygote deficiencies are also common (Zouros, Romero-Dorey, and Mallet 1988). These latter patterns could in theory stem in part from inbreeding or the Wahlund effect, but careful study has shown that natural selection and the effects of genotype on reproductive seasonality are instead responsible (Koehn 1983; Zouros, Romero-Dorey, and Mallet 1988; Hilbish and Zimmerman 1988).

Unfortunately, breeding studies in this species have not been directed toward the problems of inbreeding and outbreeding depression. There are no published data from inbreeding experiments, nor are there data on the success of matings between conspecifics from distant sites, generally referred to as subspecies (Seed 1976). Matings between *M. edulis* and *M. galloprovincialis* show no evidence of hybrid inferiority (Skibinski 1983; Lubet et al. 1984), however. This suggests that marked outbreeding depression between geographically distant conspecifics is unlikely.

The Snails *Littorina littorea* and *L. saxatilis*

The two preceding examples come from species in different phyla, but widely differing potential for inbreeding may exist within a single genus. The snails *L. littorea* and *L. saxatilis* (sometimes referred to as *L. rudis* [Hannaford Ellis 1983; Janson 1985]) are both common intertidal species found on both sides of the northern Atlantic (Johannesson 1988).

Littorina littorea has a planktonic larval phase that lasts approximately 4 to 6 weeks. Johannesson (1988) suggested that during this period a larva might travel as much as 300 km prior to settlement, and noted (based on Carlton [1982]) that *L. littorea* introduced to the North American east coast spread at a rate of 34 km per year. These data strongly imply outbreeding. The young of *L. saxatilis*, on the other hand, emerge from the mother as crawling juveniles (Janson 1987a), and studies of marked individuals indicate movement of only 1 to 4 m

over a 3-month period (Janson 1983). Several studies have shown that densities vary widely depending on habitat, ranging from less than 10 to 3,000 per m^2 (Hughes and Roberts 1981; Janson 1987b). Thus *L. saxatilis* has the potential for inbreeding due to its limited dispersal, and the effect could be quite marked where densities are low.

The two species have been extensively compared both morphologically and electrophoretically. As expected, shell shape varies more between habitats in *L. saxatilis* than in *L. littorea*. The former shows marked differences between exposed and sheltered shores only 100 m apart, while the latter does not, presumably because gene flow swamps selection when larvae are planktonic (Janson 1987a). Similarly, there is a positive correlation between geographic distance and genetic difference in *L. saxatilis*, but no significant correlation in *L. littorea* (Janson 1987a). In a detailed analysis of microgeographic variation in *L. saxatilis* along 1 km of coast, populations separated by only a few meters sometimes showed significant electrophoretic differentiation (Janson and Ward 1984). Also, the random component of inbreeding (estimated by differences between subpopulations, F_{ST}) was more often and more highly significant than was the component of inbreeding due to nonrandom mating within populations (estimated by F_{IS}). This finding, in contrast with that of Grosberg for the ascidian *B. schlosseri*, is consistent with the greater mobility of snails as adults and the apparent absence of kin recognition and association, making mating with close kin within a population much less likely. Contrary to expectation, however, *L. saxatilis* shows more genetic variability within subpopulations than does *L. littorea* (Janson 1987a). The difference holds true even within Europe, where no founder events have been hypothesized. Unfortunately, no comparisons of the two snails with respect to inbreeding or outbreeding depression have been made.

Taxonomic Patterns

In this section we review the characteristics of the life cycle relevant to inbreeding and outbreeding for the principal groups of marine invertebrates, excluding parasitic forms, and highlight cases within each group where inbreeding is most likely to occur (see table 10.2).

Porifera

Sponges are sessile or passively sedentary after the larval stage (Hyman 1940). More than 90% of all species are in the class Demospongia (Hartman 1982), and the following account is based entirely on that group.

There are two principal groups of demosponges, distinguished both

taxonomically and reproductively (Brien 1973; Bergquist 1978). Tetractinomorphs are typically gonochoric (or perhaps sequential hermaphrodites), and spawn relatively small ova that develop upon fertilization into small swimming or crawling larvae. There is evidence that the evolutionary trend in the group has been for precocious fixation and loss of mobility of the larval stage (Borojevic 1970). In contrast, ceractinomorphs are divided approximately equally between simultaneously hermaphroditic and gonochoric species; most incubate comparatively large larvae that swim, or less commonly crawl, on release.

In both groups, free larval life lasts a few hours to days among swimming forms, and from a few to 25 days in exclusively crawling species. Larval aggregation at settlement and postlarval fusion to form chimeras is apparently common, as is agametic clonal reproduction, which occurs by fragmentation, budding, and formation of reduced resting stages (gemmules) and possibly larvae (Fry 1971; Brien 1973; Fell 1974; Bergquist 1978; Wulff 1986).

Exclusively crawling larvae may disperse only a few meters or less from their mother before metamorphosing, even if they crawl for 25 days. Others that roll or bounce along the bottom probably disperse a bit further. Altogether, these entirely benthic larval forms comprise 22% of the sixty-nine species whose movements were compiled by Wapstra and van Soest (1987). A similar percentage of species with crawling larvae has been reported for intertidal sponges in New Zealand (Bergquist and Sinclair 1968; Bergquist, Sinclair, and Hogg 1970). More strikingly, all ten species examined in nearby subtidal sites have exclusively crawling larvae; these include four thinly encrusting ceractinomorphs and six massive tetractinomorphs (Ayling 1980). In addition, budding is more frequent than larval recruitment in several of these species, both intertidal and subtidal. Extensive inbreeding seems very likely among the resulting populations of parents, offspring, and siblings characteristic of such species, but there are no genetic data.

Cnidaria

The diversity of reproductive modes and life histories of cnidarians is exceptionally great. The two most diverse and abundant classes are the Hydrozoa and Anthozoa (Hyman 1940; Dunn 1982). The other two classes (Scyphozoa, Cubozoa) are primarily composed of species whose adults are free-swimming and presumably outbred.

Hydrozoa. Most hydrozoans are apparently gonochoric, although sequential hermaphroditism is hard to rule out in the absence of long-term studies of individuals. Occasional hermaphrodites (1% to 2%) in

otherwise gonochoric species are probably chimeras, as has been shown for *Hydractinia* (Hauenschild 1954; Yund and Parker 1989).

Hydroids are the most abundant and diverse hydrozoans (Hyman 1940; Dunn 1982). Many species have both sessile and mobile phases as adults; the former as solitary polyps or, more commonly, vine- or treelike colonies of polyps with interconnecting stolons; the latter as free-swimming medusae, or more rarely as planktonic polyps. Medusae typically produce gametes that fuse and develop into ciliated, mobile planular larvae that settle on the bottom and give rise to the sessile polypoid phase, although various forms of agametic budding from medusae are also known (e.g., Carré and Carré 1990). Polyps in turn agametically bud off new medusae.

There are strong indications that the mobile phases of the life cycle have been increasingly (repeatedly?) suppressed throughout colonial hydroid evolution (Hyman 1940; Mackie 1974). Presumably primitive forms have strongly swimming, frequently large, pelagic medusae. In more derived groups medusae are often smaller, less mobile, or absent (e.g., they swim only near the bottom, creep along the bottom, hold onto the bottom by their tentacles, are never released by the polyp, or are reduced to sessile gonadal structures on the polyp). Larvae also vary in their mobility, ranging from those that swim vigorously, to those that swim and crawl, crawl only, or are varyingly packaged or bound to one another or their parent by mucus (Williams 1965, 1976; Wasserthal and Wasserthal 1973). In addition, most solitary hydroids that lack medusae brood embryos that are ready to settle when they leave their parent (Rees 1957).

Highly derived colonial forms lacking both medusae and swimming larvae are abundant and diverse (Nishihira 1967; Williams 1976), comprising nearly half of the species in many habitats (e.g., Boero 1981). Larvae may disperse only a few centimeters or meters before settlement and metamorphosis (Pyefinch and Downing 1949; Nishihira 1967, 1968; Wasserthal and Wasserthal 1973; Williams 1976). Larvae settle preferentially near one another or on parental tissue, and adjacent postlarvae commonly fuse to form chimeras (Nishihira 1967, 1968; Williams 1976). In such cases inbreeding without selfing is probable, but there are no genetic data. The principal mode of dispersal of such otherwise immobile species is almost certainly by floating or rafting of entire "sessile" colonies on seaweeds, seagrasses, or other floating debris (Jackson 1986).

There are two orders of sessile hydrozoans that construct calcareous skeletons (Hyman 1940). Milliporid hydrocorals have massive encrusting or erect colonies and tiny sexual medusae that shed gametes within

a few hours of their release. They are presumably outbred. In contrast, stylasterine hydrocorals form smaller erect or encrusting colonies without a medusoid stage (Ostarello 1973, 1976; Frichtman 1974), and females brood larvae for nearly a year. In Ostarello's study, female colonies more than a meter from the nearest male were frequently unfertilized, so dispersal of sperm must be as short as reported for sea urchins (Pennington 1985). Larvae crawl away from their mother for only a few centimeters before settlement; more than half settled within 10 cm and fully 85% settled within 20 cm of their mothers. Local populations consist of parents and offspring in very close proximity, so that inbreeding must be compounded over many generations, but once again there are no genetic data.

Also included among the hydrozoans are two highly specialized planktonic orders of swimming or floating colonies, the siphonophores (e.g., the Portuguese man-of-war), and the chondrophores (velellids) (Hyman 1940; Dunn 1982). These groups must be routinely outbreeding.

Anthozoa. All anthozoans lack medusae (Hyman 1940). There are two important subclasses (Dunn 1982): the Alcyonaria, which includes soft corals, gorgonians, and pennatulaceans (sea pens); and the Zoantharia, which includes sea anemones, zoanthids, and stony corals.

Soft corals grow as sessile or sedentary encrusting, massive, or erect colonies with spicular skeletons. They are generally gonochoric or sequential hermaphrodites. Many small and some large species of soft corals and encrusting gorgonians brood exclusively crawl-away larvae that settle within a few centimeters of their parents (Gohar 1940; Benayahu and Loya 1983, 1984a, 1984b, 1984c, 1985; Sebens 1983a, 1983b, 1983d). These larvae often aggregate and may fuse to form chimeras (again with the potential to produce rare hermaphrodites in otherwise gonochoric species). These species also characteristically form extensive monospecific stands by fragmentation (Benayahu and Loya 1983, 1985). The combination of extremely short-distance larval dispersal and clonal propagation must result in extensive inbreeding. The same pattern holds for the large erect gorgonian *Capnella gaboensis* (Farrant 1985), but most larger species of soft corals and upright gorgonians spawn small ova that develop on fertilization into swimming larvae (Grigg 1979; Weinberg and Weinberg 1979; Yamazato, Sato, and Yamashiro 1981), and are certainly outbred. There are no appropriate genetic data for any octocoral.

The sea pen *Ptilosarcus gurneyi* forms extensive populations on subtidal sands (Birkeland 1974). Adults are long-lived and sedentary, al-

though some, mostly small, individuals drift into cleared areas. Sexes are separate, and gametes are spawned annually in a neutrally buoyant mucus that is not readily dispersed (Chia and Crawford 1973; Strathmann 1987: 90–91). Development is demersal and juveniles can burrow within 9 days. Settlement occurs in massive sets reflected in abrupt spatial discontinuities in size and age classes, but these commonly overlap presumably parental distributions (Birkeland 1974). Weak inbreeding is therefore possible. The life history of the Atlantic sea pansy, *Renilla*, is similar (Wilson 1883).

Sea anemones are solitary polyps that may be sedentary or mobile, the latter by pedal locomotion or passive drift (Nyholm 1949; Mackie 1974; Wahl 1985a, 1985b). Most species are gonochoric, but sequential and synchronous hermaphrodites are also found (Shick 1991). Clonal propagation by fission, pedal laceration, or ameiotic juveniles is widespread, occurring in 40% of the eighty-five species compiled by Chia (1976). Some species (or species complexes) display gonochorism, hermaphroditism, and parthenogenesis (Schmidt 1967; Rossi 1975; Shick 1991). Reports of brooding and release of crawling larvae or juveniles, limited adult movement, and coordinated spawning between neighbors (Shick 1991) suggest the potential for inbreeding in some species.

All of the best-studied anemones live principally on rocky intertidal shores. Many of these, like *Anthopleura elegantissima* and *Metridium senile*, form extensive monoclonal, unisexual populations (Sebens 1982, 1983c; Hoffman 1986; Francis 1988) so that fertilization may be limited to adjacent clones. However, these species spawn relatively small ova that develop upon fertilization into drifting or swimming larvae (Ford 1964; Jennison 1979) so that genetic exchange between populations is expected and does occur (Hoffmann 1987). In contrast, *Haliplanella lineata* (= *luciae*) is apparently exclusively clonal, at least over large parts of its geographic range (Shick and Lamb 1977; Shick, Hoffmann, and Lamb 1979).

Dense monospecific aggregations may also form by extremely philopatric dispersal of relatively large brooded larvae, as is the case for two intensively studied species of *Actinia* in New Zealand, Australia, and Britain (Black and Johnson 1979; Ottaway 1979; Orr, Thorpe, and Carter 1982; Ayre 1982, 1983a, 1983b, 1984a, 1984b, 1985, 1987, 1988; Brace and Quicke 1985, 1986). However, all larvae that have been examined in these species are apparently clonally produced. Larvae are electrophoretically indistinguishable from their brood parents at four to five polymorphic loci, and gonads of brooders may be male, female, or absent entirely. Apparently normal maturation of ova and sperm occurs in all populations investigated. Sexual reproduction, as yet un-

documented, probably involves oviparous spawning and planktonic larval development. This idea is supported by a good fit to Hardy-Weinberg expectation for different genotypes (counting each clone as one individual) at the same locality, or among localities (Ayre 1984b, 1985, 1988).

One well-studied sea anemone, *Epiactis prolifera*, begins life as a female and then develops into a simultaneous hermaphrodite. This species broods large crawl-away larvae that apparently settle in the immediate vicinity of their parents (Dunn 1975a, 1975b, 1977). Electrophoresis indicates that individuals typically self-fertilize with infrequent outcrossing, but there is no genetic evidence for clumping of genetically similar individuals, as would be expected from short-distance larval dispersal (Bucklin, Hedgecock, and Hand 1984). At least three other species of *Epiactis* brood crawl-away larvae (Uchida and Iwata 1954; Fautin and Chia 1986; Strathmann 1987: 94–96).

The natural history of several species strongly suggests inbreeding, although genetic data are absent. The burrowing anemone, *Halcampa duodecimcirrata*, has large crawl-away larvae that develop within sticky gelatinous capsules near their mothers, and females lean toward adjacent spawning males, making fertilization between neighbors highly probable (Nyholm 1949). *Aulactinia incubans* is a small, intertidal hermaphrodite that internally broods its young to the juvenile stage (Dunn, Chia, and Levine 1980). The species is not abundant, but several individuals are typically found close together where it occurs. Isolated clusters of interbreeding kin thus seem likely.

Zoanthids are simultaneously hermaphroditic, morphologically (as opposed to socially) colonial anemones that routinely fragment to form dense clonal populations (Karlson 1981, 1983, 1986, 1988a, 1988b; Fadlallah, Karlson, and Sebens 1984). However, they spawn ova that develop into potentially very long-lived larvae (Scheltema 1971), and are presumably outbred.

Scleractinian corals are typically sessile, solitary or colonial polyps that secrete a calcareous exoskeleton. Most tropical corals are colonial simultaneous hermaphrodites, and spawn ova that develop when fertilized into swimming planular larvae (Fadlallah 1983a; Harrison et al. 1984; Babcock and Heyward 1986; Babcock et al. 1986; Szmant 1986; Richmond and Hunter 1990). Such species are almost certainly outbred, despite demonstrable self-fertilization in some mass-spawning species (Heyward and Babcock 1986; Richmond and Hunter 1990), and the likelihood that some reefs may be colonized primarily by larvae derived from the same reef (Sammarco and Andrews 1988; but see Willis and Oliver 1989).

A substantial minority of tropical scleractinians, however, including perhaps one-quarter of Pacific species and half of those in the Atlantic, brood larvae that crawl or swim and crawl (Fadlallah 1983a; Szmant 1986; Morse et al. 1988). Clutches of brooded larvae are commonly released at widely varying stages of development, with the result that some offspring are competent to settle on release, and do so. This has been shown best for two small faviids, *Favia fragum* (Duerden 1902; Lewis 1974a, 1974b) and *Manicina areolata* (Duerden 1902; Boschma 1929), and two pocilloporids, *Stylophora pistillata* (Loya 1976a, 1976b; Rinkevich and Loya 1979a, 1979b) and *P. damicornis* (Stephenson 1931; Harrigan 1972).

For *P. damicornis*, however, there is a serious problem of interpretation, because all of the hundreds of larvae examined so far are genetically identical to their brood parents at five polymorphic loci (Stoddart 1983, 1984, 1986; Stoddart and Black 1985). The situation seems very similar to that of the anemone *Actinia* (see above), except that sperm in Hawaiian populations of *P. damicornis* have been shown to be reabsorbed just before they would otherwise be released (Martin Chavez 1986). Comparison of gene frequencies among and within local populations suggests that in this case too, dispersal occurs by rare swimming, sexually produced larvae (Stoddart 1984, 1988), but this is speculation. *Pocillopora damicornis* is also commonly rafted for very long distances (perhaps across the entire Pacific!) on pumice and other floating debris (Jokiel 1984, 1990). Bioenergetic estimates and laboratory studies of larvae show that they remain competent to settle after 100 days, allowing them in theory to travel successfully from the central to the eastern Pacific (Richmond 1987).

Two species in the genus *Goniastrea* show apparently related patterns in life history and self-compatibility. Both *G. aspera* and *G. favulus* are common inshore shallow-water species on Australian reefs, although *G. favulus* is generally less common in and less restricted to these disturbed habitats (Babcock 1984). Both are mass-spawning synchronous hermaphrodites with external fertilization and similar investments in sexual reproduction, but *G. aspera* produces more numerous and smaller eggs (Babcock 1984, 1991). This species exhibits the common pattern of releasing buoyant egg/sperm packets that break up and typically mix with gametes from other members of the population prior to fertilization, and the resulting swimming larvae continue to float for at least several days. *Goniastrea aspera* shows some ability to self-fertilize in the laboratory, but self-fertilization is delayed and limited in extent relative to cross-fertilization (Heyward and Babcock 1986). In contrast, *G. favulus* releases negatively buoyant eggs embedded in

sticky mucus, and sperm are often released synchronously (Kojis and Quinn 1981; Heyward and Babcock 1986). Spawning occurs during the time of minimum water flow, and fertilized eggs typically remain on or next to the mother colony (Kojis and Quinn 1981). Larvae are at least initially benthic, although they begin to swim after several days in the laboratory (Kojis and Quinn 1981). Consistent with this life history is the finding of high selfing rates in laboratory crosses, with little or no delay in the onset of selfing (Heyward and Babcock 1986; Stoddart, Babcock, and Heyward 1988). Genetic data for one natural population do not show the expected reduction in heterozygotes associated with regular selfing, however, suggesting either that selfed progeny do poorly or that selfing is only common where population densities are not high (Stoddart, Babcock, and Heyward 1988).

Most scleractinians outside the tropics are small, solitary or encrusting, colonial corals. *Balanophyllia* are solitary, gonochoristic brooders that release large crawl-away larvae, which settle less than half a meter from their mothers (Gerrodette 1981; Fadlallah 1983b; Fadlallah and Pearse 1982a) and are almost certainly inbred. In contrast, *Caryophyllia smithi* and *Paracyathus stearnsii* spawn gametes that develop upon fertilization into pelagic larvae that can swim for up to 10 weeks (Lacaze-Duthiers 1897; Fadlallah and Pearse 1982b; Tranter, Nicholson, and Kinchington 1982).

Polychaeta

Polychaetes are the most diverse and abundant worms in the sea (Pettibone 1982) and exhibit a bewildering array of reproductive modes. They include forms ranging from minute to large, and sessile to highly mobile. Fauchald (1983) has outlined three general patterns of polychaete life histories. Annual species are commonly mobile, with moderately large eggs and planktonic larvae. Perennial species are typically sedentary, with moderately large to large eggs and benthic larval or direct (i.e., no free-living larva) development. Lastly, multiannual species (two or more generations per year) are typically sedentary, with relatively small eggs and benthic larval or direct development. This common association of sessile or sedentary adult habit with exclusively benthic development and dispersal suggests the possibility of inbreeding for the latter two categories. Reproductive patterns in polychaetes are not commonly taxonomically constrained, and many closely related forms have very different life histories (Grassle and Grassle 1977, 1978; Blake and Kudenov 1981; McEuen, Wu, and Chia 1983; Wilson 1983, 1991; L. A. Levin 1984b). Moreover, variation is not just a function of egg size; there are also differences in the relative composition of eggs

that correlate with developmental patterns and probably reflect differences in the energy requirements of different types of larvae (Eckelbarger 1986).

Most species of polychaetes, particularly those that are large, are gonochoric and spawn small ova (median oocyte volume 300 μ^3, n = 13 species), which develop when fertilized into pelagic swimming larvae that feed or develop on stored yolk (Schroeder and Hermans 1975). Many of these species also produce specialized swimming adults that swarm high in the water column to spawn. On all counts outbreeding is inevitable.

In contrast, a substantial minority of species, particularly small, sessile or sedentary filter feeders, show a different pattern. Approximately one-third of the species surveyed by Wilson (1991) have reproductive characteristics suggesting restricted larval dispersal. Clonal reproduction, sequential and simultaneous hermaphroditism, and potential for self-fertilization are also common. Many of these species brood relatively few, large eggs (median oocyte volume 2,050 μ^3, n = 16 species) that develop into juveniles without an intervening larval stage (Schroeder and Hermans 1975). Moreover, the size, growth rate, and behavior of the larvae depends in many cases on the number of nurse eggs or siblings consumed during development by the individuals that survive to hatch. The greater the number consumed, the more benthic the life history and the lower the probability of dispersal (Blake and Kudenov 1981).

Twelve of seventy-one species listed by Strathmann (1987: chapter 8) and L. A. Levin (1984a) do not swarm, and brood larvae that are benthic or demersal. Of these twelve species, three intertidal tubeworms (*Sabella media, Fabricia limnicola,* and *Axiothella rubrocincta*) brood exclusively benthic larvae (McEuen, Wu, and Chia 1983; Wilson 1983; L. A. Levin 1984a), so that inbreeding may occur despite densities of 20,000/m^2 or more. The possibility of inbreeding is strengthened for *F. limnicola* by its absence from plankton tows, recruitment experiments, and cleared areas studied over 4 years (L. A. Levin 1984a). *Sabella media* may also self-fertilize, since it is synchronously hermaphroditic, sedentary, solitary, and uncommon, although individuals may be able to collect and store sperm picked up in feeding currents (McEuen, Wu, and Chia 1983). Several intertidal Spionidae also have life histories that could result in inbreeding, including clonal reproduction and brooding of bĕnthic larvae, but these worms are very small, occur in enormous numbers, and actively move or are moved about over short distances (Dauer, Maybury, and Ewing 1981; L. A. Levin 1984a).

The size dependence of brooding is clearly evident among sessile

calcareous tubeworms of the families Serpulidae and Spirorbidae. Larger species of genera like *Pomatocerus* and *Hydroides* tend to be sequential hermaphrodites that spawn gametes and lack clonal reproduction (Schroeder and Hermans 1975). Aggregation at settlement (Wisely 1958; Scheltema et al. 1981) is by distantly related larvae that have been dispersed in the water column, just as for gregarious sabellarid tubeworms (Wilson 1968; Pawlik 1988). Alternatively, species of *Salmacina*, *Filograna*, and *Spirorbis*, all of which are very small, include both sequential and simultaneous hermaphrodites, brood larvae in the parental tube, and, except for *Spirorbis*, undergo extensive clonal reproduction (Schroeder and Hermans 1975). All spirorbids brood (Bailey 1969), but larvae of some species, such as *S. borealis*, usually swim briefly upon release, whereas others, like *S. rupestris*, *Pileolaria pseudomilitaris*, and *Janua brasiliensis*, settle and metamorphose immediately if suitable substratum is available (Gee 1963; Beckwitt 1980; Fauchald 1983). Selfing is possible among all spirorbids tested, but results in significant inbreeding depression (Gee and Williams 1965; Potswald 1968; Beckwitt 1982). Nevertheless, inbreeding among adjacent parents, offspring, and siblings appears inevitable for species in which offspring settle near their parents.

Polychaetes that live among sand grains, all of which are relatively small, also show a strong relationship between adult size and larval dispersal. Mean adult length of species with planktonic larvae is 9.8 mm ($n = 7$), while mean length of species with offspring released as juveniles is only 2.1 mm ($n = 8$) (Westheide 1984).

Members of the *Ophryotrocha labronica* species complex are small worms, and include both self-fertile hermaphrodites and gonochores capable of sustaining intense inbreeding for many generations (Åkesson 1977, 1984). In the closely related, less estuarine *O. diadema*, however, selfing does not occur despite gametic self-compatibility. Rather, simultaneous hermaphrodites reciprocally spawn in pairs (Sella 1985). In polychaetes generally, routine selfing does not appear to be common, although Smith (1950) provides strong circumstantial evidence for its occurrence in one burrow-dwelling, estuarine species with direct development.

Mollusca

There are five important classes of mollusks: Polyplacophora (chitons), Gastropoda (snails), Cephalopoda (octopuses, squids, nautiloids), Bivalvia (clams), and Scaphapoda (tusk shells). Clonal reproduction is rare in all groups. Cephalopods are gonochoristic with direct development, but are highly mobile as adults (Arnold and Williams-Arnold

1977; Wells and Wells 1977; Ward 1987); inbreeding is very unlikely. Scaphopods are sedentary burrowers in sediments. They are mostly gonochoristic, with external fertilization and pelagic larvae that settle within 2 to 6 days after fertilization, again making outbreeding inevitable (McFadien-Carter 1979). The other classes all have probable examples of both inbreeding and outbreeding.

Gastropoda. Prosobranchs are the commonest shelled snails in the sea. Many species are highly mobile, but there are also sedentary and cemented forms. Most are gonochoric with sex ratios commonly close to 1:1 or slightly biased toward females (Webber 1977; Hughes 1986). The most primitive reproductive systems occur among the archaeogastropods, which typically broadcast gametes and develop pelagically. Members of all other groups typically copulate, and juveniles develop partially or completely within external egg capsules. Protandric hermaphrodites and brooders are also fairly common. Overall, direct development (no free larval stage) is found in 39% of the 142 species of snails listed by Webber (1977). Clonal reproduction is very rare and occurs only by parthenogenesis.

The likelihood of inbreeding among free-living prosobranchs with entirely direct development depends primarily upon postlarval mobility, behavior, and abundance. For example, some species are highly mobile but aggregate to breed, so the critical data are the size of breeding groups and the faithfulness of snails to their parental group (see Breden [1987] for an analysis of a comparable situation in the toad *Bufo woodhousei*). Sufficient data are available for two intertidal species to suggest that some inbreeding may occur. Approximately 80% of over four thousand surviving marked individuals of *Nucella* (= *Thais*) *lamellosa* returned annually to the same sites and breeding populations over 5 years of observations (Spight 1974), and genetic data are consistent with these observations (Grant and Utter 1988). More strikingly, all marked *Nucella emarginata* moved less than 10 m over 1 year at two sites, and were almost as stationary at a third site (Palmer 1984). Moreover, there are striking morphological, physiological, and genetic differences in local populations of these snails with no regular clinal pattern (Campbell 1978; Crothers 1980, 1981; Palmer 1984; Day and Bayne 1988), just as would be expected if inbreeding occurs. Palmer (1984) did not, however, detect any reduced viability in offspring from matings between individuals from widely distant sites, suggesting that there is little or no intraspecific outbreeding depression.

Vermetids are cemented tubiculous snails that characteristically live in dense aggregations (Hughes 1986); they are dioecious, copulate, and

brood embryos for varying periods. Among ten species for which data are available, only two invariably produce planktonic larvae, five hatch crawling juveniles, and three produce planktonic or crawling juveniles, depending on the number of nurse eggs consumed by the developing embryo (Hadfield et al. 1972; Hughes 1978). Because of the sessile habit of adults, inbreeding is possible for species with crawling larvae, but there are no genetic data.

Opisthobranch gastropods have reduced shells or lack shells entirely. Most are simultaneous hermaphrodites with enormously complex reproductive anatomy, and copulation apparently precludes self-fertilization (Beeman 1977). Most species spawn small eggs, which develop quickly into tiny larvae that drift for hours to weeks before settlement. Some are viviparous, including the planktonic pteropods. Clonal reproduction is unknown. Populations of an intertidal nudibrach from sites separated by 3 km showed stable genetic differentiation in patterns suggesting limited gene flow, despite a pelagic larva (Todd, Havenhand, and Thorpe 1988). Nevertheless, outbreeding seems inevitable for all but the ectoparasitic pyramidellids, which usually lack a free larva and develop on their hosts (Hyman 1967).

Polyplacophora. Chitons are sedentary grazers, and most are gonochoric; there are two simultaneous hermaphrodites and one confirmed sequential hermaphrodite (Pearse 1979; Strathmann and Eernisse 1987; Eernisse 1988). Eggs are spawned free or in mucus packages. Fertilization apparently occurs while the eggs are still protected by the female. Most embryos hatch as immature larvae, but in some species are sufficiently developed to settle. Time in the plankton for nonbrooding species is 0 to 19 days with a median of 3.5 days (n = 11 species). About thirty species from half the known families brood larvae until they become juveniles; most are smaller than 2 cm as adults but some are much longer. A few other species lay benthic egg masses from which emerge crawling larvae. Most chitons aggregate for spawning. Inbreeding seems likely for species with crawling larvae if adults are stationary (territorial) or return to the same breeding aggregations. Brooders are very patchy in distribution (Eernisse 1988), which suggests limited movement of adults. Where they occur, brooders sometimes reach high densities (e.g., 500 per m^2), but these large populations may be the descendants of only a few colonists (Eernisse 1988). Eernisse (1988) found that gonochoristic brooders were less diverse genetically than free-spawners, a pattern consistent with inbreeding caused by limited dispersal. The two simultaneous hermaphrodites, *Lepidochitona fernaldi* and *L. caverna*, are small brooders capable of self-

fertilization (Eernisse 1988), and they self in culture even when they have the opportunity to outcross (Eernisse 1984, cited in Strathmann and Eernisse 1987). The preponderance of ovarian tissue in their gonads also suggests that selfing occurs regularly (Charnov 1982: 261), although parthenogenesis (Eernisse 1988) or reciprocal spawnings of animals in pairs (Fischer 1981; Sella 1990) are alternative explanations.

Bivalvia. Most bivalves are sedentary or sessile. Like *Mytilus edulis,* they are usually gonochoric with sex ratios of approximately 1:1 (Sastry 1979; Mackie 1984). Various types of hermaphroditism occur, however, particularly among sessile forms like oysters, shipworms, and giant clams, but also in the mobile scallops and cockles. Most species spawn small ova that are fertilized externally and develop in the plankton through a series of feeding or nonfeeding larval stages. Larval life ranges from 3 to 53 days, with a median of 18 days (n = 22 species). Self-fertilization may occur in some simultaneous hermaphrodites, but at lower rates than cross-fertilization, and parthenogenetic development may be induced in offspring of full-sib crosses of the oyster *Crassostrea virginica* (Longwell 1976). Inbreeding seems extremely unlikely in these spawning species.

Brooding is common among bivalves, especially in small, hermaphroditic species and in high latitudes and the deep sea; larvae are brooded within the mantle, gills, or external egg capsules (Sellmer 1967; Sastry 1979; Mackie 1984). Many brooded embryos are released as advanced pelagic larvae, but more are released as miniature adults (thirteen as larvae versus nineteen as juveniles [Sastry 1979]). Given their sedentary adult existence, inbreeding among close relatives seems possible for brooding bivalves that release benthic juveniles and live in low-energy environments (e.g., Jackson 1968), but there are no appropriate genetic or behavioral data. Most clams in the genus *Lasaea* are minute, intertidal, brooding, simultaneous hermaphrodites. Self-fertilization has been proposed for some species (Beauchamp 1986; Ó Foighil 1987; Tyler-Walters and Crisp 1989).

Crustacea

All crustaceans except barnacles are potentially mobile as adults, although symbionts or crevice dwellers may be quite sedentary (Bruce 1976). Clonal reproduction is uncommon except among Cladocera. The great majority are gonochoric or sequential hermaphrodites and have swimming larvae that pass through one to four stages and many more molts before settlement (Williamson 1982). Simultaneous hermaphroditism is rare except in barnacles. Some barnacles self-fertilize when

isolated. They do so only after a delay, however, and such offspring sometimes exhibit reduced viability (Barnes and Crisp 1956; Barnes and Barnes 1958). Barnacles also have long-lived pelagic larvae. Inbreeding is unlikely for all these groups.

Most crustaceans that develop directly into juveniles are small. The most important such group in the ocean is the Peracarida, which includes amphipods, isopods, mysids, tanaids, and cumaceans (Williamson 1982; Highsmith 1985). Small intertidal isopods such as *Sphaeroma serratum* have visible chromatic polymorphisms, and early work on these species revealed striking differences in karyotypes and color patterns along continuous stretches of coast (Bocquet and Lejuez 1974; reviewed in Hedgecock, Tracey, and Nelson 1982). Limited dispersal, highly biased sex ratios, population bottlenecks, and microgeographic genetic differentiation in *Jaera albifrons* strongly suggest inbreeding within subpopulations living in individual crevices (Carvalho 1989). Considerable morphological differences occur among local populations of the isopod *Excirolana braziliensis* on nearby isolated beaches in Panama (Weinberg and Starczak 1988), although these may represent different species (H. A. Lessios, personal communication, 1990).

The harpacticoid copepod *Tigriopus californicus* is abundant in high intertidal and supratidal rock pools (Dethier 1980; Burton and Feldman 1981; Burton 1986). Despite having demersal larvae, adults are free-swimming, and might be expected to disperse readily. Gene flow is extensive among neighboring pools on the same outcrop, but is highly restricted between outcrops separated by stretches of sandy beach. Moreover, F_2 hybrids between distant populations show reduced tolerance to extreme salinities and increased development times compared with offspring from crosses within a single population (Burton 1986, 1987, 1990a, 1990b). Outbreeding depression between widely separated populations does not imply close inbreeding within populations, however. Close inbreeding leads to the disappearance of females within four to five generations in another harpacticoid, *Tisbe reticulata* (Ginsburger-Vogel and Charniaux-Cotton 1982).

In contrast to these forms with direct development, intraspecific geographic variation in heterozygosity and gene frequencies among species with swimming larvae is commonly much lower (Hedgecock, Tracey, and Nelson 1982). Intense selection may result in much local differentiation over very short distances (Hedgecock 1986; Achituv and Mizrahi 1987), however, and the strong swimming ability of crustacean larvae may limit their passive drift to a greater extent than would be predicted by the duration of the larval stage (Burton and Feldman 1982).

Brachiopoda

Brachiopods are bivalved animals that were the dominant shelly fauna of the Paleozoic, but are only locally abundant now. There are two classes, Articulata and Inarticulata. Both groups have separate sexes, but they otherwise differ considerably in aspects of life history important to inbreeding (Jablonski and Lutz 1983; Reed 1987a). Most inarticulates spawn relatively small eggs that develop as planktonic larvae (Paine 1963; Chuang 1977), so that outbreeding is inevitable. In contrast, articulates spawn or brood larger eggs that are competent to settle within about 4 days after fertilization. Larvae are demersal, and in brooding species some percentage may settle just after leaving the mother (Doherty 1979). Thus inbreeding may occur among some brooding species. This possibility is consistent with the frequently clumped distributions of articulates, and the apparently preferential settlement of larvae upon adults (Logan and Noble 1971; Thayer 1977, 1981; Doherty 1979; Noble and Logan 1981). There are no genetic data.

Bryozoa

Bryozoans are sessile or sedentary and colonial. There are two marine classes: Stenolaemata, which includes the cyclostomes, and Gymnolaemata, which includes the ctenostomes and cheilostomes (Ryland 1970, 1982). All bryozoans are hermaphrodites. Some presumably primitive gymnolaemates spawn gametes that develop into planktonic larvae, but the great majority of bryozoans brood short-lived, nonfeeding larvae that settle within a few seconds to hours of release (Ryland 1974; Zimmer and Woollacott 1977; Reed 1987b; Ström 1977). Moreover, many species produce viable larvae when reared in isolation, so self-fertilization or parthenogenesis may be widespread (Maturo 1991).

Brooded larvae are typically positively phototactic on release in the laboratory, swimming upward during part of the brief period before they settle (Cook 1985; Cancino and Hughes 1988). This should prevent inbreeding, but a variety of evidence suggests otherwise. First, recruitment of *Bugula neritina* may fail to occur in favorable habitats less than 100 m away from dense, reproductively active populations, and transplant experiments show that the vacant habitats are indeed suitable (Keough and Chernoff 1987). Second, larvae of *B. neritina* settle preferentially next to siblings (Keough 1984), a phenomenon difficult to understand if larvae were carried more than a few meters from their parents. Third, in the only such experiment done for bryozoans, larvae of the cyclostome *Tubulipora tuba* settled on the same small piece of kelp as their parents at densities ten times greater than on similar pieces of

kelp only 1 m away (C. S. McFadden, personal communication, 1989). Moreover, cyclostome larvae multiply clonally in the brood chamber before release (Ström 1977), so the numbers of genotypes present among locally derived recruits should be low. Thus the probability of extensive inbreeding seems high for *T. tuba*.

Echinodermata

There are five extant classes of echinoderms: Echinoidea (sea urchins), Asteroidea (sea stars), Ophiuroidea (brittle stars), Holothuroidea (sea cucumbers), and Crinoidea (sea lilies) (Hyman 1955). All are mobile to varying degrees, and unstalked crinoids can swim. The great majority of all echinoderms are exclusively sexual, gonochoric, and spawn small ova that develop into pelagic larvae, which feed or live on yolk for several days to months before settling (Hyman 1955). For example, of fifty-three common species of echinoids, asteroids, ophiuroids, and holothurians from the American Pacific Northwest, thirty-six spawn pelagic eggs with a median diameter of 236 μm, whereas median egg diameter of the seven brooding species is 850 μm (Strathmann 1987). Outbreeding appears inevitable for the free-spawning species, and this conclusion is supported by genetic data (e.g., the crown-of-thorns sea star [Nishida and Lucas 1988]).

There are cases of clonal fission or autotomy of adults or larvae, hermaphroditism, and brooding scattered through each class (Hyman 1955; Emson and Wilkie 1980; Bosch, Rivkin, and Alexander 1989). The most extensive data are for tropical brittle stars (Emson, Mladenov, and Wilkie 1985; Hendler and Littman 1986; Hendler and Peck 1988; Mladenov and Emson 1988). Of thirty-seven reef-dwelling species from Belize whose reproductive mode is known, twenty-four have planktonic development, nine brood, and four are predominantly clonal species that probably rarely spawn gametes. Small, cryptic habitats, such as branching calcareous algae or the cavities of sponges, support abundant small brooding or clonal species. Clonal species typically build up large populations of sexually immature individuals. Moreover, when individuals with gonads are present, sex ratios are highly biased, presumably due to founder effects (e.g., only males of one species are known from Bermuda). Sexual reproduction, when it occurs, involves free spawning and planktonic development, so outbreeding seems inevitable. In contrast, brooders in the same habitats are hermaphroditic, possibly facultatively parthenogenetic (Hendler 1975), and commonly lack any planktonic stage. Given their cryptic habits and size, adult mobility is probably low, so inbreeding is expected; there are no genetic data.

Sea stars in the genus *Asterina* show a comparable diversity of repro-

ductive modes (Komatsu et al. 1979). Some are gonochores with widely dispersing larvae, and at least one is primarily clonal (Achituv and Sher 1991), while others lack dispersing larvae and are thus potential candidates for inbreeding (Strathmann, Strathmann, and Emson 1984). *Asterina phylactica* is a small simultaneous hermaphrodite that broods its young. Isolated individuals in the laboratory produce viable offspring, and there are no apparent differences in early viability of young from aggregated versus solitary brooders in the field. The abundance of solitary brooding individuals in the field, plus the dominance of ovarian tissue in the gonad (see above) suggest that selfing commonly occurs (Strathmann, Strathmann, and Emson 1984). This species is sometimes found in abundance in large, deep, high-elevation pools on exposed coasts (Emson and Crump [1979] estimate at least ten thousand individuals in one pool), but pools could be initially colonized by a few individuals with generally limited movement between pools. Thus inbreeding may occur even in sizable aggregations. Both *A. phylactica* and the larger *A. gibbosa* (which does not self or brood but also lacks dispersing larvae) showed no enzyme variability at six scorable loci (Bullimore and Crump 1982). *Asterina minor* is another simultaneous hermaphrodite capable of selfing; it lacks dispersing larvae but does not brood and regularly breeds in aggregations whose members are of unknown genetic relatedness (Komatsu et al. 1979).

Inbreeding is also possible for the two small holothurians *Cucumaria lubrica* and *C. pseudocurata*, which occur in dense, stationary aggregations, sometimes exceeding 4,000/m^2 (Rutherford 1973; Engstrom 1982; McEuen 1987). These species are dioecious, with a sex ratio of 1:1, and females brood eggs externally, with nearly all brooding at peak season. Juveniles are slow to leave their mother and presumably wander very little. Again, local populations are likely to be derived from small numbers of founders, but populations have not been analyzed genetically. Genetic studies of the infaunal brooding holothurian *Leptosynapta clarki* showed no evidence of selfing, close inbreeding, or fine-scale genetic differentiation, however (Hess et al. 1988).

Ascidiacea

Ascidians are usually small and sessile, and include both solitary and colonial forms, often within the same family. Most ascidians are simultaneous hermaphrodites and the few exceptions, including *Botryllus schlosseri*, are sequential hermaphrodites (Millar 1971; Kott 1974; Berrill 1975; Cloney 1987). All species of several large families or genera are self-fertile, but routine self-fertilization is not well documented (Ryland and Bishop 1990).

Colonial ascidians are viviparous, with an average period of embry-

onic development of 5 to 70 days within the atrium or body of the parent. After release, the large larvae may crawl, drift, or swim for a few minutes to 3 hours before settlement (van Duyl, Bak, and Sybesma 1981; Young 1986; Cloney 1987; Davis and Butler 1989). In *Podoclavella muluccensis* the average larva travels only 2.2 m, and at many sites densities are less than four colonies per square meter (Davis and Butler 1989). Inbreeding seems likely for species with larvae that swim little or not at all, but there are no genetic data except for *B. schlosseri* as noted above.

Most solitary ascidians spawn ova into the sea, where they develop into swimming tadpole larvae within 2 days, and subsequently swim free for a few hours to 6 days before settlement. Inbreeding is unlikely. However, two solitary species show a variety of characteristics that should promote inbreeding. *Corella inflata* is a "fugitive," shallow-water species that can self-fertilize eggs within the atrium; larvae are brooded there until they are ready to settle, often near their parents. There is no evidence of inbreeding depression, in contrast to the closely related, subtidal *C. willmeriana*, which has external fertilization, swimming larvae, and some self-sterility (Lambert 1968; Lambert, Lambert, and Abbott 1981). Many populations of *C. inflata*, however, have genetic characteristics indicating outcrossing, suggesting that self-fertilization occurs naturally only when potential mates are scarce (Cohen 1990). *Molgula pacifica* occurs in patchy aggregations of up to 50/m^2 (Young et al. 1988). Isolated individuals are completely self-fertile. Eggs are spawned but sticky and adhere to the bottom and to one another; development is entirely within the adhesive coat and without a larval stage. Juveniles hatch 36 hours after fertilization and settle near the parent. Nonbrooding solitary ascidians in the same habitat also build up large populations, but do so by aggregation of presumably unrelated pelagic larvae at settlement.

Summary of Patterns

The preceding review has been necessarily inferential, based as it is almost entirely upon comparative life history traits, particularly the mobility of all phases of the life cycle, and evidence for selfing. The species listed in table 10.2 are those whose life histories are most suggestive of inbreeding. Conclusive demonstration of inbreeding would require direct measurements and experiments (Ralls, Harvey, and Lyles 1986). Such information is unavailable except for *Botryllus schlosseri* (Grosberg and Quinn 1986; Grosberg 1987), and even those data are incomplete. Population genetic surveys are not on their own partic-

TABLE 10.2 Marine Invertebrate Species in Which Inbreeding Is Likely

Taxon	Characters	References
Demospongia[a]		
Stylopus sp. (orange)	*,SH,Fr,V,C	Ayling 1980
Stylopus sp. (pink)	*,SH,V,C	Ayling 1980
Anchinoe sp.	*,SH,V,C	Ayling 1980
Chondropsis sp.	*,SH,Fr,V,C	Ayling 1980
Polymastia robusta	*,O,M,C	Borojevic 1967
Polymastia granulosa	*,O,M,C	Bergquist, Sinclair, and Hogg 1970
Tetilla serica	*,O,M,C	Watanabe 1957, 1960
Tetilla cranium	*,V,C	Borojevic 1970; Bergquist 1978
Raspalia pumila	*,O,M,C,A,F	Lévi 1956; Borojevic 1970
Halichondria moorei	*,G/GH,V,C	Bergquist, Sinclair, and Hogg 1970
Hydroidea[b]		
Sertularia miurensis	*,G,V,B,C,F	Nishihira 1967, 1968
Tubularia larynx	*,G,V,B,C,Exp	Pyefinch and Downing 1949
Clava squamata	*,G,V,B,C,Al	Tardent 1963; Williams 1965, 1976
Plumularia alleni	*,V,B,M,C,Al,F	Williams 1976
Plumularia setacea	*,V,B,C	Williams 1976
Kirchenpaueria pinnata	*,V,B,C,Al	Williams 1976
Nemertesia antenina	*,G,V,B,C,M,Al	Williams 1976; Hughes 1977
Nemertesia ramosa	*,V,B,C,M,Al,F	Williams 1976
Eudendrium rameum	*,V,B,C,M	Wasserthal and Wasserthal 1973
Stylasterina		
Allopora californica	*,G,B,C	Ostarello 1973, 1976
Alcyonacea		
Alcyonium siderium	*,GH,V,B,C,Al,Exp	Sebens 1983 a,b,d
Xenia macrospiculata	*,G,Ma,Fr,V,B,C,M, Al,Exp	Benayahu and Loya 1984a,b,c; 1985
Gorgonacea		
Capnella gaboensis	*,G,Ma,Fr,O,B,M,C	Farrant 1985
Parerythropodium fulvum fulvum	*,G,Fr,O,B,M,C,Al	Benayahu and Loya 1983, 1985
Actinaria		
Epiactis prolifera	#,SH,O,B,C,Self	Dunn 1975a,b, 1977; Bucklin, Hedgecock, and Hand 1984
Epiactis japonica	#,SH,O,B,C	Uchida and Iwata 1954
Epiactis ritteri	#,SH,O,B,C	Strathmann 1987
Halcampa duodecimcirrata	#,G,O,C	Nyholm 1949
Cereus pedunculatus[c]	#,SH,V,C	Rossi 1975
Scleractinia		
Favia fragum	*,SH,V,B,Syp,C/S,A	Duerden 1902; Lewis 1974a,b; Szmant 1986
Manicina areolata	*/#,SH,V,B,C/S,F	Wilson 1888; Duerden 1902; Boschma 1929; Peters 1978

continued

TABLE 10.2 *(Continued)*

Taxon	Characters	References
Siderastrea radians	*/#,G,V,B,C/S,Al,F	Duerden 1902,1904
Stylophora pistillata	*,SH,V,B,Syc,C/S	Loya 1976a,b; Rinkevich and Loya 1979a,b
Goniastrea favulus[d]	*,SH,O,Syp,M,C/S,Self	Kojis and Quinn 1981; Heyward and Babcock 1986
Balanophyllia elegans	*,G,V,B,C	Gerrodette 1981; Fadlallah and Pearse 1982a; Fadlallah 1983b
Balanophyllia regia	*,G,V,B,C	Fadlallah 1983b; Tranter, Nicholson, and Kinchington 1982
Polychaeta		
Axiothella "rubrocincta"[e]	#,O,B,M,C	Strathmann 1987; Wilson 1983
Capitella capitata IIIa	#,B,C	Grassle and Grassle 1976, 1977, 1978
Sabella media	#,SH,O,B,C,Self	McEuen, Wu, and Chia 1983; Strathmann 1987
Fabricia limnicola	#,O,B,C	L. A. Levin 1984a
Fabricia sabella	#,G,B,C	Thorson 1946; Rasmussen 1973
Manayunkia aestuarina	#,SH,B,C	Muus 1967; S. S. Bell 1982
Spirorbis rupestris	*,SH,V,B,C	Gee 1963; Bailey 1969
Pileolaria pseudomilitaris	*,SH,V,B,C,Self,Exp	Beckwitt 1982; Fauchald 1983
Janua brasiliensis	*,SH,V,B,C,Self,Exp	Beckwitt 1982; Fauchald 1983
Prosobranchia		
Nucella emarginata	+,G,V,B,C,Aa,Cop	Palmer 1984
Nucella lapillus	+,G,V,B,C,Aa,Cop	Spight 1974; Crothers 1980, 1981
Littorina saxatillus	+,G,V,B,C,Cop	Janson and Ward 1984; Janson 1987a
Bivalvia		
Lasaea subviridis	#,SH,V,B,C,Self	Ó Foighil 1987
Lasaea rubra	#,SH,V,B,C,Self	Tyler-Walters and Crisp 1989
Polyplacophora		
Lepidochitona thomasi	#,G,O,B,C	Eernisse 1988
Lepidochitona caverna	#,SH,O,B,C/S,Self	Eernisse 1988
Lepidochitona fernaldi	#,SH,O,B,C,Self	Eernisse 1988
Isopoda		
Sphaeroma serratum	+,G,V,B,C,Cop	Bocquet, Lévi, and Teissier 1951; Bocquet, Lejuez, and Teissier 1960; Kaestner 1970
Jaera albifrons	+,G,Fe,V,B,C,Exp,Cop	Carvalho 1989
Excirolana braziliensis	+,G,V,B,C/S,Cop	Weinberg and Starczak 1988
Cyclostomata		
Tubulipora tuba	*,SH,V,B,C,Exp	C. McFadden, pers. comm.; Reed 1987b
Asteroidea		
Asterina phylactica	+,SH,O,B,C,Self	Strathmann, Strathmann, and Emson 1984

TABLE 10.2 (*Continued*)

Taxon	Characters	References
Holothuria		
Cucumaria lubrica	#,G,O,B,C	Engstrom 1982; McEuen 1987
Cucumaria pseudocurata	#,G,O,B,Syp,M,C	Rutherford 1973; McEuen 1987
Ophiuroidea[f]		
Amphioplus abditus	+,O,B,M,C	Hendler 1975
Axiognathus squamatus	+,SH,V,B,C	Hendler 1975; Emson, Mladenov, and Wilkie 1985
Ascidiacea		
Trididemnum solidum	*,SH,B,V,C/S	van Duyl, Bak, and Sybesma 1981
Molgula pacifica	*,SH,O,B,M,C,Self	Young et al. 1988
Botryllus schlosseri	*,GH,V,B,C/S?,Al,F,Exp	Grosberg and Quinn 1986; Grosberg 1987
Corella inflata[g]	*,SH,O,B,C/S?,Self	Lambert 1968; Lambert, Lambert, and Abbott 1981
Podoclavella moluccensis	*,B,C/S,Exp	Davis and Butler 1989

Note: This table includes sixty-eight species in which inbreeding is likely based upon life history characteristics. Species that produce larvae asexually and for which sexual larvae have not yet been demonstrated are not included. Symbols: *, sessile adults; #, sedentary adults; +, mobile adults; SH, simultaneous hermaphrodite; G, gonochore; GH, sequential hermaphrodite; Fe, sex ratio female-biased; Ma, sex ratio male-biased; Fr, fragments; P, polyembryony; V, viviparous; O, oviparous; B, broods; Syc, synchronous larval release within colony but not population; Syp, synchronous larval release within population; M, mucus tethering or adhesive packaging of larvae; C, crawling larvae; C/S, crawling or swimming larvae; Al, larvae aggregate with presumed kin; Aa, adults aggregate to copulate with presumed kin; F, larvae fuse with presumed kin; Exp, field experimental evidence for extremely philopatric recruitment; Self, self-fertilizing; Cop, copulates.

[a]Not including six brooding ceractinomorphs of Ayling (1980) for lack of additional information.
[b]All hydroids listed lack free medusae.
[c]Roscoff population.
[d]Genetic data for one population do not show evidence for routine inbreeding (Stoddart, Babcock, and Heyward 1988).
[e]False Bay population.
[f]Not including many brooding species of Emson, Mladenov, and Wilkie (1985), Hendler and Littman (1986), and Hendler and Peck (1988) due to lack of additional information.
[g]Genetic data (Cohen 1990) indicate that inbreeding may only occur in the field when potential mates are rare.

ularly useful for these purposes because such data are subject to widely varying interpretations: equally heterogeneous, fine-scale differentiation of populations may result over a few meters either from natural selection upon widespread recruits or from extreme philopatry and inbreeding (Burton and Feldman 1982; Burton 1983; Hedgecock 1982, 1986). Another important problem is how to evaluate anecdotal information on population densities and the potential for population bottle-

necks in species with dispersal patterns suggestive of inbreeding. With all these limitations in mind, a number of patterns are clearly evident.

1. Life histories that almost certainly result in outbreeding are the norm in every major invertebrate phylum in the ocean. Nevertheless, the potential for inbreeding is just as widespread, with likely candidates in all phyla surveyed (see table 10.2). Species with traits conducive to inbreeding are scattered throughout many families and genera that are dominated by species with traits more conducive to outbreeding. Some higher taxa appear to include species with only one set of traits or the other, but we suspect these are the minority in most phyla. This taxonomic pattern is strikingly similar to that found for obligately clonal organisms (Hughes 1989).

2. The taxonomic distribution of species with life history traits conducive to inbreeding suggests that they are secondarily derived from taxa that were primitively exclusively outbred (Hyman 1940; Mackie 1974; Schroeder and Hermans 1975; Webber 1977; Bergquist 1978; Strathmann 1978; Sastry 1979; Boero 1984; Boero and Sarà 1987; McKinney and Jackson 1989; but see Chaffee and Lindberg 1986). The potential for inbreeding has apparently evolved independently many times within each phylum, but there is little evidence for transitions from inbreeding to outbreeding. Again, the same pattern holds for obligately versus facultatively clonal organisms (Hughes 1989).

3. Of the various mechanisms that could lead to inbreeding in marine invertebrates, very low mobility at *all* phases of the life cycle is the most common. Exclusively crawling larvae occur in 84% of the sixty-eight species in table 10.2, and nearly all of the remaining species produce at least some larvae that do not swim before settlement. Moreover, adults are sessile in 59% of the species, sedentary in 28%, and mobile in only 13%. This extreme philopatry must lead to a high incidence of mating among siblings.

4. In striking contrast to the high incidence of philopatry, demonstrated cases of self-fertilization are uncommon. Selfing is found in only thirteen of the sixty-eight species (19%) in table 10.2, despite the high incidence of simultaneous hermaphrodites among those species (54% of the fifty-four species whose mating systems are described). Moreover, experimental confirmations of self-fertilization by isolated individuals commonly result in some form of inbreeding depression (Potswald 1968; Sabbadin 1971; Beckwitt 1982; but see Strathmann, Strathmann, and Emson 1984; Grosberg 1987), even though these same species apparently mate routinely with close relatives. We are unaware of any well-substantiated case of obligate or routine self-fertilization among marine invertebrates, with the exception of the anemone *Epiac-*

tis prolifera (Bucklin, Hedgecock, and Hand 1984) and probably the clams *Lasaea subviridis* and *L. rubra* (Ó Foighil 1987; Tyler-Walters and Crisp 1989). In only three other species does the domination of gonads by ovarian tissue suggest that selfing is common (*Lepidochitona caverna*, *L. fernaldi* [Eernisse 1988], and *Asterina phylactica* [Strathmann, Strathmann, and Emson 1984]), although parthenogenesis and reciprocal spawning by pairs (see Sella 1990) remain alternative explanations in the absence of other data. We may have underestimated the prevalence of selfing because of inadequate data, but selfing is clearly not the major form of inbreeding in marine invertebrates (Ghiselin 1974: 118). Moreover, genetic data have not supported the hypothesis of regular selfing in several cases where it was predicted from laboratory studies of fertilization and development (Stoddart, Babcock, and Heyward 1988; Cohen 1990).

5. Species with life histories conducive to inbreeding are typically smaller than those unlikely to inbreed, even within the same taxonomic group. The sponges in table 10.2 are thin encrusting or small massive forms rather than large vases, cylinders, or ropes, all of which seem to have dispersed larvae (Bergquist 1978; Ayling 1980). Colonies of potentially inbreeding hydrozoans, alcyonarians, and scleractinian corals are also typically small compared with the species in these groups that dominate most coral reefs and broadcast gametes. Similar patterns occur in most sessile unitary animals. The primary contributor to this pattern is the well-known association between brooding and small size (Strathmann and Strathmann 1982; Strathmann 1990). Simultaneous hermaphroditism is also common among brooders (Strathmann, Strathmann, and Emson 1984), however, and brooding species that self tend to be smaller than closely related brooders with separate sexes (Emson and Crump 1979; Eernisse 1988).

6. Modular and unitary species are equally likely to inbreed (thirty-three versus thirty-five species respectively in table 10.2). However, effective population sizes are generally much lower for modular species, so the chances of inbreeding are much greater. Contrary to previous assertions (Jackson 1985, 1986), chances of strong inbreeding are not closely associated with clonal propagation, which is characteristic of only 7% of the species in table 10.2. Clonal species do have, on average, much shorter periods of larval dispersal than aclonal species (Jackson 1985, 1986; Strathmann 1990), and have other characteristics that reduce effective population size (see above). But the extreme larval philopatry that is probably necessary for strong inbreeding is most common among species that do not commonly undergo budding, fission, or fragmentation (but see below).

7. The environmental distributions of species likely to inbreed are different from those of species that are obviously outbred. Many of the animals in table 10.2 occur principally in intertidal or otherwise highly disturbed environments, including high rocky shores, tide pools, mud flats, reef flats, shallow lagoons, and estuaries (Duerden 1902; Lewis 1974a, 1974b; Bocquet and Lejuez 1974; Beckwitt 1980, 1982; Fauchald 1983; L. A. Levin 1984a; Burton 1986; Emson 1986). This trend can even be seen when comparing potentially inbreeding species with close relatives that inbreed to a lesser extent or not at all (e.g., *Corella inflata* versus *C. willmeriana* [Lambert, Lambert, and Abbott 1981], *Asterina phylactica* versus *A. gibbosa* [Emson and Crump 1979], *Ophryotrocha labronica* versus *O. diadema* [Åkesson 1977; Sella 1985] and the "morphs" of *Cereus pedunculatus* [Rossi 1975] and *Bunodactis verrucosa* [Schmidt 1967]). This environmental pattern is less apparent for many modular or clonal groups, particularly among the sponges, for which it may not apply at all (Bergquist, Sinclair, and Hogg 1970; Ayling 1980). Among reef corals, all the species in table 10.2 are characteristic of shallow subtidal or intertidal habitats, but subtidal brooding species have not been sufficiently studied for comparison. It is possible that the differences in habitat distributions between unitary and modular animals in table 10.2 merely reflect the characteristically greater relative proportions of unitary species in marginal environments (Jackson 1977, 1985) and a relative dearth of comparably detailed work in subtidal habitats (e.g., subtidal, brooding, clonal corals in the genus *Porites*). Nevertheless, Shields' (1982) statement that inbreeding marine invertebrates are characteristic of stable environments is incorrect.

Explanations of Patterns

The association between various life history traits and the probability of inbreeding or outbreeding is relatively straightforward. Much more difficult to disentangle are the arrows of causality in these correlations, because characteristics that increase or decrease inbreeding typically have other important selective consequences (D. Charlesworth and B. Charlesworth 1987). This is clearly true for a feature like dispersal, but most characters involved have complex associated costs and benefits. For example, fusion between close kin may prevent close inbreeding when combined with alternating sequential hermaphroditism (Grosberg and Quinn 1986), but may also maximize the benefits of increased size while decreasing the costs of intraspecific parasitism (Buss 1982; Grosberg 1988; Grosberg and Quinn 1988). Added to this is the problem of inadequate data to test alternative hypotheses regarding

energetic or demographic trade-offs between alternative developmental and life history patterns (Strathmann 1985).

We consider in turn ecological, functional, and genetic constraints on the breeding systems and life histories of marine invertebrates. We use these terms loosely, realizing that the distinctions are somewhat arbitrary and that the explanations are unlikely to be mutually exclusive. Taxonomic constraints are clearly not an overwhelming factor because of the widespread co-occurrence of alternative life histories among closely related lower taxa within most major phyla. Although taxa certainly differ to some extent in their intrinsic potential for inbreeding (Strathmann 1985), we will not further explore this issue here.

Ecological Constraints

Several ecological arguments predict the observed association of extreme larval and adult philopatry with small adult size. First are a series of models analyzing the relative importance of risk reduction and spreading for large and small individuals (Strathmann 1974; Strathmann and Strathmann 1982). For example, small adults are likely to die sooner and have less total energy available for reproduction than large adults. Thus they cannot produce as many larvae over as long a period of time as can large organisms. Small adults may have the same mean success rate per larva as larger adults producing similar-sized propagules from the same location, but their variance in reproductive success will be necessarily greater. Species that brood typically have less variable recruitment patterns than do species that broadcast (Thorson 1946, 1950), so the hypothesis that brooding reduces variance in reproductive success seems reasonable. The selective advantage of reducing variance is particularly strong when intergenerational variance is involved (Gillespie 1973), as would be likely in small, short-lived species.

Second, the linkage between small size and direct development can be derived from models of the evolution of life cycles in marine invertebrates without considering variance in reproductive success (Roughgarden 1989). Whenever both planktonic habitat quality and benthic habitat quality decline simultaneously, Roughgarden's models predict that adults should become sexually mature at smaller sizes and larvae should develop benthically. The observed correlation between direct development and small adult size would therefore depend on a correlation between the quality of planktonic and benthic habitats. The models also assume that recruitment is limited by intraspecific crowding. We know of no environmental data that broadly support these assumptions.

Third, extremely short-distance dispersal in sessile organisms may permit one of the offspring to grow into space liberated by the death of the parent in situations where space is limiting (e.g., Sebens 1983b, 1986). The probability of parental death per unit of time is often much higher for smaller organisms (Hughes and Jackson 1985; Jackson 1985). Hence inbreeding may be associated with small size because offspring have a higher probability of inheriting parentally controlled space in small, short-lived species than in large, long-lived species (Willson and Burley 1983: 36).

Finally, the link between small size and philopatry may be explained in the context of the other major pattern observed, that of philopatry and highly disturbed habitats. There are three common solutions to the problem of guaranteeing the nearby presence of conspecifics for mating or for other beneficial aspects of group living (Buss 1981; Bertness and Grosholz 1985; Jackson 1985): larval philopatry, clonal propagation, and aggregative larval recruitment. Among serpulids and brittle stars, for example, rapid local buildups of populations can occur by fission, by brooding of sexually produced larvae that crawl a short distance from their parents, and by aggregative larval settlement (Wisely 1958, 1960; Gee 1963; Jackson 1977, 1985; Emson, Mladenov, and Wilkie 1985; Mladenov and Emson 1988). Solitary ascidians cannot propagate clonally, but they also employ aggregative settlement of widely dispersed larvae, or, more rarely, hatch directly as juveniles on substratum adjacent to or on their parents with similar effect (Young et al. 1988).

Which of these three alternatives is favored depends on the ecological and morphological characteristics of the species involved. Aggregative larval recruitment probably overwhelms the effects of either fragmentation or brooding when conditions are favorable. This option, however, is only reliable for species that are abundant, fecund, and widely distributed, because it depends on the regular or synchronized presence of larvae in the water column, and often entails substantial decreases in fecundity and increases in mortality due to excessive crowding. The second alternative, clonal propagation, requires a body plan compatible with fragmentation or budding. This automatically excludes most members of some taxa, for example, mollusks, crustaceans, and solitary ascidians, and is less likely for certain growth forms of modular species. In addition, one of the advantages of producing fragments rather than larvae is that the propagule begins its benthic existence at a relatively large size, and thus avoids the early vulnerable period associated with small size after larval settlement (Jackson 1985). However, if the adult is itself very small, this advantage associated

with fragmentation may be lost because the survival of fragments drops sharply with decreasing fragment size (Hughes and Jackson 1985; Knowlton, Lang, and Keller 1989). Thus when adults are themselves small, the production of large, philopatric larvae that are capable of active microhabitat choice (Morse et al. 1988) may be favored over the production of very small fragments. This should be true whether larvae are sexually or asexually produced. Two species of *Goniastrea* illustrate some of these points. Both *G. aspera* and *G. favulus* are massive corals that do not regularly fragment but nevertheless exhibit clumped distributions. The former is more abundant and fecund, and has widely dispersed larvae that apparently aggregate at settlement, while the latter has restricted dispersal of eggs and larvae (Babcock 1984, 1991).

Ecologically, the above three mechanisms may all result in rapid establishment of high-density populations, albeit at potentially very different levels of parental investment in reproduction. The probability of encountering a potential mate will also be increased by each of these mechanisms, except for clonal species that are gonochores or have strict self-incompatibility systems. The evolutionary implications of these mechanisms are entirely different, however. Aggregative recruitment of widely dispersed pelagic larvae leads inevitably to outbreeding, and the production of a few highly philopatric larvae strongly favors extensive sib-sib or parent-offspring matings. Clonally propagating, colonizing species may or may not self-fertilize, depending on their mating system.

Functional Constraints

Strathmann and colleagues (Strathmann and Strathmann 1982; Strathmann, Strathmann, and Emson 1984; Strathmann 1985) argue that large size selects directly against brooding because of changes in fecundity and brood-space relationships with increasing parental size, which secondarily result in increased larval dispersal and outbreeding. Among unitary animals, large masses of eggs may be difficult to ventilate because of surface-to-volume constraints, so brooding should generally be limited to species with small adults. Such physiological constraints may explain why large animals should broadcast (or at least not brood) their eggs, but not why many, but not all, small animals should brood (e.g., contrasting patterns for the small, solitary corals *Balanophyllia*, *Caryophyllia*, and *Paracyathus* discussed previously). Some unitary taxa also fail to show the predicted allometric relationship between body weight and egg volume (H. Hess, personal communication, 1991).

Modular animals provide an important test of the functional argu-

ment. Brooding is usually carried out in discrete modules (polyps, zooids) which are typically arranged in two-dimensional arrays (Jackson 1977, 1979), so surface-to-volume constraints should not apply except for extremely large modules (discussed for colonial animals in Strathmann and Strathmann [1982]). Caribbean corals, for example, include abundant species with polyps smaller than 2 mm that brood (*Porites* and *Agaricia* spp.) or broadcast (*Acropora* spp.), and species with polyps 1 cm or larger that also brood (various Mussidae) or broadcast (*Montastrea cavernosa*) (Fadlallah 1983a; Szmant 1986; Morse et al. 1988). Two groups, the faviids and siderastriids, include among them four brooding species (median polyp diameter = 5 mm) and four broadcasters (median = 4 mm). In contrast to this overall similarity in polyp size, *colony* size of these brooding species (*Favia fragum, Manicina areolata, Siderastrea radians,* but not *Diploria labyrinthiformis*) is much smaller than that of their broadcasting relatives (*Montastrea annularis, M. cavernosa, Siderastrea siderea,* and *Diploria strigosa*). Similarly, in *Porites,* all of which have small polyps, species with small adult colony sizes brood, while larger forms are spawners (Szmant 1986; Richmond and Hunter 1990). This correlation of small colony size and brooding within scleractinian families and genera supports an ecological explanation, as discussed above (Babcock 1991). So also does the trivial difference in average polyp size between western Pacific and Caribbean corals (Coates and Jackson 1987), despite the 43-fold difference in the apparent proportions of brooding and broadcasting species in the two regions (Richmond and Hunter 1990).

Genetic Constraints

Many analyses of breeding systems have considered their genetic implications (e.g., Williams 1975; Maynard Smith 1977, 1978; Lloyd 1979; Charlesworth 1980a; D. Charlesworth and B. Charlesworth 1987; Shields 1982, 1987; Lande and Schemske 1985; Schemske and Lande 1985; Campbell 1986; Templeton 1986; Uyenoyama 1986; Holsinger 1988a, 1988b; Hamilton, chapter 18, this volume). Outbreeding is thought to be favored when (1) populations contain large numbers of deleterious recessives or loci that show heterosis, (2) individuals are vulnerable to genetic arms races with parasites and pathogens, and (3) sib-sib competition favors genetic variability. On the other hand, factors favoring inbreeding include (1) the so-called twofold cost of sex, (2) the cost of producing males, (3) coadapted gene complexes, and (4) local adaptations to spatially varying environments.

The patterns we have documented can be plausibly derived from purely genetic considerations. First, selective pressures from parasites

might be higher in stable environments, where predictable and adequate abundance of hosts facilitates the persistence of parasites. Long-lived organisms should also be more vulnerable to the effects of arms races with short-lived parasites. The tendency for inbreeding to occur primarily in weedy and small organisms would be a logical consequence of these arguments (Hamilton, chapter 18, this volume). Second, species that colonize new areas with a very small number of propagules would tend to lose deleterious recessives during these population bottlenecks (Lande and Schemske 1985). This would also tend to produce an association between some forms of weediness and inbreeding. Third, large organisms that spawn both eggs and sperm are more likely to suffer from low to moderate levels of accidental selfing. Adults are unable to control the movements of gametes once spawned, and the dispersal of gametes prior to fertilization will be limited relative to the size of the adult. This would result in increased selection for mechanisms to prevent gamete wastage caused by the low viability of selfed offspring. Selfing would be reduced before loss of deleterious recessives occurs, thus preserving outbreeding (Maynard Smith 1978: 136). Finally, large organisms are often more fecund, which could potentially lead to greater intensity of sib-sib competition and thus favor outbreeding (Shields 1982). This last argument is weaker, however, because the extensive larval dispersal characteristic of most outbred marine invertebrates makes sib-sib competition very unlikely (Maynard Smith 1977; Jackson and Coates 1986).

Genetic mechanisms may also strengthen patterns of inbreeding and outbreeding generated by ecological and functional constraints through disruptive selection and positive feedback loops built into the selective processes (Lloyd 1979; Strathmann, Strathmann, and Emson 1984; Waller 1984; Lande and Schemske 1985). Outbred species tend to maintain large numbers of deleterious recessives and heterotic associations that produce substantial inbreeding depression and selective pressures to maintain outbreeding. However, once enforced inbreeding is established through population bottlenecks or low dispersal, then coadapted gene complexes and local adaptation lead to outbreeding depression and increased benefits associated with inbreeding. The models of Lande and Schemske (1985) thus predict that inbreeding and outbreeding are alternative stable strategies. The interaction of these opposing pressures with mating systems can be complex, however, even when only genetic factors are considered (Campbell 1986; Uyenoyama 1986; Holsinger 1988b). Neither can one neglect the costs of the mechanisms required to achieve the genetically optimal level of inbreeding or outbreeding (e.g., dispersal in models by Bengtsson [1978]

and Waser, Austad, and Keane [1986]). These and other factors undoubtedly help to break the positive feedback loops leading to higher levels of inbreeding or outbreeding.

Several types of genetic arguments also support the observation that the transition from outbreeding to inbreeding should be more common than the reverse. First, whenever inbreeding occurs through reduced larval dispersal, it may be argued that the loss of a specialized planktonic form is easier to achieve than its creation once lost (Strathmann 1978, 1985). Second, the loss of deleterious recessives during a population bottleneck is a much more rapid process than their accumulation during intervals of large population size (Nei, Maruyama, and Chakraborty 1975). Third, a dioecious or self-incompatible species will lose deleterious recessives during a population bottleneck, but species with nonrandom inbreeding will not reacquire deleterious recessives when large population sizes are reached (Lande and Schemske 1985).

Plants versus Sessile Marine Invertebrates

In both plants and sessile marine invertebrates, all genetic movement occurs in the gamete (pollen/egg and sperm) and young (seed/larva) stages, or by clonal propagation, suggesting natural parallels between the two groups. The summary of patterns of inbreeding in marine invertebrates was compiled without reference to the extensive literature for plants on inbreeding and outbreeding. When this literature was consulted, we found striking similarities and intriguing differences (see also Strathmann 1990).

Similarities

1. Outbreeding in plants tends to be the norm, but inbreeding has repeatedly evolved in a variety of taxa. Inbreeding in plants is a secondarily derived character, and the transition from outbreeding to inbreeding appears to be more common than the reverse (Stebbins 1950, 1957; Jain 1976).

2. Plants show a strong relationship between adult size and the probability of inbreeding. Trees are notable in being more likely than herbs to be dioecious or self-incompatible (Bawa 1974; Bawa and Opler 1975) and to have seeds that are carried by animals (Bawa 1980) and thus are probably more widely dispersed (Howe and Westley 1986).

3. Inbred plants are often ecologically weedy in the sense of being characteristic of highly disturbed environments (Stebbins 1950; Baker 1974).

4. Cloning plants do not tend to be strong inbreeders (Stebbins 1950). Indeed, Baker's (1974) alternatives of selfing in annual and clon-

ing in perennial weeds are strikingly parallel to the alternatives we present for marine invertebrates of larval philopatry, clonal propagation, and aggregative settlement by dispersed larvae (the latter not being an option for plants except when animals disperse seeds to distant but spatially restricted sites).

Differences

1. Inbreeding is more extreme in plants than in sessile marine invertebrates. In contrast to marine invertebrates, routine selfing is common in plants; discussions in the plant literature of inbreeding typically refer primarily to selfing (e.g., Jain 1976). Sib and parent-offspring matings are also common in plants (Levin 1986), although comparing the relative frequency of such matings in plants and marine invertebrates is not currently possible. Some plants show both substantial selfing and mating with close relatives (Waller and Knight 1989).

2. Inbreeding in plants is most conspicuously achieved by changes in the mating system, while in sessile marine invertebrates it is the potential for movement, particularly in the larval stages, that is most strikingly affected. In each group there are correlated shifts in mating and dispersal systems, however (see above).

3. Inbreeding is probably more common in plants than in sessile marine invertebrates. Allard (1975) estimated that one-third of all plant species are regularly selfing and thus highly inbred. It seems unlikely that one-third of sessile marine invertebrates are highly inbred, although the scarcity of data makes it difficult to estimate the frequency with any accuracy.

4. At the gamete stage, dispersal is generally more limited for marine invertebrates than for plants. In plants, the transport of pollen by animals and the ability of pollen to move from plant to plant increases the potential for long-distance dispersal in many species. Plant breeders are routinely concerned about unwanted fertilizations from dispersal of pollen over distances of 300 m or more (Levin 1986), while the limited studies of sperm and egg transport prior to fertilization in sessile marine invertebrates (reviewed above) suggest much shorter distances.

5. At the seed or larval stage, marine invertebrates have a much greater potential for dispersal. That larvae can profitably grow while they move, whereas seeds cannot, probably explains why the dustlike seeds of most orchids (Dressler 1981: 12) are the exception while planktotrophic larvae are the rule (Roughgarden 1989; Strathmann 1990). The tail of dispersal distributions is probably longer for marine invertebrates than for plants, even when most recruitment is local, because of the buoyancy provided by water. Dispersing propagules tend to be

expensive in plants because they must attach to or attract the interest of animals, whereas in marine invertebrates, dispersing planktotrophic larvae are cheap to produce compared with those that are immediately ready to settle (Strathmann 1990).

6. At the adult stage, sessile marine invertebrates are more mobile than plants, because marine invertebrates do not need to be attached to acquire nutrients and because water provides a much better medium than air for the rafting and floating of large organisms. Thus marine invertebrate colonists are more likely to arrive in a form that permits sexual reproduction without selfing (small groups of adults or an already fertilized adult) than are plants, which typically arrive as seeds and are often dependent on animals to carry their pollen.

Conclusions

In this review of inbreeding in marine invertebrates we have found that characteristics suggesting inbreeding are not uncommon, that there is little evidence for taxonomic constraint on the traits affecting the potential for inbreeding, and that there are morphological and environmental correlates of inbreeding in marine invertebrates that parallel those found in plants. Shields' (1982) claim that ecological arguments could not be consistently applied to both plants and marine invertebrates has not been upheld; more detailed review of the ecological characters associated with inbreeding in the latter group has shown that as in plants, inbreeding is commonly associated with unstable habitats.

A variety of ecological, functional, and genetic models make predictions compatible with the patterns observed. Whenever different models make the same general predictions, it is difficult to dissect their relative importance, particularly when derivative hypotheses are not equally amenable to testing. Moreover, many processes may contribute to the patterns, and the importance of various processes may vary among groups. Detailed studies of closely related species or populations with differing degrees of inbreeding offer the best hope of addressing the problem (May 1979). The many complexes of sibling species in marine invertebrates remain largely unexplored from this perspective. Comparative studies should include direct and indirect measures of mating patterns and dispersal, studies of inbreeding and outbreeding depression, and descriptions of ecological and morphological differences. Comparisons of the species listed in table 10.2 with more outbred close relatives (where they exist) is a logical starting place, and we pointed to a few examples above. Conspecific populations differing in inbreeding potential could also be examined.

While awaiting this information, we offer a few tentative conclusions based on the data at hand. In marine invertebrates, the primary characteristics that influence the potential for inbreeding or outbreeding are adult and larval mobility. These features are such fundamental components of ecology and life history that it seems parsimonious to assume that genetic systems initially respond to a level of inbreeding dictated by ecological and functional constraints. This conclusion is supported by the prevalence of inbreeding in plants, with their intrinsic limits on mobility, and the general rarity of close inbreeding in the more mobile vertebrates. Also supporting this interpretation is the fact that both plants and sessile marine invertebrates exhibit various solutions to the problem of colonization that have drastically different implications for inbreeding. In sum, at least on a coarse scale, inbreeding or outbreeding seems more likely to arise due to selection in response to a specific ecological situation rather than as the result of selection for inbreeding or outbreeding per se (see also Grosberg 1987).

Once the basic potential for inbreeding and outbreeding has been determined, however, intrinsic genetic factors appear to have some effect. This is seen most clearly when all members of a group have limited dispersal but only the smallest and weediest species show evidence of selfing. The same process may influence dispersal itself (i.e., general philopatry with selection for extreme philopatry in the smallest, weediest forms), but the data are generally not adequate to detect such subtle differences in dispersal potential.

Note added in proof: Recent evidence suggests that brooding bivalves in the genus *Lasaea* are parthenogenetic rather than self-fertilizing (Ó Foighil and Thiriot-Quiévreux 1991).

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