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Body Shape / Competition / Hydrodynamic Forces / Materials: Strength / Territoriality / Wave Forces, Measurement of

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SNAILS

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Snails are members of the Gastropoda, the most diverse class in the phylum Mollusca, and are characterized by a spiral, conical shell of calcium carbonate ($CaCO_3$), a large muscular foot, and a rasping tongue called a radula. Intertidal snails feed on algae or various invertebrates (e.g., mussels, barnacles, other snails) or are scavengers. They represent an important group of intertidal organisms that operate as both predators and prey within food webs and play key roles in regulating the structure of intertidal communities.

BIOLOGY

The most distinctive feature of a snail is its spiral $CaCO_3$ shell (Fig. 1), which protects the soft anatomy from abiotic and biotic stresses and can vary dramatically within and among species in response to spatial and temporal environmental variation. Among species, the shell can vary from a simple conical cone as found in limpets to highly spiraled forms found in periwinkles and whelks. The snail is attached to the shell via the columellar muscle and cannot be removed from the shell. The shell is divided into the body whorl—the most recent and largest whorl—and the spire, the whorls above the body whorl. The main opening to the shell is the aperture, where the head and foot of a living animal extend through. When snails are disturbed, they retract their head and foot into their shell and seal off the aperture with the operculum (trap door).

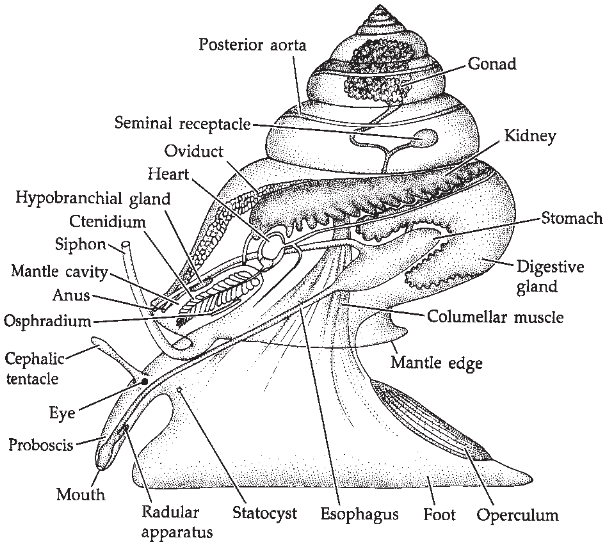

FIGURE 1 An illustration of a typical marine snail showing the major features of the external and internal anatomy. Reprinted from Brusca and Brusca (2003).

Most intertidal snails are highly mobile and use the muscular foot and pedal secretions (mucus) to move over the substrate. In addition, adhesion develops between the substrate, pedal mucus, and foot, allowing snails to "hold on" to the substrate and avoid dislodgement from currents or the hydrodynamic forces that attend breaking waves.

Snails have well-developed sensory systems, including sight, smell, and touch. The eyes are located at the base of each cephalic (head) tentacle (Fig. 1) and vary in complexity from simple pits containing photoreceptors that can detect differences in light to highly developed structures with a cornea and lens that can form an image. In most snails, the eyes are used primarily to detect differences in light intensity. A pair of cephalic tentacles is used for both touch and smell. The osphradium, in the mantle cavity, provides additional chemosensory (smell) capability. The ability to detect and track smells is critical for many predatory and scavenging snails to find their prey.

Gas exchange takes place at the ctenidium (gill) located in the mantle cavity (Fig. 1). Water circulates through the mantle cavity and across the ctenidium, where gases diffuse in and out of the blood. The blood has a special copper-containing protein called hemocyanin, similar to hemoglobin, which binds with oxygen and transports it through the circulatory system. A two-chambered heart pumps blood through the ctenidium and to the other tissues.

The primary feeding structure of snails is the radula (Figs. 2, 3), essentially a tongue covered with rows of teeth that is scraped across a surface to tear off tissues for consumption. Herbivorous snails use the radula to feed on algae growing on intertidal rock surfaces, while predatory snails use it to scrape tissues from their prey and sometimes to drill through protective shells. The size, shape and morphology of the radular teeth vary within and among species and, like teeth in terrestrial mammals, are indicative of what snails eat. The radula is contained within the proboscis (Fig. 1), which is composed of the esophagus, buccal cavity, radula, and mouth. In predatory snails the proboscis can be highly extensible, sometimes extending three times the shell length.

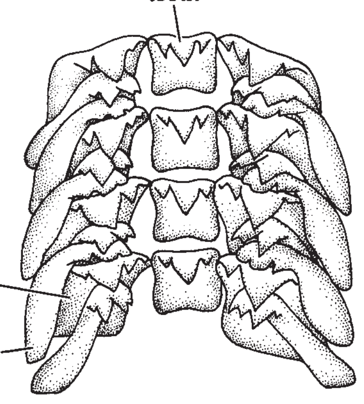

FIGURE 2 Four rows of radular teeth in a marine snail showing median, lateral, and marginal teeth. The teeth are arranged in a series of rows and attached to the odontophore. Reprinted from Brusca and Brusca (2003).

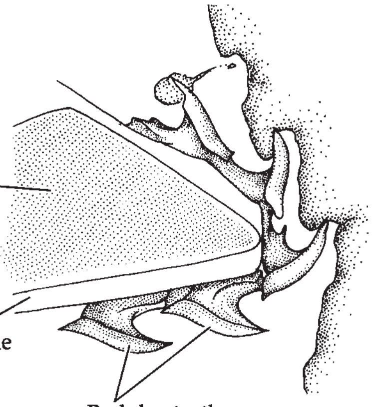

FIGURE 3 An illustration showing how the radula is scraped along the tissues of the prey. As the radula is pulled back towards the snail, the teeth dig in and tear off pieces of tissue. Reprinted from Brusca and Brusca (2003).

AUTECOLOGY

Environmental Heterogeneity

The intertidal zone is an extremely heterogeneous environment, and snails often exhibit considerable morphological, physiological, and life history variation within and among shores. The variation develops in response to two major physical gradients. Within shores, tidal height (vertical position on the shore relative to mean low tide) determines the length of time snails are out of the water and exposed to air, which influences thermal stress, desiccation, feeding time, and predation intensity. The higher on the shore, the longer individuals are exposed to air and the more severe the physiological stresses. Because most snails feed only when immersed, those higher on the shore have greater constraints on foraging. Predation intensity is generally greater low on the shore but can be complex because snails are preyed on by both terrestrial and marine predators. When snails are immersed, lobsters, crabs, fishes, sea stars, and other snails prey on them; while emersed, predators include shorebirds, rodents, and humans.

Among shores, wave action can vary dramatically from sheltered bays and inlets with little wave energy to open coast headlands that are pounded by enormous oceanic swells. Breaking waves impart tremendous forces that directly and indirectly affect the ecology of intertidal snails. For example, the hydrodynamic forces that attend breaking waves can rip snails off the shore, depositing them in the shallow subtidal zone, where they are typically consumed by predators. Indirect effects of waves are more subtle but can alter the nature and amount of food available to snails, their foraging efficiency, the efficiency of their predators, and the intensity of physiological stress.

Whether intraspecific variation develops in response to these gradients depends on the amount of gene flow relative to the spatial scale of environmental variation, the intensity of selection, and the degree of phenotypic plasticity. Gene flow represents the exchange of individuals/genes among populations and tends to retard adaptation to local selective pressures. The mode of larval development determines, to a large extent, how much gene flow occurs. Snails that produce larvae that spend part of their development in the water column drifting with ocean currents tend to have greater gene flow among populations than do species that brood their young or deposit benthic egg capsules releasing crawl-away juveniles. Snails with greater dispersal potential generally exhibit much less phenotypic variation in response to environmental heterogeneity. For example, *Littorina littorea* is a very common periwinkle with a broad distribution encompassing the eastern and western North Atlantic. It releases larvae that drift for several weeks in the water column and shows little morphological, physiological, or life history variation among shores. In contrast, two closely related congeners with similar geographic distributions, *Littorina obtusata* and *L. saxatilis*, deposit benthic egg capsules or brood their young, respectively, and they vary considerably among shores.

Tidal Height

Because the vertical gradient within the intertidal zone is small relative to the mobility of snails, there is little opportunity for populations to diverge, and only modest intraspecific phenotypic variation emerges. For example, there is a positive correlation between tidal height and snail size for many species. This pattern may reflect higher settlement rates lower on the shore, size-specific movements, or differential mortality. Various life history characteristics (growth, reproduction, mortality) can differ between upper and lower-shore populations for some species with very limited dispersal. For example, *Littorina saxatilis* grows more quickly, attains a larger size, and produces more offspring at low levels on the shore than at higher levels.

Interspecific differences are much more apparent across the tidal gradient. Different species exploit different levels within the intertidal zone and are highly adapted to those zones. One of the key adaptive characteristics is their ability to withstand physiological stress. Snails higher in the intertidal are exposed to air longer and suffer greater thermal and desiccation stress. Thermal stress can involve higher heat loads, induced by the higher air temperatures and absorption of solar radiation, or freezing when air temperatures fall below 0 °C, both of which can severely stress or kill snails. As the tide recedes, snails begin to lose water, and this desiccation is more severe higher on the shore. Not surprisingly, the physiological tolerances of snails to thermal and desiccation stress are correlated with their height on the shore. In fact, the upper distribution limit of some species is set by their physiological tolerances.

Although physiological tolerances can set the upper limit for snails, they are not as prevalent as for sessile organisms. Instead, a number of biotic forces control the vertical distribution of intertidal snails. The reason many snails live within the intertidal zone, instead of the more benign subtidal, is because it provides a refuge from major predators that are intolerant of emersion. Predators, especially those from the subtidal, are often thought to limit the downward spread of intertidal snails. For example, the lower limit of the trochid *Tegula funebralis* in the eastern Pacific is set by predation from the sea star *Pisaster ochraceus*. The sea star is not very efficient at foraging in the intertidal, so *T. funebralis* can avoid being eaten by remaining high enough that *Pisaster* cannot feed. Interestingly, *Pisaster* also probably sets the lower limit of various whelks, both directly through feeding on them, as well as indirectly, by setting the lower limit of their prey (mussels and barnacles). A similar situation occurs for *Nucella lapillus*, a whelk in the North Atlantic. Its lower limit is set directly by predation from subtidal fishes, sea stars, and crabs, as well as indirectly by these same predators setting the lower limit of their barnacle and mussel prey.

Prey distributions can play an important role in setting the vertical distributions of both predatory and herbivorous snails. Because of their limited mobility, intertidal snails rarely live far from their prey. Thus, the biotic and abiotic forces that regulate the vertical distributions of their prey can affect indirectly the vertical distributions of snails.

Competition with other species also can delimit vertical distributions within the intertidal. For many species, their spread across the intertidal zone is constrained by other species that are competitively superior at higher or lower regions of the intertidal. For example, *Acmaea digitalis* is typically found higher on the shore than *Acmaea paradigitalis*, but when *A. digitalis* was experimentally removed, *A. paradigitalis* extended its range to higher levels on the shore. In control areas where *A. digitalis* was not removed, *A. paradigitalis*'s range did not change, suggesting that its upper boundary is set by competition with *A. digitalis*. Competition can be mediated through a variety of mechanisms, including superior feeding efficiency, greater physiological tolerances, and differential susceptibility to predation. A slightly more complex example involves *Littorina subrotundata*, which can live throughout the intertidal but is restricted to the high intertidal because it grows more slowly than *L. sitkana* and is more vulnerable to predators in the low intertidal. The faster growth rate and lower mortality rate of *L. sitkana* in the low intertidal make it competitively superior in this zone.

Because snails often are adapted to exploit particular levels within the intertidal, it is essential that they avoid moving outside their typical zone and that they can find their way back if displaced. A number of environmental cues are used to regulate their level on the shore, including light, gravity, temperature, desiccation, and chemosensory responses to predators and prey. For example, snails that are dislodged by waves and washed downshore become positively phototactic and negatively geotactic, which tends to move them back up the shore. Responses to gravity are usually stronger than those to the direction of light. In some cases, waves could displace snails upshore, depositing them in the high intertidal, where positive phototaxis and negative geotaxis would move snails in the wrong direction. However, the higher thermal and desiccation stresses experienced in the upper intertidal can switch the behavioral responses such that they become negatively phototactic and positively geotactic. In addition to light and gravity, snails use chemosensory cues from their predators and prey to help determine position in the intertidal. Both predators and prey release chemicals into the water that many snails can detect. When snails pick up these chemical cues, they tend to move towards their prey and away from their predators. Together, these behavioral patterns allow snails to maintain their level within the intertidal and, if displaced, to find suitable microhabitats.

Wave Action

MORPHOLOGY

The morphology of snails with limited dispersal varies dramatically among shores differentially exposed to waves. On sheltered shores, snails tend to be large and narrow and produce heavier shells with thick shell walls and a narrow aperture (Fig. 4). These morphological features are thought to represent adaptations to the greater intensity of predation on sheltered shores. The larger size and thicker shell reduces the efficacy of shell-crushing predators such as crabs, fishes, and birds. For example, when crabs are provided both thick- and thin-shelled prey, the thin-shelled morphs suffer much greater mortality because they are easier to break. Size is important because as snails increase in size, fewer predators can feed on them and eventually they may often attain a size refuge, where they are sufficiently large that most predators are unable to consume them. In addition to crushing, some crabs will hold snails by the spire with one claw and use the other to peel back the shell from the aperture to gain access to the soft tissues. The narrow aperture and thick shell wall make it more difficult for crabs to insert a claw and peel back the shell. Some snails (e.g., whelks) produce apertural teeth that reinforce the aperture wall and narrow the opening (Fig. 4). The narrow aperture also makes it more difficult for birds that prey on snails by turning them over and tearing off any tissues they can reach with their beak.

FIGURE 4 Examples of *Nucella lapillus* from exposed (top row) and protected (bottom row) shores. Note that the exposed shore forms are smaller with broader apertures and thinner shell walls. Photograph by the author.

In contrast, on wave-swept shores, predation is much less, and snails are often smaller and wider with thin-shelled walls and a broad aperture (Fig. 4). These morphological features are thought to represent adaptations to the powerful hydrodynamic forces that attend breaking waves. A thick shell is unnecessary, because predation intensity is considerably reduced on wave-swept shores, and a thinner shell wall reduces the energy required to produce and transport the shell. High wave energies reduce the abundance and efficiency of the guild of mobile, durophagous predators that typically feed on snails (e.g., crabs, fishes). The pounding surf makes it difficult for even terrestrial predators to forage during low tides. Snails tend to be smaller on wave-swept shores because they grow more slowly and suffer much greater mortality (see subsequent discussion). The smaller size is favored because the intensity of hydrodynamic forces (e.g., drag) increase with increasing size, and it allows snails to exploit small cracks and crevices, where hydrodynamic forces are reduced. The wider shell and broader aperture are necessary to accommodate a larger foot, which is favored on exposed shores to reduce the likelihood of dislodgement.

Contrary to earlier views, snails use adhesion, not suction, to maintain their position on shore and resist dislodgement. Adhesion develops between two hard surfaces separated by a thin layer of fluid (e.g., a wet microscope slide cover is more difficult to remove from a slide than a dry one). In snails, the foot and substrate act as the two hard surfaces and are separated by a thin layer of pedal mucus. The adhesive force that develops is proportional to the surface area of the foot and the viscoelastic properties of the pedal mucus. The strength of attachment increases with pedal surface area, so the production of a larger foot allows snails to withstand stronger hydrodynamic forces. Pedal surface area increases with snail size but increases more quickly on exposed shores, such that snails from wave-swept shores produce a much larger foot (Fig. 5).

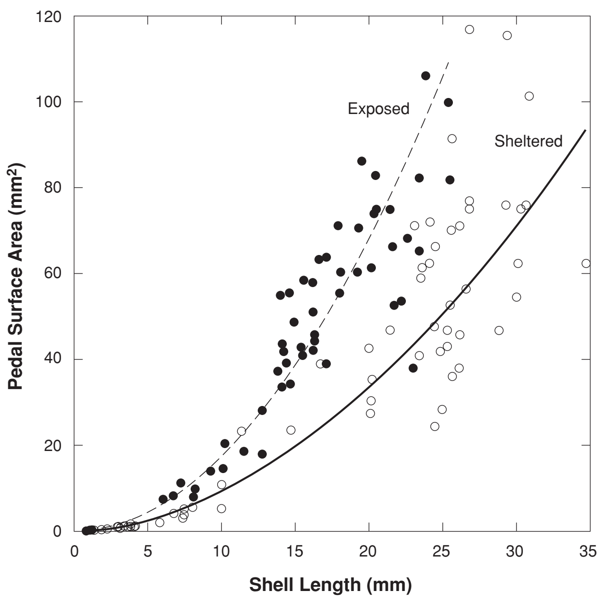

FIGURE 5 Pedal surface area as a function of shell length for *Nucella lapillus* from exposed (solid circles) and sheltered shores (open circles). Snails from exposed shores produce a much larger foot to reduce the likelihood they will be dislodged by breaking waves.

LIFE HISTORY

The intensity of waves impinging on a shoreline also has a profound influence on the life-history characteristics of snails. Life histories are a suite of characters molded by natural selection to maximize fitness and include traits such as growth rate, age and size of maturity, fecundity, and life span.

Snails on sheltered shores grow more quickly than do those on wave-exposed shores. Growth is depressed on exposed shores because the relentless pounding of breaking waves reduces foraging time and efficiency. For example, whelks that feed on barnacles and mussels forage less on exposed shores and take longer to handle a particular prey item. To avoid the powerful hydrodynamic forces that develop as waves break, snails spend most of their time in cracks and crevices, severely reducing foraging time. In addition, crawling along the shore reduces tenacity and increases the risk of being dislodged. The breaking waves continually jostle the snail, making it more difficult to drill its prey and feed, increasing prey handling time.

Despite lower predation intensity on exposed shores, snails experience much higher mortality, often because they are dislodged by waves. After dislodgement, snails are either transported high in the intertidal, where they can succumb to physiological stress, or are washed down into the subtidal, where they can be consumed by a more diverse guild of predators. Consequently, life spans tend to be much shorter on exposed shores. For instance, *Nucella lapillus,* the common predatory whelk in New England, may live for 2 to 3 years on exposed shores, while those on nearby sheltered shores live for 6 to 8 years.

The lower growth rate and higher mortality result in much smaller snails on exposed shores. The higher mortality also selects for snails to become sexually mature at a smaller size (earlier age) and channel most of their energy into reproduction. For whelks on a New England shore, 4 times more offspring were produced on exposed shores than by similar sized snails on sheltered shores. The greater reproductive effort, in part, offsets the higher mortality on wave-swept shores.

Plasticity

Many of the characters that change along these two major environmental gradients may not reflect genetic differences, but instead may be environmentally induced. For example, numerous experiments have shown that if snails are exposed to the chemical effluents of their predators, or from predators feeding on other members of the same snail species, they will produce a thicker shell. Similarly, pedal surface area is highly plastic and can be altered by changes in wave energy. Snails from a protected shore reared on an exposed shore will produce a much larger foot than will their counterparts remaining on the protected shore. Life-history characteristics will also respond to environmental changes. Snails from sheltered shores transplanted to exposed shores grow more slowly than conspecifics remaining on sheltered shores. These examples demonstrate that the morphological, physiological, and life history differences among snails from different habitats may not reflect genetic differences. The ability to produce a flexible phenotype may be an important adaptive characteristic for dealing with the pronounced spatial and temporal environmental heterogeneity of the intertidal.

COMMUNITY STRUCTURE

Because they are important components of intertidal food webs, snails play a key role in shaping the structure (abundance, composition, and diversity) of intertidal communities. As consumers, they can control the distribution and abundance of their largely sessile prey and thereby determine membership in local species assemblages. In addition to directly altering the abundances of their prey, snails can have profound indirect effects on intertidal systems via habitat modifications, trophic cascades, and positive and negative feedbacks on nontarget species. For example, by feeding on competitive dominants in local assemblages, snails can reduce competition and allow competitively inferior species to coexist (see subsequent discussion). The relative importance of herbivorous and predatory snails in controlling the composition and diversity of intertidal communities reflects a complex interplay between physical (e.g., tide levels, tide cycle, wave energy, temperature, desiccation, algal canopy) and biotic processes. For instance, snails tend to have a much greater impact in regulating communities on sheltered and moderately exposed shores because high wave energies reduce the efficacy of mobile consumers. However, even on sheltered shores, their role can be influenced by physiological stresses that change seasonally, monthly (lunar cycle), and with tidal height, or by spatial and temporal variation in the presence of their predators.

Herbivores

Herbivorous snails feed on diatoms, microalgae, algal spores, and macroalgae and can profoundly alter intertidal algal communities. For many species, the diet is fairly eclectic; the snail simply moves along the substrate scraping up whatever algae (diatoms, microalgae, and algal spores) it encounters. For others, especially those that consume macroalgae, the diet is much more restricted and clear preferences exist. For example, the fleshy unprotected tissues of ephemeral forms (e.g., *Ulva*, *Enteromorpha*, *Porphyra*) are favored over perennials (e.g., *Fucus*, *Laminaria*, *Ascophyllum*), which typically invest in structural or chemical antiherbivore defenses.

The feeding preferences of herbivorous snails can be important in regulating patterns of algal distribution and diversity. Ephemeral forms are found primarily on wave-exposed shores. On sheltered shores where herbivorous snails are abundant and efficient grazers, ephemerals are rare because they are preferred over perennials. Although ephemerals often settle on sheltered shores in winter and early spring while snails are relatively inactive, they are quickly removed once snails become active. On highly exposed shores, herbivorous snails are rare and less efficient, and ephemerals flourish.

By feeding preferentially on one particular group of algae, snails can exert a powerful control on algal diversity. A classic example of this comes from Jane Lubchenco's work on New England intertidal algal communities (Lubchenco 1978). The common periwinkle *Littorina littorea* feeds preferentially on the ephemeral algal species. She found that algal diversity within tidepools varied parabolically with the density of periwinkles, resulting in maximum diversity at intermediate snail densities (Fig. 6). In these tidepools, ephemerals were the competitive dominants. At low snail densities, the ephemerals outcompeted the perennials and eventually excluded them. As snail densities increased, herbivory on the competitive dominant

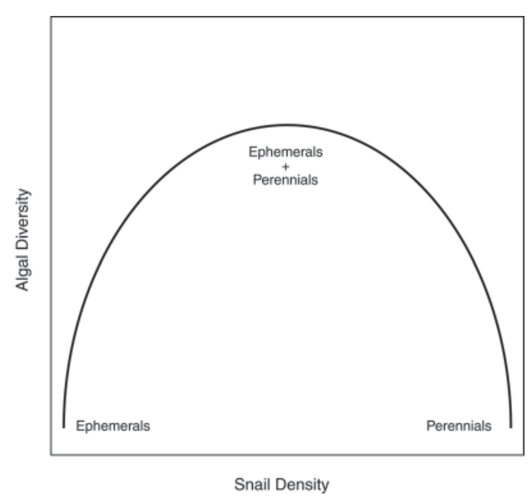

FIGURE 6 Algal diversity as a function of herbivore snail density. The major composition of the algal community is shown for various snail densities. Algal diversity peaks at intermediate levels of herbivore pressure because the snails feed on the competitive dominant algal forms preventing them from monopolizing space.

ephemeral forms prevented them from monopolizing space and allowed the competitively inferior perennial species to coexist. At high snail densities, herbivory was so intense that both the ephemerals and most of the perennials were consumed, leaving only inedible forms. Interestingly, the pattern was quite different on nearby emergent substrata (not in tidepools), where diversity simply decreased with increasing herbivore density. Although the feeding preferences were the same, the perennials were competitively superior on emergent substrata. In this case, both competition and herbivory acted to preclude ephemerals and reduce diversity. Thus, the composition and diversity of these algal communities reflect a complex interplay of wave energies, herbivore density, feeding preferences, and algal competitive abilities.

On sheltered shores, where snails can reach very high densities, grazing by limpets and periwinkles can be so intense that they effectively denude patches of the shoreline of diatoms and microalgae. If herbivorous snails are experimentally excluded, a luxuriant and dense growth of diatoms and microalgae rapidly develops. The transformation of the intertidal from a rich algal community to bare rock indicates snails can be important habitat modifiers—substantially altering the nature of the intertidal.

The impact of *L. littorea* on very sheltered southern New England cobble shores provides a stark example of how a single herbivorous snail species can lead to dramatic habitat modification. On these cobble beaches, snail densities reach 600 to 1000 individuals per square meter and impose intense consumer pressure on algal communities, essentially excluding all algae except for a couple of herbivore-resistant algal crusts. If snails are excluded, the cobble landscape develops a dense and rich algal canopy, which leads to sediment accumulation and the colonization of soft-sediment organisms. Tube-building organisms and perennial grasses further stabilize the sediment, and eventually the habitat transforms into a typical New England marsh. The presence of this snail in such high densities keeps the rock surfaces clear and prevents the typical succession from protected cobble beaches to marsh. Moreover, Mark Bertness (1984) has suggested that *L. littorea* may be responsible for shifting these habitats from soft-sediment marshes, typical of highly sheltered New England shores, to hard substrates. *Littorina littorea* was introduced to New England within the last century, so these modifications are relatively recent and ongoing.

Predators

Most intertidal predatory snails feed on shelled prey such as barnacles, mussels, oysters, and other snails. They typically use the radula and acidic chemical secretions that soften the $CaCO_3$ to bore a hole through the shell of their prey. Once the shell is penetrated, they extend their proboscis (in some species three times their body length) into the prey and use the radula to rasp off tissues. In some cases (e.g., barnacles), snails can use the edge of their shell to pry open the valves and insert their proboscis to feed. Feeding times vary with the type of predator and prey but can be quite long. For instance, a whelk feeding on a mussel can take from 4 to 36 hours to drill and consume a single individual.

As with herbivores, predatory snails can exert a powerful influence on the distribution of their prey and the structure of intertidal communities. A classic experiment by Joe Connell (1961) demonstrates just how effective whelks can be in controlling the distribution of their barancle prey. He used cages to exclude the predatory whelk *Nucella lapillus* from various regions of the shore in Scotland. The results showed that the impact of *N. lapillus* was greater at lower levels of the shore and could effectively set the lower boundary of the barnacle *Semibalanus balanoides*.

Many whelks feed on mussels, the dominant competitor for space in the intertidal, especially on temperate shores in the Northern Hemisphere. On exposed shores, where mobile predators are rare and inefficient, mussels monopolize the shore, excluding most other space occupiers, including barnacles, macroalgae, tunicates, anemones, and bryozoans. On more sheltered shores, predatory snails, as well as other predators (crabs, fishes, seabirds), consume mussels, creating bare patches that allow competitively inferior species to coexist. By cropping down the competitively dominant mussels, predatory snails can regulate diversity in much the same way herbivores control algal diversity in tidepools. In fact, the predators that control the distribution of mussels often have a greater impact on the distribution of intertidal algae than do herbivores. Clearly, snails can profoundly affect the abundance, distribution, and diversity of intertidal organisms.

SEE ALSO THE FOLLOWING ARTICLES

Adhesion / Competition / Dispersal / Limpets / Predator Avoidance / Wave Exposure

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SPONGES

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Sponges (phylum Porifera) are animals, often with colorful bodies that, in the intertidal, form crusts or clumps, primarily on rocky surfaces. Sponges are unique among animals in having a body perforated by canals open to the surface. This may be a significant factor in limiting species intertidal occurrence and distribution because of low tolerance of physical stresses such as desiccation, temperature, and salinity. Also, like other filter feeders, sponges feed only when fully submerged. Given that many subtidal sponges feed continuously, the mid- and upper regions of the intertidal habitat may be food-limited for sponges.

GENERAL MORPHOLOGY

Sponges are best described as encrusting, globular, massive, vase-shaped, reticulate, or branching. Of these types, the first is most common in intertidal habitats, and there the encrusting forms are usually no more than a few millimeters thick, while massive and globular sponges may be as large as 10 to 20 centimeters in diameter. Colors are often vibrant—brilliant red, violet, mustard yellow, or green. The surface of most sponges is completely clear of sediment and debris, even in muddy bays; they are soft to hard and slippery to sandpaper-like to the touch, and a few have pungent odors if scraped.

INTERNAL ANATOMY

The sponge is essentially a suction pump that draws water through minute canals, extracting food and oxygen from the fresh supply and excreting wastes into exhalent canals. There are three functional regions (Fig. 1): the apical pinacoderm, which allows water into the animal through pores (ostia); the choanosome, the bulk of the body, which contains chambers with pumping cells (choanocytes); and the osculum (a chimney-shaped extension of the canal system and apical pinacoderm), which vents water out of the animal. Each of these regions is composed of two epithelia separated by a collagenous mesohyl with some crawling cells. The outer epithelium, the exopinacoderm, is formed of flat cells called exopinacocytes, and the inner epithelium, the endopinacoderm, is formed by elongate cells called endopinacocytes.

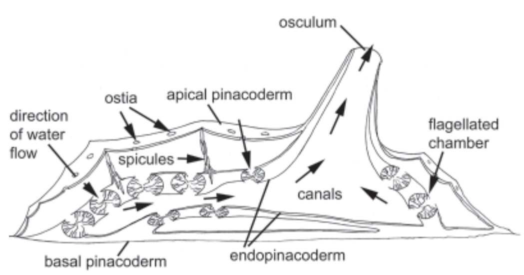

FIGURE 1 Internal anatomy of a juvenile demosponge, showing the inner and outer cell layers and the pathway that water follows as it is drawn through chambers and particles extracted for food.

INDIVIDUAL OR COLONY

Though texts often refer to sponges as colonies, the individual unit within the colony is difficult to define. One definition is that any animal enclosed by a single and continuous outer epithelium (or apical pinacoderm) can be considered an individual. Another view suggests that the individual unit within a multiosculum sponge consists of a single osculum and the chambers and canals that it drains. Typically, sponges are quantified by the percent of the substrate they cover or their volume, rather than their specific pumping and feeding capacity.

FEEDING

Choanocytes, specialized cells with a collar of microvilli surrounding a flagellum, generate the force for the feeding current. The beat of the flagellum draws water down to its base, and the combined effort of 80–100 or more choanocyte pumps in one or more chambers draws water through the sponge (Fig. 2). (While one deepsea