CHAPTER 2

The Concept of Larvae

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DEVELOPMENT CONSISTS OF A SERIES OF COORDINATED stages from egg through adult (Figure 2.1). The fertilized egg, or **zygote**, undergoes a series of mitotic divisions called **cleavage**, during which it is converted into a population of many cells. Then, in the process of **gastrulation**, the cells of the embryo become rearranged, giving rise to the basic organization of the body. After organs develop in the embryonic stage, the organism is often not a mature form capable of reproduction. Rather, it is an immature stage of that organism. The immature stage of some animals generally resembles the adult organism, in which case it is called a **juvenile**. The juvenile progressively develops, or matures, into the adult. On the other hand, many animals possess a free-living immature form unlike the adult. Such an immature stage is a **larva**. In some cases there is a series of larval stages in the life history of an animal. The larva undergoes a more or less dramatic transformation into the adult, which frequently involves new organogenesis and sometimes reorganization of the basic body plan. The development of a larva into an adult is called **metamorphosis**.

Since larval forms are unlike adults, they frequently carry out special functions in the life cycles of organisms. Included among these functions are feeding, dispersal, and habitat selection. Some larvae, especially among the insects, become dormant and may be the only form in which a population survives adverse environmental conditions.

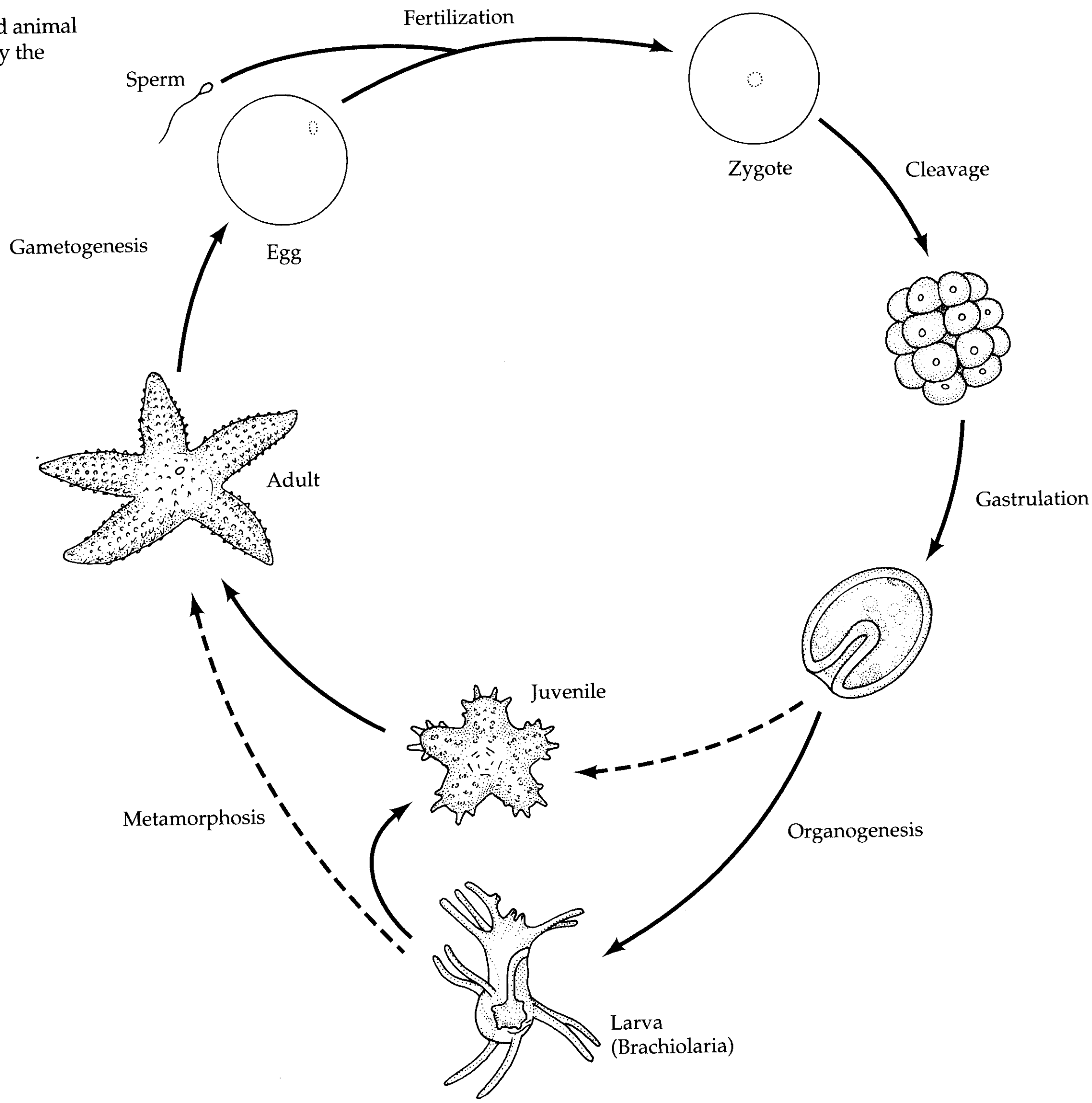
Feeding

Some larvae, including sponge *parenchymellas*, some coelenterate *planulae*, and tunicate *tadpoles*, do not feed. They spend only a short time in the plankton before settling and metamorphosing into adults. The larvae of certain other organisms are relatively long-lived and are the only feeding stage in the life history; the adults reproduce and die within a short time following metamorphosis. For example, this situation is found in a number of insects and the brook lamprey. The *caterpillar* of the cecropia silkworm moth eats leaves, increasing in mass 5000-fold during its six-week existence. The *ammocete* larva of the brook lamprey burrows into the sediments of streams and feeds on diatoms. The larval period may last for as long as 6.5 years. In both cases, the larva gives rise to a complex adult with all the nutritive reserves needed for producing gametes and completing reproduction before it dies.

In most cases both the larvae and adults feed, but the diets of these different stages may be very different. For example, the *pluteus* larvae of sea urchins feed on phytoplankton, whereas the adults eat macroalgae (seaweeds) and other larger foods. Although the larva of the sea lamprey, like that of the brook lamprey, feeds on diatoms, the adult is an ectoparasite/predator on other fish. During the course of metamorphosis, the *tadpole* of the leopard frog is transformed from an aquatic herbivore into a semiterrestrial carnivore that preys on a variety of animals, including insects. Such situations eliminate competition between larvae and adults for food and may allow each stage to exploit appropriate seasonally abundant food sources.

Many animals, especially marine invertebrates, produce large numbers of small eggs containing relatively little yolk. An oyster may produce 60 million eggs during a reproductive season, and some sea urchins produce up to 400 million eggs per female each year. The nutrient reserves of the eggs are adequate for the development of very simple feeding larvae, but not for the development of complex larvae or adults. These simple larvae must begin to feed immediately since they rapidly deplete their yolk stores. As they feed, they grow and increase in complexity (Figure 2.2). The more complex late-stage larvae then meta-

Figure 2.1 Generalized animal life cycle, exemplified by the starfish *Asterias*.



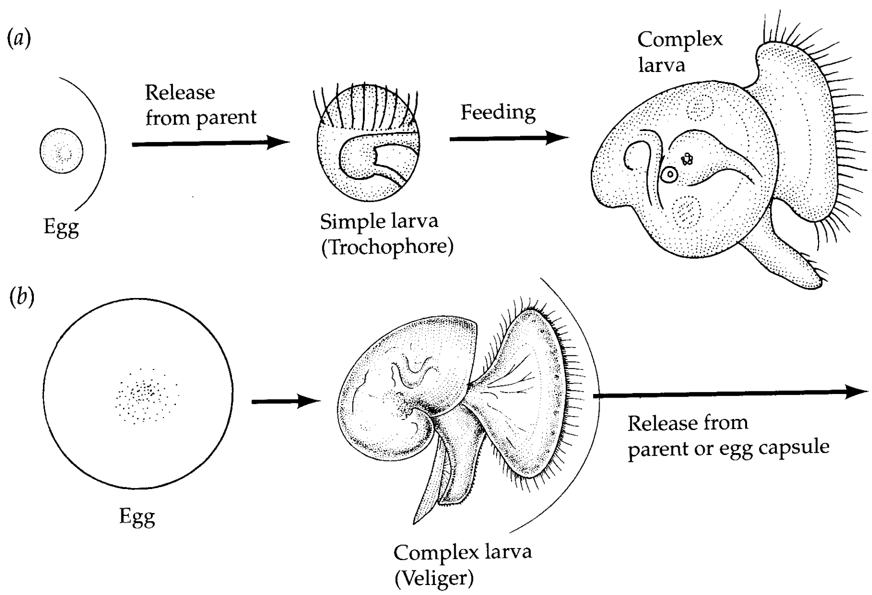


Figure 2.2 Larval development. (*a*) From a small egg with very limited yolk stores (e.g. the oyster *Crassostrea virginica*). (*b*) From a large egg with more abundant yolk (e.g. certain marine snails). (Part *a* after Galtsoff 1964.)

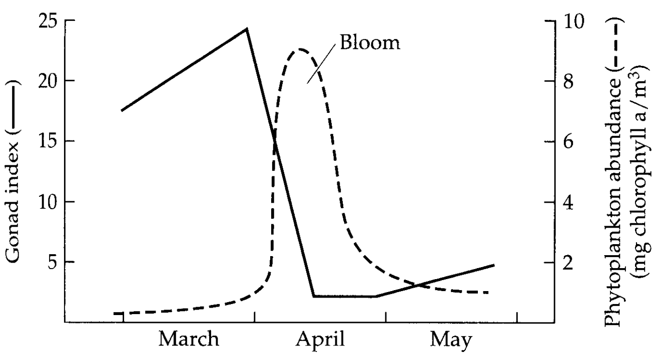


Figure 2.3 Spawning by the green sea urchin *Strongylocentrotus droebachiensis* in relation to the spring phytoplankton bloom. As spawning occurs, the gonad index (wet weight of the gonads expressed as a percentage of the total wet weight of the animal) rapidly declines. (After Himmelman 1975.)

morphose into small juveniles or adults. The eggs and larvae of such animals typically experience a high rate of mortality, often becoming the food of other organisms.

Other animals produce fewer larger eggs that may develop directly into complex larvae which then begin to feed. These larvae may be able to survive for at least short periods when food is scarce or absent. Development up to the feeding stage sometimes takes place within special protective capsules or parental **brood pouches**, and the embryos generally exhibit a lower rate of mortality compared to those developing from very small eggs.

For animals that produce feeding larvae, it is important that the larval period coincides with an abundance of larval food. In aquatic environments, the larval food is often phytoplankton. The spawning of gametes by some animals with plankton-feeding (**planktotrophic**) larvae and the release of such larvae by other animals that brood embryos have been shown to be highly correlated with phytoplankton blooms (Figure 2.3) and to be stimulated by phytoplankton. For example, when sea urchins and mussels, collected prior to their normal spawning period, are maintained in the laboratory without phytoplankton, they either do not spawn or exhibit at most a low incidence of spawning. However, the addition of phytoplankton stimulates spawning by many individuals within a few days. The spawning response depends upon the concentration of phytoplankton. Thus in these instances, phytoplankton directly signals the abundance of food. This situation is advantageous because the occurrence of phytoplankton blooms depends upon a number of interacting factors and cannot be reliably predicted on the basis of any one. The actual spawning inducer apparently is a phenolic compound released by phytoplankton (Starr et al. 1990, 1992).

In barnacles, which brood embryos, first-stage *nauplius* larvae (Figure 2.4) hatch within the mantle cavity of the parent and escape into the surrounding water in response to phytoplankton. However, phytoplankton does not act directly on the larvae. In the spring when the adults resume feeding on plankton, they secrete a fatty acid compound into the mantle cavity. This substance stimulates vigorous muscular activity in the larvae which results in their breaking out of the egg capsules (Barnes 1957; Clare and Walker 1986; Song et al. 1990).

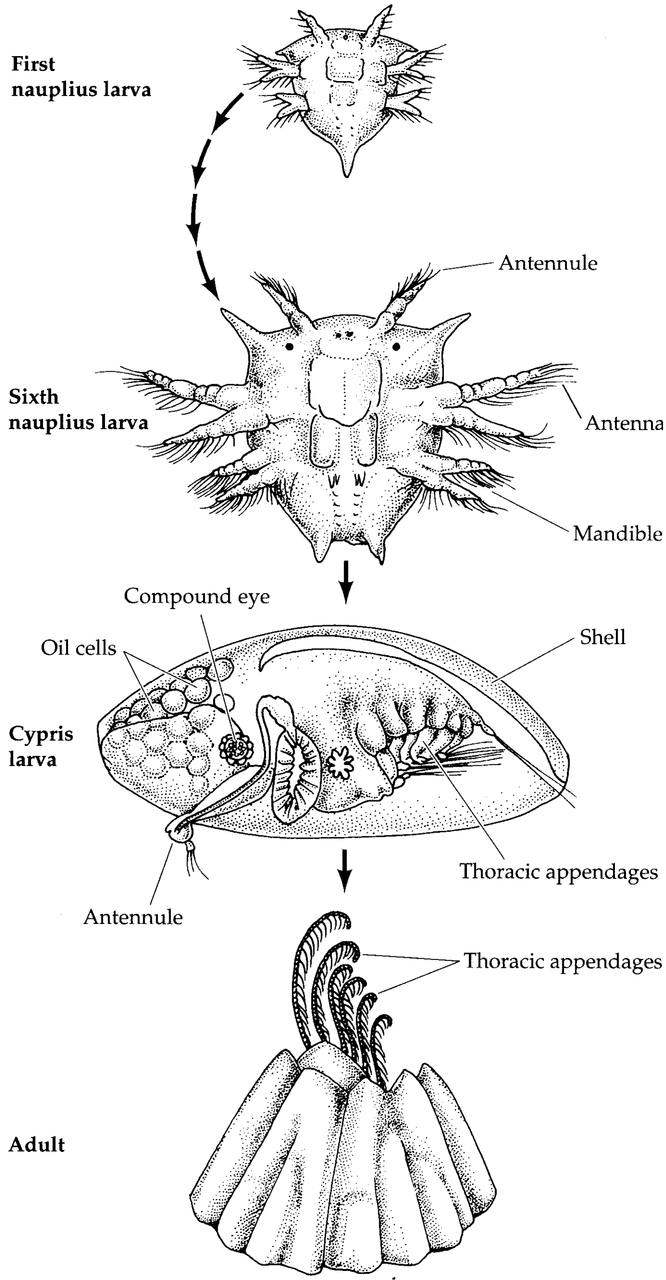
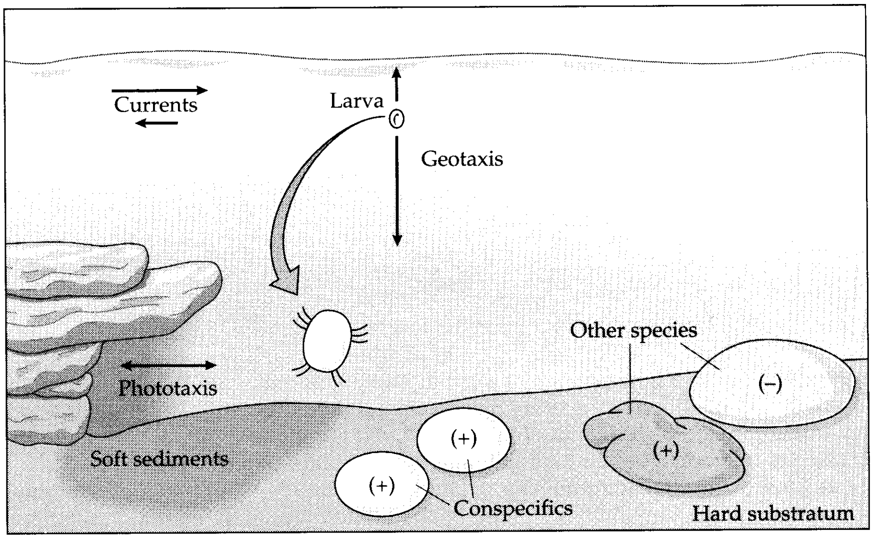


Figure 2.4 Larval stages and metamorphosis in the common rock barnacle *Semibalanus balanoides*. (After Costlow and Bookhout 1957 and Walley 1969.)

Dispersal and Settlement

Although the adults of some organisms travel over much greater distances than their larvae, the larvae of many ani-

Figure 2.5 Factors influencing patterns of larval dispersal and settlement.



mals play an important role in dispersal. Most aquatic larvae are small and their rates of movement are frequently very slow compared to those of water currents. Therefore, to a large extent, they are passively distributed within the environment. Although this is true, larval behavior may be a significant factor in determining the final distribution pattern. Many larvae exhibit a **phototaxis**, moving toward or away from light. They may also respond positively or negatively to the force of gravity (**geotaxis**) (Figure 2.5). The larvae of many organisms possess eyes, statocysts, and other sense organs. Various stimuli may interact to influence larval behavior, and responses to individual stimuli may change during the larval period (see Crisp 1974; Chia and Rice 1978). For example, some larvae move toward the bottom when they are exposed to light but move upward when they are carried under an object that shields them from the light. Larvae may swim near the surface of the water during early larval life and move along the bottom when they are older.

Behavior, which regulates the position of larvae in the water column, may determine which currents will be used for dispersal. At different depths, the currents may flow with different velocities and/or in different directions. By riding different currents that move in opposite directions, at various times during the larval period, aquatic larvae may be retained within a limited area rather than being dispersed into potentially unfavorable habitats. For example, the larvae of estuarine animals tend to be flushed from an estuary with the outward flowing river water. Certain crab larvae reduce this tendency by rising in the water column during the flooding tide that carries them up river and then descending during the ebbing tide to a position where the seaward currents are relatively slow (Cronin and Forward 1979).

In some other aquatic animals, many aspects of the larval period have been highly modified to minimize the risk of dispersal into unfavorable situations. Freshwater lampsilid mussels provide a striking example. These mussels produce a *glochidium* larva (Figure 2.6*a*) that develops from the fertilized egg within a brood pouch formed by portions of its mother's gills. Following expulsion from the brood pouch, the glochidium clamps onto the gills of a fish with its two shell valves. The tissues of the fish grow progressively over the glochidium, forming a cyst in which the larva completes development (Figure 2.6*b*). At the end of the parasitic phase, during which the larva ap-

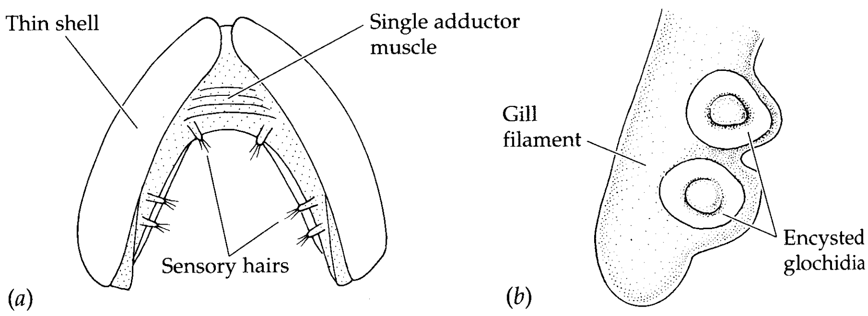


Figure 2.6 Glochidium larvae of a freshwater mussel. (*a*) Free-living larva with gaping shell valves. (*b*) Glochidia encysted in the gills of a fish. (After Coker et al. 1919.)

parently absorbs nutrients from its host, a juvenile mussel breaks out of the cyst and falls to the bottom. If attachment to a fish does not occur, the glochidium dies within a short period of time. Contact between glochidia and fish is promoted by structural and behavioral adaptations of the brooding female mussel. Adult females of some species possess fishlike lures that develop from the posterior mantle folds. These lures exhibit eyelike spots at one end and a rhythmically waving tail at the other. When a predatory fish is attracted to the lure, the female mussel discharges masses of glochidia that are eaten by the fish. Many of the larvae evidently are moved into the gut and digested, but some become attached to the gills of the fish. Such transfer to a fish host prevents the larval mussels from being carried downstream by currents (Welsh 1969).

Other freshwater mussels release glochidia that fall to the bottom of the river or stream. These larvae attach to the fins or other body regions of fish that come into chance contact with them. The glochidia of many such species possess a prominent hook at the free margin of each shell valve, and these facilitate attachment to the fish host (Welsh 1969).

A phenomenon related to larval dispersal is **site selection**. This is especially important for nonmotile and sedentary organisms. After a period of dispersal and development, larvae of numerous species acquire the ability to settle and initiate metamorphosis. Such larvae are said to be **competent**. Competent larvae, which have reached a stage preceding metamorphosis, explore surfaces with which they come in contact. When a larva encounters a favorable substratum, it may settle almost immediately. On the other hand, if a larva fails to locate a suitable site, settling may be delayed or prevented. Such postponement of settling increases the likelihood that a favorable site will be found. For example, the larvae of the red abalone (*Haliotis rufescens*), which have a very specific substratum requirement for settling, become competent for settling at 7 days following fertilization; then, at any time for up to a month, they rapidly settle out of the water column upon making contact with an appropriate substratum. (Also see the discussion later in this section on *Haliotis rufescens* larval settlement.) However, beyond this period, they exhaust their energy stores and are no longer capable of settling (Morse 1991). In selecting a place for settling, larvae may respond to a number of factors including texture, chemical composition, light, and currents.

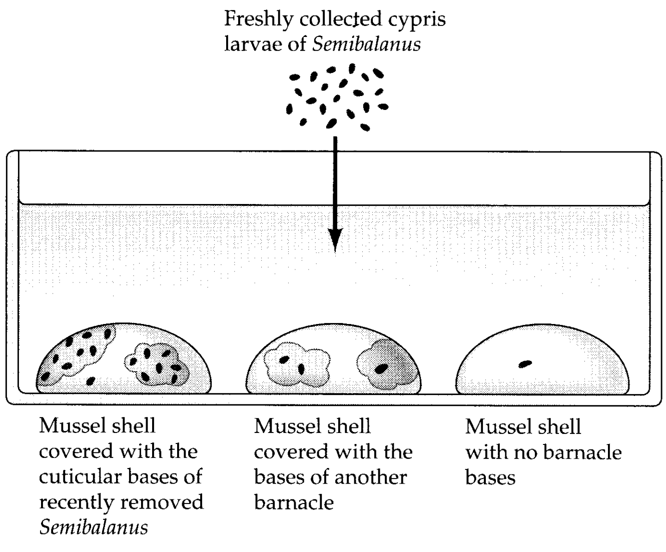
Barnacles, such as *Semibalanus*, develop a series of six *nauplius* larvae that are characterized by the possession of three pairs of head appendages: antennules, antennae, and mandibles (Figure 2.4). These larvae feed on phytoplankton. The last nauplius molts and gives rise to a nonfeeding *cypris* larva that functions in site selection and settlement. The cypris possesses a bivalve shell, compound eyes, antennules, cement glands, and six pairs of thoracic appendages that are used for swimming. When the larva has found a favorable place for settling, it adheres to the substratum by means of its antennules and releases attachment cement. The shell and compound eyes are shed, and the larva metamorphoses into a small adult-like juvenile (Walley 1969).

Barnacle larvae settle gregariously. That is, they settle in clusters. The settlement of a few larvae on a surface greatly increases the chances of other larvae settling there. The protein, arthropodin, present in the cuticle of settled barnacles promotes larval settlement; and this effect is species-specific (Figure 2.7). Slate panels soaked in an aqueous extract of barnacles, containing arthropodin, strongly stimulate cypris larvae to settle in contrast to untreated panels (Crisp and Meadows 1963). Gregarious larval settling is important for these nonmotile organisms, which are cross-fertilizing **contemporaneous hermaphrodites** (adults simultaneously produce both spermatozoa and eggs), because fertilization is internal. An acting male deposits spermatozoa in the mantle cavity of a receptive individual by means of a highly extensible penis. Obviously, if two individuals are not within a certain limited distance of each other, breeding can not take place. Even if the problem of fertilization did not exist, the presence of barnacles on a surface would serve as a cue to the larvae that the site is a favorable one for settling, but such a cue is not infallible.

Larvae of the honeycomb worm *Phragmatopoma* also settle gregariously. These worms construct tubes of sand grains and debris held together by a proteinaceous cement, and large reefs are formed as new recruits settle on the tubes of established adults. The larvae are induced to settle by the cementing protein (Morse 1991).

The larvae of certain species of the annelid *Spirorbis*, which possesses a calcareous tube cemented to a surface, exhibit a high degree of substratum selectivity during settlement. Closely related species of *Spirorbis* occupy differ-

Figure 2.7 Experiment demonstrating gregarious larval settlement in barnacles. (After Knight-Jones 1954.)



ent substrata even when they occur together in the same general area. *Spirorbis borealis* is found on the brown alga *Fucus serratus*, whereas *Spirorbis corallinae* occurs on the red coralline alga, *Corallina officinalis*. A third species, *Spirorbis tridentatus*, is attached to rocks. When the larvae of *S. borealis* are given a choice of settling on *Fucus* and/or *Corallina* in the laboratory, they settle predominantly on *Fucus*. In the same situation, the larvae of *S. corallinae* settle almost exclusively on *Corallina*. The larvae of *S. tridentatus* do not settle on macroalgae but readily colonize stones (de Silva 1962). Exposure of panels to an aqueous extract of *Fucus* greatly increases the number of *S. borealis* larvae settling on them compared to untreated control panels (Williams 1964).

The larvae of a number of animals, besides *Spirorbis corallinae*, are induced to settle by contact with coralline red algae. One of these is the red abalone *Haliotis rufescens*. The larvae of this mollusc respond to a small algal peptide that has properties similar to those of gamma-aminobutyric acid (GABA), a neurotransmitter; and GABA is effective in inducing larval settlement. The newly metamorphosed juveniles eat coralline red algae, but older abalones have a diverse diet (Morse 1991).

In these cases, a substance(s) produced by another organism makes a substratum specifically attractive for larval settlement. In other cases, it appears that a potential settling site may be made specifically unattractive by a similar mechanism. The bryozoan *Bugula* is often overgrown and smothered by the colonial tunicate, *Diplosoma*; and it would be beneficial if the larvae of *Bugula* could avoid settling close to this competitor. Interestingly, *Bugula* larvae can be reversibly prevented from settling by placing them into sea water in which *Diplosoma* has been previously kept (Young and Chia 1981).

Reproduction

Although larvae cannot reproduce sexually (see the discussion of neoteny below), **asexual reproduction** may occur at any stage in the life cycle of an organism, even in the larva. For example, the oceanic larvae of certain starfish produce embryo-like to larva-like **embryoids** that develop from various regions of the larval body (Figure 2.8). These "embryos" detach from the primary larva and take up an independent planktonic existence. Such asexual propagation by larvae may promote long-distance dispersal by currents and increase the probability that some larvae will find a suitable place to settle (Jaeckle 1994).

Larval Structure and Function

Larvae, like all stages in the life history of an organism, are subject to evolutionary change. Over time larvae may become more efficient in their feeding, acquire increased capacity for locomotion, become better adapted to stressful environments, and/or change in a variety of other ways (see Emlet and Ruppert 1994). The larvae of some animals undergo dramatic transformations during metamorphosis; and within certain limits, changes in the larvae may have little direct influence on the adults. For example, in certain aquatic larvae that have a long planktonic life, structures related to swimming, suspension feeding and/or the reduction of sinking velocity may be highly developed and then they are absorbed or discarded at the time of metamorphosis. The *veliger* larva of the mud snail *Ilyanassa obsoleta*, possesses a large bilobed structure associated with its head known as the **velum** (Figure 2.9*a*). This structure, which is ciliated, functions in feeding and locomotion. During metamorphosis, the velum becomes severed from the rest of the body and the young snail creeps away, leaving this larval organ behind (Scheltema 1962).

In other cases, changes in larval structure/function are carried over to the adult stage. Such changes are selected for or against depending upon how they affect

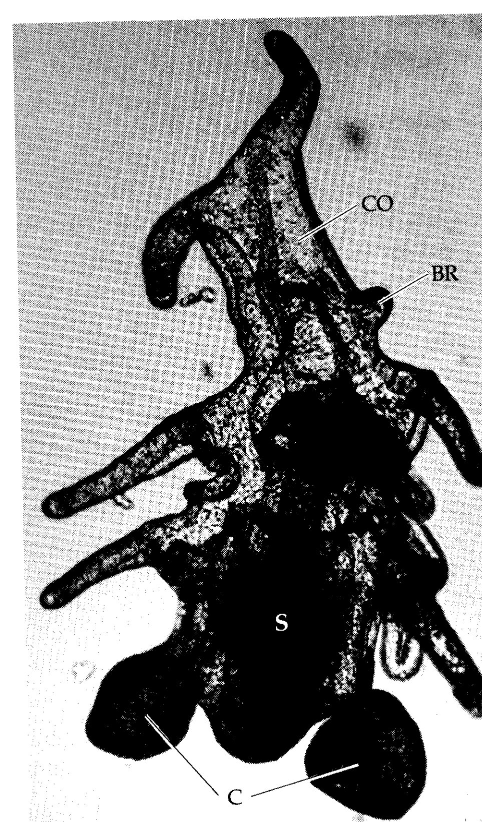


Figure 2.8 Asexual budding by a sea star brachiolaria larva. Note the secondary larvae (C), and the coelom (CO), stomach (S), and brachiolar arm (BR) of the primary larva. (From Jaeckle 1994.)

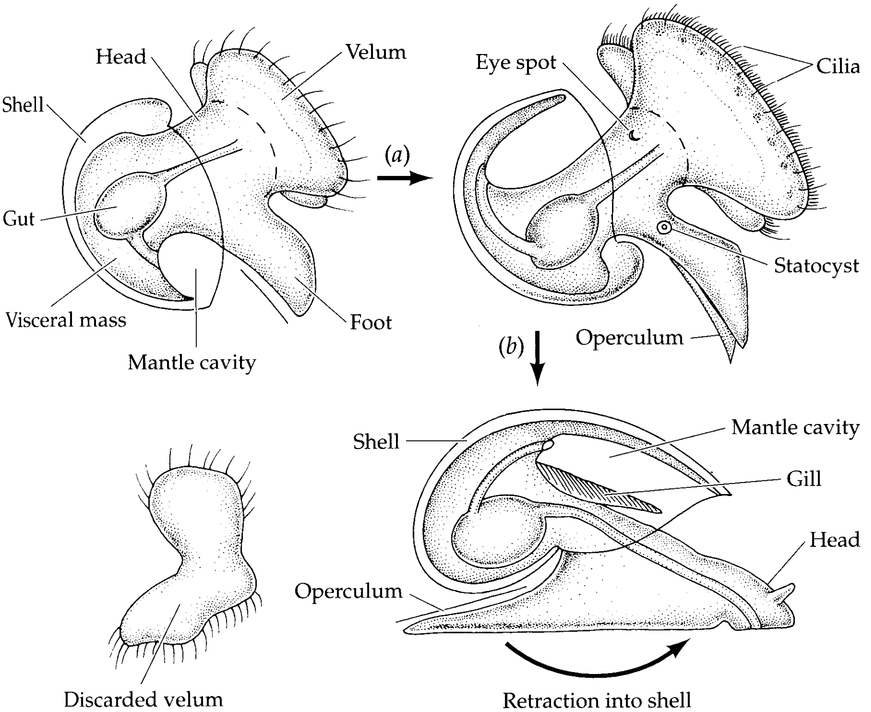


Figure 2.9 Development of a gastropod mollusc. (*a*) Torsion in the veliger larva, shifting the mantle cavity to a dorsal position behind the head. (*b*) Metamorphosis of the advanced veliger larva into a juvenile snail. During this process, the larval velum is shed. (Modified from various sources.)

both the larva and the adult. For example, the caterpillar of the tiger moth *Utethesia ornatrix* feeds on plants containing toxic alkaloids. These alkaloids accumulate within its body and are transferred during metamorphosis to the adult stage, protecting both the larva and the adult from predators. Furthermore, the newly laid eggs of this moth contain alkaloids derived not only from the female adult, but also from male semen. Thus chemicals ingested by the larva protect all other stages of development as well (Dussourd et al. 1988). This defense mechanism of the moth obviously depends upon its resistance to the toxic effects of the alkaloids from the egg through the adult. Another example is torsion in gastropod molluscs (Garstang 1928). In the early veliger larva, the mantle cavity is in a ventral position behind the foot. However, as development continues, the visceral mass is rotated 180° in relation to the head and foot, bringing the mantle cavity into a dorsal position behind the head (Figure 2.9*b*). This rotation is brought about by contraction of an asymmetrically positioned retractor muscle and/or differential growth. At the end of the torsion, the head and velum can be drawn into the shell, followed by the foot, which often bears a horny operculum on its dorsal surface. It has been suggested that torsion is an adaptation for protecting the head of the larva and the adult. Another possible advantage of torsion for the adult is that the osphradium, a chemoreceptor situated in the mantle cavity, is exposed to a current of water coming from in front of the animal.

Neoteny

Neoteny is the phenomenon brought about by the maturation of the reproductive system in a larval form that fails to undergo metamorphosis. As a result, the former adult stage is lost. For example, a number of salamander species are neotenic. These include the mudpuppy *Necturus maculosus*, the Mexican axolotl *Ambystoma mexicanum*, and the Texas salamander *Eurycea neotenes*. Since metamorphosis is normally induced by the thyroid hormones, triiodothyronine and thyroxine, there are several different levels at which mutations could result in neoteny: the hypothalamus, the adenohypophysis, the thyroid gland, and the target tissues of the larva. Depending upon where the block to metamorphosis occurs, some neotenic amphibians can be experimentally stimulated to undergo metamorphosis.

In *Ambystoma mexicanum*, the adenohypophysis apparently does not release thyroid stimulating hormone that promotes the synthesis of thyroid hormones by the thyroid gland. This salamander can be induced to undergo metamorphosis by transplanting the adenohypophysis of another species into it (Blount 1950) or by treatment with thyroid hormones (Huxley 1920; Prahlad and De Lanney 1965). On the other hand, the tissues of *Necturus* are unresponsive to thyroid hormones (Frieden 1981).

The northwestern salamander *Ambystoma gracile* inhabits moist woodlands along the Pacific coast at altitudes ranging from sea level to approximately 3500 m. At sea level most of the larvae undergo metamorphosis at one year of age and become sexually mature one year later. Nearly all of the remaining larvae metamorphose during their second year, but a few become neotenic. However, in montane populations, metamorphosis is rare and most individuals become neotenic (Snyder 1956). Neoteny appears to be advantageous for populations where the aquatic environment is normally more hospitable than the terrestrial one (Wilbur and Collins 1973). Predation, competition and/or climatic conditions may be important factors.

Summary

The necessity of larval forms for feeding, dispersal, and/or site selection has produced a wealth of intricate and beautiful transitory phases in animal life cycles. These stages link the embryo with the adult and have their own anatomical and physiological properties that make them fascinating to study. The larvae of some animals are specialized for feeding and growth; those of others function primarily in dispersal and site selection. However, many larval forms perform all of these functions. In some cases larvae occupy the same general habitat as the adults, whereas in other cases they live in a very different environment. The larvae of some animals may be the only stage in the life cycle to survive seasonally occurring adverse conditions.

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