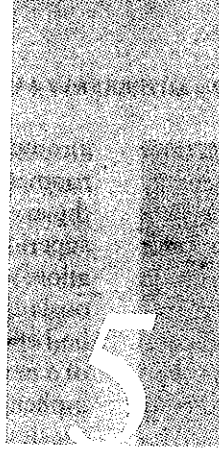take up

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Reproduction, Dispersal,

and Migration

Reproduction, dispersal, and migration are the fundamental processes that allow living populations to grow and exploit new habitats. **Reproduction** is the replication of individuals and is necessary for population growth. Nearly all species have some form of sex, which allows exchange of genetic materials among individuals. Sex and reproduction are intimately related, but many organisms can reproduce without sex, so the two processes must be kept separate. **Dispersal** is the spread of progeny to new locations, which may differ from that of the parent. Dispersal is a one way process, and often is controlled by the vagaries of water currents. Because water is a supportive medium and because water circulates rapidly over great distances, many newly hatched young can disperse over large distances, often as much as hundreds of km. As a result, marine species often have broad geographic distributions and the capability of rapid extension of their geographic ranges. Many species undergo the process of **migration**, which is a directed movement between specific areas. This process allows a multiplication of habitat use and can increase a species efficiency at exploiting the best resources at optimal feeding and spawning sites. In this chapter, we will discuss the important factors in sex, reproduction, dispersal, and migration.

Ecological and Evolutionary Factors in Sex

Benefits of Sexual Reproduction

✳ Sex is a nearly universal characteristic, despite the fact that there are considerable costs to organisms in maintaining it.

Sex is a species property whereby different individuals have the capacity to exchange or combine DNA, which causes offspring to differ genetically from their parents. Sex may involve simple transfer of DNA between bacterial cells or the union of gametes to produce zygotes. Nearly all organisms have some form of sexuality, ranging from the mating types of bacteria to the separate sexes and mating dance of humpback whales. The near universality of sex turns out to be a paradox, because there is a measurable cost to sex, at least in typical marine organisms characterized by Mendelian inheritance. In a typical diploid organism, each parent contributes the same number, n, of chromosomes to the offspring, giving the proper diploid number of $2n$. However, the mother usually invests much more into her offspring than does the father, even though half of the genes are his (think of the

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energy put into egg production and the usual greater female parental care). Why not devote all her energy to nurturing offspring that carry only her own genes?

There are other costs to maintaining sex. Finding a mate can be costly in terms of time and energy. In fiddler crabs (genus *Uca*), the males have two claws, one of which is much larger than the other and comprises over 40% of the body weight (Figure 5.1). This larger claw is used only for sexual displays and combat with other males. Because the claw is not used for feeding, males must compensate for this handicap by feeding longer and faster. Why should so much cost be attached to sex and sexual differences such as these?

The most obvious benefit of sex is the **increase of genetic diversity**. Genetic variation allows a population to live in a broader variety of habitats. There is also an increased **evolutionary potential** when the environment changes. Without sex, all offspring are genetically identical to the parent. No evolutionary change is possible, unless rare mutations occur. Asexual populations are therefore clones, with little or no genetic diversity. In contrast, sex provides continually new combinations of genes, and changes of gene arrangements because of chromosome crossover during meiosis. Crossing over increases intragenic changes, but also produces new combinations of alleles on different chromosomes. This gives the flexibility required for the appearance of offspring with new g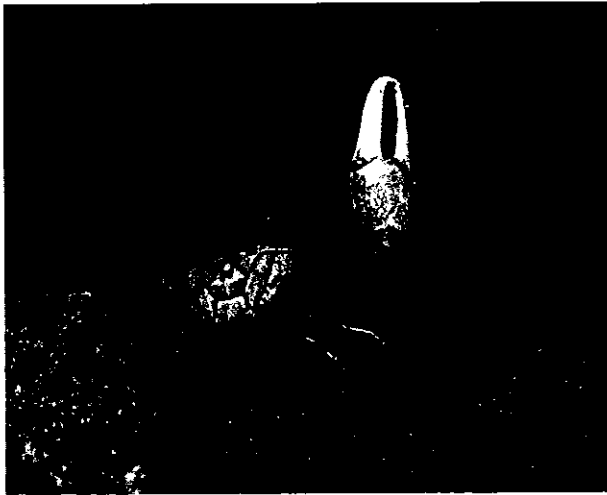ene combinations, which may be better able to exploit the environment and superior in meeting a changing environment. The process of natural selection results in the eventual dominance of these new and adaptively superior genetic variants. Genetic variation may also allow some of the population to survive the continual onslaught of diseases that confront a species. It would be better to possess a gene for resistance in the face of a new disease, rather than only one that determines a phenotype susceptible to the disease. A study of a species the snail genus *Potomopyrgus* demonstrates this well. This species, living in freshwater of New Zealand, has populations that reproduce sexually and asexually. The asexual populations are far less able to resist invasions of parasites.

Once sex exists, the differences between the sexes can be enhanced by **sexual selection**, the selection for secondary sex features (e.g., the antlers of deer, and the large claw of fiddler crabs) that increase mating success. Genetic variants that have the most successful mating abilities will increase in the population. Success might involve being the largest in overall body size, or having the largest antlers or the most conspicuous colors. For example, fiddler crab males with larger claws may be better at attracting mates or in holding high quality territories where females can incubate eggs. This would set a selective process in motion that could lead to selection for larger and larger claw size.

Types of Sexuality and Their Value

* Sexes may be separate (gonochoristic species), simultaneous, or sequential in the same body.

Nearly all kinds of organisms (with the exception of bacteria and some protozoa) have two sexes. Why only two is a story in itself, but we shall focus on the types of sex. Species that have separate sexes, or **gonochoristic** species, are the most familiar. In animals, this characteristic entails the need for a mechanism of sperm transfer. The presence of sea water permits the simple shedding of sperm (and possibly eggs) in the water. Planktonic gamete production often involves simultaneous spawning of males and females, which is often keyed into tidal or lunar rhythms. To avoid interspecific matings, the simultaneous presence in the water of eggs and sperm of many species requires extremely precise egg–sperm chemical recognition. Recent studies of abalone species on the west coast of the United States show that sperm–egg recognition proteins are extremely specialized to the degree that

Fig. 5.1 Displaying male of the fiddler crab, *Uca pugilator*. Note the large major claw, which is used for displays and male–male combat.

interspecific zygote formation is nearly precluded. In sea urchins, sperm that penetrate an egg's jelly coat have a protein that binds specifically with a receptor of only an egg of its own species. It may be that speciation in externally fertilized species is strongly controlled by such recognition proteins, and the rapid evolution of the recognition proteins may be the major factor in species isolation.

An **hermaphrodite** can produce gametes of both sexes during an individual's lifetime. In **simultaneous hermaphrodites**, sex cells for both eggs and sperm are active at the same time. Despite this, self-fertilization is rare, probably because inbreeding problems result in selection against such behavior. Being a simultaneous hermaphrodite means never having to say you're sorry, because an encounter between any two individuals guarantees that mating can occur. For example, acorn barnacles need to copulate in order to reproduce, but they are stuck with a sessile life style and can reach only nearby barnacles. Simultaneous hermaphroditism is a great advantage because the nearest individual must always be of the complementary sex. Barnacles have an extraordinarily long penis, which allows the barnacle to reach relatively distant fixed mates. One of the most fascinating aspects of simultaneous hermaphroditism is the common continual trading of mating roles. In many simultaneously hermaphroditic fishes, for example, members of a mating pair change sex roles every few minutes, first producing sperm, then spawning eggs (as the other individual, who also has changed roles, now deposits sperm).

Sequential hermaphrodites start their mature sex life first as one sex, and then they transform into the opposite sex. If they are male first, they are said to be **protandrous**, while if they are female first, they are **protogynous**. Many invertebrates, including some oysters, polychaetes, prawns, and coelenterates, are protandrous, whereas some fishes, particularly coral-reef fishes, are protogynous. In some cases, such as the diminutive protandrous polychaete species of the genus *Ophryotrocha*, sex change can involve a mere switch from the manufacture of oocytes to manufacture of spermatocytes. In protogynous reef fishes, however, the sex change also involves color, size, and morphological transformation. The snail *Crepidula fornicata* usually occurs in stacks, with larger and older females below and smaller and younger males on top (Figure 5.2). In their case, the stimulation to change sex involves contact with other individuals. Members of the stacks are oriented with the right an-

Fig. 5.2 A stack of the sequentially hermaphroditic snail *Crepidula fornicata* on a gravel beach. Females are on the bottom (right). Males are the smallest and topmost individuals and transitional forms are in the middle.

terior margin in contact with the same margin of the lower member. This allows insertion of the penis of the upper snail into the female gonopore of a lower snail.

* The relative contributions of different sexes to zygotes in the next generation determine the value of hermaphroditism, and the relative sizes of males and females.

Why be a simultaneous hermaphrodite? In a sense, one might turn the question around and ask: Why aren't all organisms simultaneously hermaphroditic, given the obvious advantage of finding a potential mate in every individual? The answer may lie in the limitations of being a jack-of-all-trades and master of none, versus being a specialist. Simultaneous hermaphrodites must invest not only in an apparatus to form gametes, but in the secondary sexual attributes necessary to attract another mate. If one started with a population in which genetic variants for hermaphroditism and for separate sexes coexisted, one might find that sexual selection would favor the "pure" males and females, because they can devote all their respective resources to either male or female mating structures and activity. The hermaphrodite would lose out in the competition, because it serves both functions, but each less efficiently. Hermaphroditism is favored only in cases in which the value of always being able to find a mate compensates for the disadvantage of not being a sexual specialist. The acorn barnacle may be just such a case. Simultaneous hermaphroditism is far more common in fresh-water in-

vertebrates, where it is generally harder to find a mate, owing to the lower population densities and the uncertainties of fresh-water existence.

Sequential hermaphrodites would seem to have all the advantages, given that they can be both sexes at different times. Unlike simultaneous hermaphrodites, however, they never have the advantage of always being able to find a mate in another individual. Then what is the advantage of changing sex? Here, the answer lies in the advantage of being a male or female at different ages or sizes. Consider protandry, or the quality of first being a male, and later a female. As a general rule, it costs more to produce eggs than sperm. It is also usually true that a larger and older animal has more energy at its disposal than does a smaller and younger one, simply because of the former's size. Then it would be best to be a male while still small, when a relatively small investment in sperm could produce many offspring. Above a certain threshold size, however, more offspring may be parented by being a female, because the available energy can produce more eggs. The threshold size of switching (Figure 5.3) should be that size at which the number of offspring parented would be the same if the animal were

either male or female. Below that threshold size, the animal would sire more offspring if it were male; above that threshold size, it would parent more offspring were it a female. The considerations are thus simply those in a cost–benefit game.

Commercial fishers inadvertently performed an experiment that tested certain aspects of the theory explaining the size at which sex switching occurs. Species of the prawn genus *Pandalus* are fished widely in both the North Atlantic and Pacific Oceans. The prawns mature first as males, but, after a variable period of time, switch to being females for the rest of their lives. A fishery in which such prawns were caught commenced in Danish and Swedish waters about 1930. Following this, the average body size of the catch decreased and the threshold size of switching to females also decreased. This can be interpreted as follows: Due to increased mortality (from fishing), females become relatively rare if males continue to switch sex only when they have reached a large body size. If a new genetic variant appears that switches at a smaller size, it will produce more offspring. Owing to natural selection for these variants, the size of sex switch will decline over time. If fishing pressure is very severe, in might "pay" for some individuals to mature first as females, rather than going through a male stage. Such populations exist.

Why in general should an organism be female first, then male? Here we must consider the common role of males as competitors for matings with females. Success as a male often entails agility at combat, bright colors, rapid swimming, and so on. Most of these traits are enhanced with increased size and experience. Many territorial coral-reef fish have flashy males and are protogynous. For example, the cleaner wrasse *Labroides dimidiatus* can usually be found in a group of 10–15 fish. All but the largest fish in the group are relatively dull in color and are females. By contrast, the largest fish is brightly colored and male. The male constantly tries to prevent the females from mating with interlopers. If this male is removed from his harem, the largest female will transform itself into a male and then serve the same function. In other species of wrasses, individuals can either be terminal-phase males (Figure 5.4), which hold territories, initial-phase males, or females. Initial-phase males do not hold territories and either spawn in groups with females, or attempt to sneak into the territories of the flashier terminal-phase males. Both initial-phase males and females are capable of changing into terminal-phase males. The proportion of initial-phase
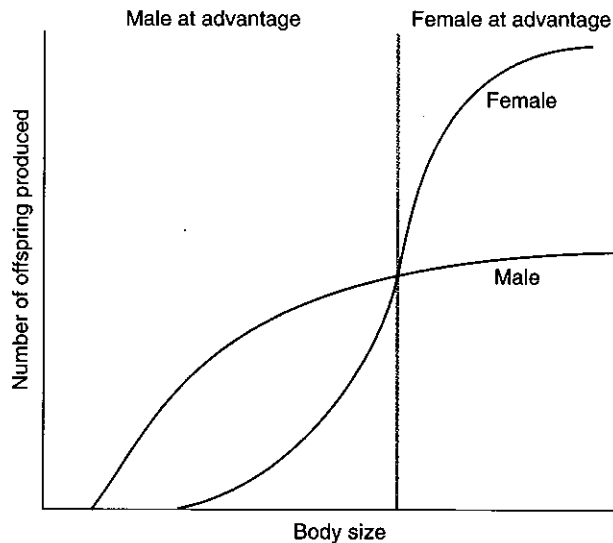

Fig. 5.3 A graph showing how to find the optimal size for a switch from male to female in a protandrous hermaphrodite. Shown are curves of offspring that an individual would parent if it remained either male or female for its entire life. The curves cross once, and output as a female surpasses that for a male as the crossover is reached and passed. For sizes smaller than the crossover, output is greater as a male.
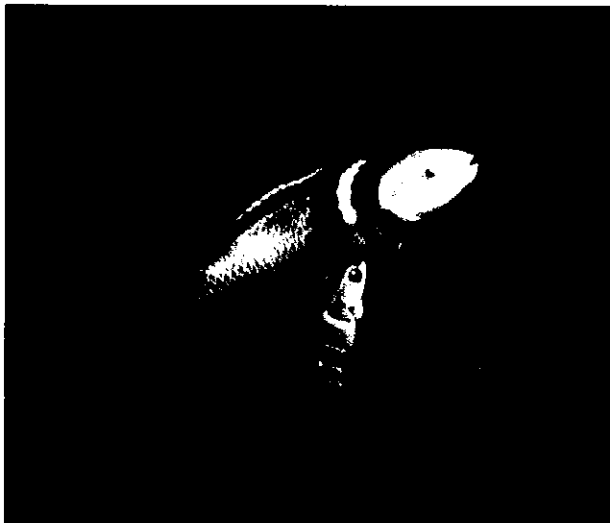
Fig. 5.4 A terminal-phase male of the bluehead wrasse *Thalassoma bifasciatum* courting a female. The two are about to mate. (Photography courtesy of Robert R. Warner.)

Fig. 5.5 A female brittle star, *Amphilycus androphorus*, carrying a dwarf male. The two are attached mouth to mouth. (From Hyman, 1955.)

Fertilization Success

✳ Fertilization success is affected by the mode of sperm transfer, the volume of gamete production, the distance between males and females, water turbulence, timing, and behavior.

males varies from place to place. This suggests that there are places where being a small male results in successful matings.

Although it is possible to classify types of sequential hermaphroditism, it is important to realize that many natural populations contain considerable geographic variation in sex change. This is especially true of coral-reef fish. Certain species may be locally protogynous, but could be gonochoristic in other sites. Hermaphroditism is not necessarily a fixed trait of a species and may be under active natural selection in different directions in different populations.

✳ Dwarf parasitic males are found in some species, in which it is difficult to find mates.

Where the sexes are separate and mate location is difficult, males may be small and either attach to or reside very close to larger females. Good examples are found among some barnacles, where tiny dwarf males attach within the mantle cavity of normal-sized females (e.g., the stalked general *Scalpellum* and *Ibia*, and the boring Acrothoracica). Many deep-water fish have dwarf males. Males show varying degrees of modification, and may be parasitic upon the female. In some cases, males are miniature versions of the female, except for the reproductive organs. This is common in some brittle stars (Echinoderm class Ophiuroidia), whose dwarf males cling to the much larger females (Figure 5.5).
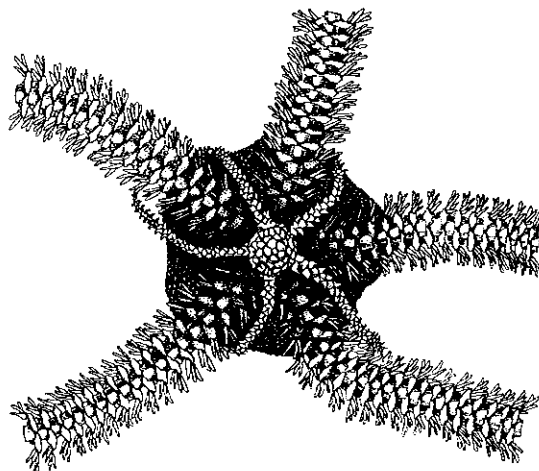
Many animal species use a variety of specialized means of sperm transfer involving direct male-to-female contact. In the simplest cases, found in some polychaetes and fishes, the male applies sperm to the body surface of the females or to an egg clutch as the female lays her eggs. Males of many species (e.g., gastropods, crustacea, and fishes) have copulatory structures . This mode of sexual contact increases the probability of fertilization and allows for mate selection. Many species, ranging from migratory fishes to intertidal drilling gastropods, form breeding swarms at the time of mating to further ensure the finding of a mate.

Although direct contact and copulation guarantee sperm transfer, many marine species take advantage of the presence of water and shed their gametes directly into it. At best, the gametes will mix and fertilization frequency will be high, because the sperm are so much more numerous than the eggs. However, turbulence or large distance between spawning individuals greatly reduces fertilization success. Studies by Don Levitan[1] and colleagues show that fertilization success in sea urchins can be greatly reduced by low volume of sperm production, combined with turbu-

1. See Levitan, Sewell, and Chia, 1992 in Further Reading.

lence and great distance between males and females. In one respect, however, turbulence can be a positive factor, because it permits sperm to be mixed with eggs shed by females. However, turbulence also dilutes gamete concentration and may reduce the probability of fertilization. Some species, such as the Pacific sea star *Acanthaster planci*, produce such large volumes of gametes that high rates of fertilization can occur between males and females separated by tens of meters.

Spawning by one or a few individuals may induce **mass spawning** of an entire local population. Mussels will spawn in response to phytoplankton in the water; the mussel larvae then can eat the phytoplankton. Timed spawning is usually keyed into lunar tidal cycles. In some reef sponges, all male individuals spawn simultaneously, spreading a fog of sperm over the reef. Many polychaete annelids can change morphology radically to transform themselves into **epitokes**, individuals that are essentially swimming sacs of gametes. Operating on a lunar cycle, they may swim to the surface and perform a nuptial dance, in which males and females swim rapidly about each other while releasing gametes into the water. South Pacific peoples take advantage of this behavior by harvesting swimming polychaete Pololo worms. Many coral-reef fish shed their gametes, but the fishes often locate themselves strategically on the downstream end of patch reefs, to minimize turbulence and gamete dilution. As a result fertilization success is surprisingly high, often exceeding 90%.

Parental Care

✳ Parental care is non-existent in many marine animal species, but in some cases females or males care for the young.

Marine species often exhibit absolutely no parental care. Many of these species spawn eggs and sperm, which unite to form zygotes, which, in turn, develop into free-swimming larvae that are completely at the mercy of the seas. However, in some groups, such as the fiddler crab *Uca*, the female incubates the eggs for a couple of weeks, and then releases swimming larvae into the water. Many species care for their young to an even greater degree. In some species, the young are reared to a juvenile stage within the mother. This is of course true for all marine mammals, but it is also the case for certain species of many of the invertebrate groups and fishes. The Atlantic and Pacific intertidal clam *Gemma gemma*, which is only a few mm long,

nurtures its young within the mantle cavity and releases them as shelled juveniles.

In some species, courtship is strongly related to male parental care. The male of the three-spined stickleback, *Gasterosteus aculeatus*, has a vivid red belly during courtship. It uses it to lure females to lay eggs in its hidden nest, usually among rocks on the bottom. Many aquarium enthusiasts have observed the male dance in a zig-zag motion, in order to lure the female to the nest. The great behaviorist Niko Tinbergen showed that the reproductive females have a stereotypical territorial response: They are strongly attracted even to silver disks painted red on the bottom. Behaviorist Susan Foster[2] has recently shown that in some locations the female participates, perhaps to a dominant degree, in mate selection and often swims up rapidly to a male and jumps onto on his back! During the courtship process, a female enters the nest and lays her eggs, which are fertilized externally by the male. Subsequently, the male aerates the eggs until they hatch. It is in the male's interest to rear the young of all females that have laid eggs in his nest, because they are his progeny. When a female enters, however, the eggs that have already been laid there by other females are—well—just food. Commonly, such a female will gobble up the eggs already present, and then bolt.

Nonsexual Reproduction

✳ Nonsexual reproduction permits the same genetic type to increase rapidly in an open environment.

Although sexuality is nearly universal in marine organisms, many of them are capable of reproducing without the formation of a zygote. Asexual reproduction lacks the cost of sexual reproduction and permits the spread of a genotype that has successfully colonized a given habitat. A population of genetically identical individuals, all deriving from one founder, is known as a **clone**.

The exact style of asexual reproduction varies, depending upon the biology of the individual group. Diatoms, a major group of marine phytoplankton, consist of cells or cell chains and can reproduce asexually by fission. The diatoms are usually unicellular and have a silica skeleton composed of two valves. At cell division, each daughter cell inherits one valve. Although the rate of cell division varies, most form fall

2. See Foster, 1990 in Further Reading.

within the range of 0.6 to 6 doublings per day under optimal laboratory conditions. The genetic clone with the highest combination of survival and doubling rate will come to dominate the local population.

In multicellular organisms, fragmentation can serve the same function as fission. Some annelids fragment, while others divide by forming head segments midway down the body and then splitting into two new individuals. Many seaweeds (e.g., *Gracilaria, Polysiphonia*) and many corals (e.g., the Caribbean stag horn coral *Acropora cervicornis*) may reproduce mainly by fragmentation. Tropical storms may benefit a stag horn coral population by dispersing newly created fragmented individuals.

Colonial invertebrates may reproduce asexually by fission of whole individuals in the colony. This mode is utilized by such colonial animals as encrusting sponges, coelenterates, and bryozoans. Marine algae and angiosperms include many **vegetatively reproducing** species. The marsh grass *Spartina alterniflora* usually consists of a large number of plants connected together by a rhizome system. It can be demonstrated by biochemical marker techniques that tens of square meters may be covered by genetically identical plants, all of which have derived from one progenitor. A marsh meadow is thus typically a series of clones.

The value of vegetative spread varies with the biology of the individual group. In some corals and sponges, the overall form of the colony is important in the collection of food. In certain cases, the strength of the colony is helpful in resisting strong currents. Large colony size may also be an advantage. Larger colonies will have a greater ratio of living surface to periphery exposed to moving sediment. They will therefore be superior to small colonies in surviving the movement of sediment along the bottom. For the same sort of reason, colonial forms may survive the attacks of predators, at least those attacking from the side.

Group living is of greatest value when it benefits related individuals. In this case, all individuals increase the survival of their own genes by group living. In groups that consist of unrelated individuals, some of the disadvantageous aspects of group living actually decrease an individual's probability of passing on its own genes. Consider the poor members at the periphery of a colony, which are more likely to succumb to predators. Their residence in the colony would be counterproductive to them as a group if the individuals in the center were unrelated to them. Because they are related, their exposure helps protect the in-

dividuals farther inside, and helps ensure the continued existence of the genetically identical group. As the famous biologist J.B.S. Haldane once said, "I would give my life for my brother, or for eight of my cousins."

Colonies of the colonial ascidean *Botryllus schlosseri* are usually founded by a single sexually produced larva, which attaches to a hard surface, metamorphoses (transforms into an immature adult), and then reproduces asexually. However, sometimes the larvae settle in aggregations. Using a unique genetic marker at an enzyme locus, Richard Grosberg demonstrated that such aggregations consist of larvae that are ge-
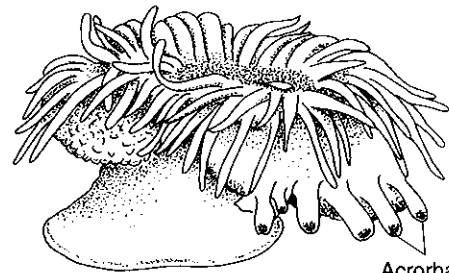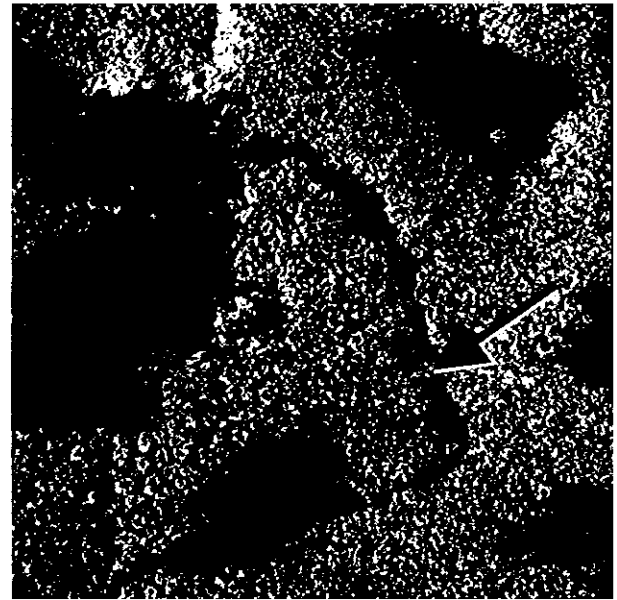

Acrorhagi

Fig. 5.6 The anemone *Anthopleura elegantissima* (top) often occurs as clones of a few hundred, but different clones have a bare zone between them (arrow, lower center of photograph). When an individual at the edge of one clone encounter members of another (bottom), they rear up and expose acrorhagi, which sting the individuals of the other clone. (Courtesy of Lisbeth Francis.)

netically similar in tissue compatibility. These larvae can fuse and form larger initial colonies, which are more resistant to predation, and may reproduce sexually at an earlier age, because the initiation of reproduction is size dependent.

The phenomenon of immunological recognition of genetically related individuals seems widespread among groups that may benefit from group living. On eastern Pacific shores, the anemone *Anthopleura elegantissima* (Figure 5.6, Plate VI.3) lives in large clones of several hundred to several thousand individuals. All derive from a single colonizing larva that repeatedly divides asexually. At any time, some individuals can usually be caught in the middle of fission. Lisbeth Francis[3] found that contacts between individuals of different clones result in a stereotyped aggressive response. The affected anemones raise their tentacles, and expose acrorhagi, which sting individuals from the other clone. No such aggression occurs between individuals within the same aggregation. This behavior can be interpreted as the defense of a communal territory, but it is not known what benefit is obtained from the defense.

Reproduction, Demography, and Life Cycles

Natural Selection of Reproduction

✳ The age of first reproduction, reproductive effort (resources devoted to reproduction), and longevity may be partially determined by patterns of mortality and predictability of reproductive success in the population.

Not all marine organisms spawn for the first time at the same age, nor do all devote the same proportion of available resources to reproduction. Consider the several Pacific species of salmon. All spend three years or so at sea while feeding as adults. They then make the long return trip to the tributary from which they originally came, and then spawn. During the trip upriver, they change morphology significantly, and, by the time they spawn, they have no ability to return to the sea. They are so weak after spawning that they lie on the spawning beds and soon die. By contrast, Atlantic salmon spawn, but then may go through at least one more migration–spawning cycle.

Why should there be such a difference among species? Differences among species can be found in the age of first reproduction, proportion of energy de-

voted to reproduction, or **reproductive effort**, and whether the animal spawns only once (**semelparity**) or more than once (**iteroparity**). The theory explaining these differences is based partially upon the premise that there is a **cost of reproduction**. We would expect that evolution would maximize the total reproductive output over the lifetime of an organism. If there is a cost to reproduction, it then matters how reserves are allocated to reproduction versus somatic growth. If more reserves are devoted to reproduction, there will be fewer that can be devoted to growth. If mortality during reproduction is heavy, then any investment of resources into growth may be wasted, because the organism will probably die before getting a chance to reproduce again. High adult mortality therefore selects for earlier reproduction. If adult mortality is low, then it may pay to invest in additional growth to ensure repeated reproduction, because larger adults can often produce more gametes and are often more experienced at winning mates than are smaller adults. Low adult mortality therefore selects for later age of first reproduction, and for repeated reproduction.

Commercial fishing pressure should strongly influence the distribution of life histories of the exploited fish species. After all, species with low reproductive effort and late age of first reproduction will be the first to be seriously affected by intensive fishing. By contrast, species with early reproduction and high reproductive effort would be best suited to withstand the onslaught. It also stands to reason that life histories may evolve as a response to fishing. Again, fishers have inadvertently performed an experiment for us. The spiny dogfish *Squalus acanthias* is fished heavily in Europe, but up to recently, was hardly fished off the American Atlantic coast. As a result, spiny dogfish populations are far more dense in American waters. The European populations have an earlier age of first reproduction, and higher reproductive effort in the first spawning season. Assuming that all other things are equal, this would indicate that fishing pressure has selected for reproductive tactics that ensure more reproduction. Recent increased fishing pressure on North American populations will probably yield the same effect.

Environmental uncertainty is also an important factor, and can be related to the potential success of a new year class. If environmental uncertainty is high, a new group of juveniles may not survive. This im-

3. See Francis, 1973 in Further Reading.

Table 5.1 The relationship between variation in spawning success (recruitment of young in the best year divided by recruitment in the worst year) and age of first reproduction and total reproductive span (both in years). Variation in spawning success seems to cause natural selection for increased age of first reproduction and prolonged total reproductive life span. (Data from Murphy, 1968.)

Population	Age at first maturity	Reproductive span	Variation in spawning success
Herring (Atlantic-Scandian)	5–6	18	25
Herring (North Sea)	3–5	10	9
Pacific sardine	2–3	10	10
Herring (Baltic)	2–3	4	3
Anchoveta (Peru)	1	2	2

poses a selective force for repeated reproduction, to ensure that some year class of juveniles will carry on the population. In effect, a female engaged in such repeated reproduction is hedging its bets against a bad year. Table 5.1 shows the age of first reproduction and the reproductive span as compared with variation in spawning success. Fishes with relatively high spawning variability tend to have a longer reproductive span than those with low variability.

Migration

✳ Fishes, crustaceans, turtles, and marine mammals often migrate between spawning and feeding grounds.

Many marine species have a reproduction and migration cycle similar to the scheme in Figure 5.7. Juveniles drift from a spawning area to a nursery ground and then move to an adult feeding ground as they grow older. Adults then migrate back to the spawning

Fish Migration: Which Way to Go?

Fish migration is one of the most perplexing phenomena in marine biology. Some species breed in fresh water but migrate, sometimes thousands of miles, to feed in salt water. Others do the reverse. Why should some species move in one direction, whereas others take the opposite tack?

Migration should make sense as a way to increase the growth rate of a fish population. After all, if migration was costly, genetic variants that did not migrate would win out in the evolutionary race. Migration costs a lot. Such a journey increases the risks of starvation, predation, and simply becoming lost! It must be that migration produced increased benefits in terms of increased reproduction at a suitable spawning ground and increased growth in a good feeding area.

As it turns out, there is a systematic variation in the relative abundance of anadromous and catadromous fish species in different regions. Anadromous fishes are more common in high latitudes, whereas catadromous fishes seem to dominate tropical habitats. There are, however, some glaring exceptions. The Atlantic eels are catadromous but live as adults in the North Atlantic. Overall, the pattern does hold well.

Zoologist Mart R. Gross and colleagues have recently discovered an important key to success in migration. Food abundance is obviously important for fish survival and growth. As it turns out, high latitude rivers and streams have lower overall productivity, and therefore less fish food, than the adjacent oceans. Thus anadromous fish spend their time feeding in the ocean but come into fresh-water bodies during a brief period to spawn. By contrast, tropical oceans are very low in productivity, but tropical rivers and streams are very productive. This suggests that the difference in migration is not really paradoxical. Fishes are feeding where the food is. An interesting experiment confirms the hypothesis. The Arctic char is anadromous, but experimental additions of food to fresh waters decreased the migrations back to sea.

Further Reading

Gross, M. R., R. M. Coleman, and R. M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. *Science*, v. 239, pp. 1291–1293.
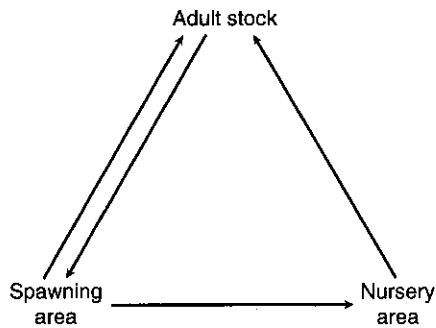
Fig. 5.7 A schematic pattern of migration. The two-way arrow between the spawning area and the adult stock area applies to cases where an adult migrates more than once to spawn. (After Harden Jones, 1968.)
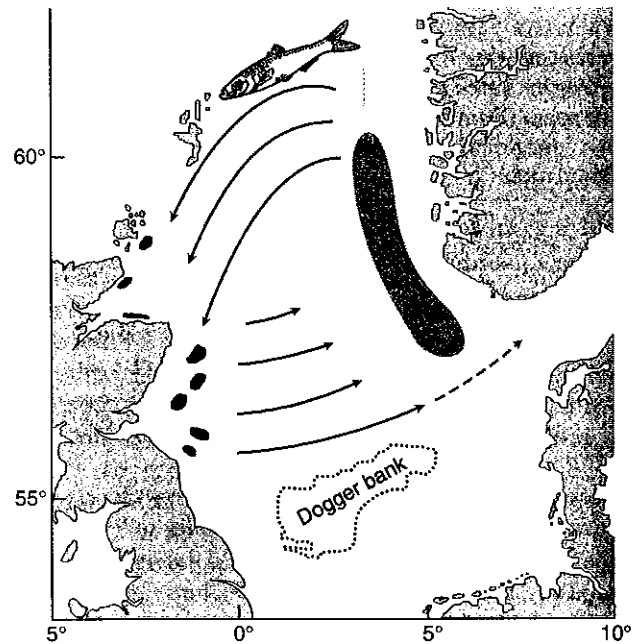

Fig. 5.8 The migration of the herring *Clupea harengus* in part of the North Sea, between spawning grounds (dark ovals) and feeding grounds (grey area). (After Harden Jones, 1968.)

area, The cycle of spawning, drift, and active migration back again reflects a maximization of reproductive success by feeding and spawning in the optimal sites. The movement from nursery grounds to different adult feeding grounds may reflect competition between juveniles and adults for limited food resources, or may result from differing food requirements of the different age classes. In many cases, fishes spawn for more than one reproductive season, so there is repeated migration between the adult stock area and the spawning area.

Migratory patterns are classified on the basis of the location of spawning and adult feeding grounds. **Anadromous** fishes (e.g., salmon, shad, sea lamprey) are those that spend most of their time in the sea but breed in fresh water. **Catadromous** fishes (e.g., eels of the genus *Anguilla*) spend their adult lives in fresh water, but move to the sea to breed. Many species (e.g., herring, cod, plaice) feed and breed in open sea water, though they migrate between different localities.

Migratory species vary in their degree of homing. Pacific salmon species are born in fresh water tributaries, and migrate to the sea after a few months. They then return several years later, almost always to the same tributary. By contrast, the early larval stages of the herring *Clupea harengus* (Figure 5.8) drift shoreward from the spawning grounds. As they grow, the herring move to deeper water and feed upon larger zooplankton. They return to a spawning ground after a year, but homing is not exact. The herring, (like cod and other species) often occur in distinct **stocks**, or separated populations that maintain separate migratory routes.

The American eel *Anguilla rostrata* and European eel *Anguilla anguilla* undergo one of the world's most spectacular and enigmatic migrations (Figure 5.9). Both species migrate from freshwater rivers, ponds, and estuaries in eastern American or European waters to spawn in partially overlapping areas in the Sargasso Sea. The trip to the spawning site is very poorly known, but adults are believed to swim in deep water. After spawning and zygote formation, the larvae then drift north and eastward in the Gulf Stream. American eels then move across the continental shelf towards shallow water eastern American rivers and estuaries, whereas European eels continue to drift across the Atlantic and are carried by currents into shallow waters there. The two species are distinctive in chromosome count, various biochemical genetic markers, and even in the number of vertebrae (which is determined at birth).

It is not clear at all why the two species migrate so far to their spawning grounds. Could such an area be optimal for spawning? If so, how was it "discovered" at such a great distance? One wonders whether this cycle started millions of years ago, when the Atlantic was narrower. The movement of larvae must be pas-
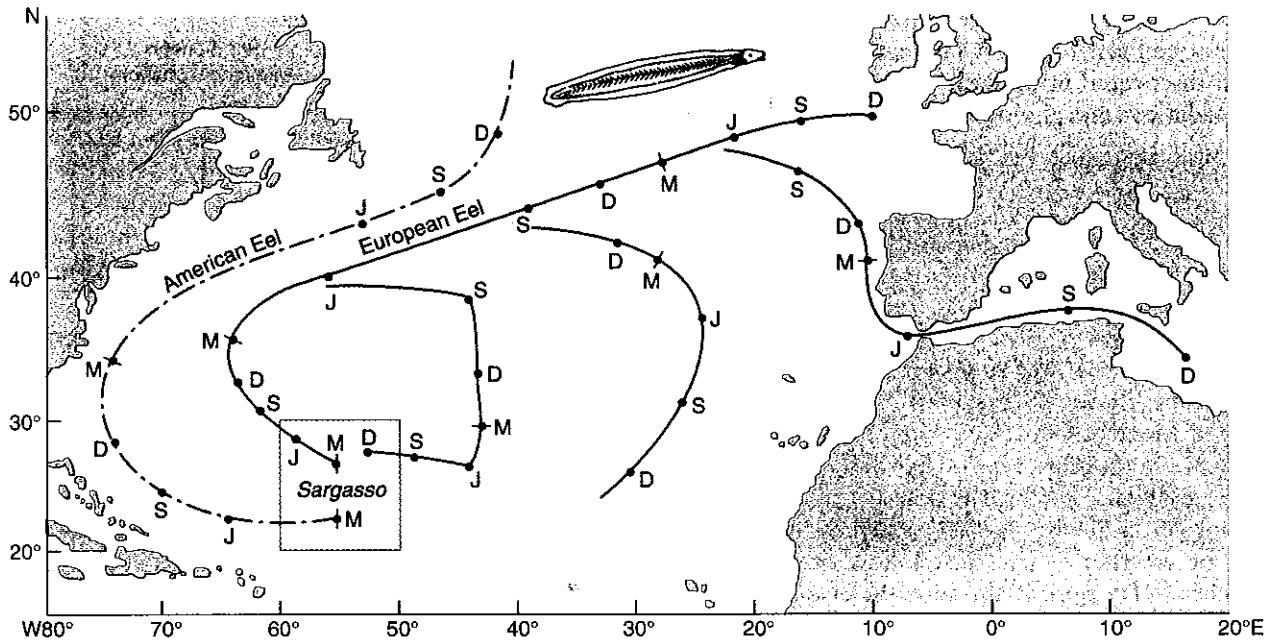
Fig. 5.9   The drift of larvae (leptocephali) from the spawning areas of the American eel and the European eel. The geographic positions of larvae hatched in March (M) in the two spawning area are plotted at quarterly intervals: June (J), September (S), December (D), and March (M). (From Harden Jones, 1968.)

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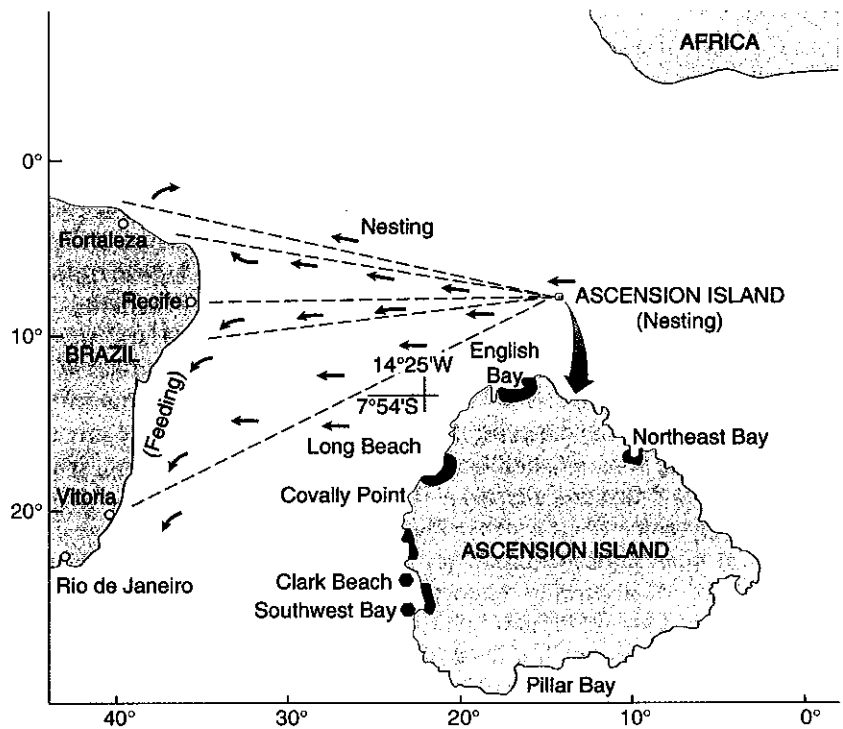ers whether this
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Fig. 5.10   The location of egg laying and feeding grounds of the Ascension island nesting populations of the migrating green turtle, *Chelonia mydas*. Nesting sites are shown in green on expanded map of Ascension island at lower right. (After Koch et al., 1969.)

sive, so the further passage of European eels must be determined genetically. A fascinating population has been discovered in Iceland, which appears to be intermediate in morphology and genetic markers. These individuals may be hybrids between *A. rostrata* and *A. anguilla*.

Green turtles (*Chelonia mydas*) are still something of an enigma to marine scientists. It is clear that they migrate hundreds to thousands of kilometers between feeding grounds and beaches where females lay eggs. Turtles that lay eggs at Tortuguero on the Atlantic coast of Costa Rica, for example, can be found at other times throughout the Caribbean, including Venezuela, Mexico, Cuba, and Puerto Rico. Tagged females seem to return repeatedly to the same beach to lay eggs (Figure 5.10). It is unclear whether this behavior starts at birth, when hatchlings move to the sea, or whether females just follow others to good beaches to lay eggs. Right now, the evidence is in favor of the hypothesis of imprinting at birth. Female turtles from different beaches are genetically distinct, but turtles from the same beach are very similar. This can be shown by studies of the DNA in their mitochondria, which are inherited maternally. Populations from different beaches have probably been isolated from each other long enough to have diverged genetically.

Larval Dispersal: The Long and the Short Haul

Modes of Dispersal

✳ Dispersal and range extension of marine populations are strongly controlled by currents that transport larvae and may have important ecological consequences.

Planktonic dispersal does not guarantee the ability to survive a long trip across the ocean, or to colonize new habitats successfully. The overwhelming majority of planktonic larvae die in the water column. They are swept to inappropriate habitats, are eaten by predators, or starve. Most recruits, even of planktonic larvae, probably come from nearby. Figure 5.11 shows the general possibilities of larval transport. Depending upon the local current regime, larvae might be swept off shore, or they might even by brought onshore by wave trains (see following discussion on larval mortality). Longshore drift is common and larvae usually are moved parallel to coastlines to some de-
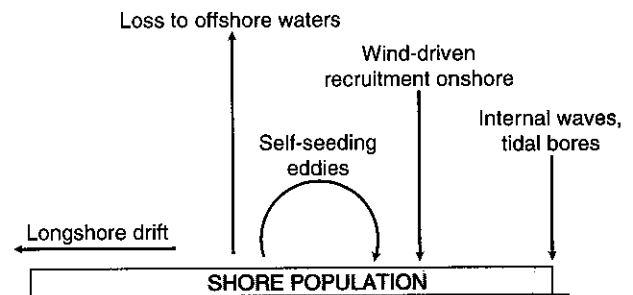

Fig. 5.11   General types of movement of larvae of benthic invertebrates with respect to the coastline.

gree. This may permit rapid extension of a species' biogeographic range. Finally, inhomogeneities in the coastline often create eddies, which may concentrate planktonic larvae (see further discussion in Chapter 7 on the movement of plankton by currents).

Surprisingly reduced dispersal of planktonic coral larvae was demonstrated for corals by Paul Sammarco (1989) who monitored larval settling in the vicinity of an isolated patch reef in the Great Barrier Reef of Australia. Settling plates were placed at various distances from the patch reef and a detailed study of local water currents allowed a prediction of sites where larvae might be concentrated. Settling occurred mainly in the close vicinity of the patch reef (Figure 5.12), suggesting that most larvae come from within the patch system itself. Settlement was greatest in a vortex of currents, where water was trapped and recirculated for a while before being swept to sea.

Although average dispersal distance is probably short, the potential exists for long-distance dispersal, and this potential must increase with the planktonic larval life span, and with the favorable nature of ecological opportunities at the distant site. Rudolph Scheltema discovered that many planktonic larvae of coastal invertebrate species could be found in the open sea (Figure 5.13), particularly in major trans-oceanic surface currents. He termed such larvae **teleplanic larvae** and found trans-oceanic similarities in species, whose larvae were common in the open ocean. Another particularly interesting case is that of the larvae of the coral *Pocillopora damicornis*, which is widespread and dominant throughout Pacific coral reefs. Robert Richmond has shown that these larvae can live in the plankton and are competent to settle and metamorphose for periods greater than 100 days. This may explain the coral's broad geographic distribution. The larva's symbiotic zooxanthellae (see
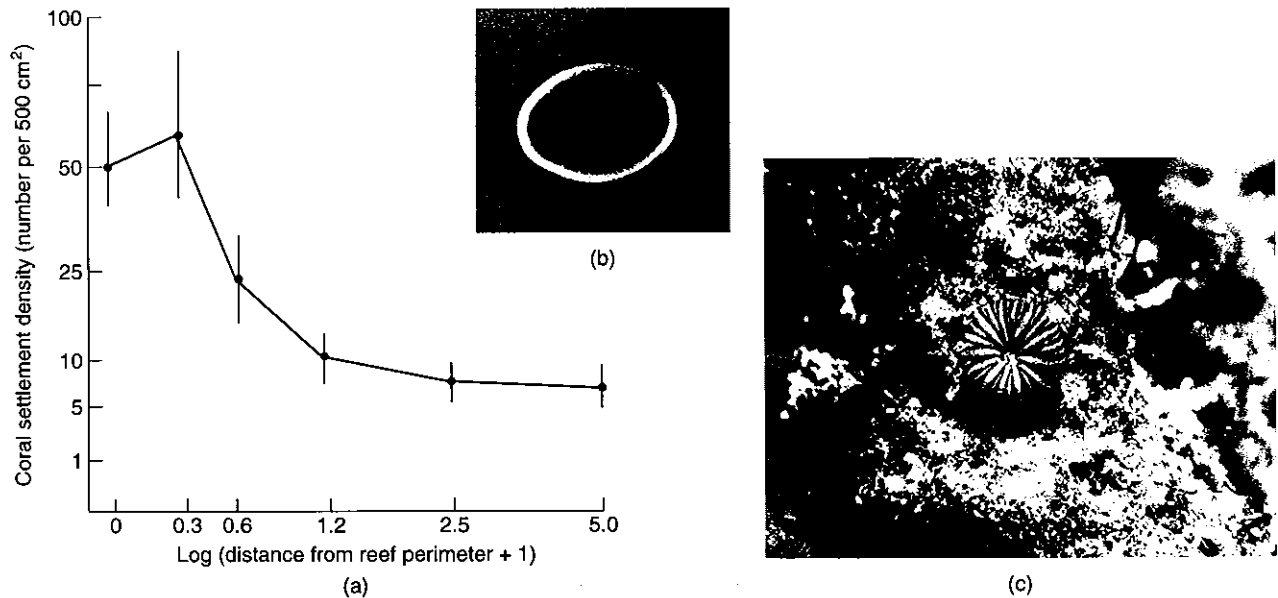
Fig. 5.12 (a) Diagram illustrating settlement onto settlement plates of planktonic coral larvae around a patch reef on the Great Barrier Reef of Australia, as estimated by counts of newly settled coral colonies. Note that settlement was highest near the patch reef, indicating that most settlers came from within the patch itself. (After Sammarco, 1991); (b) a coral planula larva; (c) a newly settled coral, only a few mm across (b and c photographed by Robert Richmond).

Chapter 15) photosynthesize and provide food to the larva, which fuels its journey over long distances across the open sea.

If some ecological opening exists, arriving larvae may flourish, reproduce, and continue to extend the species' geographical range along a coastline. Such invasions have happened several times during the last century, and the sudden expansions may have been aided by commercial shipping. In the mid-nineteenth century, the shore periwinkle *Littorina littorea* arrived on the shores of Nova Scotia, and then spread southward. It arrived at Cape Cod, Massachusetts, by the turn of the century and has now reached the Middle Atlantic States. It is unlikely that the species will spread much further southward, given its thermal and geographic ranges in Europe.

* Marine invertebrate offspring may be (1) brooded or released as small adults, (2) dispersed only to a small degree by means of relatively short-lived, yolk-dependent lecithotrophic larvae, or (3) dispersed great distances by means of longer-lived plankton-feeding planktotrophic larvae.

The hallmark of larval production and dispersal is a complex life cycle. An adult stage gives rise to a dispersing larva, which moves to a new site and completes the cycle by establishing itself and eventuallly growing to reproductive maturity. Figure 5.14 shows an example of such a cycle. Although there is a continuum of dispersal distances, several qualitatively different types of release and spread of larvae result in modes of dispersal distances. **Direct release** of individuals next to adults is the shortest type of dispersal. Many species are **viviparous**, or bear live embryos and they then release juveniles as crawling miniature adults. Such young may then crawl directly on the mud or on the rocks. The Atlantic periwinkle *Littorina saxatilis* broods fertilized eggs in a modified oviduct, and fully shelled young snails are later released. Many Antarctic species of feather stars (comatulid crinoids) develop their eggs in brood chambers located near the gonads in the arms at the pinnule bases. Other species are **oviparous**, or produce young that hatch from egg cases. Several species of the drilling genus *Thais* lay egg capsules that they attach to rocks. Embryos develop in the eggs and hatch as fully-shelled juveniles. Some of the eggs may serve as nurse eggs and are consumed by the hatchlings. It is extremely common for meiofauna to have direct release, since any sort of current-driven dispersal will likely
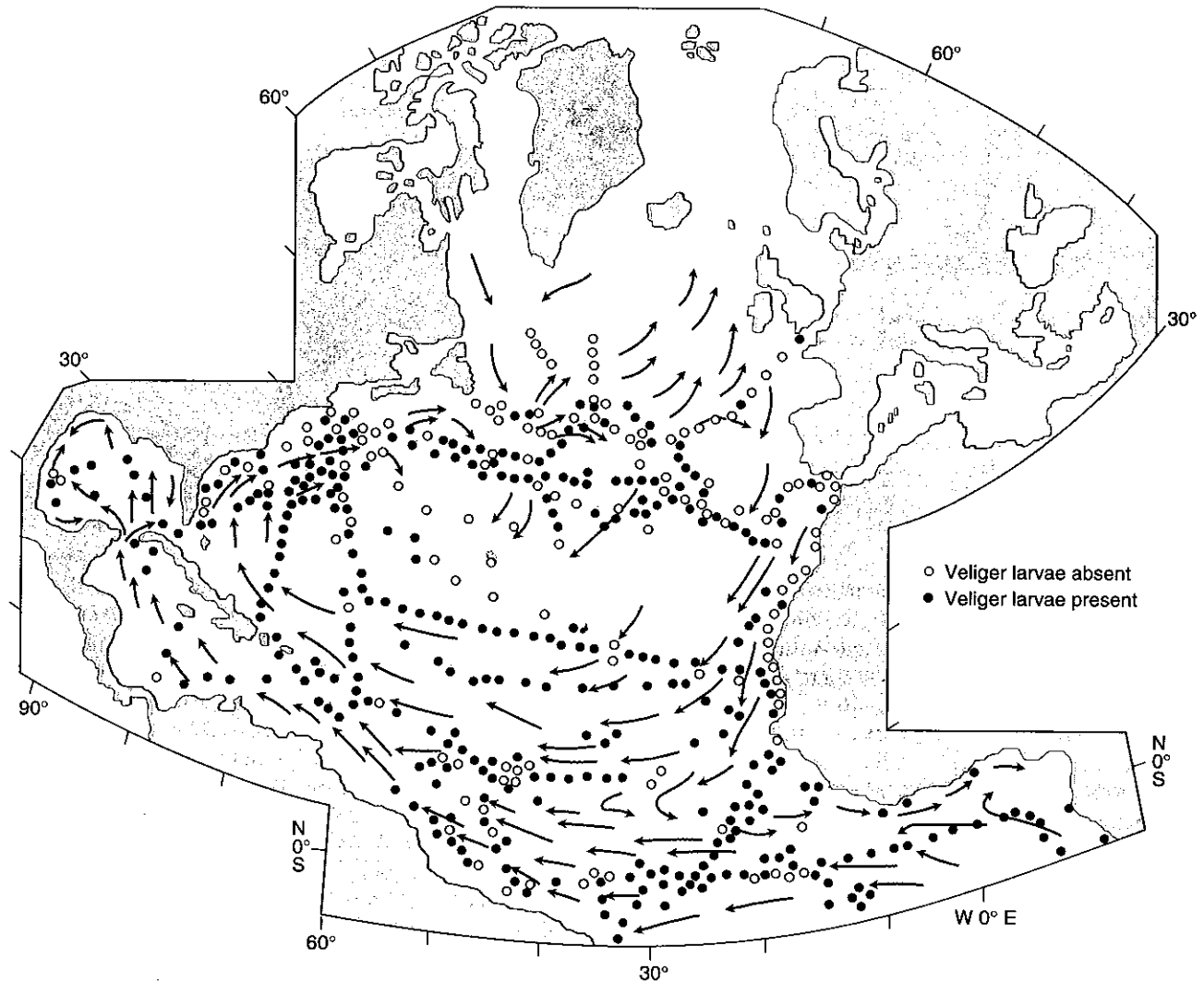
Fig. 5.13 Geographic distribution of teleplanic gastropod veliger planktonic larvae, based on samplings taken in the tropical and North Atlantic Ocean. (After Scheltema, 1971.)

take them to inappropriate habitats. The small size of meiofauna also restricts them to releasing very few young, which puts a premium on maximizing survival. Dispersal encumbers great risks (see following discussion), so direct release is therefore favored in these forms.

Most invertebrates have larvae that swim for varying amounts of time before settlement and metamorphosis. **Lecithotrophic larvae** (Figure 5.15) are swimming larvae that depend on nourishment from the yolk provided in a relatively large egg; the larvae have no feeding or digestive structures. They are capable of limited swimming, and spend a few hours to a day

or so moving either along the bottom or up in the water column. This mode of larval development cannot permit dispersal for much more than 10–100 meters. Lecithotrophic larval development occurs in species of many phyla, including mollusks, annelids, and ectoprocts.

Planktotrophic larvae feed while they are in the plankton. They usually have specialized larval feeding structures and digestive systems. They feed on planktonic bacteria, algae, and smaller zooplankton and usually drift for one to several weeks in the water column (Figure 5.16). Because of the time they spend in the open waters, they have a great capacity for long-
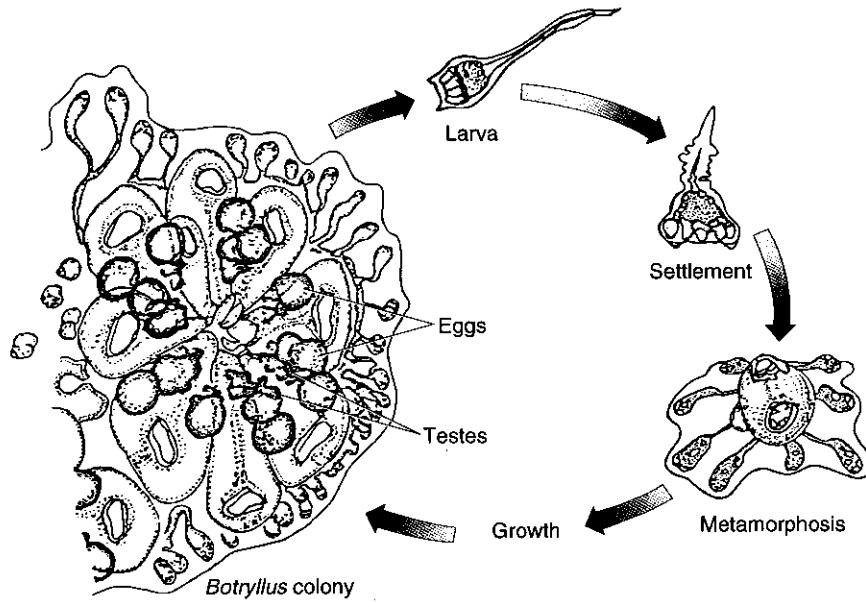
Fig. 5.14 Example of a complex life cycle of a marine invertebrate with a dispersing phase. The colonial sea squirt *Botryllus schlosseri* is a colonial hermaphroditic species. Sperm move through the water from one colony and fertilize a nearby neighbor. Larvae emerge and move only a couple of meters to settle, metamorphose, and establish a new colony.

distance dispersal. In most groups, development proceeds through a number of planktonic developmental stages. Until it reaches a terminal stage of development, the larva cannot find the adult habitat and is incapable of metamorphosing into the benthic adult stage. This requires a minimum time to be spent in the plankton. If a suitable adult substratum is not found, the larva may be capable of delaying metamorphosis.

Lecithotrophic larvae are often covered with ciliary bands, which are used for locomotion. However, planktotrophic larvae use ciliary bands or tufts to move and to feed upon the planktonic food (Figure 5.17). The small size of the cilia and the low velocities of ciliary movement cause planktonic larval feeding to operate at low Reynolds number (see Chapter 6),

meaning that viscosity dominates inertial forces in fluid behavior. The cilia must beat to propel water and food particles. Particles don't move through the water like a sinking stone. The domination of the role of viscosity makes them stop when water movement stops. Although there is a great deal of variation in morphology, a surprising number of taxonomic groups of organisms have ciliated bands (Figure 5.18). The cilia beat and create a current across the band. In order to capture a particle, it appears that a cilium suddenly reverses its rowing motion toward downstream. The reverse beat captures the particle and traps it upstream of the ciliary band.

A good example of a typical planktotrophic larva is that of the blue mussel *Mytilus edulis*, which lives on intertidal and shallow subtidal rocks and cobbles.

Fig. 5.15 An example of a lecithotrophic larva: a "tadpole" larvae of the colonian ascidian *Botryllus schlosseri*. This larva lives for only a few hours, is a poor swimmer, and moves only a few meters from the parent colony. (Courtesy of Richard Grosberg.)
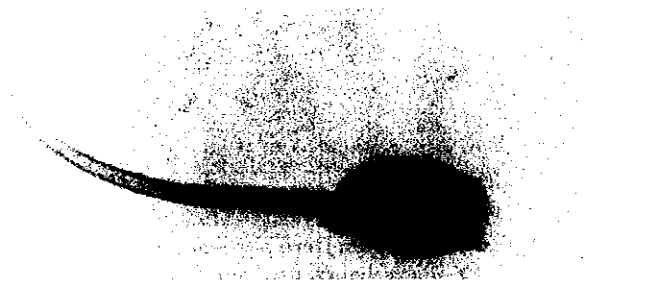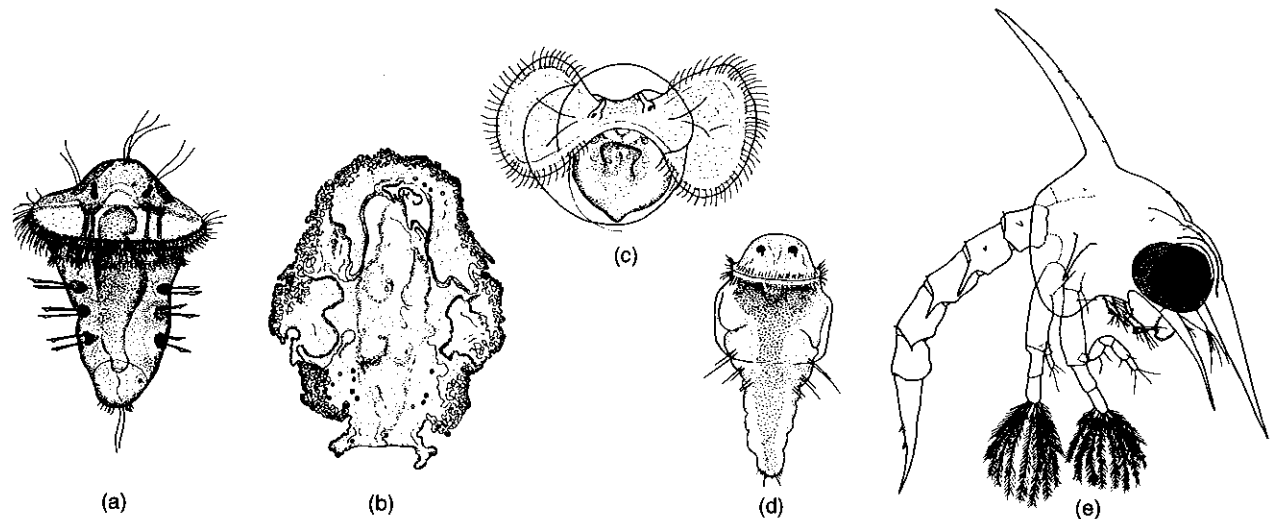
Fig. 5.16 Planktonic larvae: (a) the polychaete *Spirobranchus giganteus*, which is planktotrophic for 1–2 weeks; (b) the sea cucumber *Auricularia nudibranchiata*, which is planktotrophic and teleplanic, capable of many months in a plankton; (c) the gastropod *Ilyanassa obsoleta*, which is planktotrophic for 12 days to 6 weeks; (d) the polychaete *Spirorbis spirorbis*, which is lecithotrophic for less than one day; (e) a planktotrophic zoea-stage larva of the crab *Portunus sayi*. Adults live on pelagic *Sargassum* seaweed. (Drawings a–d by R. Scheltema, drawing e by I.P. Williams.)

Sexes are separate and the animals release eggs and sperm into the water. Within nine hours after fertilization, the larvae are completely ciliated and are strong swimmers. Within 5–7 days, fully developed feeding veliger larvae develop. Normally, larval life

may be 4–5 weeks. By contrast, the Atlantic mud snail *Ilyanassa obsoleta* produces fertilized eggs laid in cases that are attached to rocks. Larvae emerge from the cases and swim away. Planktotrophic larvae may also be released directly from the mother, as in the acorn barnacles.

Animals living or breeding in the highest part of the intertidal zone must have precise larval release schedules because the animals may be inundated only once every two weeks during spring high tides. The Atlantic marsh snail *Melampus bidentatus* lives in the highest part of the tide zone and breathes air, but lays eggs that develop into swimming larvae (Plate VIII.4). These larvae are launched at a spring high tide, and return to settle during the next spring high tide. The Pacific American grunion *Leuresthes tenuis* comes onto sand flats to spawn at spring high tide at night. Females dig a pit in the sand and lay eggs at the highest level of the tide, while males curl around and deposit sperm. For about two weeks, the high tides fail to reach this level, but the next spring high tide washes out the eggs, which hatch into swimming larvae.

* Variation in egg size is considerable among marine species and this may relate to different consequences in terms of mortality.

Although variation in age of reproduction is considerable, equally noticable is the great variation in egg
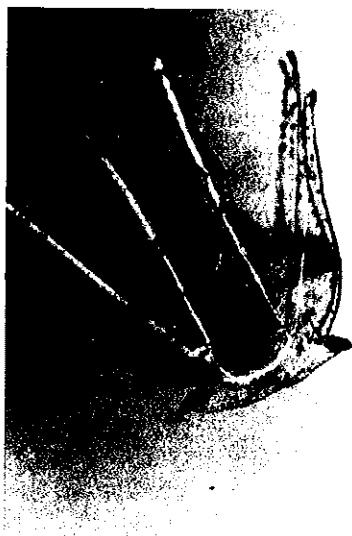

Fig. 5.17 Planktotrophic larva of the red sea urchin *Strongylocentrotus franciscanus*. Dark pigment spots are concentrated near the ciliary bands used for feeding and swimming. (Courtesy of Richard Strathman.)
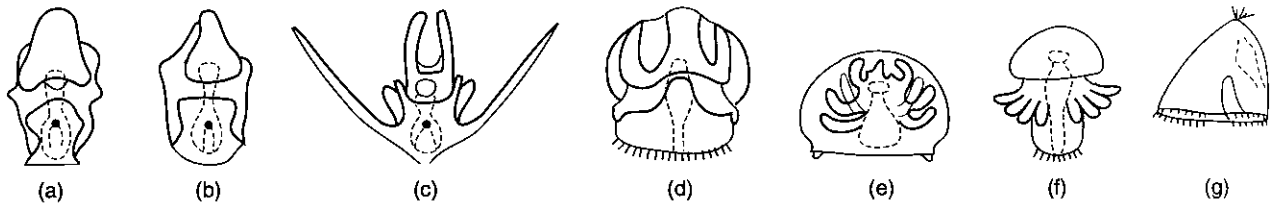
Fig. 5.18 Many different groups have evolved ciliary bands (green) for feeding on plankton. (a) sea star; (b) sea cucumber; (c) brittle star; (d) hemichordate; (e) inarticulate brachiopod; (f) phoronid worm; (g) bryozoan. (Courtesy of Richard Strathman.)

size in marine animals, sometimes between closely related species. In large measure this variation is unexplained as yet, but there are some general patterns. As mentioned above, lecithotrophic larvae develop from eggs that are much larger than planktotrophic eggs. Eggs of directly released juveniles are largest of all. As a general rule, planktotrophic eggs are also much more numerous than lecithotrophic eggs, which are in turn more numerous than the eggs of directly releasing species. This suggests a strategy, which in turn may determine egg size. Planktotrophic larvae swim in the water far longer and probably have much higher mortality rates than do lecithotrophic larvae, which are in the water for only a few hours. In turn, directly releasing species deposit their young in appropriate habitats (namely, those of the adults), thus further minimizing mortality. It seems likely then that the large number of planktotrophic eggs produced by a female "hedges her bet," because far fewer young will survive, relative to lecithotrophic eggs. Some have suggested that the intermediate strategy of producing an intermediate size egg with intermediate numbers may be the worst of both worlds, producing high mortality with relatively few numbers of eggs and young. Thus, we expect either the low-number–quality-care approach or the high-number–leave-them-alone approach.

Larval Settlement, Metamorphosis, and Early Juvenile Survival

✳ Larval settlement and metamorphosis involves active choice, aided by chemical and physical cues of the substratum.

Planktonic larvae reach a stage at which they must locate the adult habitat, and then settle and attach before metamorphosis. Although the vast majority of larvae die before reaching a potential adult habitat, the road ahead is still dangerous for the survivors.

Natural selection and evolution favor any larval features that enhance location and settlement on the proper substratum. Figure 5.19 provides a general outline of the stages of larval selection.

In the plankton, larvae pass through one or more stages of photopositive and photonegative behavior. These permit the larvae to remain near the sea surface to feed, and then to drop to the bottom in order to settle on the proper habitat. Larvae of intertidal animals are photopositive during their entire larval life, so that they may feed in the surface waters and settle in the intertidal zone. Richard Grosberg examined the water-column distribution of intertidal barnacle spe-
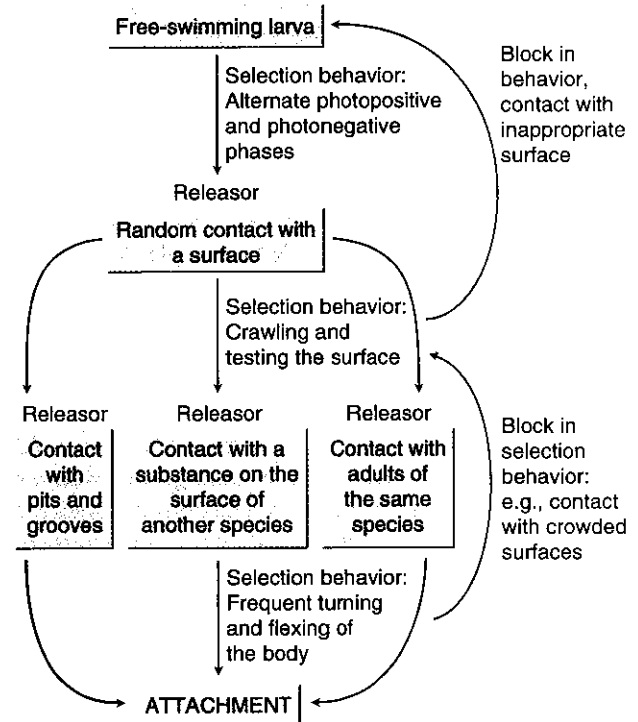

Fig. 5.19 Stages in the selection of a suitable substratum by planktonic larvae. (Modified after Newell, 1979.)

cies in California and found that the highest intertidal species was to be found at the surface during larval life, but that species living in the mid-intertidal were found a meter or two below the surface. Intertidal larvae are apparently capable of subtle adaptations to maintain the proper tidal height at the time of settlement. Subtidal species, by contrast, are first positively phototactic, but then switch to negative phototaxis just before the time of settling. Larvae are also capable of responding to pressure differences that might enable them to select a specific depth during the period of feeding, dispersal, and settlement.

Planktonic larvae must maintain their proper depth in the water column during the dispersal phase, either to feed on phytoplankton that are abundant near the surface or simply to avoid sinking before development is completed. Most larvae are slightly negatively buoyant, but simple turbulence retards sinking. Larvae can be simple and ciliated, but planktotrophic larvae usually have a swimming organ (for example, the velum of gastropod larvae, which is lost at the time of metamorphosis). Young postlarval mussels (e.g., *Mytilus edulis*) secrete monofilamental byssal threads that are more than a hundred times the larval shell length. The filaments exert viscous drag force sufficient to reduce greatly the sinking rate, thereby enhancing dispersal.

Amazingly enough, deep-sea hot-vent environments (see Chapter 16) have species with planktotrophic larvae. As judged from submarines, hot vents are scattered throughout the deep-sea floor and are ephemeral, because the hot nutrient-rich sources give out after a time. Dispersal might thus be expected. The protoconch (larval shell) size of hot-vent bivalve mollusks is of the typical small size for planktotrophic larvae, and isotope data from the larval shell (isotope ratios of oxygen in the shell can be used as a sort of thermometer) show that the larvae spend a time in water that is warm, which is characteristic of surface oceanic water and not the deep sea. Vent bivalve larvae must make the seemingly impossible trip to the surface waters, and then some manage to locate an incredibly rare appropriate deep-bottom environment. By contrast, archaeogastropods (a group of snails) near the vents have large yolky eggs and probably have larvae with quite limited dispersal. It may be that these eggs hatch as swimming but nonfeeding larvae, with strong dispersal abilities, relative to their non-vent relatives.

After touching the bottom, larvae must be able to determine whether or not the substratum is suitable for adult existence. Larvae use chemical cues and mechanical cues to detect suitable settling sites. Almost all larvae prefer surfaces coated with bacteria. Sterilized sand or rock usually inhibits larval settling. Larvae of some sand-dwelling polychaetes can select sand grains of the appropriate size, whereas rock dwelling barnacles have larvae that move preferentially to surfaces with pits and grooves, which provide a secure attachment against wave action, predators, and competing barnacles that might overgrow or undercut them. Although barnacles are often found in cracks, it is often not clear whether this is the result of preferential settlement or differential survival after settlement (Figure 5.20).

In **gregarious settling**, larvae settle on adults of their own species. This usually requires direct contact of larvae with adults, because the chemical cue is a relatively insoluble molecule, such as arthropodin in barnacles. Recently, Richard Zimmer-Faust and colleagues discovered that the cue for settling of oyster larvae is a soluble peptide (which is a string of amino acids). Such a waterborne settling cue only exists in effective concentrations within a few mm of the bottom, but larvae sinking within the bottom boundary layer can detect this cue and settle. The greatest concentration of such a settling cue would likely emanate from the water coming from adult oysters, which would concentrate settling of oyster larvae on adults of their own species.

Gregarious settling allows a larva to settle in a site where adults have previously settled and survived.
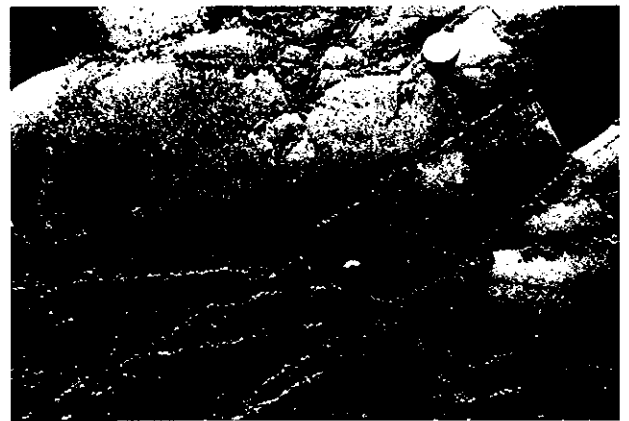

Fig. 5.20 Preferential recruitment of barnacles into cracks, on a rocky shore near Nahant, Massachusetts. It is not clear whether this pattern results from preferential larval settlement or from differential post-settlement mortality; or a combination of both processes.

There is the disadvantage, however, of being eaten by adults of the same species. There also is the problem of how, in a gregarious species, a "pioneer" can ever manage to colonize a new site. Recently Toonan and Pawlik[4] discovered that the colonial tube-dwelling polychaete worm *Hydroides* has two distinct types of planktonic larvae: one seeks adults of its own species, and another is specifically a "pioneer" larvae that seeks new bare hard substratum.

Planktonic larvae may also cue in on the chemical characteristics of other benthic species. For example, adults of the hydroid family Proboscidactylidae live on the tubes of members of the polychaete annelid family Sabellidae. At settling time, the larvae can detect and settle on the tentacles of the worm. After settling they move down the tentacles and live as adults on the tube. The mechanism probably involves **chemical attraction**. Some bryozoan larvae are attracted to seaweeds, and organic substances can be extracted from some seaweeds that will attract larvae onto another nonliving surface. In other species, **mechanical attraction** is involved. Planktotrophic larvae of the mussel *Mytilus edulis* are attracted to filamentous red algae, but the larvae will also settle on fibrous rope that has approximately the same texture. This attraction is used to great advantage in mussel mariculture.

After settling, larvae may move a short distance, no more than a few centimeters, to a better site. This is be very important for larvae of sessile species, whose movements at this point commit themselves to life at one location. Newly settled barnacle larvae can move to a small degree, locate optimal microsites, and space themselves away from other barnacles. The tubeworm *Spirorbis borealis* settles randomly on the seaweed *Fucus serratus*, but individuals then crawl and space themselves evenly. Avoidance of crowding reduces overgrowth and competition for food. In barnacles where settlement is often very dense, reduction of crowding, which follows a period of mortality after settlement, greatly enhances the susequent expectation of life (Figure 5.21).

When they reach the substratum, marine planktonic larvae encounter a complex physical and chemical environment. As we have discussed, many chemical cues can be used by larvae to select an appropriate site upon which to settle. However, there are probably a number of chemical cues that may lead to avoidance of a local site. Unfortunately, we know very little about these cues, even though they may be a major means of local site selection. Recently, Sara Ann Woodin and colleagues[5] demonstrated that noxious
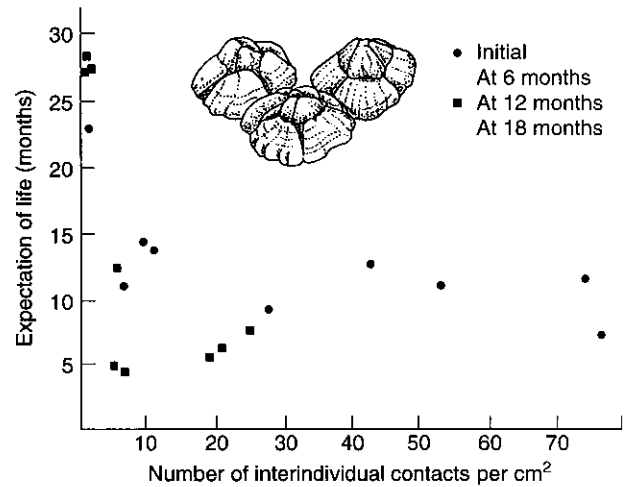

Fig. 5.21 Relation between crowding, as measured by number of interindividual contacts per square centimeter, and future expectation of life of the intertidal barnacle *Semibalanus balanoides*. Expectation of life is shown for barnacles that were first observed at either first settling, 6, 12, or 18 months of age. (After Deevey, 1947.)

chemicals released by benthic animals may reside in the sediment pore waters and can inhibit settlement by larvae. In soft-sediment intertidal flats of Washington, the infaunal terebellid polychaete *Thelepus crispus* is locally abundant and harbors toxic bromine-containing aromatic compounds. These compounds are found in the sediment pore waters adjacent to the worm. Woodin and colleagues demonstrated that such sediments are actively rejected by settling larvae of the nereid polychaete *Nereis vexillosa*, a common resident of sandy shores in the area. This result suggests that negative chemical interactions may also be important in determining the settling and metamorphosis of planktonic larvae.

Finally, a larva commits itself and metamorphoses into an adult stage. (Recall that metamorphosis is the process whereby a larva changes dramatically into the adult form.) In the case of barnacles, for example, the football-shaped cypris develops adult appendages, and a basal plate is laid down. The energetic cost of metamorphosis often is so severe that the animal must feed immediately afterwards. Some sea star species have been shown to die unless they find a prey item within a couple of days after metamorphosis. If larvae

4. See Toonan and Pawlik, 1994, in Further Reading.
5. See Woodin, Marinelli, and Lincoln, 1993, in Further Reading.

of the plaice *Pleuronectes platessa* are starved of zooplankton for more than eight days, a point of no return is reached and they will not have the energy to feed subsequently. Older larvae can survive at least 25 days before the point of no return is reached. It may be that early larval development in these fish is also very costly.

＊ Planktonic larvae suffer extensive mortality from predation, transport away from appropriate bottom substrata and food shortage.

The vast majority of planktonic larvae never make it to their destination. One gets an inkling of this by counting the number of eggs produced by most female invertebrates that spawn and produce planktotrophic larvae. In the small Atlantic American bivalve mollusk *Mulinia lateralis*, females can mature at lengths of less than 1 cm and produce hundreds of thousands of eggs. Although larvae of this species can settle in spectacular densities locally, one cannot account for the total larval output in terms of successful settlement. This is the general picture for most marine organisms. Where do the larvae go?

The problem is easiest to visualize for organisms that have restricted habitats. Larvae of rocky-shore invertebrates are released in currents and may easily be swept to inappropriate habitats. Along the southern New England coast, a longshore current would tend to sweep larvae from the rocky coasts of Rhode Island to the sandy south shore of Long Island, New York, and most larvae of the rocky-shore species would be doomed. Species with nonplanktonic larvae dominate the Galapagos Islands, off Ecuador, where currents carry surface waters offshore for a large portion of the year. As a result, species with planktonic larvae are relatively rare in the Galapagos.

Currents may cause net movement toward the shore. General eastward currents and winds tend to keep eastern Atlantic larvae pressed against the shorelines of the Atlantic coast of Europe. Off most open ocean coasts, one can observe surface slicks that contain jetsam that seems to move toward shore. Surface floats off the California coast are often carried 1–2 km shoreward in 2–3 hours. Planktonic invertebrate and fish larvae are 6–40 times more concentrated in these slicks than in the surface waters between the slicks. The slicks are formed by the interaction with the sea surface of tidally driven internal waves (waves within the water column). Planktonic larvae may therefore be "trapped" against the shoreline. In recent years, episodic recruitment has been discovered to be the rule for settling megalopa larvae of the blue crab *Callinectes sapidus*, both on the east and Gulf coasts of North America. In some cases, these recruitment events last only a day and may be simultaneous over several hundred kilometers of coastline. Recruitment in the mid-Atlantic states region appears to be correlated with onshore transport caused by wind stress and by spring flood tides, although other factors may also be important.

Many species have apparently taken advantage of such current effects. Many estuarine species spawn within the estuary, but larvae and juveniles may spend some period of time in coastal waters (Figure 5.22), perhaps to avoid predation within the estuaries (see the following). Because they are entirely dependent upon currents for transport, they must take advantage of the various wind and tide-driven transport sources discussed earlier to return to the estuary from adjacent coastal waters.

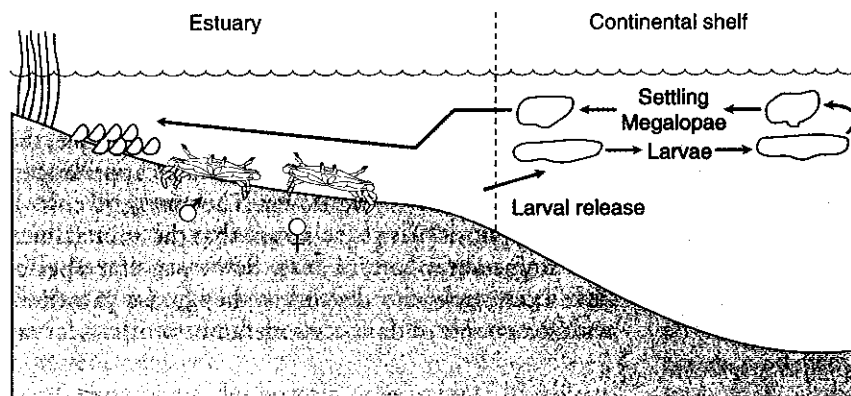As was discussed in Chapter 2, surface water flows seaward in moderately stratified estuaries, whereas

Fig. 5.22   Reproduction of many invertebrates and fishes, such as the blue crab *Callinectes sapidus*, occurs within the estuary. Larvae and juveniles, however, move into coastal waters, and later move back into the estuary to spend their adult lives. (Courtesy of Steven Morgan.)

the more saline bottom layer moves landward. If estuarine planktonic larvae held their position near the surface, they would be carried out to sea. Although we know far too little as yet, it appears that many estuarine species move actively to avoid the seaward surface flow. Oyster larvae (*Crassostrea virginica*) studied in the James River estuary, Virginia, differ in depth distribution from inert particles, and are found in surface waters more frequently at the time of flood tide, which would tend to move them upstream. Larvae of the mud crab *Rhithropanopeus harrisii* gradually concentrate up the estuary during the larval dispersal season. This suggests that they are actively moving up and down the water column with the tide, in order to avoid being swept from the estuary to the coastal ocean. Mud crab larvae appear to spend more time at the bottom at the time of low tide and move higher in the water column during the flood. Larvae (especially the later developmental stages) that are retained within estuaries tend to spend more time near the bottom, which places them in the landward moving layer of the estuarine water column. As mentioned before, other species have larvae that start within the estuary, but stay in the surface waters and are dispersed out to the coastal zone. They may return to the estuaries after a larval life in coastal waters, and larval recruitment depends very strongly on often quite irregular onshore winds.

The water column is filled with predators that cause considerable planktonic larval mortality. In temperate waters, planktivorous fishes and ctenophores are important grazers in the spring and summer. Ctenophores are especially abundant in the inner shelf waters and are major predators of zooplankton. Predation is a major problem for those larvae that are adapted to be retained in estuaries. Steven Morgan has shown that three species of crustacea retained in a North Carolina estuary have evolved pronounced spines. The mud crab *Rhithropanopeus harrisii* for example has movable spines, which are erected when fishes come close (Figure 5.23). Other crustacean species whose larvae spend time in coastal waters experience less predation and have less-completely-developed spination.

Although primary production is often sufficient to feed larval populations, shortages or failures of phytoplankton can devastate a planktonic feeding larval population that might be produced only once a year for a brief period. Harold Barnes encountered a bad phytoplankton year in British waters in 1951 (Figure
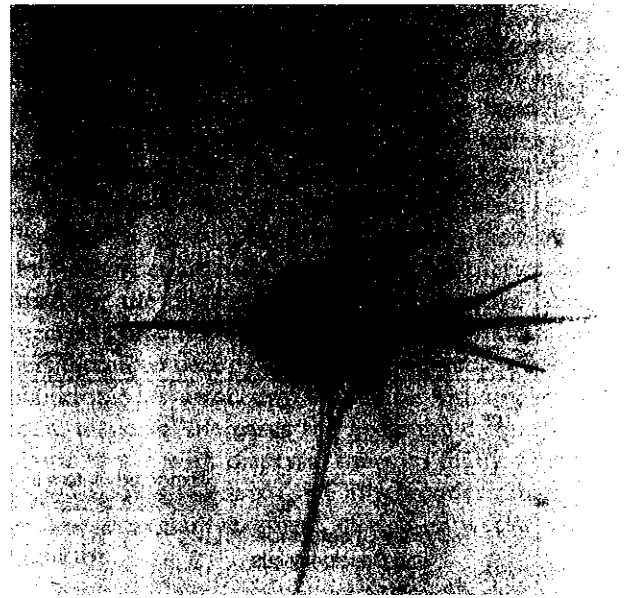

Fig. 5.23 Larvae of the mud crab *Rhithropanopeus harrisii* have erectible spines, which make them very difficult for fishes to attack. This is a necessary defense for larvae that are retained within estuaries, where predation by fishes is intense. (Courtesy of Steven Morgan.)

5.24). Early larval stages of barnacles could be found at first, but soon disappeared because of starvation. It would be best for larvae if their release could be coupled to the spring phytoplankton bloom. Such coupling has been found in sea urchins and mussels living in the St. Lawrence estuary of eastern Canada, which spawn in response to high concentrations of phytoplankton. The response is similar when urchins and mussels are exposed to only the filtered water in which the phytoplankton lived. The response is also advantageous because zooplankton predators tend to be rare at the peak of the phytoplankton bloom, so larvae can eat and not be eaten.

Sometimes the presence of even copious amounts of phytoplankton does no good, because they are either indigestible or inedible. Such has been the case in recent years in coastal bays of New York, New Jersey, and Rhode Island. So-called **brown tides**, or dense blooms of small-celled phytoplankton, have developed, but these cannot be digested very efficiently by larvae or adults of the bay scallop *Argopecten irradians*. Some other as yet unknown factor also causes these phytoplankton to harm the scallops. As a result, the scallop fishery has nearly collapsed in the Peconic
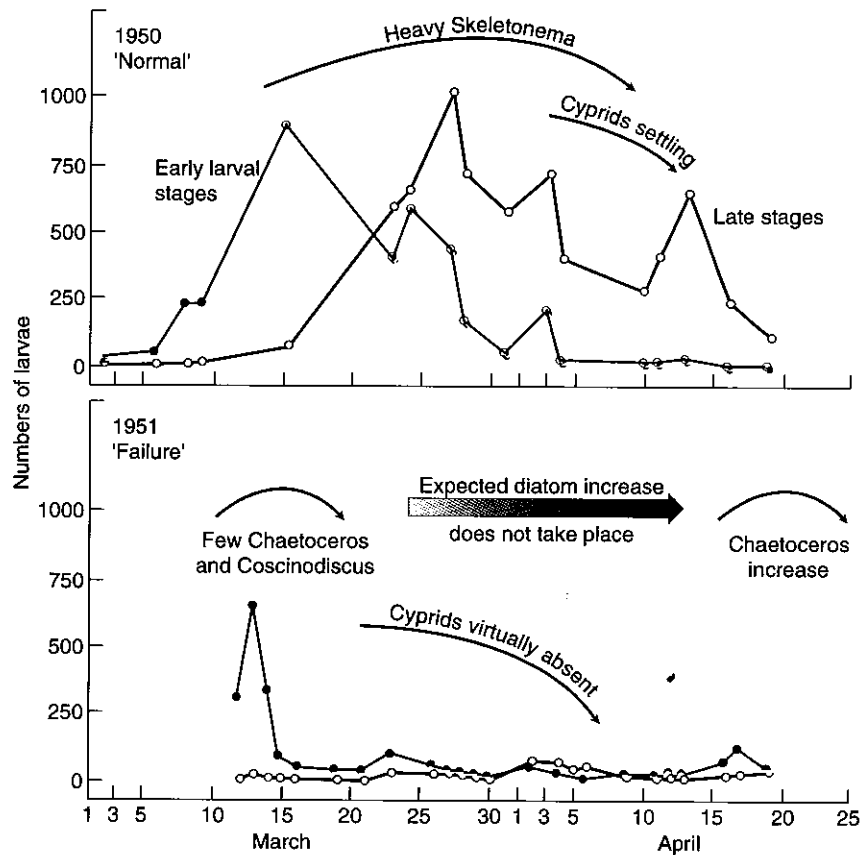
Fig. 5.24 Successful settlement and failure in the barnacle, *Semibalanus balanoides,* in good and bad phytoplankton seasons. (After Barnes, 1956.)

Bay (eastern Long Island, New York), which was formerly an area rich in these scallops.

There may be cases in which larvae do not suffer especially from food shortages. Echinoderm larvae may survive well despite an absence of phytoplankton, and many bivalve mollusk larvae are also resistant to the effects of food shortages. It is possible that these groups are able to survive on dissolved organic matter in sea water. (The interested student should consult Olson and Olson (1989) for more on this subject.)

∗ Larval recruitment is the combined result of larval habitat selection and early mortality.

In March, the rocks in Long Island Sound waters begin to be covered by small red specks—the cypris stages of the barnacle *Semibalanus balanoides*—which soon metamorphose into tiny white-shelled barnacles. **Recruitment** represents the residue of those larvae that have: (1) dispersed; (2) settled at the adult site; (3) made some final movements toward the adult

habitat; (4) metamorphosed successfully, and (5) survived to be detected by the observer. Recruitment, therefore, could obscure much of the life cycle of the dispersing larva. When the observer arrives on the scene, all that is usually known is how a combination of larval selection and mortality has resulted in the final distribution of recruits.

If we find a set of recruits living under the most favorable adult conditions, it is potentially fallacious to conclude that the larvae are good at finding the proper adult habitats. The final match between recruit and optimal environment may result from extensive mortality just after settling in suboptimal sites. Consider, for example, the lecithotrophic larvae of the bryozoan *Bugula neritinea* on sea grass blades in the Gulf of Mexico. Colonies were found mainly at the tips of the blades, where suspended food was more plentiful. By transplanting young colonies away from the blade tips, Michael Keough showed that survival was reduced. Settlement occurred mostly on the blade tips, but some larvae settled in suboptimal sites and

did poorly. Recruitment in this case was mainly the result of selective larval settlement, but mortality enhanced the concentration of recruits at the blade tips. There is a similar complexity in recruitment patterns of the Atlantic oyster *Crassostrea virginica*. Resident adults, such as sea squirts, tend to inhibit settling, but larvae often avoid the residents and settle on adjacent open space. Even though sea squirts eat oyster larvae, and other species preclude settling, there may be enough space such that overall recruitment is not affected very much.

Biogeography and Function of Larval Dispersal

* The geographic range of a species with planktonic dispersal is greater than for species without planktonic larvae.

Planktonic dispersal gives some species the opportunity to invade distant shores, merely by being passengers on the ocean's transport system of currents. We rarely see this in action, but several species have invaded new coasts in the past 100 years and their spread has been documented. We mentioned earlier in this connection the shore periwinkle *Littorina littorea*, which invaded Nova Scotia waters in the late 1800s and has now spread as far south as New Jersey. While there are some exceptions, invertebrate species with planktonic larvae appear to have far greater geographic ranges than those species with direct release. Figure 5.25 shows a series of biogeographic zones on the Atlantic coast of North and South America, identified for the distinctness of their respective benthic species. Note that species with nonplanktonic dispersal tend to occupy 2–3 zones, whereas those with planktonic larvae occupy 4–5 zones. Although planktonic dispersal increases the geographic range, teleplanic larvae with dispersal times of many weeks or months do not seem to have any broader range than those whose larvae spend only 2–6 weeks in the plankton.

* Why disperse? Dispersal of planktonic larvae ensures that local habitat destruction will not lead to extinction.

Given the dangers of planktonic dispersal, one might wonder why this mode has evolved at all. Richard
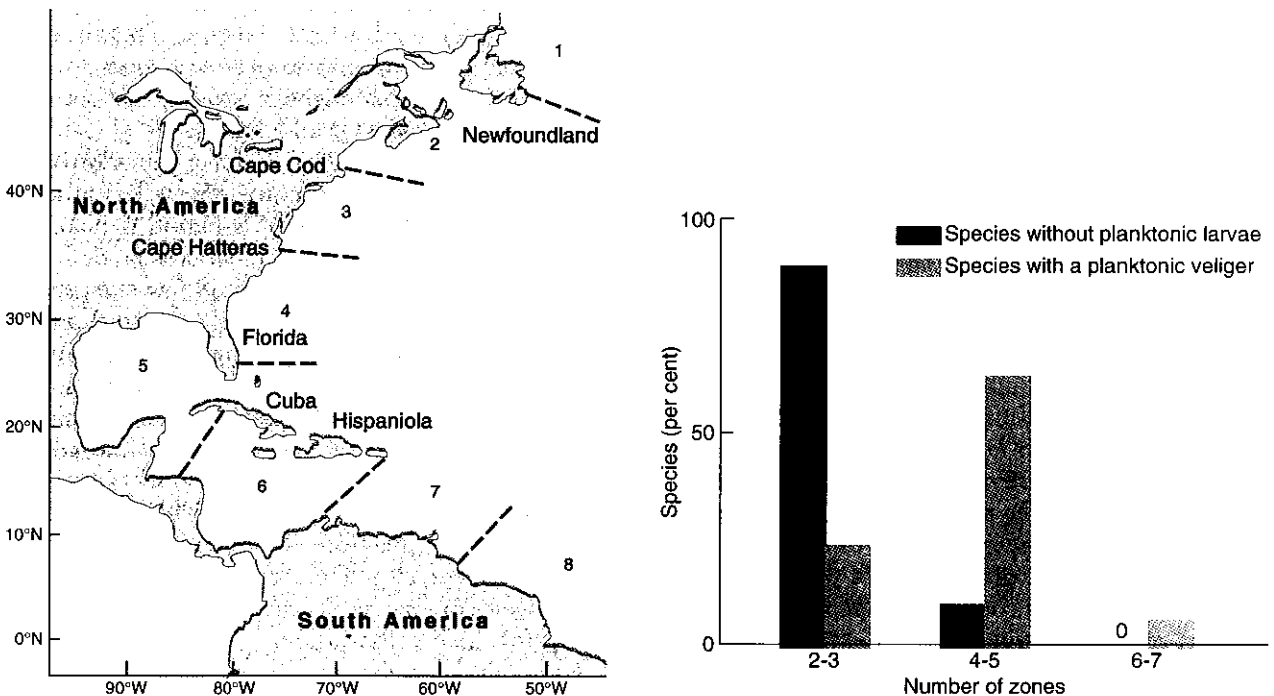

Fig. 5.25 (Left) Diagram of biogeographic zones of shore benthic invertebrates in the Western Atlantic. (Right) Number of zones occupied by invertebrate benthic species with and without planktonic larvae. (After Scheltema, 1989.)
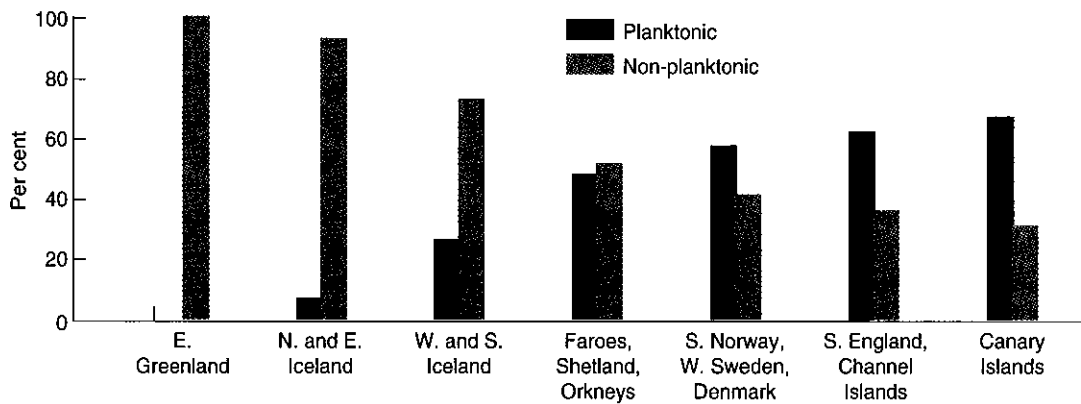
Fig. 5.26 Latitudinal variation in the abundance of prosobranch gastropod species with planktonic larvae. (After Thorson 1950.)

Strathman has pointed out that many evolutionary lines have lost the ability to produce feeding planktonic larvae, simply because it is fairly easy, in the evolutionary sense, to lose a swimming or plankton-feeding structure, but hard to reacquire it. However, the great majority of marine invertebrates have planktonic feeding larvae. Planktotrophic dispersal is rare only in high latitudes (Figure 5.26), where the phytoplankton season is very short and the water temperature is low. This may stem from the danger of failing to synchronize reproduction with the short phytoplankton production season, combined with the very long development times caused by low temperature, which would increase the danger of predation and of being swept to sea.

Avoidance of crowding is one significant benefit of dispersal. Many marine habitats are severely space limited and dispersal to an open habitat would ensure population increase. The rate of destruction of local marine habitats may also make dispersal beneficial. All marine habitats suffer major alterations. Coral reefs, which are often represented to students as benign environments, are continually disturbed by major storms and some by temperature fluctuations. No rocky shore long escapes the force of the waves, ice, hot and dry weather, or an influx of predators. If an organisms's offspring could not disperse, the chances are that its genes would become extinct. Dispersal therefore ensures that some of the progeny will escape a catastrophe. It is of interest in this regard that paleontologists have discovered that mollusk species characterized by long-distance dispersal have lower extinction rates. One should not forget, however, that

many species have reduced dispersal and have still managed to survive. They have the advantage of giving their young access to a habitat that has at least proved suitable to the parents.

Long-distance dispersal also has the advantage of spreading the young over a variety of habitat types. In carrying out said dispersal, a parent is hedging its bets on the success of its offspring. Instead of investing heavily in one site, dispersal allows settling on many sites. In any year, one site may be very poor for settling, whereas another might be good. In the long run, survival is averaged over all habitats.

The minimum time required for a planktotrophic larva to develop and the distance that the larva travels in the water column during this period is puzzling. Why should a larva travel for two weeks or more, when it could sample a diversity of new sites only a few hundred meters (and a couple of days) away? Strathman suggests that planktotrophic larvae might not have evolved as an adaptation for long-distance dispersal, but that the larvae may have evolved planktotrophy in order to take advantage of the phytoplankton food source, much in the same way a juvenile fish exploits a nursery ground. The exact length of dispersal may therefore be something of an evolutionary accident, even if wider dispersal does have the consequence of lowered species extinction and the potential for rapid colonization.

Although long-distance dispersers are common, many colonial animals, such as bryozoans and coelenterates, are known to have short-distance-dispersing lecithotrophic larvae. Indeed, this form of dispersal has been underemphasized in the past. The

bryozoan *Bugula neritinea* lives in Florida on blades of turtle grass. Areas with dense populations are self-maintaining, but nearby areas without *Bugula* also exist for several years without any significant colonization. Thus, marine populations in certain areas may be limited by dispersal potential, especially in the case of species with no planktonic larvae or with lecithotrophic larvae.

Further Reading

SEX, FERTILIZATION, AND LIFE CYCLES

Andersson, M. 1994. *Sexual Selection*. Princeton, Princeton University Press.

Babcock, R.C. and C.N. Mundy. 1992. Reproductive biology, spawning and field fertilization rates of *Acanthaster planci*. *Australian Journal of Marine and Freshwater Research*, v. 43, pp. 523–534.

Bacci, G. 1965. *Sex Determination*. New York, Pergamon Press.

Berglund, A. 1990. Sequential hermaphroditism and the size-advantage hypothesis: an experimental test. *Animal Behavior*, v. 39, pp. 426–433.

Christy, J.H. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behavioral Ecology and Sociobiology*, v. 12, pp. 169–180.

Denny, M.W., and M.F. Shibata. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *American Naturalist*, v. 134, pp. 859–889.

Foster, S. 1990. Courting disaster in cannibal territory. *Natural History*, November issue, pp. 52–60.

Francis, L. 1973. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. *Biological Bulletin*, v. 144, pp. 73–92.

Ghiselin, M.T. 1987. Evolutionary aspects of marine invertebrate reproduction. In A.C. Giese, J.C. Pearse, V.B. Pearse (editors), *Reproduction of Marine Invertebrates, V. IX, General Aspects: Seeking Unity in Diversity*. Palo Alto, CA: Blackwell Scientific, pp. 609–665.

Hughes, D.J., and R.N. Hughes. 1986. Life history variation in *Celloporella hyalina* (Bryozoa). *Proceedings of the Royal Society of London*, B 228, pp. 127–132.

Hughes, R.N. 1989. *A Functional Biology of Clonal Organisms*, London, Chapman and Hall.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution*, v. 36, pp. 1–12.

Levitan, D.R., M.A. Sewall, and F.-S. Chia. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology*, v. 73, pp. 248–254.

Maynard Smith, J. 1971. What use is sex? *Journal of Theoretical Biology*, v. 30, pp. 319–335.

Murphy, G.I. 1968. Pattern in life history and the environment. *American Naturalist*, v. 102, pp. 391–403.

Peterson, C.W. 1991. Variation in fertilization rate in the tropical reef fish *Halochoeres bivattatus*; correlates and implications. *Biological Bulletin* (Woods Hole), v. 18, pp. 232–237.

Pianka, E.R. and W.S. Parker. 1975. Age-specific reproductive tactics. *American Naturalist*, v. 109, pp. 453–464.

Robertson, D.R. 1972. Social control of sex reversal in a coral-reef fish. *Science* v. 177, pp. 1007–1009.

Stearns, S.C. 1976. Life history tactics: A review of the ideas. *Quarterly Review of Biology* v. 51, pp. 3–47.

Vahl, O. 1981. Age-specific residual reproductive value and reproductive efforts in the Iceland Scallop, *Chlamys islandica* (O.F. Moller). *Oecologia*, v. 51, pp. 53–56.

Warner, R.R. 1975. The adaptive significance of sequential hermaphroditism in animals. *American Naturalist*, v. 109, pp. 61–82.

Williams, G.C. 1975. *Sex and Evolution*. Princeton, NJ: Princeton University Press.

MIGRATION

Gross, M.R., R.M. Coleman, and R.M. McDowall. 1988, Aquatic productivity and the evolution of diadromous fish migration. *Science*, v. 239, pp. 1291–1293.

Harden Jones, F.R. 1968. *Fish Migration*, Second Edition. London, Edward Arnold.

Koch, A.L., A. Carr, and D.W. Ehrenfeld. 1969. The problem of open-sea navigation: the migration of the green turtle to Ascension Island. *Journal of Theoretical Biology*, v. 22, pp. 163–179.

Meylan, A.B., B.W. Bowen, and J.C. Avise. 1990. A genetic test of the natal homing versus social facilitation models for green turtle migration. *Science*, v. 248, pp. 724–727.

LARVAL DISPERSAL AND RECRUITMENT

Barnes, H. 1956. *Balanus balanoides* (L.) in the Firth of Clyde: the development and annual variation of the larval population, and the causative factors. *Journal of Animal Ecology*, v. 25, pp. 72–84.

Butman, C.A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales explained by active habitat selection and the emerging role of hydrodynamic proceses. *Oceanography and Marine Biology Annual Reviews*, v. 25, pp. 113–165.

Butman, C.A., J.P. Grassle, and E.J. Buskey. 1988. Horizontal swimming and gravitational sinking of *Capitella sp.* 1 (Annelida: Polychaeta) larvae: implications for settlement. *Ophelia*, v. 29, pp. 43–57.

Cronin, T.W. 1982. The estuarine retention of larvae of the crab *Rhithropanopeus harrisii. Estuarine and Coastal Shelf Science*, v. 15, pp. 207–220.

Deevey, E.S. 1947. Life tables for natural populations of animals. *Quarterly Review of Biology*, v. 22, pp. 283–314.

Eckman, J.E. 1983. Hydrodynamic proceses affecting benthic recruitment. *Limnology and Oceanography*, v. 28, pp. 241–257.

Gaines, S.D., and J. Roughgarden. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science*, v. 235, pp. 479–481.

Grosberg, R.K. 1987. Limited dispersal and proximity-dependent mating success in the colonial ascidian *Botryllus schlosseri. Evolution* 41, pp. 372–384.

Grosberg, R.K., and J.R. Quinn. 1986. The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature*, v. 322, pp. 456–459.

Hoek, C. van den. 1987. The possible significance of long-range dispersal for the biogeography of seaweeds. *Helgoländer Meeresunters.* v. 41, pp. 261–273.

Innes, D.I. 1984. Genetic differentiation among populations of marine algae. *Helgoländer Meeresunters.* v. 38, pp. 401–417.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. *American Fishery Society Symposium*, v. 2, pp. 17–29.

Hunt, J.H., W.G. Ambrose, Jr., and C.H. Peterson. 1987. Effects of the gastropod *Ilyanassa obsoleta* (Say) and the bivalve *Mercenaria mercenaria* (L.) on larval settlement and juvenile recruitment of infauna. *Journal of Experimental Marine Biology and Ecology*, v. 108, pp. 229–240.

Judge, M.L., J.F. Quinn, and C.L. Wolin. 1988. Variability in recruitment of *Balanus glandula* (Darwin, 1854) along the central California coast. *Journal of Experimental Marine Biology and Ecology*, v. 119, pp. 235–251.

Levin, L.A. 1986. The influence of tides on larval availability in shallow waters overlying a mudflat. *Bulletin of Marine Science*, v. 39, pp. 224–233.

Lutz, R.A., D. Jablonski, and R.D. Turner. 1984. Larval development and dispersal at deep-sea hydrothermal vents. *Science*, v. 226, pp. 1451–1453.

McConaugha, J.R. 1988. Export and reinvasion of larvae as regulators of estuarine decapod populations. *American Fisheries Society Symposium*, v. 3, pp. 90–103.

Mileikovsky, S.A. 1974. Types of larval development in marine bottom invertebrates: an ecological scheme. *Thalassia Jugoslavica*, v. 10, pp. 171–179.

Miller, S.E., and M.G. Hadfield. 1990. Developmental arrest during larval life and life-span extension in a marine mollusc. *Science*, v. 248, pp. 356–358.

Morgan, S.P. 1990. Impact of planktivorous fishes on the dispersal, hatching and morphology of estuarine crab larvae. *Ecology*, v. 71, pp. 1639–1652.

Mullineaux, L.S., and C.A. Butman. 1991. Initial contact, exploration, and attachment of barnacle cyprids (*Balanus amphitrite*) settling in flow. *Marine Biology*, v. 110, pp. 93–103.

Olson, R.R. 1985. The consequences of short distance dispersal in a sessile marine invertebrate. *Ecology*, v. 66, pp. 30–39.

Olson, R.R., and M.H. Olson. 1989. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? *Annual Review of Ecology and Systematics*, v. 20, pp. 225–247.

Osman, R.W., R.B. Whitlatch, and R.N. Zajac. 1989. Effects of resident species on recruitment into a community: larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica. Marine Ecology Progress Series*, v. 54, pp. 61–73.

Pawlik, J.R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology Annual Reviews*, v. 30, pp. 273–335.

Pawlik, J.R., C.A. Butman, and V. Starczak. 1991. Hydrodynamic facilitation of gregarious settlement of a reef-building tube worm. *Science*, v. 251, p. 421–424.

Peterson, C.H., and H.C. Summerson. 1992. Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallopi implications for recruitment limitation. *Marine Ecology Progress Series*, v. 90, pp. 257–272.

Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science*, v. 253, pp. 548–551.

Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series*, v. 107. pp. 125–138.

Richmond, R.H. 1985. Reversible metamorphosis in coral planula larvae. *Marine Ecology Progress Series*, v. 22, pp. 181–185.

Sammarco, P.W. 1988. Localized dispersal and recruitment in Great Barrier Reef corals: The Helix experiment. *Science*, v. 239, pp. 1422–1424.

Sammarco, P.W. 1991. Geographically specific recruitment and postsettlement mortality as influences on coral communities: The cross-continental shelf transplant experiment. *Limnology and Oceanography*, v. 36, pp. 496–514.

Sammarco, P.W., and M.L. Heron (editors) 1994. *The Bio-Physics of Marine Larval Dispersal.* Washington, D.C., American Geophysical Union.

Scheltema, R.S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin*, v. 140, pp. 284–322.

Scheltema, R.S. 1989. Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species. In *Reproduction, Genetics, and Distributions of Marine Organisms*, 23rd European Marine Biology Symposium, ed. J.S. Ryland, P.A. Tyler. Fredensborg, Denmark, Olsen and Olsen, pp. 183–188.

Shanks, A.L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Marine Ecology Progress Series*, v. 13, pp. 311–315.

Starr, M., J.H. Himmelman, and J.-C. Therriault. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science*, v. 247, pp. 1071–1074.

Strathman, R.R. 1974. The spread of sibling larvae of sedentary marine invertebrates. *American Naturalist*, v. 108, pp. 29–44.

Strathman, R.R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics*, v. 16, pp. 339–361.

Strathman, R.R. 1987. Larval feeding. In A.C. Giese, J.C. Pearse, V. B. Pearse, Editors, *Reproduction of Marine Invertebrates, V. IX, General Aspects: Seeking Unity in Diversity*. Palo Alto, CA, Blackwell Scientific, pp. 465–550.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews*, v. 25, pp. 1–45.

Toonan, R.J., and J.R. Pawlik. 1994. Foundations of gregariousness. *Nature*, v. 370, pp. 511–512.

Woodin, S.A., R.L. Marinelli, and D.E. Lincoln. 1993. Allelochemical inhibition of recruitment in a sedimentary assemblage. *Journal of Chemical Ecology*, v. 19, pp. 517–530.

Young, C.M., and F.-S. Chia. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. In A.C. Giese, J.C. Pearse, V.B. Pearse (eds.), *Reproduction of Marine Invertebrates, v. IX, General Aspects: Seeking Unity in Diversity*. Palo Alto, CA, Blackwell Scientific, pp. 385–463.

Review Questions

1. Why are not all sexual species hermaphroditic?

2. What is the "cost of sex," biologically speaking?

3. What might be the benefit of sex to organisms?

4. Under what circumstances does it make sense for a hermaphrodite to be protandrous? Protogynous?

5. When might you expect the presence of dwarf males attached to females?

6. What is the advantage of clonal reproduction? The disadvantage?

7. Why do fishes such as Pacific salmon species reproduce only once?

8. What might be the value, if any, of long-distance dispersal across an ocean?

9. What are the advantages of having planktotrophic larvae capable of settling and metamorphosing upon any substratum? What are the disadvantages?

10. Why are species with planktotrophic larvae more common in the tropics, than at polar latitudes?

11. How might planktonic larvae be able to find adults of their own species?

12. What is the value of planktonic-feeding larval development?

13. What are the potential sources of mortality for planktonic larvae?

14. What effect does planktotrophic larval dispersal tend to have on the geographic range of a coastal marine invertebrate species?

15. Do you think that the total evolutionary life spans of species with planktotrophic larvae are liable to be greater than those with lecithotrophic larvae? Explain your answer.

16. Anemones often occur in clones of large numbers, that have arisen by fission from a founder individual. What experiment might be performed to determine the benefit of large numbers of adjacent anemones, as opposed to smaller groups or solitary individuals?