BARNACLES
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Barnacles are crustacean arthropods, which means they are distantly related to such animals as crabs, lobsters, and shrimp. However, unlike their mobile cousins, barnacles have adopted a sessile existence. Barnacles are found on hard substrates in virtually all marine habitats and on all levels of the shore, often in vast numbers. This, coupled with the fact that they have a typical marine life cycle with an easily identifiable, planktonic larval stage, has made them a model study organism. Consequently, much is known about the biology of barnacles.

LIFE CYCLE

The life cycle of a typical barnacle includes two stages: a free-swimming larval stage and a sessile adult stage. As with all crustaceans, a barnacle’s body is encased in a hard exoskeleton made of chitin. What distinguishes this group from other crustaceans, however, is that as adults they also secrete an outer calcareous “shell,” called a test, which provides them additional protection against both predators and the elements. This test is made up of several plates that are attached either directly to the substrate (acorn barnacles) or to a fleshy stalk (gooseneck barnacles). Although some barnacle species are parasitic as adults, most are free-living filter feeders. Instead of being used for locomotion, their legs have been modified into a netlike structure called a cirral net. When under water, this net is extended out through an aperture in the test, called the operculum, to filter food out of the water column (Fig. 1).

Adult barnacles are generally hermaphroditic (although there are some amazing twists on this), meaning they have both male and female reproductive organs. Prior to mating, one individual, the “male,” first polls the reproductive state of its immediate neighbors. It does this by using its elongated penis to “tap” nearby barnacles, a process thought to determine whether they carry eggs. If eggs are present, insemination occurs. Because fertilization is internal, the penis needs to be quite long and can be twice the length of the barnacle itself (Fig. 2).

Following fertilization, eggs are brooded within the test, where they develop into naupliar larvae, which are released into the water. This stage is the start of the mobile and dispersing larval period, which lasts between 10 and 45 days. While in the plankton, barnacles usually progress through six naupliar larval stages, all of which feed on phytoplankton and deposit lipid (fat) reserves. The final larval stage, the cyprid, is a nonfeeding stage, and it survives by utilizing the fat reserves built up

FIGURE 1 Some of the morphological features of (A) acorn and (B) stalked barnacles. Note that the cirral net pictured is only partially deployed; when fully deployed, it adopts a fanlike shape. Photograph by D. Lohse.
during the previous stages (Fig. 3). The cyprid is the stage that ultimately settles on the shore and undergoes metamorphosis into the adult form. Because adults are sessile, finding a good spot to settle (the location it will reside in for the rest of its life) is very critical. As such, cyprids utilize both chemo- and neuro-receptors to detect environmental cues that facilitate finding a suitable settlement site.

**SETTLEMENT CUES**

Since relocating after settlement is impossible, selecting a good settlement site is probably the most critical decision a barnacle larva will make. To aid in this decision, barnacles use cues from the environment to distinguish good sites from bad. A good cue is one that reliably predicts locations on the shore where individuals are likely to survive and reproduce. Hence, one of the most potent settlement cues used by cyprids is the presence of other individuals of the same species; if a site already has barnacles, then this is a strong indication that survivorship and mating opportunities are good. Other cues that have been demonstrated to influence the selection of a settlement site include bacterial films, surface texture, and even the presence of predators.

**INTERACTIONS**

Many studies have shown that once a barnacle settles on the shore, it must deal with a suite of physical and biological factors in order to survive, grow, and reproduce. One of the earliest, and perhaps most influential, of these studies was done by Joseph Connell in the mid-1950s on the rocky shores of Scotland. In this system were two species of barnacles: *Chthamalus stellatus* and *Semibalanus* (formerly the genus *Balanus* *) balanoides*. Connell observed that as adults, *Chthamalus* were restricted to a region of the shore above *Semibalanus*, but as juveniles their distribution extended down into the region of the shore occupied by *Semibalanus*. To determine why the distribution of adult *Chthamalus* was smaller than that of the juveniles, Connell performed the first manipulative field experiment in ecology. He first transplanted rocks covered with *Chthamalus* into the region where *Semibalanus* was abundant. Then, after allowing *Semibalanus* to settle on them, he removed the *Semibalanus* from half of each rock. Thus, half of each rock contained a mixture of *Semibalanus* and *Chthamalus*, while the other half had only *Chthamalus*. This treatment tested the idea that *Semibalanus* had a negative affect on the survival of *Chthamalus*. Cages to keep out predators were erected over half of the rocks to determine whether predation could explain the distribution of *Chthamalus*. Subsequent observations revealed that, when by themselves, *Chthamalus* survived just fine, but those in the mixture treatment were either crushed or undercut by the faster-growing *Semibalanus*. The presence/absence of predatory snails had little effect on this outcome. Based on this, Connell concluded that *Chthamalus* was actually capable of living...
lower on the shore but was prevented from doing so by the competitively superior *Semibalanus*. Additional observations suggested that the upper limit of *Chthamalus* was determined by physical factors such as desiccation. Thus, this study showed that competition for space is important in determining the structure of intertidal communities and that lower limits are determined by biological factors, upper limits by physical factors.

Studies done since Connell’s have shown that barnacle abundances are affected by a variety of other processes in addition to interspecific competition. For example, barnacles are attacked by a myriad of predators including sea stars, flatworms, nemerteans, predatory snails, and, in the case of gooseneck barnacles, even shore birds. Most predatory snails attack barnacles by drilling through the barnacle’s test. The time needed to drill through the test can take many hours and increases with the size of the barnacle. Beyond a certain size the time needed to successfully attack becomes so great that the predator would have to continue drilling even while exposed during low tides. Since doing so would increase the snails’ risk of desiccation, they usually do not attack barnacles beyond a certain size. Thus, one way barnacles can protect themselves from predation is by growing rapidly enough to reach this size.

One species of barnacle found in the Gulf of Mexico, *Chthamalus anisopoma*, has evolved a different method of protecting itself from attack. Instead of drilling, its principal predator, *Acanthina angelica*, sits atop the barnacle and uses a large “tooth” to pry its way through the operculum. However, if exposed to *Acanthina* when young, *C. anisopoma* can adopt a “bent” morphology. That is, they grow in such a way that the operculum shifts from the top to the side of the test (Fig. 4). Since *Acanthina* has great difficulty accessing the operculum in this location, adopting this bent morphology greatly reduces the risk of attack by *Acanthina*. However, this protection comes with a cost: to grow bent requires the loss of part of the gonad. Thus, while a bent individual may have a higher chance of survival than a normal barnacle, it also has a lower reproductive potential. This trade-off has important evolutionary consequences and prevents the entire population from adopting the bent morphology. Since the abundance of mussels and algae in this system is affected by the relative abundance of the two types of barnacles, this, in turn, also has important consequences for the structure of the community.

Other studies have shown that, high on the shore, limpets can also affect barnacle abundances. However, exactly how they do so depends upon several different direct and indirect interactions. Barnacles and limpets compete directly for space, so a decline in abundance of one can lead to an increase in abundance of the other. However, barnacles offer juvenile limpets protection from desiccation, so limpet recruitment is enhanced by the presence of barnacles. Thus, an increase in barnacles could actually cause the number of limpets to increase. Likewise, because barnacles and algae compete for space, by grazing on algae limpets actually assist the barnacles by reducing the abundance of a competitor. Thus, whether and how much a change in limpet abundance affects the number of barnacles depends upon the relative strengths of each interaction that makes up the complex interaction web among limpets, barnacles, and algae.

Intraspecific interactions also play an important role in determining barnacle abundances on the shore. Because barnacles need to be near each other to reproduce, and living together can also reduce the risks of desiccation, it is beneficial to live near conspecifics. However, because this strategy is true for all individuals, it is not uncommon for barnacles to experience severe crowding. Studies have shown that crowding can lead to higher mortality, slower growth, and lower reproductive output. Thus, this type of intraspecific competition has profound negative effects on an individual’s fitness.

In some cases, crowding manifests itself through the production of hummocks. Hummocks are areas in which the densely packed barnacle cover has developed a dome-like, or mounded, appearance (Fig. 5). Although barnacles typically grow by increasing in diameter, crowded individuals are prevented from doing so by their neighbors. Instead, they grow upward, which causes them to adopt a cylindrical shape instead of the typical conic morphology. Not all
crowded individuals grow at the same rate, and, as a result of differences in water flow and food availability, those that grow the fastest (and are therefore the tallest) end up surrounded by slower-growing (and therefore shorter) individuals. The end result is a hummock. Although individuals in hummocks can be quite tall, their area of attachment to the substrate tends to be relatively small. Further, because they are crowded, their tests tend to be thinner, which increases their fragility. Thus, hummocks tend to be inherently unstable. Any disturbance that kills even just a few barnacles can end up destabilizing the entire formation; the loss of a few individuals can result in the denudation of barnacles from large areas of rock.

Interestingly, in some cases it is the barnacles themselves that sow the seeds of their own destruction. Although many species compete for space with barnacles, for some their presence actually facilitates settlement. For example, along the shores of California the settlement of both mussels (*Mytilus*) and algae (*Endocladia*) is enhanced by the presence of barnacles. However, because this interaction ultimately results in the barnacles being smothered, it is usually detrimental to the barnacles. Such facilitation is often needed for succession to occur following a disturbance.

NEW DIRECTIONS IN RESEARCH

While past studies have shown that processes such as competition and predation affect barnacle abundances on the shore, recent studies have demonstrated that what happens to larvae while in the plankton is also important. For example, while in the plankton, larvae are subject to predation by planktonic predators and to being carried about by currents and other oceanographic processes. In fact, given the length of time they spend in the plankton (10–45 days), and assuming a current velocity of 10 cm/s, barnacle larvae could end up 80 to 400 km from where they were released by their parent. Thus, current thought is that the larvae that settle at a site are probably not produced by the local population. This decoupling of larval input from local production, and how it affects population abundances on the shore, is of great interest to marine ecologists.

Interestingly, recent genetic data suggests that, although they have the potential to travel great distances, barnacle larvae typically disperse much less than this. Recent advances in coupled biological–oceanographic models, which link larval behavior with realistic depictions of oceanography, suggest that directed swimming behavior (e.g., swimming to maintain position in surface water) may be responsible for the local retention of larvae. These models have implications beyond barnacles and may be fundamentally important to the management of harvested species such as rockfish, abalone, and sea urchins.

SEE ALSO THE FOLLOWING ARTICLES

Competition / Facilitation / Larval Settlement, Mechanics of / Limpets / Recruitment / Succession

FURTHER READING


Beaches are the loose deposits of sand, gravel, or shells that cover the shoreline in many places. Beaches serve as buffer zones or shock absorbers that protect the coastline, sea cliffs, or dunes from direct wave attack. They also provide important coastal recreational areas for millions of residents and visitors around the world, and they are the most intensively used parts of the coastal environment. The landward edge of the beach may be a sea cliff, sand dune, vegetation line, or seawall. In the seaward direction beaches extend to water depths of about 10 meters beyond where there is usually little seasonal sediment movement due to normal wave action. Although beaches may appear wide and stable during the summer months under periods of low, gentle waves, they can erode very quickly when attacked by hurricanes, large storms, or heavy surf. In winter they change their entire character or may even disappear altogether. Beaches can undergo significant change in response to human activity in addition to their seasonal and storm cycles. The sources and losses of beach sand, the interaction of waves, tidal action, and wind are each important in determining the composition, size, and shape of any individual beach. About 5280 km, or 30%, of the entire continental coastline of the United States consists of beaches.

**FORMATION OF BEACHES AND SOURCES OF BEACH SAND**

Beaches form where there is enough loose or unconsolidated material available and where there is some suitable coastal environment in which the waves and coastal landforms will allow these sediments to accumulate. The materials making up beaches can vary in size from very fine-grained sand to pebbles, cobbles, and even boulders (Fig. 1A–C). The sediment may be either terrigenous or land-derived, having been transported to the shoreline by rivers and streams, or through erosion of the coastal bluffs or cliffs. In tropical areas or where land-derived material is lacking, beach sediment may be biogenous in origin and consist of broken bits of coral or shells of nearshore organisms (Fig. 2A, B). On volcanic islands such as Hawaii, beaches may be black and consist almost entirely of broken lava and volcanic minerals (Fig. 3).

Fine-grained sand beaches tend to be quite flat (usually a slope of only a few degrees), whereas coarser pebble or cobble beaches are usually much steeper, often as much as 15 to 20 degrees or more. These slope differences are due to the differing permeabilities of the materials and the resulting balance between wave uprush and backwash. Where the beach consists of fine-grained sand, permeability is low, and little of the broken wave that washes up the beach face can percolate into the sand. Thus the backwash, or the water returning to the surf zone, will
carry the fine-grained sediment in suspension back down the beach face, maintaining a low-sloping beach. With a cobble beach, in contrast, the voids between the cobbles are large, permeability is high, and much of the uprushing wave percolates into the beach face, so much less water washes back down the beach face, reducing the seaward movement of the cobbles. Thus the coarser materials can accumulate on the beach, where they are transported by larger winter waves.

**THE MOVEMENT OF BEACH SAND AND BEACH SHAPE**

The sediment on beaches is in constant motion, being driven by the waves breaking on the shoreline and also wave-induced near-shore currents. The lower, less energetic, and longer-period summer waves tend to pick up the fine sand that is suspended where the waves break and to carry it up the beach, where it is deposited before the next wave breaks. Through the late spring, summer, and early fall months, these lower-energy waves transport the sand onshore, building up a high berm and broadening the beach (Fig. 4A). By the end of summer many beaches are at their widest extent, providing lots of area for beachgoers. Where the beach is very wide and a persistent onshore wind blows, dunes may even begin to form on the back beach, and in some cases, where there are no topographic barriers and an abundance of sand, large dune fields may form and migrate inland.

With the arrival of the first winter storms, which bring higher, shorter-period, and more energetic waves, the sand is thrown into suspension, scoured off the beach face, and carried back into the surf zone, leading to erosion or narrowing of the summer berm. As the winter storm waves continue, the beach face is lowered, the sand moves offshore to form a series of bars and troughs, which serve to protect the beach by causing the winter waves to break further offshore. Winter beaches are then narrower, usually coarser-grained, and may be completely eroded (Fig. 4B, where the sand has not disappeared but has only been carried offshore into bars and troughs that are parallel to the...
beach). Most beaches undergo some seasonal change each winter and then return or reform the following spring and summer. In some cases, beaches may be 2 to 4 meters lower in the winter than in the summer months, and pebbles or cobbles may be exposed as the sand is moved offshore.

In addition to the seasonal on- and offshore movement of sand, in any location where the waves approach the shoreline at an angle, sand or beach materials are also transported alongshore, either up-coast or down-coast. As each wave breaks, it stirs up the sand in the surf zone and carries the sand up the beach face. When a wave breaks at some angle to the shoreline, this path of the sand grains up the beach face is also at an angle that depends on the direction of wave approach. When carried back down the beach face by backwash, the individual particles move perpendicular to the shoreline (Fig. 5). So sand grains are transported in a zigzag or saw-tooth pattern alongshore. This process is called littoral drift and is responsible for transporting thousands to hundreds of thousands of cubic meters alongshore each year.

So, although beaches may appear to be wide and stable environments in the middle of summer, they are constantly adjusting their size and shape in response to changing wave conditions. Sand moves on- and off-shore seasonally as the beach is eroded and then rebuilt. Beach materials are also often moved alongshore by waves approaching the shoreline at an angle. Beach sand is transported many miles alongshore until it is ultimately transported offshore onto the continental shelf, carried down to the deep sea floor through a submarine canyon, or blown inland into a dune field.

Human activities have greatly altered beaches along many coastlines. The construction of dams and reservoirs in coastal watersheds, and sand and gravel mining along streams, have trapped or removed millions of cubic meters of sand that would formerly have been delivered to the shoreline to nourish beaches. Armoring coastal bluffs with seawalls and revetments temporarily halts bluff erosion but also eliminates these bluffs as a source of sand for the adjacent beaches. Large jetties, breakwaters, and groins all disrupt or trap littoral drift and serve to widen upcoast beaches but in many places have reduced the size of downcoast beaches. There are other locations where large volumes of sand have been added to the beaches, known as beach nourishment, to widen them or to make up for losses caused by upcoast human activities or construction.

SEE ALSO THE FOLLOWING ARTICLES
Coastal Geology / Sea Level Change, Effects on Coastlines / Surf-Zone Currents / Tidepools, Formation and Rock Types

FURTHER READING
BENTHIC-PELAGIC COUPLING

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Benthic-pelagic coupling (BPC) refers to the linkage between the water column and the bottom. The process can be relatively passive, such as the sinking of particles, or highly energetic, such as upwelling or downwelling. This key process impacts all types of bottom communities including those on rocky shores, on coral reefs, and in soft-bottom habitats. BPC delivers particulate food, organic and inorganic nutrients, and offspring in the form of larvae, spores, or propagules to the seafloor. BPC is an integral component of food webs, resulting in bottom-up regulation (control by nutrients, food resources) of marine webs. Furthermore, it can trigger a linkage between bottom-up and top-down (regulation by predation, grazing) control.

ECOLOGICAL IMPORTANCE

The ecological importance of BPC has been appreciated in deep-sea and coastal sedimentary habitats for decades, but it is only recently that the role of BPC in coral reefs, rocky intertidal, and subtidal habitats has been investigated. Earlier theories predicting the distribution and abundance of organisms in these habitats were focused on the roles of biotic interactions and environmental stress acting at local (0–20 km distance) spatial scales. The emerging recognition of the importance of oceanographic processes in marine benthic ecosystems has led to the development of models of community structure applicable to larger landscape (20–200 km) and regional (200–4000 km) spatial scales. Major forms of BPC are sedimentation, upwelling, downwelling, and Langmuir circulation.

Sedimentation

Sedimentation is defined as the settling of solids out of a liquid. Sedimentation can be of inorganically or organically derived material. Inorganic sediments are either chemical precipitates or geologically derived material. They include a broad range of sedimentary particles—from sands, silts, and muds washing off the land, to volcanic material of all sizes, to dust deposited from the atmosphere. Major sedimentation of organic material occurs from the coastal zone to the deep-sea floor. Organic material sinking to the bottom includes phytoplankton and zooplankton of all sizes, macroalgae and marine angiosperms, flocculents (marine snow), woody debris, and animal carcasses. Reflecting this input, bottom sediments are a mixture of inorganic and organic matter.

Generally, sedimentation rates of small passive particles are inversely proportional to water velocity and particle size, as predicted by Stokes’s law. BPC sedimentation forms soft-bottom habitats in places where water velocity is not high enough to keep particles in suspension. Sedimentation blankets the seafloor, creating a layer of soft-substrate habitat for invertebrates and fish that is, on average, 1.2 km thick.

Sediments are named after the type of material from which they were created. There are calcareous oozes composed of plant and animal skeletal material such as foraminiferal oozes (mostly *Globoquadrina*), pteropod shell oozes, and coccolith oozes composed of algae in the Coccothophoridae. Siliceous oozes of radiolarians and diatoms are another major category of organic sediments. The biomass, distribution, and growth rates of invertebrates are correlated with the organic content of the sediment, which represents food for deposit feeders. The sedimentation of organic matter thus has a bottom-up influence on soft-bottom food webs.

Sedimentation occurs on rocky shores as well as soft-bottom habitats. On rocky shores it represents a major source of stress and disturbance for algae and invertebrates. By hindering settlement, growth, and survival of algae and epifaunal invertebrates, sedimentation reduces abundance and species diversity in rocky-shore communities. Many aggregation-forming species such as subtidal kelp beds, polychaete reefs, and mussel beds trap sediments, causing other direct and indirect ecological effects among the associated species and habitat formers (foundation species).

Development, pollution (sewage, industrial), and ocean dumping resulting from human activities have greatly increased the sediment load of many coastal waters. Consequently, negative ecological impacts of sedimentation are increasing and widespread. There is a need for more experimental studies of sedimentation effects on rocky shores and coral reefs.

Upwelling

Upwelling is a major type of BPC created by a variety of mechanisms including wind forcing, Coriolis deflection, and flow–topography interactions operating on a range of spatial and temporal scales. At the largest spatial scales, upwelling is driven by wind that blows parallel to a coastline, pushing a current of surface water in the same direction (Fig. 1). As a result of the Coriolis
The Coriolis effect also plays a major role in equatorial upwelling phenomena. Equatorial upwelling occurs when winds blowing westward along the equator drive currents from east to west. The Coriolis deflection causes the current on the Northern Hemisphere side of the equator to deviate to the right, whereas the currents moving parallel to the equator in the Southern Hemisphere diverge to the left. These deflections push the surface water away from the equator, which triggers upwelling as deep water replaces surface equatorial water. Moving deeper from westward-flowing equatorial surface currents, one finds equatorial countercurrents flowing to the east. For example, the eastward-flowing equatorial countercurrent drives upwelling in the Galápagos Islands, when it runs into the western side of the archipelago.

One of the first ecological effects of upwelling noted was due to elevated nitrate levels in upwelled waters. It was hypothesized to stimulate the growth and production of macroalgae and explain the high abundance of macroalgae along shores bathed by the Benguela upwelling system. This hypothesis was tested and confirmed in the Chilean rocky intertidal, where the growth rates and biomass of a red alga were higher at sites of strong upwelling.

Researchers working along the coast of California discovered that wind-forced upwelling affects the supply of larvae as well as nutrients. When winds blowing along the central coast relax, upwelling currents stop and are replaced by onshore currents transporting invertebrate larvae entrained in surface waters to the coast. Pulses of high barnacle and crab settlement occur in the rocky intertidal as the water flows onshore during these upwelling relaxation events. The opposite situation occurs when upwelling resumes, as barnacle larvae are transported far offshore by surface currents (Fig. 1), explaining low barnacle settlement during upwelling periods.

Since intertidal recruitment varies with the timing and spatial extent of wind-forced upwelling, it is logical to hypothesize that species interaction strength and community structure varies with upwelling as well. This hypothesis has been tested along the West Coast of the United States and Chile. One of the effects is that cold water delivered by upwelling decreases the feeding rate of a keystone species, the predatory sea star, Pisaster ochraceous. Broad regions of the U.S. West Coast have been classified as the Intermittent Upwelling Region (IUR) in Washington and Oregon, the Persistent Upwelling Region (PUR) off central to northern California, and the Weak Upwelling Region (WUR) in southern California. Phytoplankton food concentration and the recruitment of mussels are highest in the IUR, indicating a bottom-up effect of upwelling. Interaction strength, measured as the per-capita and per-population rates of sea star predation on mussels, show regional-scale trends driven by upwelling. For example, per-population predation rates are higher in strong- than in weak-upwelling areas, lending support to the notion that BPC links bottom-up and top-down effects in intertidal food webs. To understand the causes of the often large variability in community structure observed from site to site, several authors have suggested that the upwelling regime should be measured at the same local scale as the study sites.

Rocky intertidal community structure and the recruitment of mussels and barnacles is sharply demarcated on a
regional spatial scale along the coast of Chile. Recruitment is low in the strong upwelling region, north of 32° south latitude, and high south of it, where upwelling is weaker. High mussel recruitment in the weak-upwelling area leads to high cover of adult mussels, which typically outcompete other intertidal species. In this manner, upwelling changes intertidal community structure on large, regional spatial scales. In the Chilean intertidal system, the bottom-up effects of upwelling do not typically extend up the food web to herbivores of macroalgae and predators of barnacles and mussels, indicating that the extent of linkage between bottom-up and top-down control may be limited by factors other than prey availability such as predator recruitment, predator diet, and removal of predatory species by humans.

Internal Waves

Upwelling is often caused by the interaction of flow and topography. Internal wave upwelling and downwelling occurs in density-stratified waters worldwide as the tide flows over abrupt bottom topography (banks, ledges, reefs, continental slopes). Depending on the nature of the stratification, lee waves propagate forward obliquely or horizontally as a packet of internal waves as the tide changes (Fig. 2). Downward-flowing currents are followed by upwelling currents as the internal wave train moves away from the ledge. As observed on rocky shores of California, Chile, and on coral reefs, the train of internal waves breaks and becomes an internal tidal bore when it moves into shallow water. Internal tidal bores are well developed during periods of strong water column stratification. They deliver subthermocline water to the shore.

Similar to wind-forced upwelling, internal waves affect larval transport and recruitment and create bottom-up effects on benthic food webs. For example, internal waves can transport invertebrate larvae across the coastal shelf toward shore. In some cases, the cross-shelf larval transport has been linked to higher intertidal settlement and recruitment of bivalves, barnacles, and crustaceans. Two mechanisms have been proposed to explain larval transport by internal tides. One maintains that larvae are concentrated at or near the surface in convergence zones (slicks, Figs. 2, 3) above weak downwelling limbs of internal waves. The larvae and propagules are then carried along near the surface and toward the shore as the wave train propagates forward. Another mechanism involves larvae entrained in the downwelling phase of the internal tidal bore, which is conspicuous as a front of warm water. Larvae are transported to the intertidal as the front moves onshore.

**FIGURE 2** Diagram of an internal wave forming on the lee side of a bank. When the tide ebbs over the bank, water that was held on the lee side of the bank during the flood tide rushes forward forming an initial internal wave that depresses the thermocline and pycnocline. This is the downwelling phase. The parcel of water that was depressed by the initial tidal energy reaches a depth at which it is lighter (less dense) than water at the surrounding depth, so it rises. This is the upwelling phase of an internal wave. A convergence zone forms above the trough of the internal wave and is often visible as a slick. Repeated depression of the thermocline/pycnocline as the water flows over the bank generates a packet or train of internal waves.

Bottom-up effects of internal waves and bores are related to the strong vertical motion of internal waves that mixes nutrients and phytoplankton in the water column and pushes planktonic food and nutrients to the sea floor. During the stratified season, an energetic internal wave regime drives the subsurface chlorophyll maximum (SCM) layer 15 to 30 meters down to the bottom several times per day on subtidal pinnacles in the central Gulf of Maine. Enhanced food supply at the internal-wave downwelling zone at the tops of the pinnacles resulted in faster growth rates of mussels and sponges, indicating a bottom-up effect on subtidal food webs.

**FIGURE 3** Photograph of a slick from part of a large packet of internal waves on Cashes Ledge, Gulf of Maine. Downwelling by these internal waves pushes a midwater layer of dense phytoplankton to the rocky sea floor where filter-feeding invertebrates thrive. For scale, the dark object to the right is a 5.5-meter-long inflatable boat. Photograph by J. Witman.
Internal tidal bores break and run up the reefs in the Florida Keys, delivering water that is rich in nitrate, phytoplankton, and zooplankton. The effect of breaking internal bores is well developed on the deep reef (>35 m). Upwelled water during the internal-bore phase is 10–40 times higher in nutrients (nitrate, phosphate) than during nonbore periods. Demonstrated biological responses to the internal bore regime on these coral reefs include use of nitrogen by benthic macroalgae, which are most abundant deeper on the reef, and elevated growth of a branched coral in the zone of internal-bore influence. In general, nutrients supplied to coral reefs by breaking internal waves may be a vitally important source of nitrogen for corals in the nutrient-limited environment of tropical oceans.

One of the few studies of upwelling in the subtidal zone suggests that the pace of community change may be faster at upwelling sites, because the diversity of epifaunal invertebrates doubled in a year at a strong subtidal-upwelling site in the Galápagos, as a result of high recruitment. Larvae are not necessarily advected offshore by localized upwelling in this subtidal system in which local physical regimes are often dominated by internal wave–generated upwelling and downwelling.

**Langmuir Circulation**

Like internal waves, Langmuir circulation results in convergence zones at the surface of the ocean, visible as slicks that aggregate biological material, but the mechanisms that produce them are completely different. For example, Langmuir circulation is driven by the wind, requiring wind speeds of greater than 3.0 meters per second to generate the characteristic rotating tubes of water aligned parallel to the wind. The slicks often contain lines of foam and are known as windrows. They are caused by wind shear acting on the surface of the water, which dissipates with water depth. Basically, the rotating tubes or vortices are caused by variation in the wind speed and resulting shear. Downwelling currents are formed in the convergence zone between the tubes; they typically exceed the velocity of the upwelling limbs. Small fish and jellyfish may reach greater abundances in Langmuir slicks than elsewhere. Although discovered in 1938, the biological potential of Langmuir circulation as a mechanism influencing benthic communities is only beginning to be realized. For example, in some cases the rotating Langmuir circulation can span the entire water column to a depth of 15 meters, as observed off the coast of New Jersey in the United States. The vertical flow in these supercells vigorously resuspended bottom sediments, apparently transporting sediment near the bottom. As downwelling phenomena, the BPC implications of such supercells are that they are likely important mechanisms to supply larvae, propagules, and food to the shallow sea floor on an episodic basis.

**SEE ALSO THE FOLLOWING ARTICLES**

Food Webs / Near-Shore Physical Processes, Effects of / Nutrients / Upwelling / Waves, Internal

**FURTHER READING**


**BIODIVERSITY, GLOBAL PATTERNS OF**

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Biodiversity, although present at all levels of organization of organisms, is most commonly measured by ecologists and biogeographers as species richness, or the number of species found at a particular point in space or time. By
this definition, a section of rocky intertidal coast where 100 different species of fish, algae, and invertebrates can be found has greater biodiversity than a location of similar size where only 50 different species are found. Understanding patterns of global biodiversity, and the underlying processes, will continue to be a major priority as issues such as global climate change, conservation, and sustainable resource use increase in importance worldwide.

MEASURING BIOLOGICAL DIVERSITY
Although historically the number of species has been the most commonly used measure of biodiversity, scientists increasingly emphasize alternative methods of characterizing biological diversity, looking beyond the mere number of species to consider, for example, diversity in morphologies, genetics, or ecological relationships of organisms. Thus, although many of the hypotheses for global patterns of biodiversity use species richness as the measure of biodiversity, it is important to keep in mind that other ways of measuring the diversity of organisms may lead to important insights into the dynamics underlying biogeographic patterns.

GLOBAL PATTERNS OF BIODIVERSITY
Biodiversity varies spatially on the globe. The study of this variation has made rapid advances in recent decades through improvements in available datasets and analytical tools such as geographical information systems and remote sensing techniques. Interest in global patterns of biodiversity and the main factors determining species richness has also increased with the need to understand how biodiversity might change under different scenarios of global climate change, as well as to inform conservation and sustainable resource use efforts.

Although the total number of species on earth is yet unknown, it is clear that the tropics harbor many more species than colder environments. The latitudinal gradient in species richness, wherein species richness peaks near the equator and declines toward the poles, is a widely recognized phenomenon that holds true for many taxa, from marine to terrestrial organisms, and in habitats as diverse as the open ocean, coastal zones, rainforests, deserts, rivers, and lakes. In the ocean, the typical decline in species richness at high latitudes has been reported on continental shelves, in the open ocean, and surprisingly, in the environmentally stable deep sea. The pattern is so general that it has been observed from microscopic to macroscopic organisms, including the most conspicuous and abundant groups such as molluscs (Fig. 1), crabs, and fishes. Moreover, diversity gradients not only exist for species but also for higher taxa (baurpans). However, some authors have claimed that there is not convincing evidence for the latitudinal gradient in species diversity across all marine taxa, comparable with that found for terrestrial taxa, based on exceptions to this pattern (e.g., infauna, certain peracarid crustaceans, southern oceans). Figure 2 shows one of these exceptions: the inverse latitudinal diversity pattern exhibited by molluscs (bivalves, gastropods, and placophora) in the southeastern Pacific.

![Figure 1: The relationship between bivalve diversity and latitude (after Stehli et al. 1967).](image1)

![Figure 2: Relationship between diversity of molluscs and latitude in the southeastern Pacific (after Valdovinos et al. 2003).](image2)

In the ocean, species richness also varies with depth. The number of species peaks at about 2000 meters depth and then declines toward shallower and deeper waters in all taxa and oceans. Although our knowledge of the
biodiversity of the deep ocean is particularly limited, and a remarkable number of new species are being discovered in the world ocean, the patterns reported seem unlikely to reverse even as more species are described.

Biodiversity patterns are scale dependent. It is interesting that the generalization of increased diversity with decreasing latitude applies to large-scale analysis (e.g., number of species per one-degree latitudinal band) but not necessarily to the number of species living within a small area (e.g., a square meter). For example, using a simple three-unit scale—local (patch dynamics), regional, and global—different biodiversity gradients can be obtained at different scales. The latitudinal species richness gradient is most detectable at broader scales. At a regional scale using latitudinal bins or blocks of 5–10 degrees latitude, strong gradients have been demonstrated in both hemispheres for bivalves, gastropods, coastal fishes, sea stars, planktonic foraminifera, benthic foraminifera, and pelagic copepods. These observed gradients are not uniform, but they do have highest diversity values between 0 and 30 degrees latitude and lowest values between 60 and 90 degrees.

A number of recent studies have suggested that if samples are taken on significantly smaller spatial scales, it can be far more difficult to detect a latitudinal diversity gradient. A famous early study by Thorson on a small scale found no evidence of an equatorial–polar gradient for macrobenthic taxa associated with soft substrates. One complication of gradients and scales is that diversity is highly variable among habitats. For instance, coral reefs, which are restricted to low latitudes, host higher marine biodiversity than any other habitat. This factor alone could explain the hotspots of diversity found at low latitudes. The question of diversity gradients on smaller scales will require further work in all habitats from the tropics to the poles. Explicit consideration of the relevance of scale may allow for a more nuanced view of global patterns of biodiversity, hopefully leading to insights into and improved understanding of the dynamics that cause these patterns.

**PRIMARY CAUSES OF LATITUDINAL BIODIVERSITY GRADIENTS**

Although some authors have stated that an almost universal pattern must have a common explanation, the processes behind one of the most universal and intriguing features of nature, the latitudinal biodiversity pattern, have not yet been elucidated.

**A Common Pattern or Common Cause**

Several authors have stated that the general latitudinal pattern in species numbers must be related to some climatic factor, or combination of factors, that change in a consistent manner with latitude. Several factors could serve as suitable candidates, from contemporary variation in average temperature, primary production, or seasonality, to historical perturbations of the physical environment.

The major risk of looking at a common cause is confounding correlation with causation. However, a strong correlation between diversity and some physical parameters may be a powerful indicator of a possible cause. Evidence relating temperature and species diversity of terrestrial and marine organisms has been accumulated for decades. Temperature is also an excellent predictor of the diversity of planktonic, benthic (crabs, bivalves, gastropods), and pelagic organisms (e.g., fish) in the world oceans. It is also remarkable that the rate of change in crab diversity with changes in sea surface temperature is exactly the same in the southern Atlantic and Pacific oceans (Fig. 3). In spite of the striking associations between temperature and diversity among marine organisms, ecologists have so far failed to find the primary cause linking biological diversity...
and temperature. The variation in diversity with depth, where there is no temperature difference, also remains unexplained.

Although most of the studies on causal factors have focused on latitudinal patterns of diversity, a factor that influences biodiversity on one spatial gradient, such as latitude, may also likely influence biodiversity along other spatial gradients for which the factor also varies (e.g., depth in the ocean, altitude on land). Thus, many of the hypotheses presented in the following subsections, developed to explain latitudinal gradients of diversity, may also inform our understanding of other types of spatial diversity gradients, such as gradients along depth in the marine environment. These hypotheses are broad, in that they apply to marine and terrestrial systems, but are also limited, in that they have been developed primarily using only species richness to measure biodiversity.

**Identification of the Primary Cause of the Relationship between Temperature and Diversity**

Considering the evidence linking temperature and diversity, the challenge is to identify the processes that link temperature and species diversity. A number of different hypotheses have been proposed to explain and understand the underlying causes of latitudinal biodiversity patterns, but only some of them have been tested in marine systems.

**SPECIES–ENERGY HYPOTHESIS**

A possible interpretation of the correlation between temperature and species diversity is that species richness is limited by energy supply. Solar energy is the most basic source of energy for photosynthesis and is also stored as the ambient temperature of the air or water in which organisms are immersed. Solar energy itself exhibits a strong latitudinal gradient, declining from the tropics to the poles. If productivity really represents the main constraint on biological diversity, then species richness might be strongly associated with the climatic factors that influence productivity, such as temperature. As has been shown previously, on a broad geographic scale, net primary productivity is higher at lower latitudes. It should be recognized, however, that other factors such as nutrients affect primary production and may affect diversity patterns, especially over smaller spatial scales. Therefore, the species–energy hypothesis proposes that the high biodiversity in the tropics compared to the poles is related to the fact that tropical regions exhibit greater primary productivity. Proponents of the species–energy hypothesis point to widespread evidence that productivity (or its climatic proxies) describes broad-scale diversity gradients better than alternative explanatory variables do.

According to the species–energy hypothesis, net primary productivity is critically important in determining biodiversity. In other words, somewhat simplified: Where there is more energy from the sun to allow more photosynthesis, there will be more algal matter, which will provide more food for herbivores, increasing their populations, thus providing more food for carnivores, increasing their populations, so that the total number of organisms will be greater than in areas with less primary productivity. The species–energy theory predicts that species richness for a given area is controlled by the population size of the total number of organisms of all species; therefore, the population sizes of individual species are relatively unimportant. However, there is a logical limitation to this hypothesis: Why do a small number of species not monopolize the available energy? The hypothesis that species richness is limited by energy supply also assumes that habitats are saturated with species, which remains controversial.

As described previously, the species-energy hypothesis is partially based on the somewhat controversial idea that patterns in diversity observed at ecological and biogeographical scales can be explained by solely examining the population sizes of the total number of all species, without examining the specific biology of individual species. This approach requires the theoretical assumption that all individuals are identical and that all species are equal in competitive ability—a hypothesis known as the neutral or symmetric hypothesis. Because there is much support that species do, in fact, vary significantly in competitive ability, the neutral hypothesis is usually invoked more as a thought experiment and a structure for beginning to analyze biodiversity patterns, not as a stand-alone hypothesis. Its value is that it provides a simplified, unified structural approach that highlights factors long recognized as jointly influencing species richness: population density, area, and speciation rate.

**NICHE–ASSEMBLY HYPOTHESIS**

In contrast to the neutral hypothesis, the niche–assembly hypothesis incorporates from the start the idea that species are different in a variety of ways, including their niches and competitive abilities. The niche–assembly hypothesis of biodiversity views ecological communities as societies foremost, structured by species interactions as well as organisms’ life histories, habitats, and trophic levels. The key concept in the niche–assembly hypothesis is
adaptation of organisms to the climate and to each other. Classical niche–assembly hypothesis emphasizes the inherent uniqueness of all species in ecological communities. According to this perspective, competing species coexist in closed, stable assemblages by partitioning limiting resources through niche differentiation.

There are a number of ways that the niche-assembly hypothesis can be used to explain the latitudinal gradient in species richness. For example, the tropics might support more species than the higher latitudes because species in the tropics tend to occupy narrower niches, possibly because the resources in the tropics are more reliable and tend to be available year-round. This climatic stability allows for species to become increasingly specialized, so that one broad niche can be subdivided into multiple narrower niches, thus accommodating more species. In contrast, at higher latitudes, where significant climatic variation (e.g., seasonality in solar radiation, in temperature) is more common from season to season and year to year, such niche subdivision is not possible, because species that become too specialized for a specific narrow niche are at a higher risk of extinction when resource availability or climatic variables change. An important question, however, is what might drive this pattern: whether there are more species in the tropics because tropical niches tend to be smaller, allowing evolution of more species; or if niches are smaller in the tropics because the larger number of tropical species forces the subdivision of broader niches into narrower ones.

**EVOLUTIONARY SPEED HYPOTHESIS**

The difficulties encountered when trying to explain greater species richness in energy-rich environments, such as the tropics, disappear when energy (particularly temperature) is not related to species number but to evolutionary speed. Differences in evolutionary speed at different latitudes have been implicitly or explicitly assumed by several authors, and there is a considerable body of data that indicates higher evolutionary rates in the tropics. Several processes have been proposed to support the evolutionary speed hypothesis. One proposal is that since the climate in the tropics is warmer, generation times tend to be shorter, evolution tends to occur more rapidly, and therefore speciation is faster. The counterargument for this hypothesis, however, is that species' extinction rates, also tied to generation time, should increase as well, canceling out the effects of faster speciation rates, assuming speciation and extinction are in equilibrium. Higher mutation rates at higher temperatures can also favor higher speciation rates, and there is evidence supporting this process. This may be accompanied by faster physiological processes at higher temperatures, which accelerates selection, leading to fixation of favorable mutants in populations. Although it can also be argued that the high diversity in tropical areas could be generated by reduced extinction rates, the limited fossil record does not provide evidence in this direction.

**CENOZOIC RADIATION HYPOTHESIS**

Finally, several authors have pointed out that the substantial increase in biodiversity during the Cenozoic Era, when a pronounced radiation event took place in the ocean, may explain why higher latitudes have lower biodiversity. Even though some polar marine taxa, especially in the Antarctic, went through intense radiation, most of the Cenozoic radiation took place in tropical and low-latitude regions. In fact, the latitudinal diversity patterns that we observe today can be traced back to the Cenozoic Era.

**ALTERNATIVE WAYS OF MEASURING DIVERSITY**

Although species richness has been the most commonly used measure of biodiversity, it is now frequently viewed as an inadequate metric taken by itself. Alternative definitions of biological diversity try to capture the true variety of life by looking beyond simply the number of taxa to include everything from genetic to ecological diversity. Species richness has been deconstructed, for example, to examine the morphologic, physiological, phylogenetic, and ecological relationship diversity among organisms.

The deconstructive approach to measuring biodiversity starts with the assumption that species richness does not sufficiently represent the true diversity of life, because it ignores the ways in which species differ from one another and in their responses to environmental changes. This approach emphasizes that it is critical to consider that the mechanisms controlling the number of species at a given location (migration, extinction, and diversification) are not independent of the life histories or physiological and ecological attributes of the species involved, because these attributes determine what environmental aspects are relevant to their survival. In other words, because the number of species in a given time and place depends on the interaction between the organisms’ strategies and attributes and the characteristics of the environment in which they exist, any hypothesis that measures only numbers of species, while ignoring the similarities and differences in species’ attributes, gives an incomplete picture of the complexity of the biodiversity.
pattern. To view the complete picture, one must consider biological attributes such as dispersal abilities, energetic demands, life history traits, physiological attributes, taxonomic distinctions (vertebrates vs invertebrates), ecological attributes such as food web position (decomposers, producers, primary consumers, and secondary consumers). For example, applying this deconstructive approach to the effects of energy availability on biodiversity would mean disaggregating mere species richness to examine the patterns in the attributes of species that are most relevant to the environmental variable of energy availability. For example, patterns in energy metabolism, endothermism versus ectothermism, body size, or diet.

An acknowledged characteristic of the deconstructive approach is that species richness can be disaggregated or deconstructed in many different ways and therefore achieve a better understanding of the environmental factor affecting biodiversity. With regard to the neutral or symmetric hypothesis, the deconstructive approach asserts that it is logical to first properly qualify the complexity of biodiversity patterns before attempting unification. Although some other approaches, such as the species-energy hypothesis, view environmental factors as causal and species as equivalent, the deconstructive approach claims that any hypothesis derived from environmental factors alone gives an incomplete view of the complexity of the biodiversity pattern. Although hypotheses driven by external factors may correlate to observed gradients of biodiversity, deconstruction allows researchers to explore in more complex detail how diversity patterns change depending on the criteria used to disaggregate richness, and it can be useful for explaining why certain groups with similar biological attributes, such as mollusks that show asymmetric patterns in the Northern and Southern Hemispheres, run counter to expected gradient patterns.

CONCLUSION

Global patterns of biodiversity, especially the latitudinal diversity gradient, have led to the development of numerous hypotheses to attempt to elucidate the underlying causes of this intriguing global pattern. Although each of the current hypotheses offers insights, no one mechanism seems to explain all instances of the observed patterns. Furthermore, many of the hypotheses are not mutually exclusive, and multiple hypotheses may play some role in determining the observed global patterns. Focusing on the complexities of biodiversity, including alternate methods of measuring diversity beyond number of species and the importance of scale in the patterns observed, may lead to a more nuanced view and improved understanding of the dynamics underlying diversity patterns. Understanding patterns of global biodiversity, and the underlying processes, will continue to be a major priority as issues such as global climate change, conservation, and sustainable resource use increase in importance worldwide.

SEE ALSO THE FOLLOWING ARTICLES

Competition / Dispersal / Temperature Change

FURTHER READING


Biodiversity, Maintenance of

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One of the most important attributes of ecosystems on land and the ocean is the number of species that can be found coexisting in a local habitat. In the ocean, this essential component of biodiversity is first constrained by the ability of species to disperse and settle in appropriate habitat. Once there, a suite of local postsettlement biological and physical processes can maintain or alter biodiversity, favoring the establishment of some species and eliminating others.
SUPPLY OF INDIVIDUALS

The maintenance of biodiversity in marine environments depends critically on the successful arrival or supply of new individuals of different species to the local habitat. This is true of all systems, but it acquires special relevance in marine environments because the mere presence of healthy adults of a given species does not guarantee that new individuals will arrive and maintain that population over time. This is an obvious, but often times underappreciated, factor in the study and discussions of biodiversity of marine environments. In these systems, local communities are usually dominated by species with life histories that include a free swimming pelagic larva, which can spend from hours to months in the water column and have no means to remain close to their parents.

Let us assume that we are examining the number of species that occur in a small fraction of adult habitat, say a single rocky bench or a medium-size tidepool along a rocky shore. Let us also assume that we start with an empty tidepool and observe, over time, how this tidepool is colonized by individuals of different species. Clearly, the number of species that settle in our tidepool will be a function of the total number of species present in the area surrounding the tidepool and whose propagules—larvae and spores—have the potential to reach this pool. Note that in the case of invertebrates with long-lived pelagic larvae, the area supplying species to our pool can be several tens of kilometers up or down the coast. In the simplest case, our pool receives at least one individual of all the species within dispersal distance, in which case, at the time of settlement, our pool will be a faithful representation of the diversity in this region (Fig. 1A). However, this is highly unlikely. Our small pool will most likely receive only a fraction of those species within dispersal distance. Rare species or those producing few propagules or larvae at the time we start our observations will probably not reach the pool (Fig. 1B). In some cases, there might be sufficient individuals of one or a few species to completely fill the pool and this could prevent the arrival of new individuals. In these cases, the pool will no longer receive individuals of other species and will reach saturation (Fig. 1C). The later situation is common among sessile animals that require rock surface to settle and can quickly occupy the entire space.

POSTSETTLEMENT FACTORS: ONE TIDEPOOL

After our species colonize the pool, the individuals that settle grow in size and have to withstand the physical and biological conditions in the adult habitat. A number of postsettlement processes can then cause differential mortality of individuals of different species and affect the number of species that we observe in the pool after some period of time. These processes can both decrease or help maintain the number of species that can coexist in the tidepool following settlement.
**Competition for Limited Resources**

**EQUAL COMPETITIVE ABILITIES: THE LOTTERY MODEL**

If the species that arrived at our pool have similar colonization and competitive abilities, as well as similar requirements and tolerances of abiotic conditions, then individuals will be able to hold their space without being overgrown, crushed, or displaced by others. When an individual dies, it will be replaced by an individual of the same or different species. Under these circumstances, species cannot secure the space beyond their lifetime, but can improve their chances of recolonizing the lost space by having more propagules available. In a way, this is like buying lottery tickets; buying more tickets improves your chances, but there is no certainty that you will win the prize and colonize the available space. Competition occurs in an indirect manner, through the appropriation and therefore pre-emption of space that otherwise will be available for colonization by self- and other species. In these cases, the final number of species will fluctuate somewhat over time, but it will be similar to the number of species that settled initially in the pool (Fig. 2A, curve a).

**COMPETITIVE HIERARCHIES: THE EXCLUSION OF INFERIOR COMPETITORS**

Much more common than species with similar colonization and competitive abilities is the existence of strong and persistent competitive hierarchies among algal and invertebrate species. One or a small subset of species is usually able to settle on, overgrow, crush, squash, suffocate, and eventually kill all other species. As species grow, these competitive hierarchies generate successional sequences from the time of settlement. Succession does not have to be linear, and multiple successional paths might be observed in the same community, but unless disturbed by other factors, the community will end up dominated by one or very few competitive dominant species. The number of species will therefore decline over time and in many cases the pool will end up with just one single species (Fig. 2A, curve c). Numerous examples of this type of competitive structure abound in most rocky shores of the world. In many shores, mytilid mussels are dominant competitors for space at mid-intertidal elevations; in others, barnacles can take over this role and exclude other species, and in many shores different kelp species or surfgrass can form extensive monocultures that exclude all other algal and invertebrate species.

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**FIGURE 2** Processes maintaining or modifying the diversity of species after individuals have successfully settled into the new habitat and individuals grow. (A) Different forms of competition can maintain or alter biodiversity. In curve a, all species have equal competitive abilities and after settlement they hold the resource for life. In curve b, some species can outcompete and exclude others, but the process is not transitive: species A outcompeted a species B, which in turn dominates over C, but C can outcompete species A. In curve c, there is perfect competitive hierarchy, leading to monopolization of the resource by one or a small subset of competitively superior species. (B) Effect of predation on species diversity. Once predators start consuming prey (red arrow), they can increase species diversity by removing the dominant competitor as depicted in curve a, or can decrease diversity by removing inferior competitors (curve c), accelerating the effects of competitive hierarchies alone (curve b). (C) Effect of positive interactions among the established species on species diversity. In curve b, a settled species provides habitat for other species, diminishing the effects of competitive exclusion (curve a). In curve d, a settled species modifies local conditions for the settlement of other species, allowing the colonization of new species that otherwise could not even settle there. In curve c, the facilitator species favors the establishment of a superior competitor, which after some time accelerates the exclusion of other species.
COMPETITIVE NETWORKS: INTRANSITIVE INTERACTIONS

In intertidal systems there are few examples of coexisting species having equal colonization or equal competitive abilities. The most common pattern is the existence of competitively superior species that can overgrow competitively inferior ones. In some cases, however, competitive abilities might not be transitive; that is, species A might be able to exclude species B for the use of resource (e.g., space), species B might in turn exclude species C, but it is possible that C excludes A (Fig. 3). When all species are in contact and competition occurs simultaneously among them or in different sections of our pool, these intransitive networks can allow species to coexist. Species diversity in the pool should persist over time, amid continuous competitive interactions within the pool (Fig. 2A, curve b). It is unlikely, however, that the rates of competitive exclusion are similar among all pairs involved in the network; and therefore, some of the original species that settled will most likely be excluded from the pool. Lack of transitivity in competitive networks is usually produced by the existence of different mechanisms of competition between species. For instance, a species A could shade and kill a species B, which in turn might overgrow and suffocate a species C; this latter species could be shade resistant and outcompete species A for food. Few examples of intransitive networks have been documented in intertidal systems.

Facilitation and Other Positive Interactions

For years ecologists have emphasized the importance of negative interactions among species, such as competition, in discussions and theoretical models about the maintenance of species diversity. However, in real systems species not only compete for resources, having negative effects on each other, but they can also have positive effects on other species. Besides the positive effect that prey have on consumers, which are better treated in the context of predatory (trophic) interactions, species can indeed have a myriad of positive nontrophic effects on many species with which they interact. These positive effects might be long lasting or temporary, and they need not be reciprocal between species (i.e., mutualistic) to have dramatic effects on species diversity. Some definitions of positive interactions—"those that cause a positive effect on one species and cause no harm to neither"—are not particularly useful in the context of our tidepool community, because they underestimate the true importance of these interactions in the maintenance of species diversity and put an enormous burden on empirically demonstrating that the species recipient of the positive effect has no negative effects on the donor.

Among the most widespread and important biological interactions in rocky intertidal systems is the facilitation of settlement of invertebrate species by algal turfs and other invertebrates, or the refuge provided to mobile consumers by algae and invertebrates (e.g., limpets found under algal fronds, gastropods, crustaceans, and many other mobile species found inside beds of intertidal mussels, tunicates, or kelp holdfasts). This habitat enhancement can halt the negative effects of competition and help maintain species diversity (Fig. 2C, curve b). In many of these cases, the only means by which species can settle or survive is because another "facilitator" species is there. In our tidepool, this effect will lead to an increase in the total number of species as new ones can now settle in the habitat (Fig. 2B, curve). Now, it is entirely possible and actually very common that species have positive effects on their enemies or on the friends of their enemies; for example, algal turfs facilitate the settlement of competitively dominant mussels, which eventually overgrow the turf and all other species. Similarly, algal mats acting as bioengineers can prevent desiccation of many herbivore species, a positive effect on diversity, but these grazers can remove algal biomass, limit their growth, and potentially eliminate rare species, a negative effect. In these cases, the positive effect leads to temporary increase in the number of species in the pool, but eventually accelerates the decline of species diversity produced by competitive exclusion or over exploitation (Fig. 2B, curve c).

Predation

PREDATION ON COMPETITIVE SUPERIOR SPECIES

One of the most influential and striking experimental results in ecology has been the demonstration that predators can increase the local diversity of species. Experimental
manipulations have repeatedly shown that carnivore and herbivore consumers—whelks, starfish, littorines, chitons, sea urchins—can control the abundance of a competitively dominant species, thus stopping the succession and preventing the exclusion of inferior competitors (Fig. 2C, curve a). The simplest way to observe this positive effect of consumers on species diversity is when they preferentially consume the competitively superior species over other prey. But even if they do not exhibit individual preferences for prey species, if the competitively superior species is relatively more affected by predation (e.g., slower to recover from predation), consumers can under some conditions still favor coexistence of species over local scales.

**PREDATION ON SUBORDINATE COMPETITORS AND BEHAVIORAL EFFECTS**

Of course, predators can also decrease species diversity. A common case of negative effects of predators on species diversity occurs when they preferentially consume competitively inferior species, thus accelerating the decline in diversity produced by competition alone (Fig. 2C, curve b). Even when predators prey preferentially on the dominant competitor, if the intensity of predation is too high, diversity of the prey assemblage will be reduced. A less well-studied negative effect of predation on diversity of intertidal systems occurs through behaviorally mediated indirect effects. In many cases, the mere presence of a predator (e.g., birds) can be perceived by its prey and cause a behavioral change that forces them to use and compete for refuges (e.g., crabs restricted to forage inside refuges during daytime). The intense competition for refuges produced by predators could lead to competitive exclusions and segregation by the mechanisms discussed in the section “Facilitation and Other Positive Interactions.”

**Disturbance and Species Diversity**

Physical disturbances can kill or remove biomass from intertidal animals and plants. Physical disturbances include large waves that dislodge individuals or roll rocks inside tidepools, floating logs that crush sessile species when they land on the shore, the scouring action of ice sheets at high latitudes, and many other forms of death and destruction. In all cases, physical disturbance can alter the number of species that can coexist in the local habitat. The effect of disturbance on diversity, whether positive or negative, depends on a number of variables, including the intensity and frequency of disturbance, and the competitive and colonization abilities of the species that constitute the local community. A simple and intuitive hypothesis that relates all these factors is the Intermediate Disturbance Hypothesis, which has proven to be a useful framework in many empirical studies. The hypothesis predicts that over a gradient of increasing disturbance frequency, diversity follows a unimodal trend; number of coexisting species peaks at intermediate levels of disturbance (Fig. 4). When disturbance is infrequent, the dominant competitor excludes other species and diversity is low. When disturbance is too high, only those species with fast colonization and growth rates can get established in the habitat. At intermediate levels, removal of biomass by physical disturbances keeps the dominant competitor under checked and still allows for other species to colonize and grow.

**INCREASING THE SCALE OF OBSERVATION**

So far we have focused on a given rocky bench or tidepool, where we followed the fate of the species that colonized that small area over time, as they undergo a suite of postsettlement processes that alter or maintain local species diversity. But in real situations, colonization by new individuals is occurring at the same time many of the postsettlement processes discussed here are taking place. As a predator removes biomass of a dominant competitor, the space or resource can be colonized by the same or a different species. If a tidepool or rocky bench is monopolized by a species, as we increase the spatial scale of observation, we are bound to find that predators and physical disturbances release resources (e.g., space) and allow the settlement and at least the temporal establishment of other species. Thus, processes maintaining biodiversity in marine systems are dynamic, can interact with each other, and their relative importance vary somewhat in different coasts of the world. Since the processes that determine the dispersal...
and colonization (settlement) of new individuals are fundamentally different from those taking place in the local habitat (e.g., species interactions), maintenance of diversity over larger scales, say a section of the coast, will be a function of the number of species in the region within dispersal distance, the rate of provision of new resources through natural death, predation and disturbance, and the balance between positive and competitive interactions. Moreover, plain counts of the number of species can confound these processes (colonization and postsettlement) and lead to wrong conclusions about the importance of local processes, such as species interactions in maintaining patterns of biodiversity. Studies of biodiversity in marine systems must therefore separate new settlers from those individuals that have "experienced" the local habitat.

SEE ALSO THE FOLLOWING ARTICLES
Competition / Disturbance / Facilitation / Predation / Succession

FURTHER READING

BIODIVERSITY, SIGNIFICANCE OF

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Biodiversity refers to the numbers of different kinds of life forms present at a location. Biodiversity occurs at the species level (the number of species and their evenness), below the species level (genetic diversity within species), and above the species level (higher taxonomic or functional-group diversity). The aesthetic beauty of tidepools and rocky shores is in large part due to the wide variety and diverse coloration of the seaweeds and animals that inhabit them, and so the high biodiversity of these environments is also what often draws people to them. But there is growing evidence that biodiversity enhances the stability of marine systems by providing a form of biological insurance against changing conditions.

FIGURE 1 Tidepools of similar size from Bodega Bay, California: (A) a pool with high diversity; (B) a pool that has lower diversity. Photographs by the author.
that this appeal has something to do with the fact that the former has a greater diversity of species. But does that diversity matter to the tidepool ecosystem?

In light of declining global diversity, scientists have become increasingly interested in whether biodiversity might have more quantifiable effects on communities. Do ecosystems with more species have greater productivity or stability than those with fewer species? As of mid-2006, relatively few papers had been published in this new, but rapidly expanding area of research, and a consensus had not yet emerged in marine systems. Thus some of the generalizations portrayed in this article may be subject to revision as the field matures. In discussing the significance of biodiversity, species-level effects are most easily ascertained, because available experimental data focus mostly on manipulations of richness. However, some examples of the effects of diversity at the genetic and functional-group level can also be considered.

POSSIBLE EFFECTS OF DIVERSITY ON ECOSYSTEM STRUCTURE AND FUNCTION

That diversity should somehow result in “higher” levels of ecosystem processes has some intuitive appeal and has long been part of conventional wisdom. The following are several mechanisms that have been posited to cause diversity effects on ecosystems. The reader should be aware, however, that there is considerable disagreement among scientists as to the relative importance of each of these mechanisms and indeed as to the definitions of some of the mechanisms themselves. More than one of these mechanisms may be in operation at any one time.

Complementarity

Resource levels or environmental conditions influence species’ performance, such that different species often exhibit optimum performance at different resource levels or are limited by different resources. Because species have different ways of exploiting resources or use different parts of the resource spectrum, increasing diversity can lead to increased resource use and ultimately higher productivity. In some cases, species use resources in the same way as other species do but do so at different times of the year, or in different microhabitats, resulting in temporal or spatial complementarity.

Facilitation

Facilitation occurs when one species ameliorates some biological or physical stress, benefiting other species in the system. This can happen when, for example, a canopy-forming seaweed shades the substratum at low tide, permitting the growth of other species that are highly productive but less tolerant of drying out.

Sampling

The sampling effect occurs because more diverse communities may have a greater probability of containing a species that has a dominant effect on ecosystem functioning. This can result in an “apparent” effect of diversity in experiments that assemble communities of randomly selected species: Communities with more species have a greater chance of having the dominant species. This effect can also occur when increasing species richness increases the likelihood of including an important facilitator (see the preceding paragraph). Intertidal community structure and functioning often change dramatically depending on the presence of a single facilitator (such as a canopy-forming seaweed) or a single keystone predator (such as a sea star or sea otter).

Redundancy and Insurance

Often, species are redundant (i.e., they perform the same function or role in the community as some other species), but they may respond differently to environmental stress. For example, seaweeds may have different tolerances to changing temperature, such that the species that are the most productive under normal conditions die when temperatures are elevated. In these cases, less productive species that are tolerant of stresses can still persist, maintaining production. This observation implies that there may be a trade-off between achieving maximum performance at a single instant and consistent performance over time. Thus, diversity may have no significance in the short term but be essential for maintenance of ecosystem functioning in the longer term. Some think of this as similar to a “portfolio effect,” analogous to a diversified investment strategy. Relying on a single stock can result in high payoff if the stock is up, but if it crashes, the investor loses everything. Similarly, spreading out resources over many species protects against wild fluctuations in the abundance of any one of those species.

Experimental studies on the functional consequences of biodiversity have been conducted in a wide range of marine environments, but relatively few have been conducted on rocky shores. Thus, the following examples also include examples from other shallow-water coastal habitats to illustrate mechanisms that will likely be shown to operate on wave-swept rocky shores.

SEAWEED AND SEAGRASS DIVERSITY

Most marine studies of diversity’s consequences have focused on consumer diversity. What is known about the
functional consequences of seaweed diversity on rocky shores is that effects of diversity on community stability can be overwhelmed by extreme physical forces or consumers. In fact, disturbances may affect diverse communities more than depauperate ones because more diverse communities have a greater biomass or cover of algae to begin with. However, communities with a diversity of functional types of algae are often able to recover from disturbances more quickly than those with lower diversity, consistent with the idea of diversity as biological insurance. The degree to which these effects are due to a single species that is resistant to stress rather than to species with complementary responses to stress is not yet clear. It is clear, however, that seaweeds respond differently to variation in the availability of different forms of nutrients, and thus having more species may allow greater and more consistent conversion of available resources into seaweed mass.

Seaweed diversity might also affect community function via bottom-up mechanisms that are independent of total production. For example, if particular invertebrates associate with certain seaweeds, then increasing seaweed diversity should lead to increasing animal diversity. Similarly, some grazing invertebrates grow, survive, and reproduce better on a mixed diet that includes a diversity of seaweeds. This kind of “diet mixing” can be favored because different foods provide complementary nutrients to grazers. Seaweed diversity could thus facilitate the health of grazing invertebrates in the same way that a balanced diet helps humans obtain proper nutrition and maintain health.

Similar effects of diversity below the species level has also been shown to stabilize communities against environmental change. For example, research on the seagrass *Zostera marina* suggests that genotypic diversity within monospecific *Zostera* meadows allows these important primary producers to persist in the face of natural (consumers) or anthropogenic (high temperatures) environmental change. Abundances of seagrass-associated invertebrates are also higher in more genetically diverse plots, perhaps because they offer a more reliable habitat. In these studies, the mechanisms appear to be very similar to those underlying the effects of species diversity previously discussed.

**SESSILE INVERTEBRATE DIVERSITY**

Although little is known about the functional significance of rocky-shore sessile invertebrate diversity, work on similar organisms on natural and artificial hard substrates in bays and harbors has been particularly informative regarding the role of diversity in determining the resistance of a community to invasion by exotic species (see Fig. 2). This resistance occurs when native species are complementary in their use of resources so that as diversity increases, the amount of unused resources dwindles, leaving fewer “leftover” resources for invaders to use. In sessile invertebrate communities, decreasing native diversity increases the survival and overall abundance of invaders. High native diversity decreases the availability of open space, the limiting resource in this system, by buffering against fluctuations in the cover of individual species. Each species has a distinct seasonal pattern of abundance, so space is most consistently and completely occupied when more species are present. Diversity decreases invasion by providing insurance against fluctuations in the abundance of any one species.

However, field surveys tell us that diversity is only one of many factors affecting community resistance to invasion. Some surveys do find a strong and consistent negative relationship between native and non-native diversity, but many find a positive correlation between native and invader diversity. This may be because some locations are inherently capable of supporting more species, both native and exotic, perhaps because of high resource levels or high levels of habitat heterogeneity. Such areas both have more natives and more invaders because both native and exotic diversity are similarly affected by some third variable (for example, the rate of settlement or frequency of disturbance). Still, within a location (when all else is equal), the loss of species should lead to an increase in invasion by exotic species as a result of a freeing of resources.
Another possibility is that there is some positive causal relationship between native and exotic diversity. For example, increasing richness may increase the probability of including species that facilitate the colonization and establishment of new species. However, it is unlikely that, on balance, natives facilitate only invaders or vice versa. The invasive bryozoan *Watersipora subtorquata*, for example, enhances three-dimensional habitat structure, facilitating both native and non-native species similarly. Interestingly, where this bryozoan is abundant, the relationship between native and exotic diversity is positive, whereas where it is absent, the relationship becomes negative, reflecting the influence of biotic resistance.

A study of genetic diversity in barnacles illustrates the potential effect of within-species diversity on intertidal community dynamics. Researchers compared settlement rates of barnacle larvae from a single brood (with a single pair of parents) to those of larvae from a mixture of two or three different broods and found that treatments with more broods had higher overall rates of settlement and metamorphosis. Although this study was conducted in the laboratory, in the absence of flow, it suggests that genetic diversity may enhance recruitment of an important intertidal species.

**CONSUMER DIVERSITY**

Mobile consumers play a large role in temperate coastal ecosystems, and single species such as sea otters, sea urchins, and sea stars can have dramatic effects that may overwhelm the bottom-up effects of diversity at the producer level. Additionally, because of the threats of overfishing and direct harvest, top predators are the most likely group of marine species to go locally extinct. An understanding of the significance of predator diversity is of great importance because of the cascading effects of predators on entire food webs. These “trophic cascades” appear to be most common in simple food chains, whereas diverse food webs are thought to be less likely to exhibit major shifts in community states when individual consumers are removed. For example, in the relatively simple food webs of Alaskan kelp forests, kelp biomass is maintained by sea otter predation on herbivorous sea urchins. In kelp forests containing a greater diversity of predatory and herbivorous fish and invertebrates, such as those of southern California, the extirpation of otters appears to have not had as large an impact on kelp. Both experimental and observational studies suggest that predator richness decreased grazing by herbivores, leading to a decrease in the biomass of the giant kelp *Macrocystis*. This occurs because predators have complementary effects on different species of herbivores such that total grazing is minimized only in a diverse predator assemblage. As kelps both serve as important habitat-providing foundation species and provide a significant energy source for much of the food web, declining predator diversity may have significant consequences for kelp forest ecosystem structure and function.

Other studies have pointed out that the presence of omnivores (consumers that eat both algae and herbivores) can overwhelm any effects of predator diversity. Given that many marine consumers are omnivores, these studies suggest that our ability to predict the consequences of changing diversity in food webs that include omnivores will be difficult and perhaps context-dependent. It is increasingly clear that the significance of diversity at any one trophic level cannot be understood without knowing the levels of diversity (and species composition) of other trophic levels.

**BIODIVERSITY’S IMPORTANCE FOR ECOSYSTEMS**

Although a growing number of examples suggest that diversity increases the absolute rates of processes such as production, many other examples indicate that a single dominant species (e.g., kelp) largely determines community productivity. However, diversity also buffers ecosystems from fluctuations in the environment or from the loss of particular species. Even if many species turn out to be functionally “redundant” because they perform similar ecological roles, having more species in a system may provide a critical insurance policy. Without the biological insurance provided by enhanced diversity, the ecosystem may collapse over the longer term and in the face of changing conditions.

Many of the community processes and ecosystem functions discussed in this article can be directly related to the benefits provided to humans by coastal ecosystems. It has been estimated that, globally, natural ecosystems provide humans with at least $16 trillion worth of goods and services per year (Costanza et al. 1997). If the effectiveness of these services is somehow linked to biodiversity (as evidence suggests that it is), then the loss of biodiversity will not only cost us our natural heritage but also cause us serious financial pain as we pay to develop technical means to provide the goods and services that the oceans currently provide us for free.

**SEE ALSO THE FOLLOWING ARTICLES**

Algae / Facilitation / Genetic Variation and Population Structure / Introduced Species / Predation / Surveying

**FURTHER READING**

Biofilms are assemblages of microorganisms that have colonized hard surfaces immersed in water. They cover rocks in the intertidal and even on the outer surface of marine plants and animals. These films are fundamental to the ecology of rocky shores, influencing settlement of invertebrates and algae and providing an important food resource for grazers. However, on man-made surfaces formation of a biofilm is described as “fouling” and is often seen as a nuisance; fouling on the hull of a ship, for example, reduces efficiency and increases fuel costs.

**BIOFILM FORMATION**

Biofilms begin to develop shortly after an object is immersed in water. Initial stages of biofilm formation are predictable and are driven by the physical and chemical properties of the surface, which influence adsorption of organic and inorganic chemicals from the surrounding water. Then, over longer time scales biological factors become increasingly important as the surface becomes progressively colonized by bacteria, diatoms, protozoa, yeasts, and eventually juvenile stages of larger marine plants and animals (Fig. 1). Intertidal biofilms are predominantly composed of photosynthetic organisms, mainly diatoms and filamentous cyanobacteria, which are less than 20 µm in diameter (Fig. 2A). These organisms combine to form a film around 20 µm thick, and although not visible without a microscope, they can give rock surfaces a dark green appearance because of the chlorophyll and other photosynthetic pigments they contain. Organisms within these films secrete mucous and other extracellular polymeric substances (EPS), which bind the film together, and they can also make filmed surfaces slippery.

**PHYSICAL FACTORS INFLUENCING BIOFILMS ON ROCKY SHORES**

Despite the harshness of physical conditions in the intertidal, biofilms persist throughout the year from polar regions, where they are covered with ice during the winter...
to the tropics, where rock surfaces may exceed 50 °C. However, the type and abundance of organisms within these films can vary considerably according to physical conditions including temperature, solar radiation and wave action, and even according to the type and rugocity of the underlying rock. Because they are microscopic the organisms within these films are vulnerable to physical stresses during low tide and the species composition and abundance of organisms generally shows considerable seasonal variation. This is particularly evident on the mid and upper shore, where at temperate latitudes, the abundance of microorganisms can change dramatically, peaking in late winter and early spring and then declining markedly as insolation stress increases during the summer (Fig. 3).

FIGURE 4 Number of juvenile barnacles recruiting to rock surfaces covered with biofilms of differing ages. Data were collected in laboratory choice chambers. (values are averages ± standard error). Reprinted from Thompson et al. (1998), with permission from Springer Science and Business Media.

EFFECTS OF BIOFILMS ON SETTLEMENT OF INVERTEBRATES AND ALGAE

Biofilms can influence settlement and colonization by larger organisms, most of which have a juvenile planktonic stage in their life cycle. The biofilm is the first point of contact between these juvenile stages and the underlying rock surface and can provide cues that influence the settlement of larvae (Fig. 4). Once settled these organisms grow and develop into adults, and as they do, their outer surface typically becomes colonized by a biofilm itself. Interestingly, these epibiontic biofilms are typically composed of different microorganisms than those on rock surfaces and so make an additional contribution to the microbial biodiversity of the shore (Fig. 2B, C, D).

BIOFILMS AS A FOOD RESOURCE FOR GRAZERS

Biofilms are also an important food resource for grazers, particularly molluscs such as limpets, but also for some urchins and fish. Because the organisms within these films are so small, they can multiply rapidly. This becomes apparent when grazers are removed from an area of shore, either experimentally or because of human exploitation or pollution. When this occurs the biomass of the microorganisms can double within days (Fig. 5). Although grazers directly remove organisms from biofilms, changes in feeding activity do not account for seasonal patterns in the abundance of photosynthetic microorganisms within biofilms (Fig. 3). Hence, at some times of year, there can be a mismatch between the microbial productivity of biofilms, which is negatively correlated with insolation stress, and the demand for resources from the grazers that feed on them, which is positively correlated with temperature (Fig. 3). Grazers also consume the germings...
of macroalgae such as *Fucus* that have settled in the biofilm; in doing so, they effectively control the abundance of larger plants as well as microorganisms within the biofilm. Because large macroalgae provide an important habitat for many other species of intertidal organisms, the interaction between grazers and biofilms is a key factor influencing the ecology of many rocky shores.

**METHODOLOGICAL ADVANCES IN THE STUDY OF BIOFILMS**

Despite the importance of biofilms as food resource we know little about their rates of productivity and their contribution is often omitted from estimates of inshore primary productivity. We also know little of the full diversity of microbiota within these films. In part, this has been a consequence of inadequacies in methods for enumerating and identifying these organisms. Traditionally, the standing stock of organisms has been estimated destructively by removing samples of biofilm and counting the abundance of cells using microscopy or estimating photosynthetic biomass using extracted chlorophyll as an index. Considerable advances have recently been made using confocal microscopy to examine the three-dimensional structure of biofilms, using PAM fluorescence to quantify photophysiological responses of microorganisms within biofilms and using infrared photography to quantify photosynthetic microbial biomass in situ on the shore. Because of taxonomic and logistical problems with visualization and enumeration the nonphotosynthetic components of intertidal biofilms have received far less attention than the photosynthetic organisms. This is now being addressed using molecular approaches to help characterize these organisms. Collectively, these techniques should greatly advance our understanding of the role of biofilms in shallow water habitats.

**SEE ALSO THE FOLLOWING ARTICLES**

Herbivory / Larval Settlement, Mechanics of / Limpets / Microbes / Stromatolites / Succession

**FURTHER READING**


**BIOLOGICAL MATERIALS**

**SEE MATERIALS, BIOLOGICAL**

**BIOOLUMINESCENCE**

**JAMES G. MORIN**

Cornell University

Bioluminescence is defined as visually detectable light generated by a chemical reaction originating from an organism. However, light production is largely the only unifying characteristic among luminescent organisms. Rather, diversity best describes bioluminescence. Bioluminescence is diverse taxonomically, biogeographically, ecologically, behaviorally, morphologically, physiologically, biochemically, and genetically. The available evidence
absent (the deep sea), and even less prevalent in periodically well-lit, photically heterogeneous environments, such as the rocky intertidal zone. The dominant luminescent intertidal organisms are found among the hydrozoa such as *Obelia* (Figs. 1A, B); the polychaetes, especially syllids (Fig. 1C), polynoids (Fig. 1D), and terebellids; the crustaceans (ostracods, rarely, Fig. 1E); echinoderms, especially ophiuroids (Figure 1F); molluscs (boring bivalves); and fishes (e.g., midshipmen during their mating period, Fig. 1G). However, the majority of the species in these higher taxa are not luminescent, and those that do luminesce are usually more abundant in subtidal environments; relatively few luminescent organisms are strictly intertidal.

Luminescence is found in less than 1% of all known genera worldwide, but there are still over 700 luminescent genera, which occur in 15 phyla. Seven major taxa (vertebrates, insects, molluscs, cnidarians, crustaceans, echinoderms, and annelids) account for over 90% of the known luminescent genera, and some of these occur in the intertidal. Nearly half of the luminescent genera are fishes and insects, while molluscs, cnidarians, and crustaceans add another third of the genera.

Over three-quarters of all luminescent genera are marine. Only about 1–3% of coastal (benthic and neritic) genera are luminescent, and of these only some occur in the intertidal zone. The open ocean represents the largest habitat on earth, and it is there that most of the luminescent genera occur. Light emission is highest among organisms dwelling in the mesopelagic zone of the open oceans, where well over 60% of the genera and almost every individual emits light. In the mesopelagic, luminescence is a way of life. Dominant luminescent organisms in this immense habitat are the fishes, squids, crustaceans, gelatinous zooplankton, and dinoflagellates. These forms occasionally wash into the intertidal zone, where their death throes may produce spectacular displays of light.

**CHEMISTRY OF LUMINESCENCE**

In all known luminescent systems an oxygenase (generically known as a luciferase) catalyzes the interaction of a substrate (generically known as a luciferin) with molecular oxygen or peroxide to form a peroxy intermediate, which breaks down to yield an oxidized oxyluciferin and light. However, both the luciferin substrates and the luciferases vary among taxa. It has been estimated that the ability to emit visible light has evolved over 30 times among organisms and with several distinctly different chemistries. Luciferases appear to be more diverse than their luciferin substrates. Accessory enzymes, as well as cofactors such as Ca$^{2+}$ or H$,^+$, are often involved in the
The diverse luciferins include (1) two systems that are composed of tripeptides that form an imidazolopyrazine nucleus (the coelenterazine and cypridinid ostracod systems), (2) a benzothiazole (fireflies), (3) a tetrapyrrole (dinoflagellates), and (4) several distinct aldehyde-related systems (bacteria, earthworms, a freshwater snail, and fungi). Only the firefly system uses ATP directly in the reaction. The specific luciferin is currently unknown or only partially characterized in about 30% of the known luminescent genera (representing at least 14 diverse higher taxa). Conversely, the coelenterazine system is very widespread. It occurs in about one-third of the luminescent genera, from at least eight phyla, and may have evolved independently several times using the same widespread tripeptide precursor. Other systems (e.g., earthworm, freshwater snail, firefly, and fungi systems) appear to be restricted to but one higher taxon (but appear in many species within that taxon). Both the cypridinid ostracod and the dinoflagellate systems occur in two different, distantly related taxa. The bacterial system, while being represented in five taxa (bacteria, nematodes, squids, thaliaceans, and fishes), occurs in the latter four taxa only by virtue of a symbiotic relationship between luminous bacteria and the host taxon.

FUNCTIONS OF LUMINESCENCE

The majority of emitters luminesce only in response to contact stimulation. The resulting luminescent expression is usually either a slow glow lasting more than 5 seconds or a bright single pulse or burst of rapid intracellular flashes, each with a duration of less than about 2 seconds and often as short as 50 milliseconds. The bursts often propagate away from the point of stimulation as a traveling wave of luminescence and also away from vital structures. In order to be visually effective, bioluminescence must be produced when and where it can be physically detected. Maximum bioluminescent intensities reach about $10^{-1} \mu W cm^{-1}$ (with most in the range of $10^{-4}$ to $10^{-7} \mu W cm^{-1}$), which is about equivalent to the boundary between nautical and astronomical twilight, well after the sun has set or before it rises. However, these dim to dark conditions occur virtually all of the time in crevices or under rocks.

Most bioluminescence almost certainly serves some form of communication. Communication is defined here as an exchange of a signal between a sender and a receiver to the benefit of at least the sender but not necessarily the receiver. Thus, whatever the incipient mechanisms were that gave rise to a visible chemiluminescent process, subsequent selection for enhancing the characteristics and expression of the light itself (e.g., intensity, color, kinetics, spatial distribution) was likely the result of evolutionary feedbacks between the emitter and the receiver.

There are four primary functions that bioluminescence might serve for an organism: defense (protection), offense (feeding), intraspecific communication (usually sexual courtship), and symbiosis (mutual benefit). Other potential functions are apparently relatively rare in nature. It is also important to note that most luminescent functions are not mutually exclusive, and more than one function is sometimes served by one light-emitting system.

Defense

Luminescent systems appear to have evolved most often for deterring predators or potentially damaging intruders that induce luminescence upon contact with the emitter. In these cases the emitter itself often does not have well-developed vision and often does not display complex behavior (see Figs. 1A, D, F), but the receiver, which is a different species, has both. These receivers—predators or intruders—are most likely to be fishes, crustaceans, cephalopods, or polychaetes. Many intertidal and subtidal predators visually forage in dim light, either nocturnally in the open or by day beneath rocks and epifauna. It is in both these situations where stimulated bioluminescence is most pervasive in the intertidal (or anywhere).
order to repel or deflect an intruder, nearly all the intertidal (and benthic) forms where light is used for attracting mates. In these cases the receivers of the same species (and usually also the emitter) have well-developed eyes and complex behavior. Luminescence is usually displayed as a ritualized, species-specific courtship display pattern toward potential mates in the water column above the substrate, in a way analogous to that of fireflies on land. Cypridinid ostracods (see Fig. 1E) from the shallow waters of the Caribbean, syllid polychaetes (see Fig. 1C), and perhaps midshipmen fish, which come into the shallows and intertidal to breed (see Figure 1G), use species-specific light cues to attract mates. Male ostracod crustaceans use secreted patterns of light to attract females. Female syllid polychaetes produce a single or pulsed glow to attract rapidly flashing males. Midshipmen males may use light, along with sound, to attract females to potential nest sites, although this function has yet to be verified, and these fish probably use their lights differently in their deep-water foraging habitats.

**Courtship**

Another function, but probably a secondary effect co-opted from intruder deterrence, occurs in some intertidal (and benthic) forms where light is used for attracting mates. In these cases the receivers of the same species (and usually also the emitter) have well-developed eyes and complex behavior. Luminescence is usually displayed as a ritualized, species-specific courtship display pattern toward potential mates in the water column above the substrate, in a way analogous to that of fireflies on land. Cypridinid ostracods (see Fig. 1E) from the shallow waters of the Caribbean, syllid polychaetes (see Fig. 1C), and perhaps midshipmen fish, which come into the shallows and intertidal to breed (see Figure 1G), use species-specific light cues to attract mates. Male ostracod crustaceans use secreted patterns of light to attract females. Female syllid polychaetes produce a single or pulsed glow to attract rapidly flashing males. Midshipmen males may use light, along with sound, to attract females to potential nest sites, although this function has yet to be verified, and these fish probably use their lights differently in their deep-water foraging habitats.

**Offense**

Using luminescence for obtaining prey is known for glowworms at cave mouths on land and flashlight fishes in shallow tropical waters, where they use bacterial light to detect and attract prey, and is postulated (but not demonstrated) for the lures of deep-sea anglerfishes. In these cases, a controlled, usually continuous or long-lasting expression of luminescence can act as a flashlight of and/or a lure to visually orienting, actively motile prey in dim or dark light conditions. These conditions have not yet been demonstrated for any intertidal species.

**Symbiosis**

Finally, light could be involved in complex symbiotic relationships. For instance, mutualism has been demonstrated in which some fungi use light emanating from the gills of their fruiting body to attract insects, thus providing food for the developing insect larvae, which eat the hyphae in exchange for spore dispersal by the insect, much in the same way that flowers attract insects. Such mutualisms are unknown in the intertidal, however. On the other hand, parasitism of crustaceans by luminescent enteric bacteria has been suggested. Intertidal and subtidal caprellid and gammarid amphipods infected with species of luminescent enteric bacteria (genus *Vibrio*) have been documented. The hypothesis suggests that the glowing crustacean may increase the likelihood that it will be eaten by a nocturnal predator, thereby delivering the bacteria to a rich source of nutrients in the gut of the predator, but without harming the predator. However, this relationship has not been tested, and it remains only a tantalizing hypothesis.

Overall, what emerges from an examination of potential functions of luminescence found in the intertidal is that there are relatively few luminescent species in the intertidal, but their functions are roughly consistent with a broader comparison. Among all the luminescent genera, most use their light for defense, many also use light for intraspecific communication, some use light for obtaining food, and a very few use light for mutualism.

Finally there are the incidental pelagic species that are brought to the intertidal and sometimes adorn the shore with fascinating sparks and glows, which are really epi-phenomena expressed by organisms usually in a moribund condition. Few survive their close encounter with what, to them, are foreign habitats. These incidental visitors include blooms of luminescent dinoflagellates or radiolarians, or, more rarely, clusters of deep-sea copepods, squids, or gelatinous zooplankters such as ctenophores, hydrozoan medusae, scyphozoan medusae, and thaliacean tunicates.

**SEE ALSO THE FOLLOWING ARTICLES**

Benthic-Pelagic Coupling / Camouflage / Foraging Behavior / Light, Effects of / Phytoplankton / Predator Avoidance
BIRDS

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Birds are often overlooked as important components of coastal ecosystems because they are a land-based group of animals. However, they can play significant roles in shoreline communities by changing mortalities of coastal species via predation and other activities and by importing nutrients from other systems.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Family</th>
<th>Food Resources</th>
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<tbody>
<tr>
<td>Cormorants</td>
<td>Phalacrocoraridae</td>
<td>Fishes</td>
</tr>
<tr>
<td>Herons</td>
<td>Ardeidae</td>
<td>Fishes</td>
</tr>
<tr>
<td>Ducks</td>
<td>Anatidae</td>
<td>Molluscs, crustaceans, echinoderms, annelids, fish</td>
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<tr>
<td>Geese</td>
<td>Anseridae</td>
<td>Algae.</td>
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<tr>
<td>Falcons, ospreys, and eagles</td>
<td>Falconiformes</td>
<td>Shorebirds, fishes, carrion</td>
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<td>Oystercatchers</td>
<td>Haematopodiidae</td>
<td>Large bivalves and gastropods, crabs, sea urchins, worms</td>
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<tr>
<td>Plovers</td>
<td>Charadridae</td>
<td>Crustaceans, barnacles, small molluscs, annelids</td>
</tr>
<tr>
<td>Sandpipers</td>
<td>Scolopacidae</td>
<td>Crustaceans, barnacles, small molluscs, annelids</td>
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<td>Gulls</td>
<td>Laridae</td>
<td>Wide range of invertebrates, fishes, and carrion</td>
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<td>Insects</td>
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</tr>
<tr>
<td>Sparrows and longspurs</td>
<td>Emberizidae</td>
<td>Insects</td>
</tr>
</tbody>
</table>

COASTAL BIRD GROUPS

Birds utilizing the shoreline span a remarkable range of taxonomic groups (Table 1). Birds primarily use shorelines as feeding habitats, although some take advantage of the adjacent seascape to establish nests, and many can be seen resting in these areas at low tide (Fig. 1). Coastal habitats such as offshore islands, flotsam-covered shores, and wave-carved cliffs often provide refuges from mammalian predators. The reasons shorelines make good resting areas are not well studied, but might include avoidance of territorial aggression by resident birds, a wide vista to scan for predators or offshore food sources, and a lack of physical habitat structure, which might facilitate social interaction or escape from predators. Birds divvy up the shoreline in different ways. Some species, such as oystercatchers (Haematopus),
establish and defend from other conspecifics territories, which include feeding areas. In contrast, some species, such as sandpipers (Scolopacidae), aggregate and forage in flocks. Finally, many birds, such as gulls (Larus), defend an area only immediately around them, such as the space around a prey item on which they are currently feeding.

**FEEDING**

Because of the open vistas shorelines offer, the moderately large size of the prey, the high consumption rates of birds, and the frequent presence of hard parts such as shells and scales in many prey species, the diets of birds occupying shore habitats are readily observed, making them a model group for feeding studies. The diets of birds that feed on shorelines span a wide range of prey resources (Table 1). Gulls (Fig. 1) and crows (Corvus spp.) frequently consume a broad range of animals that includes bivalves, gastropods, barnacles, sea urchins, sea stars, fishes, sea cucumbers, isopods, crabs, polychaete worms, and ribbon worms. Other birds, such as sandpipers, plovers (Charadriidae), ducks (Anatinae), and pipits (Motacillidae) are more specialized, focusing on small amphipods, particular barnacle species, or mussels. Some greese (Anserinae) feed on algae along the shore. Many groups concentrate just on fish or insects that utilize shoreline habitats. Even for those species that feed widely, diet observations or discarded hard parts in nesting territory middens often show individual specialization on particular prey species, termed “majoring.” Feeding observations often reveal differences in prey between adults and nestlings, which may facilitate consumption by small nestlings, maximize rates of food delivery per unit time, or reduce predator detection of nests by minimizing the number of food delivery trips. Feeding by different groups of birds varies through the tidal cycle, depending on the activity patterns of prey and the morphological traits of the birds. Some birds, such as sandpipers and various passerine groups, feed when the shoreline is exposed to air at low tide. Others, such as fish-feeders (e.g., alcids, kingfishers [Alcedinidae], and mergansers [Mergus]) and invertebrate-eating ducks (e.g., eiders [Somateria], scoters [Melanitta], oldsquaws [Clangula hyemalis], and harlequin ducks [Histrionicus histrionicus]), feed when the shore is immersed. In many cases, birds forage right at the water edge, where the prey are adjusting their activities to meet the challenges of being immersed in water versus air.

Methods of prey capture and of prey consumption vary among bird species that use shorelines, and they depend strongly both on prey traits, such as structural defenses and use of refuges, and on the beak morphology of the birds. Many bird groups have skinny beaks, which they use as tweezers for extracting prey from crevices in the rocks or between sessile organisms. Bills of sandpipers are some of the most specialized for this task, and they range in both length and shape (straight, turned up, or turned down), which permits exploitation of different habitats. In general, sandpipers specializing on rocky shores tend to have shorter bills than those utilizing soft sediment habitats, because most prey cannot burrow deep into rock. Oystercatchers (Fig. 2) have long chisel-like beaks that are especially well suited for handling prey once they are captured, as well as for extracting prey individuals from refuges. The long beak permits probing of larger crevices for hiding prey such as crabs, or serves as scissors to snip the attachments of prey such as sea urchins and mussels, yet its sturdy chisel shape is often used to dislodge prey such as limpets with a sharp lateral blow. Once captured, oystercatchers extract the most edible portions of prey either by chiseling at shells, or more commonly by deftly probing between shell parts and snipping the meat from the shell by using the beak like a pair of scissors. Other birds, such as gulls (Fig. 1) and crows have more generalized bills that can be used both in capturing food by probing for prey or by tugging prey from the substrate, and in extracting the edible prey parts by prying apart or hammering shells and by ripping flesh from carcasses. The majority of shore-feeding birds do little processing of prey with their beaks and swallow prey whole. In these cases, structural prey defenses such as shells, exoskeletons, or scales either are crushed physically with a muscular gizzard (e.g., many mollusc-feeding ducks and sandpipers), digested chemically, or regurgitated undigested as pellets (many gulls and birds of prey), which facilitates diet investigations. Some species use behavior to circumvent prey defenses. When feeding on bivalves, oystercatchers

![Figure 2](image-url)
Focus on situations in which bivalves are gaping open, such as when they are immersed in water and either feeding or rehydrating following extended exposure to air. Birds such as gulls and crows exhibit a notable behavior known as anvil use, where they drop prey from some height onto rocks below to crack shells. This procedure requires substantial skill because an anvil rock must be chosen that prevents the prey from ricocheting off to an inaccessible spot upon impact; the birds must be sufficiently accurate to hit the anvil from some height under challenging wind conditions; the birds must account for shell, weight, and shape properties of different prey species; and the prey must be dropped from an altitude that is high enough that the prey's shell will crack upon impact but low enough for the bird to reach the prey before lurking kleptoparasites steal it.

Because birds are derived from a terrestrial lineage, feeding on marine prey can pose special physiological problems for birds that live along the shore. Osmoregulation is an aspect that has received particular attention because many marine species have a higher salt content than terrestrial organisms and local sources of freshwater are often limited because of wave splash and local weather patterns. One solution is to feed on prey that are themselves low in salt content, such as many bony fish species and some crustaceans. As a further solution, many birds that inhabit shorelines have specialized salt excretory glands or exhibit reduced water loss from evapotranspiration.

Another problem posed by marine species is that they sometimes contain powerful toxins. For example, molluscs often filter planktonic dinoflagellates out of the water column and may sequester in their tissues the strong neurotoxins that these organisms produce, making them toxic to vertebrates. Yet there is little evidence of large-scale mortality of birds using shorelines following blooms of these dinoflagellates (“red tides”). How do birds avoid this hazard? One possibility is that they have evolved special physiological mechanisms to counteract the toxins, but to date there is little evidence of these. Instead, limited experiments on gulls suggest that they are adept at detecting and then either rejecting or regurgitating toxic food to avoid the hazard following detection. If no alternative food sources are available, the birds may be forced to move to other areas.

**COASTAL IMPACTS OF BIRDS**

Although birds are relatively rare compared to other coastal organisms, their energy requirements are great because of their large size and exceptionally high metabolic rate, so they can have substantial impacts on their prey populations in many situations. A variety of experimental manipulations and quantitative calculations have demonstrated that birds can significantly reduce populations and change the size structure of many benthic marine invertebrates, including bivalves, gastropods, crabs, sea urchins, barnacles, sea stars, and amphipods. Less is known about impacts on more mobile prey such as fish and insects. The temporal pattern of these impacts can vary as a consequence of migratory patterns; some birds such as oystercatchers, crows, and gulls tend to be resident and exert chronic impacts throughout the year, whereas migratory species such as sandpipers and pipits produce pulsed episodes of intense predation in an area. In the latter case, the effect of bird predation on prey populations depends on key life history events and points of regulation in the prey populations in relation to the timing of the predation pulse. For example, a pulsed bird presence is likely to have a much stronger effect on prey populations if it occurs just prior to the breeding season of prey than if it occurs after the population has been swelled by newly produced offspring. Birds often vary in abundance across space along the shore and consequently can generate significant spatial variation in prey populations. For example, birds such as oystercatchers, sandpipers, and passerines that feed at low tide usually require a horizontal surface on which to stand and hence cannot feed effectively on vertical walls. Many studies have found markedly higher abundance and individual sizes of avian prey on vertical walls compared to adjacent horizontal rock benches. This pattern has provided further evidence of the substantial role that birds can sometimes play on shorelines.

Bird impacts on the shoreline system are not limited to their feeding activities. First, birds can serve as prey resources for some species. Birds of prey, terrestrial mammals such as raccoons and otters, and the occasional shark will take adult birds. Furthermore, mammals, reptiles, and some birds such as gulls and crows regularly feed on the eggs and chicks of other birds. Additionally, because they often eat fish, molluscs and crustaceans, coastal birds can be a key host in the life cycles of parasites such as trematodes. In some cases these parasites can reduce the vitality of their avian hosts, but in others there seems to be little noticeable impact. Instead, the birds seem to be serving an important role as dispersal agents of the parasites to new areas, where they are released into the environment by defecation and go on to attack other invertebrate hosts in the life cycle, often severely.

Birds may also be a source of physical disturbance on the shore. As they feed, birds can sometimes cause considerable ancillary disturbance to nontarget species. Often prey hide on or under sessile organisms attached to the rocks, and birds may rip out or damage these sedentary organisms as they search for food. Because they are often structurally
Because birds are contained within a web of species interactions, strong impacts of birds on shore-dwelling organisms can have indirect effects on other species, and birds can themselves be indirectly influenced by other species. These indirect effects can arise in two general ways. First, chains of interactions can cause cascading effects through food webs. For example, experiments have shown that birds can reduce populations of grazing molluscs and sea urchins, which in turn can increase algal abundance and alter the food and shelter available for other grazers that are not susceptible to bird predators. Second, species can alter the intensity of interactions between individuals of pairs of other species. For example, experiments have shown that bird predation can change the relative abundance of different species of sedentary organisms attached to the rocks, and these species in turn can change interactions between predators and prey by making prey easier or harder for the predator to find. Similarly, subtidal predators such as large fish and sea stars often drive prey to the water surface or even out of the water, where they become easier for birds to catch.

Birds often can play an important role on the shoreline as conduits for material flow between ecosystems. Shoreline insect production, arising either from grazing on algae growing on the rocks or from scavenging algal and animal detritus washed up on the shore, can provide an important subsidy to insectivorous birds, allowing them to maintain higher populations in adjacent terrestrial habitats than would otherwise be possible. Similarly, piscivorous and zooplanktivorous birds often forage widely away from the shore and return to shoreline nesting areas, where they deliver both energy to the system in the form of dead prey and nutrients contained both within dead prey and in excreted guano. Through this mechanism, many groups of birds that do not utilize shoreline habitats for feeding, such as pelicans, alcids, and petrels, can still have substantial local impacts on the coastal zone. Several studies have investigated the consequences of nutrient inputs into coastal zones and have found varying effects. In some cases, the added nutrients promote coastal production of algae. In other cases, the high nitrogen and salts contained in guano are toxic to shoreline plants and algae, shifting the balance of the system toward more resistant species.

**EVOLUTIONARY IMPACTS**

Because of the impacts they have on coastal systems, birds may be an important evolutionary force for shore-dwelling species. Many prey species of birds, such as certain limpets, fish, crabs, and sea stars, are remarkably cryptic in their environment, effective at finding or even making refuges, resistant to being dislodged, or armored heavily. Several studies have demonstrated that bird predation exerts strong selection against more visible individuals of a species, consistent with strong evolutionary impacts, but it has been hard to prove that birds are the primary driver of prey defensive traits, for several reasons. First, other agents of mortality are expected to have similar effects, including visually foraging predators such as fishes and octopuses, and waves that deliver strong forces that impact the shore. Additionally, the offspring of many prey organisms are highly mobile, which can counteract spatially variable bird abundance by introducing a stream of locally maladapted individuals that interbreed with locally adapted individuals and thereby counteract evolutionary change.

**RELATIONSHIP WITH HUMANS**

Because they occupy positions high in the coastal food chain, birds can serve as sensitive indicators of environmental impacts and change. Shoreline birds face a variety of anthropogenic threats. Coastal zones are some of the most heavily populated areas of the world. Human activity leads to high rates of habitat loss for nesting and feeding. Simply walking along the shore can disturb shore birds, increasing susceptibility of both adults and nestlings to predators or reducing feeding rates. Humans often harvest large quantities of coastal organisms used by birds, such as various mollusc species, and hence may compete with birds for food. Exotic species introduced by humans, particularly predatory mammals on islands, can lead to changes in the prey base affecting food resources and often produce catastrophic increases in nest predation. Elevated nutrients in coastal runoff from sewers, agriculture, and deforestation may be favoring blooms of toxic algae, which, if not directly poisoning birds, still restrict the food resources that birds can use. Finally, coastal spills of oil and chemicals have led to well-documented mortality events of birds using shorelines. Generally mortality is greatest for birds that forage on the water, which suffer both from the disruption to the critical insulating function of their feathers and from direct ingestion of the toxic chemicals while attempting to clean their feathers.
Mortality caused by consumption of polluted prey is also a possibility but has been less clearly documented.

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BIVALVES

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The Bivalvia is the second largest class of the phylum Mollusca and includes clams, mussels, and oysters. Bivalves differ greatly from other molluscs, with two hinged shells, a reduced head, and a narrow foot. These differences relate to an ancestral lifestyle spent buried in sand and mud. In most bivalves, the gills are used for filter feeding. From infaunal ancestors, many lineages of bivalves evolved mechanisms to attach to or bore into hard surfaces. Bivalves are thus very successful on rocky intertidal shores worldwide, with species on or in the rock substrata, and others nestled in protected microhabitats.

GENERAL FEATURES OF BIVALVES

Bivalves are ecologically important members of all benthic marine habitats, including the rocky shore, sand and mudflats, subtidal soft sediments, and hydrothermal vents. Visitors to the rocky shore are most familiar with mussels and oysters, which can be the major space occupants and, through competition or the provision of secondary space, exert strong control over the abundance of other species. Less conspicuous bivalves also live in rocky intertidal communities but can be easily found when carefully looked for. The adaptations of both the obvious and the hidden bivalves of wave-beaten rocky shores make them superbly fit for life in this challenging environment.

Bivalves are members of the phylum Mollusca in the class Bivalvia, sometimes called the Pelycopoda. These names refer to characteristic features of most bivalves that set them apart from other molluscs: the possession of two shells (“valves”) and a typically hatchet-shaped foot. Bivalves are also unlike familiar molluscs, such as snails and squids, by having a very reduced head that lacks obvious sensory structures such as eyes. Bivalves are the only major group of molluscs that are mostly filter feeders, using a modified gill as described subsequently. The shells are laterally arranged, with the anterior-posterior body axis running between them. A soft tissue, called the mantle, lines and secretes the shells. A hinge joins the two shells dorsally and may contain interlocking teeth; shell teeth may also be found adjacent to the hinge. A proteinaceous ligament joins the two shells and also provides the impetus for shell opening by virtue of its spring-like elasticity. Posterior and anterior adductor muscles traverse the two shells and counteract the opening force of the ligament; some species, as noted below, have only one adductor muscle. As in other molluscs, the dorsal region of the body contains most of the viscera (heart, gut, kidneys, and gonads). Two gills, one on each side, lie left and right of the main body in a space, called the mantle cavity, between the interior surface of the mantle and the visceral. The foot lies ventral to the visceral region and is primitively used for burrowing. The general features of the anatomy of bivalves are illustrated in Fig. 1.

SUSPENSION FEEDING

Feeding by collecting suspended particles from seawater is a common means by which marine animals acquire energy and essential nutrients. This mode of feeding, referred to as suspension feeding, takes advantage of the enormous amount of production of bacteria, phytoplankton, and protists in seawater, as well as particulate
detritus and smaller zooplankton. Animals that use sievelike structures to capture food particles are often called filter feeders. However, not all suspension feeders use sieves; food may also be captured by collision with mucus- and cilia-lined surfaces. Moreover, particles that can fit through sieve apertures might be collected nonetheless by collision and adherence to sieve surfaces. Among marine animals, feeding structures are often modifications of body parts that originally served another function. In bivalves, the gill has been modified from a strictly respiratory structure into a bifunctional respiratory and filter feeding apparatus.

The primitive bivalve had a pair of gills (called ctenidia) lying on each side of the body, as do modern bivalves. The primitive gill is a typical bipectinate molluscan ctenidium: a central axis from which a series of flat leaflike structures (lamellae) arise on either side. The lamellae are thin, to reduce the distance over which gas must diffuse, and broad, to provide ample surface area for gas exchange to occur. Beating cilia on the surfaces of lamellae pump water through the interlamellar spaces and ensure that the gills are constantly flushed with clean, oxygenated seawater. Because seawater is filled with particles that can foul gills and occlude water paths, especially elongated cilia between lamellar edges serve as a barrier, while other cilia along the front edge carry potentially fouling particles into exhalant currents. This type of primitive gill is present in some extant bivalves and is termed a protobranch ctenidium.

The protobranch ctenidium has all the elements needed for an efficient filtering device: the ability to pump large volumes of water and a mechanism for removing particles from that water. In filter-feeding bivalves, the gill lamellae are elongated to increase the length of the frontal edge where filtering occurs. To contain the lengthened ctenidium within the mantle, the lamellae are folded, with tissue bridges holding the fold in place. Because each lamella is folded into a V shape, and each lamella lies on either side of an axis, the filter-feeding ctenidium has a W shape in cross section. Cilia carry food particles toward the mouth region where they are transferred to palps that transport the food to the mouth; other ciliary tracts carry inedible particles away. The simplest forms of these filter-feeding gills are termed filibranch, whereas more complicated forms, in which tissue bridges connect adjacent lamellae, are called eulamellibranch.

ADAPTATIONS OF BIVALVES TO THE ROCKY SHORE

One of the greatest challenges of life on a rocky shore is resisting dislodgement caused by the great wave forces encountered there. Organisms that must move to feed, such as predatory sea stars or grazing gastropods, cannot protect themselves from waves by permanent attachment and have to find a compromise between mobility and a secure grip on the rock. As filter feeders, bivalves do not need to move to feed and therefore make no such compromise. Thus, all that was needed for ancestral infaunal bivalves in soft sediments to enter the rocky shore environment was a mechanism to avoid dislodgement. Bivalves have evolved three mechanisms. The first is to attach firmly to the rock surface, the second is to burrow into the substratum, and the third is to seek protected microhabitats.

Attaching with Threads: Mussels and Mussel-Like Bivalves

Several groups of bivalves use byssal threads to attach to rock surfaces or to other organisms. Byssal threads are proteinaceous strands produced by a byssal gland located near the base of the foot. The foot itself is highly specialized, no longer having a burrowing function and typically
is used for locomotion only by juveniles. The thread is secreted as a liquid, molded by the foot into the thread shape, and attached by the foot to a hard surface with a disk-shaped plaque. Many threads are made, and the entire structure is called the byssus. While the most familiar of byssate bivalves are the mussels belonging to the family Mytilidae, byssal attachments have arisen independently in many other families (Fig. 2).

The byssus is an exemplary example of two evolutionary principles. The first is that the past and present adaptive significance of a structure can differ, and the second is that evolution tinkers with existing structures to perform new functions. The adult byssus has its origin as one or few threads used by newly settled larvae to attach to sedimentary particles while metamorphosing to juvenile clams. Larvae may also use byssal threads as a dragline to be carried by water currents. The byssal threads in ancestral and modern infaunal bivalves are quickly lost as the juvenile clam grows and gains the weight and burrowing ability needed to stay on the bottom. Mussels and several other groups of bivalves retain this larval feature into adulthood, an evolutionary change called neoteny. Instead of outgrowing the use of byssal threads, more threads are added to increase the strength of attachment, and this culminates in a strong byssus that can withstand wave shock on rocky shores.

Evolution has also changed shell shape and musculature in bivalves that adopt the byssal attachment strategy. These changes are most profound in the subclass Pteriomorphia in lineages in which both inhalant and exhalant water currents are located posteriorly. In these lineages, anterior tapering and posterior enlargement has resulted in a more or less triangular shell outline, in short the typical mussel shell shape. This posterior enlargement causes the elevation of the inhalant and exhalant water currents into the overlying water. This is thought to be an advantage in dense aggregations. The tapered anterior end leaves little interior room for soft body parts, and the anterior musculature is much reduced. This condition is called heteromyarian, referring to the asymmetry of anterior and posterior muscles, and is always associated with byssal attachment. In many mussels, there is also frequently a flattening of the ventral edges of each valve. This flattening lets the shell lie closely pressed to the rock surface, minimizing the space through which water can flow and dislodge the animal.

In byssate bivalves with anterior inhalant currents, restriction of the anterior end would be maladaptive, and these bivalves have limited success on wave-beaten hard surfaces. In the subclass Pteriomorphia, ark shells (family Arcidae) are an example of such bivalves, and one species found in the California fauna, *Acan tylus bairdi*, is limited to calmer waters or rock undersides. Byssate bivalves
from other subclasses are similarly unable to form mussel beds. Some examples from the Anomalodesmata are some species in the family Lyonsiidae; *Entodesma saxicola* and *Lyonsia californica* are common but limited to crevices or rock bottoms on the west coast of the North America.

The convergent evolution of the mussel form in distinct bivalve lineages is evidence of the survival value of these morphological changes. The most striking example is the freshwater genus *Dreissena*, which has strong resemblance to the marine genus *Mytilus* even though it belongs in a different subclass (Heterodonta). There is, however, disagreement on the evolutionary pathway leading to epibyssate bivalves, that is, byssally attached rock-dwelling bivalves. Some argue that retention of the byssus in adults first allowed attachment to rock surfaces, and this was followed by changes to shell shape and musculature. Others argue that an endobyssate stage, where infaunal byssate bivalves attached to buried stones or gravel, evolved first, and that the heteromyarian condition evolved before movement to hard surfaces. Updated phylogenetic analyses should be decisive in this debate.

Species of *Mytilus* are the most familiar of the byssally attached rocky shore bivalves, and these are among the most studied of all marine invertebrates. *Mytilus* spp. are found on most rocky temperate shores, and modern lineages appear to have arisen in the Northwest Pacific in the late Eocene or early Oligocene. Two lineages persist in the North Pacific, one leading to the modern *Mytilus galloprovincialis* on the Northeastern Pacific shore and *M. trossulus* in the Northwest Pacific; the other led to members of the *Mytilus edulis* complex, a group of morphologically similar species (*M. trossulus, M. edulis*, and *M. galloprovincialis*). *Mytilus trossulus* is found sympatrically with *M. galloprovincialis* and in the Northeastern Pacific. *M. trossulus* is usually found in more protected areas, including estuaries, than *M. galloprovincialis*. However, it is also found along the upper edges of *M. californianus* beds in Oregon and Washington. *Mytilus trossulus* expanded into the North Atlantic in the late Miocene or early Pliocene, and is now found in Nova Scotia and, curiously, in the Baltic Sea. *M. trossulus* is sister to a clade of *M. edulis* and *M. galloprovincialis*. *M. edulis* occupies the northeast and northwest Atlantic coasts. *M. edulis* expanded into the Mediterranean Sea where, upon the isolation of the Mediterranean Sea by the closure of the Gibraltar Strait, it diverged into *M. galloprovincialis*. Upon the reconnection of the Mediterranean Sea and the Atlantic Ocean, *M. galloprovincialis* expanded its range south and north of Gibraltar, coming into contact with *M. edulis* is southern Europe. *M. galloprovincialis* also has proved to be a potent invader and is now established in California, Japan, South Africa, Hong Kong, and Australia. The biogeography of *Mytilus* in the southern hemisphere is not fully understood.

Cementation: Oysters, Scallops, and Similar Forms

In the previous section, we were introduced to heteromyarian bivalves that attach to rocks by a byssus along the ventral surface. Bivalves able to cement themselves to rocks have evolved from this template. These bivalves, including oysters, scallops, and some other similar forms, lay on their sides, with the lower valve cemented firmly to the bottom. This evolutionary transition was accompanied by further modifications to the soft anatomy, including the loss of the anterior adductor, enlargement and movement of the posterior adductor muscle to a more central position, and rearrangement of gills and viscera to surround the single adductor muscle. This body plan is called monomyarian. Permanent attachment by cementation has clear functional advantages. The permanence of attachment avoids the need to frequently renew byssal threads. Too, laying on their sides, oysters and scallops have a lower profile on rock surfaces, reducing the area against which waves can push. Cemented bivalves might also be better protected from some predators than byssally attached mussels: they are more difficult to lever off the rock surface and do not have a gap between the shell valves where the byssus passes through. This gap can provide access to the soft body for predatory sea stars or a point of leverage for the claws of crabs. The enlarged adductor muscle also allows the two shells to be more strongly closed.

Oysters (family Ostreidae) are monomyarian bivalves that are important bivalves on some rocky shores. On rocky temperate shores, oysters do not rival mussels in abundance, but they do achieve impressive densities in other areas. Of course, oysters are also very abundant in protected waters and estuaries, and are the basis of valuable fisheries worldwide. Oysters become ecologically important when they settle on each other to form mounds and reefs that provide habitat for other organisms, alter water flow, filter large amounts of phytoplankton, and stabilize underlying sediments. In the Pacific Northwest of the United States, we find *Ostrea conchalepa*, a relatively small oyster that is edible and was eaten by Native Americans despite its small size. *Ostrea conchalepa* is capable of forming reefs and in that state has been called *O. lurida*. Other oysters in this region are not native and have been introduced for mariculture. These include the European
species *Ostrea edulis*, the Japanese species *Crassostrea gigas*, *C. ariakensis*, *C. sikamea*, and the American Eastern oyster, *C. virginica*. None of the introduced oysters are found on exposed rocky shores.

Scallops (family Pectinidae) are also monomyarian bivalves that lay on their right sides and can attach to hard surfaces by byssal threads while juvenile. In many species, adults are free living on soft sediments. Others, however, cement themselves to hard surfaces as they become adult. On rocky shores, high wave energy favors scallops that can attach firmly, such as *Crassoderma gigantea* (*Hinnites giganteus* in recent literature). This species attaches by byssal threads as juveniles, but can detach and actively swim to avoid predators. After reaching about 25 mm, the scallop cements itself by growing its right shell to low intertidal or subtidal rocks (Fig. 3A).

Other bivalves that cement themselves to rocks are jingle shells (family Anomiidae). These bivalves can be confused for true oysters, but in fact do not grow their shells to rock surfaces. Instead, they are attached by a modified byssus. The byssus extends through a large hole (actually a modified byssal notch extending from the shell’s edge) in the left valve, which lies flat against a rock surface and is covered by the convex right valve. The byssus is calcified and cemented to rocks. The shell can be pulled tight against the rock by muscles attached to the byssus; these muscles have the functional role of the enlarged posterior adductor of oysters and scallops. *Pododesmus macrochisma* (*P. cepio* in much of the literature) can be locally common on the rocky intertidal shore of the Northeastern Pacific shore (Fig. 3B).

Convergent evolution has given rise to yet another oyster-like group of bivalves, the family Chamidae, in the subclass Heterodonta. These bivalves, called jewel box shells, differ greatly in anatomical detail from true oysters. For example, they are not monomyarian—they have two, albeit unequal, adductor muscles. However, they share the habit of cementing one valve to rock surfaces. Although chamid bivalves are mostly tropical or subtropical in geographic distribution, some species are found on temperate rocky shores. *Chama arcana* is common from Oregon to Baja California. Interestingly, different species in the Chamidae attach by different valves; *C. arcana* attaches by its left valve.

**Boring Bivalves**

Perhaps the most dramatically modified bivalves are those that bore into rock. Date mussels, such as those in the genera *Adula* and *Lithophaga*, use chemical secretions in mucus to dissolve calcareous substrata or mechanically abrade soft rocks (shale and sandstone) with their shell. In the later case, they attach byssal threads in forward and posterior positions, and alternately contract byssal retractor muscles to move the shell back and forth against the burrow wall. Date mussels are also reported from flint rock much harder than their shells, so the range of mechanisms for boring is not fully known. They can be quite common, yet are relatively unknown due to their inaccessible habitat. *Lithophaga* are also common in live or dead corals in tropical regions.

Bivalves in the family Pholadidae show elaborate morphological specialization for burrowing. These animals, called piddocks, have a sucker-like foot that extends through a large gape between the two valves and attaches to the bore hole. The anterior end of the shell bears filelike serrations on raised ribs. The shell is pushed against the end of the bore hole, rocked forward and back, and rotated to effect further excavation. Pholads have a long siphon, much exceeding shell length, that is used to reach the opening of their bore hole. The Wart-Necked Piddock (*Chaceia ovoidea*) has a siphon that reaches 1 m in length! Several species are common in the lower intertidal of the Northeast Pacific. These include *Zirfaea pilburyi*, *Netastoma rostrata*, *Parapholas californica*, *Penitella conradi*, and *P. penita*. While piddocks are rarely seen alive, their bore holes are frequently found in eroded rocks and are evidence of their
abundance. Pholads are evolved from ancestors that bored into compact sediments; modern examples of these include the common clam *Platydont cancellatus* (family Myidae), found in packed clay in lower intertidal of bay mouths and the protected outer coast of the Northeastern Pacific.

**Nestling Bivalves**

Another strategy to avoid wave shock on the rocky shore is to nestle in protected microhabitats, such as sand pockets under rocks or in biogenic structures such as mussel beds, empty barnacle tests, or algal holdfasts. A taxonomically diverse array of bivalves have adopted this lifestyle, often by evolving a small body size that fits these small spaces. *Lasaea* is a cosmopolitan genus of tiny (to 3.5 mm), nestling clams. They are small enough to fit in spaces within and between empty barnacles shells, and can achieve densities of more than 275,000/m². A tiny (to 4.5 mm) mytid, *Musculus pygmaeus*, is also abundant in high rocky intertidal algal turfs, with reported densities of 10,000/m² in California. Like many very tiny marine invertebrates, these bivalves brood their offspring, which do not disperse far. This may contribute to their extremely high local abundances. Another example from the U.S. west coast is *Kellia laperousii*, which is unusual among bivalves for its effective crawling on hard surfaces with its long foot. *Kellia* is common in mussel beds, kelp holdfasts, empty barnacle shells, and other protected spaces such as empty pholad holes. Although *Kellia* grows larger than the previous examples, to 25 mm, it too broods its offspring. File shells (family Limidae) improve the security of their nestling sites by making a nest from byssal threads on the undersides of rocks. Limids, such as *Limaria hempiilli* in California, can swim actively by clapping its valves together, as do true scallops. They have long, sticky tentacles of uncertain function on their mantle margin that are extended, medusa-like, from the gaping animal. These break away when the animal is disturbed.

Another place to find refuge from waves is the bodies of larger organisms. Larvae of *Mytilimeria nuttallii* (family Myidae) settle on the tunics of compound ascideans in the lower rocky intertidal of the Northeast Pacific shore. They initially attach with byssal threads, but become overgrown and internalized in the tunic of their host. As internal symbionts, their shells are quite thin and fragile.

**ECOLOGY OF ROCKY SHORE BIVALVES**

The most important bivalves in rocky intertidal communities are mussels (Mytilidae) and, to a lesser extent, oysters (Ostreidae), and these dominate the middle intertidal region of rocky shores around the world. Their vertical distribution in the intertidal zone is often attributed to the stresses of exposure at low tide, which can include heat, desiccation, and reduced supply of waterborne food. It is often noted that the absolute height of mussel beds is higher in areas of greater wave splash, supporting the idea that aerial exposure sets the upper edge of mussel beds. However, the notion of physical upper limits is not necessarily universal, because consumers or competitors may exert pressure from above, as has been shown for some seaweeds. Physical conditions are benign for marine organisms at their lower tidal limits, and it is thought that predation or competition may prevent downward growth. For example, experimental removal of sea star predators resulted in downward growth of mussel beds in Washington State. In southern California, cages that excluded lobsters allowed growth of mussels below the natural lower limit. Suites of predators, including crabs, gastropods, sea urchins, and sea stars control the lower edge of *Mytilus edulis* on American and European Atlantic shores.

Bivalves are the dominant species at middle intertidal levels on most wave-exposed temperate rocky shores. *Mytilus californianus* dominates shores of western North America, while *Mytilus edulis* does the same in the northeast of North America and the northwest of Europe. *Perna perna* forms dense beds in wave-exposed south and eastern South Africa, although limpets dominate relatively protected areas. In the colder waters of western South Africa, and in rocky areas further north, *Choromytilus meridionalis* and *Aulacomya atra* (often reported as *A. ater*) are abundant. *Brachidontes rostratus* forms beds in the middle intertidal zone in Tasmania and Victoria, Australia. *Perna canaliculatus* fills this niche in New Zealand. The mid-intertidal zone of temperate regions of western and eastern South America, including parts of Peru, Chile, Argentina, and Brazil, contain beds of mussels *Perumytilus purpuratus* and *Aulacomya atra*. *Choromytilus chorus* may be locally abundant in Chile. Mussels may sometimes form beds in warmer waters. *Brachidontes exustus*, a species complex, can be abundant on intertidal rocks throughout the tropical western Atlantic. Although oysters are generally less abundant on rocky shores than mussels, the oyster *Saccostea cucullata* is common on intertidal rocks throughout the Indo-West Pacific.

When mussels are able to form continuous beds, they can compete with and exclude other species that must attach to the rock surface. Without predators or agents of disturbance, such as severe storms or wave-tossed logs, mussels can monopolize space and suppress the diversity of primary occupants of the rock surface. Indeed,
multilayered mussel beds can contain enormous numbers of individuals: *Mytilus californianus* in Washington State contain between 439 and 11,098 individuals/m²; *Mytilus edulis* from the Bay of Fundy had 700–4,000 individuals/m²; subtidal beds of *M. trossulus* in the Baltic Sea achieved densities as high as 158,000 mussels/m²; and *M. galloprovincialis* in Italy reach 633–11,536 individuals/m². Despite this monopoly of primary rock space, mussel beds promote the diversity of secondary space occupiers. Barnacles, bryozoans, sea anemones, tube worms, algae, and many other organisms are able to live on mussel shells and so are not necessarily excluded from mussel beds. Furthermore, the internal matrix of multilayered mussel beds is habitable space for organisms that would otherwise be swept away by waves, such as sea cucumbers, free-crawling polychaete worms, and isopods. These internal spaces can also become filled with sediments, providing essential habitat for infaunal organisms. Consequently, mussel beds are quite rich in numbers of species: beds of *Mytilus californianus* contain at least 303 species, 69 species were found in *Mytilus galloprovincialis* beds in Japan, *Modiolus modiolus* and *Mytilus edulis* beds in Northern Ireland harbored 90 species and 34 species, respectively. Oyster beds can be similarly diverse: *Crassostrea virginica* reefs in South and North Carolina contained between 37 and 303 species in different regions of estuaries. These numbers vary greatly between studies because of different sampling methods and taxonomic precision; however, the general idea that mussel beds are rich in species is clear.

Bivalves are important not only as living space, but also as a trophic link between planktonic primary production and higher trophic levels. Bivalves are filter feeders that can remove particles as small as 2–3 μm at 80–100% efficiency. Particles as small as 1 μm are taken with less efficiency; thus a wide range of food sources, including bacteria, phytoplankton, and detritus are available. Most studies show that bivalves grow best on diets of phytoplankton. The amount of phytoplankton consumed by bivalves is enormous: bivalve populations have been estimated to require less time to filter 100% of the water in many bays worldwide than the water is resident in those systems. Bivalves on the rocky shore have no less filtering ability per capita; one estimate is 6–12 m³ of seawater cleared of phytoplankton/m² of mussel bed per hour. Coastal primary production, especially in areas of strong upwelling, is efficiently transferred into intertidal communities by filter-feeding bivalves, which in turn are consumed by gastropods, sea stars, crabs, lobsters, fishes, otters, and birds.

Bivalves are frequent biological invaders of marine waters. Although less impacted than bays and estuaries, the rocky shore is no exception. *Mytilus galloprovincialis* has invaded the rocky coast of South Africa where it competes with native *Perna perna* and limpets. *Perna perna*, in turn, has invaded the Gulf of Mexico and Caribbean shores, and its congener *P. viridis*, an Indo-Pacific species, is now found in both the Gulf of Mexico and Australia. Because of their propensity to form beds, all mussels should be considered potential pests if introduced outside their native areas.

**CLASSIFICATION**

The classification of bivalves at higher levels has been based primarily on shell or gill characteristics, and the two systems have not been entirely compatible. Paleontologists have preferred to use shell characters, especially details of the hinge, as these are preserved in fossils. Anatomists have noted grades of gill architecture and proposed classification schemes based on those. Inclusion of more characters, including molecular data, has clarified the picture, and the most often used modern classification system recognizes the protobranch gill architecture as phylogenetically meaningful, whereas the eulamellibranch gill has evolved multiple times and reflects convergent evolution. The adaptations for life on the rocky shore discussed here are found in three of five subclasses of bivalves. An important conclusion of this chapter is that bivalves have evolved different solutions for life in the high wave energy of the rocky shores, and that each solution has evolved multiply and independently in these major groups.

Current schemes divide the Bivalvia into five subclasses: Protobranchia, Paleoherodonta, Heterodonta, Pteriomorphia, and Anomalodesmata. The subclass Protobranchia is the only one that is based primarily on gill architecture. Protobranchs are considered the most primitive of bivalves. These bivalves possess a gill that most resembles a generalized bipectinate ctenidium, as described earlier. Protobranchs are deposit feeders, using oral palp proboscides to collect food from sediments, or harbor chemautotrophic bacterial symbionts that provide nutrition. Protobranchs are mostly found in the soft and often deep sea floor and not of importance on rocky shores. The Paleoherodonta is comprised primarily of freshwater bivalves in the order Unionidae and are defined by their shells with interior nacre (mother-of-pearl) and details of their hinges.

Members of the subclass Heterodonta are very familiar to most students of marine life and to seafood eaters, and are the most specious of all classes of Bivalvia. This group includes...
the families that are known as clams and cockles. A unifying feature of heterodonts is interlocking teeth near or adjacent to the hinge. These bivalves usually have anterior and posterior adductor muscles, a eulamellibranch ctenidium, and siphons that direct water into and out of the mantle cavity. These siphons may be fused together and quite long, allowing some of these clams to burrow quite deeply in soft sediments and still maintain contact with the overlying water column. The mantle edges are often fused across the shell gape to prevent entry of sediment into the mantle cavity, with a gap only for the foot. The foot is typically muscular and wedge shaped, and used for burrowing. Heterodont bivalves discussed in this article include *Chama*, *Dreissenia*, *Kellia*, *Lataea*, and the family Pholadidae.

The subclass Anomalodesmata is a collection of ecologically and morphologically diverse bivalves that occur in most marine habitats. Ecological specialization has driven considerable morphological divergence among families. Typical features include a nacreous shell, a toothless hinge (or secondary teeth only), and a eulamellibranch ctenidium. As in heterodonts, the mantle is usually fused along the shell edge, leaving only siphons and a gap for the foot as openings into the mantle cavity. A unique feature in this group is a fourth opening, located near the siphons. Another unique feature is a special gland (arenophilic radial mantle gland) that glues sand grains to the shell. Species may live in sediments, nesting in algal holdfasts, mussel beds, and in fouling communities, or as commensals with compound ascideans or sponges. This group also includes the only carnivorous bivalves. These employ a gill that is greatly modified into a muscular pumping septum to draw small prey items through the inhalant siphon. Such gill architecture is termed septibranch. Septibranch bivalves in the Northeastern Pacific are found in deep soft sediments. Bivalves in this subclass that are mentioned in this chapter are *Entodesma*, *Lyonia*, and *Mytilimeria*.

Bivalves in the subclass Pteriomorpha are familiar as mussels, scallops, and oysters, among others. They have adapted to an epibenthic lifestyle through the evolution of various mechanisms to attach to hard surfaces and so are the most important bivalves on rocky shores. The shells of pteriomorphs are quite variable, some with similar left and right valves and others with distinctly different valves. In the latter, one valve is often flattened and lies close to the surface of the hard substratum. Pteriomorphs possess a byssal gland as larvae, juveniles, and often as adults. Most attach themselves to surfaces by byssal threads; some follow this by cementation. Pteriomorphs are heteromyarian or monomyarian. In the former case, they have two unequal adductor muscles with the posterior muscle the larger, as in mussels. In the later condition, found in oysters and scallops, only the posterior muscle is retained and is located centrally between the valves. The gills are used for filter feeding and are filibranch or eulamellibranch in structure. Pteriomorphs generally do not burrow, and the foot, which is small and finger-like, is used by adults for the placement of byssal threads. Fouling of the mantle cavity by sediments is a lesser problem for epibenthic pteriomorphs than for infaunal heterodonts, and the mantle edges are not fused. Similarly, living at the substratum-seawater interface, siphons are unnecessary and these are not seen. Water flow can, however, be guided by pressing the mantle edge together on the posterior edge. Pteriomorphs mentioned here are *Acanthocardia*, *Aulacomya*, *Brachidontes*, *Choromytilus*, *Crassodermia*, *Crassostrea*, *Lima*, *Lithophaga*, *Mytilus*, *Modiolus*, *Musculus*, *Ostrea*, *Perna*, *Perumytilus*, *Pododesmus*, and *Saccostrea*.

**SEE ALSO THE FOLLOWING ARTICLES**

Adhesion / Molluscs / Stone Borers

**FURTHER READING**


**BLENNIES**

**ISABELLE M. CÔTÉ**

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True, or combtooth, blennies belong to a large fish family (the Blenniidae) comprising 350 species found in temperate, subtropical, and tropical shallow marine waters
around the world. Blennies exhibit remarkable variation in reproductive behavior, making them ideal models for behavioral studies. They are also ecologically important because most species are herbivorous and many are very abundant on rocky shores.

**APPEARANCE**

All blennies are relatively small (<15 cm), although a few species can reach more than 50 cm in length. They have scaleless, elongated bodies with large blunt heads (Fig. 1), often adorned with cirri, which can be large and extensively branched, particularly in males. The name “combtooth” is derived from the tightly packed, comb-like row of blunt teeth they possess on each jaw. Blennies are highly variable in color, with many species exhibiting spots, stripes, or bands. Some species change colors during breeding or during aggressive interactions. Cryptic coloration is widespread.

![Figure 1](image1.png)

**FIGURE 1** Two rock-pool blennies, *Parablennius parvicornis*, resting on the bottom of a tidepool at Île de Gorée, Senegal. Note the continuous dorsal fin, typical of the blenny family, and the small cirri above the eyes. Photograph © Dr. Peter Wirtz.

**REPRODUCTIVE BEHAVIOR**

Blenny reproduction occurs either seasonally, with a spring onset, or year-round with peaks of spawning around full moon. Males compete for access to small cavities in the substratum, empty shells, or barnacles, which they clean in preparation for nesting. As a result of this intense competition, male blennies are usually larger than females and more brightly colored during the breeding period. Males attract females to spawn in their nests with a series of characteristic head bobbing displays. Females lay a single layer of adhesive eggs on the nest wall and leave males to provide sole care of the eggs until hatching. Males may care simultaneously for eggs at various stages of development, which have been deposited by different females on different days.

In several species, alternative male mating tactics exist. Some males do not defend nests and guard eggs but mimic the females’ morphology and behavior to approach nests, dart in, and parasitize fertilizations from nest-guarding males. This sneaky behavior is usually restricted to small males, who then adopt an egg-guarding strategy when larger.

Female blennies have fairly predictable mate preferences. Larger is usually better, although sometimes males with more developed cirri or nests that already have eggs are chosen. Larger males usually provide better care to the eggs in the nest, by fanning them assiduously with their pectoral fins and defending them from predators.

**ECOLOGICAL IMPORTANCE**

Most blennies are herbivores. Because of their sometimes phenomenal abundance, they exert strong grazing pressure, which is important in determining algal abundance and species diversity. Experimental exclusion of blennies from some rocky shore areas has been shown to result in drastically altered algal communities, which shifted from predominantly brown and red crustose macroalgae to green foliose species. Carnivorous blennies also have a large impact on algae. Blennies that rely on small invertebrates play a key role in controlling the abundance of herbivorous crustaceans, thus indirectly increasing the biomass and diversity of the algae upon which these crustaceans feed. Blennies therefore find themselves at the heart of many trophic cascades on rocky shores.

**LIFE ABOVE THE WATER**

Many species of blennies that live in the intertidal zone have the ability to withstand short periods of emersion. This ability is taken to extremes by a few species that have effectively become amphibious, living at the very top of rocky shores, where they are exposed to air for long periods. An amphibious lifestyle has required several adaptations, including providing internal support to the gills to prevent their collapse out of water, a flattened cornea to improve vision in air, various biochemical and physiological changes to deal with desiccation and ammonia excretion, and a phenomenal leaping ability to permit escape from aerial predators. For example, the small pearl blenny *Entomacrodus nigricans* (<10 cm) can jump more than 1 m in a single leap when threatened. This is approximately twice as far, relative to body length, as the currently held men’s long jump world record!

**SEE ALSO THE FOLLOWING ARTICLES**

Camouflage / Desiccation Stress / Herbivory / Sculpins / Sex Allocation and Sexual Selection
BODY SHAPE

STEVEN VOGEL
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The shapes of the inhabitants of tidepools and rocky shores must reflect the mechanical world in which they live—the hydrodynamic forces to which they may be subjected, the structural properties of their materials, and the arrangements with which they avoid dislodgement. But we commonly see them in tidepools at near low tide and under nearly calm conditions—mechanically the most benign and forgiving possible combination. It is as if we were listening to the instruments of an orchestra during intermission, not during the concert itself. To envision the mechanical challenges facing an organism, one must imagine a radically different situation. Intertidal areas of rocky, high-energy coastlines experience flows of rapidly changing speeds and directions together with the surge, splash, and plunge of breaking waves. Mechanically, then, a tidepool represents a particularly accessible bit of rocky intertidal, one stranded higher than the rest of the ocean when the tide recedes.

THE FORCES THAT MATTER

Drag

One first thinks of drag, a force on a body in the direction of the local flow that varies with the speed of flow, as in Fig. 1A. Older sources considered only drag, commonly with fanciful explanations of the relationship between form and drag. Applied to drag on rocky shores, our technological experience turns out to be less helpful than might be expected. In part, submarines and airplanes face directionally consistent flows and operate well away from substrata. Furthermore, both approach perfect rigidity, so shape and the forces of flow interact far less than they do in organisms. An airplane at the airport differs in shape only trivially from one going at top speed, while the shape of a macroalga in a storm surge will bear little resemblance to its shape in still water.

Acceleration reaction

Organisms face two other forces of comparable importance. The first, commonly termed the “acceleration reaction” (Fig. 1B), is a consequence not of the speed of flow per se but of the change of speed—the acceleration (and deceleration) of local flows. Accelerating or decelerating a body takes a force proportional to its mass. When a mass of fluid suddenly encounters and accelerates around a body, the body feels the effect as a force, one whose direction is that of the acceleration. One should note that whereas drag and acceleration reactions act concertedly for accelerating motion (the main present concern), for decelerating water (as when a swimming animal slows) they act in opposite directions. Drag typically depends (other things being equal) on the area of an object facing the flow; the acceleration reaction depends on the volume of the object. If both drag and attachment strength vary with area, then a large body is no worse off than a small one. But, given a volume-dependent acceleration reaction, the larger the body, the worse will be the force of flow relative to its attachment strength. So low volume has an advantage for organisms subject to severe flow surges beyond the advantage of low exposed surface for organisms in rapid but steady flows.

Lift

Yet another force is lift (Fig. 1C), defined as a force that acts perpendicularly to the direction of flow. Lift may be as hazardous for an organism clinging to a rock as it is for an automobile speeding down a highway. A low, rounded mound, something with lots of attachment area and low drag, turns out to be an especially effective lift producer. Shape changes that reduce lift often increase drag, which probably explains why the forms of some intertidal organisms (limpets in particular) either have more drag than expected or experience unexpectedly variable drag, individual to individual.

Impact Pressure

Something, whether liquid or solid, dropped on a body will make an impact. Breaking waves drop water on organisms, but the forces of impact rarely rise to significance relative
to the other forces at play, in part because compression of entrained air mitigates the suddenness of the event. But impacts of solids, mainly small rocks (“cobble”) and logs, are often significant and can even lead to temporarily or permanently bare patches.

As a result of the variability of flow magnitude and direction and of the diversity of operative forces, the classic drag-reducing streamlined form, an axisymmetric body rounded upstream and pointed downstream, is rare or absent among the sessile inhabitants of tidepools.

THE WAY THE FORCES IMPINGE

One might expect that encrusting organisms, which protrude only negligibly from their substrata (rocks or other organisms), would avoid flow forces entirely. In fact, they still experience shear, pulling them downstream, as in Fig. 2A. But even in very rapid flows and severe surges, shear forces are minimal; with large attachment areas, the resulting stresses (stress = force/area) will almost always be trivial.

Pull on a rope and you impose a tensile load. Since the line of action of the force corresponds to the long axis of the object, it is both the easiest to envision and to resist. Macroalgae with long fronds may be subject to purely tensile loading; for organisms of most other shapes loading regimes are more complex and challenging. Neither the force parallel to flow (drag plus the acceleration reaction) nor that normal to flow (lift) will impinge directly; rather, these forces will produce turning moments about the attachment. These moments represent the product of the force and the perpendicular distance from its line of action to a rotation point, as in Fig. 2B. One sees the result of such a turning moment when a rearward push on the backrest of a chair makes its front legs rise.

Erect or protruding organisms thus face several problems beyond minimizing the forces of flow and resisting tensile loads. Since most flow goes around rather than over it, a narrow, erect cylinder feels little lift. But making a cylinder taller increases the area facing the flow, the volume exposed to flow, and the length of the moment arm across which drag and acceleration reaction act. The turning moment of its drag will go up with the square of height, that due to the acceleration reaction with the cube of height. Few organisms of the rocky shore take the form of erect cylinders. Sea anemones, which do have that shape, avoid rapid flows by deflating when necessary down to a small fraction of both their extended heights and their volumes without changing attachment area. Cones do better than cylinders for the same volume and surface because the forces act on them with lower average moment arms; fairly low cones do better than high cones relative to both volume and surface. Thus tidepools contain nothing quite like branching corals except for tiny coralline algae and the like, but they host a great diversity of low, conical limpets, keyhole limpets, chitons, and such.

A purely tensile load imposes a nearly uniform stress on an attachment surface. By contrast, loads that produce turning moments create severe stress gradients. In the foregoing example of pushing the backrest of a chair rearward, its front legs rose while its back legs pressed down harder. If the chair were glued down, the push would produce upward tension in the front and increased downward compression in the back—a stress gradient from front to back. Similarly, an organism loaded in the direction of flow will feel an easily managed compressive stress at and near the downstream edge, but a tensile stress around the upstream edge. Lift, pulling outward from the substratum, will add to that tensile stress, its effect dependent on the location of the center of lift relative to the geometric center of the organism. Any glue or grapple will more likely fail at the upstream edge, where tension is maximal—the organism will face so-called peel failure, as in Fig. 3A.

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What shapes can best deal with peel failure? A tapering margin of soft material peels with useful difficulty. The softness out near the edge converts much of the upward lift at the upstream edge to sideways sliding or shear, making a tensile force into a more easily withstood shearing force. The edges of the soft feet of gastropod molluscs, whether snails, limpets, or sea slugs, almost always taper outward. The feet of molluscs with shells may extend well beyond the shells’ margins, both improving the conversion to shear and increasing contact area.

An additional device for minimizing the risk of peeling consists of using a tapered, flexible connection, a soft stalk, between an attachment pad and the rest of the organism, as in Fig. 3B. That ensures that almost any force on the organism will be taken by the pad in a more uniformly distributed combination of tension and shear, with little of the asymmetry that leads to peeling. Macro-algal holdfasts typically use such a pad-plus-joint, as do some sponges. Yet another approach involves multiple, tiny attachments, each flexibly connected to the rest of the organism (Fig. 3C). A large-area attachment will more likely peel than a small one; a very small one will simply be pulled straight or obliquely outward with more uniform stress over its contacting surface. A mussel attaching to a rock by numerous byssus threads (its “beard”) uses the device. Starfish, sea urchins, and some other echinoderms do likewise with their tube feet, combining motility with good attachment to quite irregular substrata.

**AVOIDING OTHER FORCE CONCENTRATIONS**

Materials ordinarily fail at some level of stress, not of force per se. Stress, again, is force divided by area; more specifically, tensile stress is force divided by cross-sectional area. Thus, failure most often occurs at a narrowed region, say, of a shoe lace—same force but less area. A long algal frond, for instance, should be at greater risk where narrowed by the bite of some grazing animal. In fact, the risk may be far greater than one would expect from the relative reduction of cross section caused by the grazer. Stress may be especially high right at the base of an indentation, where force gets locally concentrated. A strip of aluminum foil, pulled lengthwise, will fail at much less force if it has a small crosswise nick in one edge. Even a small reduction in overall cross section can dramatically reduce effective tensile strength. In other words, cracks propagate.

How might either the occurrence or the danger of high local stress be avoided? One device widely used among the macroalgae consists of extending the length of edge beyond what would be needed for a planar structure, making what is termed an undulate margin. Such an edge need withstand almost none of the tensile stress on the rest of the surface, with stress increasing with distance inward toward the long axis. Pressed and dried algal laminae almost always have folds near their edges because they are nontrivially three-dimensional, even if nowhere very thick. In addition or alternatively, algal laminae make use of material of low tensile stiffness—that is, material tolerant of stretching. Such stretching under load effectively reduces stress at the tips of sharp-ended indentations by rounding those sharp tips. Just this behavior underlies the greater difficulty of tearing a nicked piece of Saran Wrap compared with aluminum foil. An alternative to reducing the stress at the base of a nick is to mitigate its tendency to tear further. Grasses, in particular, do this with strong lengthwise fibers; one cannot easily tear a blade of grass transversely. But intertidal organisms seem not to make extensive use of this latter device.

Temporal as well as spatial force concentrations present hazards in the rocky intertidal. Consider the acceleration of a loosely tethered mass when hit by a wave. Its momentum (mass times velocity) will be converted to force on tether and attachments when the tether goes taut; how much force varies inversely with the suddenness with which it stops. Three devices among intertidal organisms mitigate such forces. First, concentrated masses on long tethers are rare. Second, tethers are made of extensible (low-stiffness) material, so stops are less sudden—macroalgae commonly do this. And third, tethers can be kept taut at all times—as are the byssus threads of mussels, where a specific muscle prevents slack.

**FORCES, MATERIALS, FUNCTIONS, AND FORMS**

Linking body form and environmental mechanics looks more complex than it did a decade or so ago. Flexibility—avoiding stiff, massy materials—provides no automatic benefit. Macroalgae, like the leaves on a tree, may curl and cluster in flow and thereby reduce their drag. But ordinary flags in air or water suffer several times the drag of rigid plates, so one cannot simply attribute their performance to flexibility. Furthermore, the mix of solidity and fluidity characteristic of almost all soft biological materials may make what appears soft to the touch to be anything but soft when suddenly loaded by a surge of water. The variety of forms found in tidepools reflects both the complexity of the challenges and the diversity of tactics with which they can be met. An anemone stands erect in a pool but deflates into a small, limpet-like shape when waveswept. Macroalgae appear quite large, but their...
Fungi are primarily terrestrial organisms that developed in close association with higher plants. Although only few fungal species are commonly found in saline environments, most Ascomycetes and Zygomycetes (as well as the ascomycetous and basidiomycetous yeasts) easily tolerate the salt concentrations of the marine environment and are able to survive and to grow in seawater. Most of the so-called marine fungi in fact belong to the terrestrial soil microflora and are only secondary invaders of the marine environment. Although numerous fungal spores are distributed in marine water, colonies are formed only on solid surfaces. This means that fungi can be isolated from the water column as spores, but the adults are benthic organisms associated with marine organisms such as corals or bryozoans and also with mineral substrata.

BORING FUNGI IN INTERTIDAL ROCKS

Rock surfaces in extreme environments, such as high salinities, high temperatures, and intense UV radiation, are generally inhabited by black meristematic fungi, cyanobacteria, and lichens. Meristematic fungi are known from rock surfaces in arid and semiarid environments, from hot and cold deserts, and from rocky shores. The morphology of those fungi resembles that of colonies of boring cyanobacteria, and until 1981 they were erroneously identified as such. The meristematic fungi form darkly pigmented cell clusters with a diameter of up to 500 µm both on the surface and inside the rock. The surface colonies develop stolons and extremely thin hyphae, which penetrate the rock, leading the fungus to pores and cracks where new colonies are developed. As a result of the high turgor pressure of the cells and their extremely rigid cell walls, fungi growing in the rock push on the rock’s structure, causing crystals to lose their adhesion to one another. This process finally leads to sloughing of material from the rock’s surface. The depth of penetration into the rock can be up to 5 mm. Thus, boring fungi on rocky shores play a significant role in the weathering of the rocks. This is especially true for calcitic rocks (e.g., limestone, marble); boring fungi are found less often on gneiss and granite. From the analysis of field samples taken from rocky shores there is strong evidence that both mechanical action and acid attack play a role in rock penetration (Fig. 1A, B). Although meristematic fungi do not excrete organic acid under laboratory conditions, scanning electron microscopy has clearly shown the etching activity of fungal colonies on single calcite crystals (Fig. 1C).

TAXONOMY

The taxonomy of meristematic fungi is complex. Because the morphology, both on the rock and in culture, is similar for all species, identification is possible on the basis of molecular data. Phylogenetic analysis based on
the sequences of 18S rDNA, Internal Transcribed Spacers I and II, and 5.8S rDNA showed that the meristematic phenotype occurs in several orders of the Ascomycetes: Dothideales, Pleosporales, and Chaetothyriales. Many new species of meristematic fungi have been described in recent years; in saline environments the most important are *Hortaea werneckii*, *Coniosporium perforans*, and *Trimmatostroma salinum*.

The meristematic morphology found on intertidal rocks is interpreted as an ecotype that combines several adaptations to extreme environmental conditions. The sheltering effect of cell clusters (which have a small surface-area-to-volume ratio) is enhanced by the protective action of melanin, encrusting the cell walls. Each vegetative cell can provide propagation when the environment is benign and can also lie dormant when the environment is severe. In this way the production of spores is economized. With increasing osmotic stress, fungi induce the synthesis of high intracellular levels of glycerol and other compatible solutes. High trehalose levels, which protect enzymes under matrix and osmotic stress, seem to be present all the time. Energy consumption for synthesis of sugar alcohols and trehalose is high and occurs at the cost of growth rate. Meristematic fungi grow slowly, and even under laboratory conditions colonies of some species do not exceed 5 mm in diameter within four weeks.

**SEE ALSO THE FOLLOWING ARTICLES**

Algal Crusts and Lichens / Heat Stress / Salinity Stress / Stone Borers / Ultraviolet Stress

**FURTHER READING**


**BOUNDARY LAYERS**

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A boundary layer is the transitional region from freely flowing water above a solid surface (e.g., the seabed) down to the stagnant water at the surface itself. The boundary layer is the result of friction exerted by the solid surface on the flowing water. The gradual increase in flow velocity from the bed to the free-flowing water above (the velocity gradient) determines the force the water exerts on the bottom, and on plants and animals living on the bottom. Strong velocity gradients require a very firm attachment to the bed, if the organism is to stay put. The velocity gradient also determines how quickly particles (e.g., food particles) are transported from the water column to the bed.

**VISCUS DRAG**

Viscosity is a measure of a fluid’s ability to resist deformation. In other words, it describes the “stickiness” of a fluid. Moving a teaspoon around in a cup of tea easily makes the tea swirl. Try the same in a cup of honey and one will find that it takes more effort to move both the teaspoon and the liquid because honey has a much higher viscosity than water. Although it is easier to stir water than it is to stir honey, water molecules nonetheless have a measurable tendency to resist movement relative to each other. This tendency is the basis for the formation of a boundary layer. Viscosity is not only a property of liquids. Gasses,
such as air, also resist deformation, although gas molecules are much less tightly bound to each other than are water molecules. At a temperature of 20 °C, seawater has a viscosity of \(1.07 \times 10^{-3}\) Pa s (pascal seconds), but air at the same temperature has a viscosity of only \(18.08 \times 10^{-6}\) Pa s.

Boundary layers occur on any solid surface in contact with a moving fluid. The fluid can be honey, tea, seawater or, as explained above, even air. The surface can be the inside of your teacup, the sea floor, a swimming fish, or the wing of an aircraft. For the sake of simplicity, in this article we deal with the boundary layer that exists between seawater and the rocky sea bottom; however, one should realize that the same principles apply to many different situations. The water immediately at the seabed has no motion relative to the surface of the bed. This is called the no-slip condition, and it is also an immediate consequence of the viscosity of seawater. As well as sticking to each other, the fluid molecules stick to the rocks on the bottom. Because it costs energy to move “parcels” of water relative to each other, water is slowed down near the bed. This is called viscous drag.

Figures 1A and B illustrate two velocity profiles of water flowing over a smooth bottom. Theoretically, the effect of viscous drag of the bed on the water column extends to infinity. However, at some distance away from the bed (a distance known as the boundary layer thickness, \(\delta\)), the impact becomes negligible and the flow velocity here is defined as the free-stream velocity. Generally, the boundary layer thickness is defined as the height above the bed where the velocity reaches 99% of the free-stream velocity.

**Velocity Gradients and Shear Stress**

For plants and animals attached to rocks, the velocity gradient, rather than the free-stream velocity, is often more important. The shear, that is, the velocity difference between layers of water, is what determines the force the water exerts on the bed and on the attached organisms. This shear stress is expressed in units of force per unit area, that is, N m\(^{-2}\), or pascals (Pa). A very thick boundary layer with a very gradual velocity increase is much less likely to erode sediment or dislodge an object than is a thin boundary layer with a steep velocity increase. Consider the examples in Figs. 1A and B; both show a boundary layer over a smooth bed with a free-stream velocity of 20 cm s\(^{-1}\), but one has a boundary layer thickness (\(\delta\)) of 10 cm and the other has a thickness of 25 cm. The thinner boundary layer exerts a stress on the bed of 1.2 Pa, although for the thicker boundary layer the stress is about half as large (0.6 Pa). For larvae of bottom-dwelling animals that want to settle on
the bed, this difference in stress can make the difference between being able to hold on to the bottom surface or being washed away.

A boundary layer does not appear instantaneously on a surface; it needs time to develop. The longer water flows with a particular speed over a surface, the thicker the boundary layer becomes. In deep, steadily flowing water, the boundary layer may have a thickness of several meters. In very dynamic environments such as rocky shores and tidepools, flow speed and direction constantly change as a result of waves and changing tides. In such environments, boundary layers are often thin and not fully developed. In shallow, wave-exposed sites the thickness of the boundary layer may be less than a centimeter.

ROUGHNESS AND FORM DRAG

The seabed is seldom smooth. Certainly, on rocky shores objects such as the rocks themselves, plants, and animals create a very complex, rough surface. This increased roughness increases the total drag on the water column and therefore influences the boundary layer. First, increased roughness increases the total surface area in contact with water, and thus increases viscous drag. Second, larger objects sticking up into the boundary layer (generally objects larger than about half a centimeter or so) create turbulent wakes in their lee, and the resulting eddies and vortices are mixed into the flow. The effect of this generated turbulence is an additional type of drag on the flow: form drag. The larger the area an object presents to flow and the higher the flow speed, the larger the form drag. In fact, form drag scales with the square of the flow velocity. A small increase in flow speed can therefore result in a large increase in form drag. Because in a boundary layer, flow speed increases with distance from the bottom and because drag increases with flow speed, reducing one’s size is a means to reduce the drag one incurs. For example, many aquatic plants are very flexible. In still water they stand up straight, but in flowing water they bend with the flow (e.g., see Fig. 2). The resulting decrease in area presented to flow means that for these algae an increase in flow velocity may not involve a too drastic increase in drag.

The wake behind a single object attached to a rock may interact with objects standing downstream. If more than roughly one-twelfth of a surface is covered with objects (say, a rock densely covered in snails), eddies from the wakes cannot readily penetrate the space between the snails (Fig. 3). In between the snails the water is nearly standing still, while the boundary
layer forms above the snails. This phenomenon is called skimming flow. Sheltering in the interstices of tightly packed objects is thus another means of avoiding drag. In a turbulent, wave-exposed environment, a submerged tidepool can also provide protection against the full force of flow.

In water flowing slowly over a flat, smooth surface the flow resembles the profiles from Fig. 1: neatly organized layers of increasing velocity, without any crossing streamlines and with little exchange between the layers. This type of flow is called laminar flow. Fast flowing water over rough objects, as well as the dynamic flow of breaking waves, disturbs this neat pattern, causing the type of turbulence mentioned previously. Boundary layers still exist in turbulent flow, but they have different characteristics. At any instant, flow speed may vary in a random fashion near the seabed, but the average flow speed is lower near the bed than higher up in the water column. Turbulent boundary layers tend to be much thinner than laminar boundary layers. Because in turbulent flow water movement is not limited to horizontal motion, turbulence causes increased drag and mixing. As a result, turbulence in a boundary layer promotes exchange of water between animals and plants on the seabed and water in the main flow.

MARINE LIFE IN THE BOUNDARY LAYER

Rocky shores in general, and tidepools in particular, often support abundant life with an amazing variety of forms. The rapid flow in the turbulent boundary layers characteristic of this habitat are an important supplier of food, oxygen, and other necessities of life. Because of this flow, sessile creatures can simply sit and wait for food to come to them. Many creatures are very well adapted to withstand extremely large shear forces, without getting dislodged from their surface. For larval stages of bottom dwellers settlement in such a high flow environment does pose specific problems. Many of the bottom dwellers are filter feeders, animals that filter the water flowing past them. Flow speed is obviously important for the rate at which this food is delivered, and turbulent motion enhances food supply. Filter feeders such as mussels often occur in densities of thousands of individuals per square meter (e.g., Fig. 4). In calm conditions, the upstream individuals can filter so much water that the boundary layer becomes depleted and downstream mussels get less food. As noted previously, turbulence enhances the exchange of water and food particles between the different water layers. The roughness of the mussels, and even the effects of their own feeding currents, promote turbulence and increase food supply. In general, boundary layers on wave-swept shores are thin enough not to pose a barrier to the delivery of food and the removal of wastes, but in sheltered estuaries this can be a serious limit to growth of organisms.

In principle, every organism living in flowing water interacts with the flow and changes it. Some species have such a profound effect on the structure of the boundary layer that they ultimately affect the whole physical regime near the bed. They can influence deposition and erosion of sediment, and can provide shelter from the flow for other plants or animals. Organisms that cause such a drastic change in the physical conditions of an ecosystem are called ecosystem engineers. Not only humans and beavers are capable of changing water currents. This type of engineering happens on many different levels and at different temporal and spatial scales.

SEE ALSO THE FOLLOWING ARTICLES

Hydrodynamic Forces / Larval Settlement, Mechanics of / Seawater / Size and Scaling / Turbulence

FURTHER READING

Brachiopods are a phylum of marine invertebrates that are bivalved, sessile, and use a ciliated, tentacled structure (called a lophophore) for feeding. Brachiopods are not major components of tidepool or rocky intertidal ecosystems, nor is there evidence that they have been a contributor to these environments in the geologic past. Nevertheless, brachiopods can be found in rocky intertidal environments, and they may occasionally be found inhabiting tidepools.

**BRACHIPOD NATURAL HISTORY**

Most brachiopods attach to a hard substrate using a fleshy footlike pedicle or cement themselves directly. Brachiopod shells are either hinged (articulated) or unhinged (inarticulated); inarticulated brachiopod species have either a phosphatic or calcitic shell, whereas articulated brachiopods possess exclusively calcitic shells. Brachiopods are found from the intertidal to several thousand meters deep and in all of the world’s oceans. It would seem that the aforementioned features would make brachiopods well suited to life in tidepools, but there are several reasons why they are not commonly found there.

First, compared to other marine macroinvertebrates such as molluscs, echinoderms, and cnidarians, little is known of brachiopods’ biology, either because they are inaccessible, difficult to keep alive in the lab, or are unrecognized by the nonspecialist. This may lead them to be underreported in literature reports of tidepool communities. Additionally, many brachiopodologists are paleontologists, as brachiopods are among the most common fossils of the Paleozoic Era, and the majority of brachiopod genera are extinct. Further, rocky intertidal environments are extremely rare in the fossil record, because they tend to be erosional systems rather than depositional.

Second, brachiopods of the rocky intertidal tend to be cryptic, found under boulders and large, immobile cobbles or in deep crevices. This is related to the tendency of brachiopod larvae to settle in low light areas; hence many shallow water brachiopods are found in less accessible areas such as marine caves. This impedes direct observation of their behavior and also leads to brachiopods’ being overlooked in the field.

Brachiopods may also be excluded from many rocky intertidal environments because they are likely incapable of surviving the large changes in temperature and salinity inherent to this ecological setting. Metabolism is positively correlated with temperature in marine invertebrates; brachiopods, for which there are data, are incapable of surviving short-term rises in temperature of more than 4–5 °C, although some brachiopods (*Lingula*) are found in waters with greater annual temperature variation (>20 °C). This may also contribute to shallow water brachiopods being more cryptic than their deeper water counterparts.

**INTERTIDAL BRACHIPODS**

There are two groups of brachiopods that can be found relatively commonly in the intertidal: discinids, a group of inarticulated brachiopods with a limpet-like appearance because of their conical dorsal valve, and terebratulides, which can be found intertidally in the Pacific Northwest of North America.

**Discinidae**

Discinids are inarticulated brachiopods with black, phosphatic shells that attach to hard substrates, leaving only their conical dorsal valve visible (Fig. 1). They range in size from a few millimeters to a few centimeters. Similar
to other brachiopods, they usually live in clusters, so their
distribution on a large scale tends to be patchy. Although
brachiopods have been reported to live for a year with-
out a food source, discinids tend to be found in areas
with high nutrient availability, such as the tropical and
subtropical Eastern Pacific. They may be found on the
bottom of boulders, encrusting the substrate along with
serpulids, bivalves, and bryozoans. Discinids may in turn
be encrusted as well. As fossils, they can be found either
encrusting a hard substrate or as free valves.

Terebratulida
Terebratulides are the dominant modern brachiopod group
and are easily the most recognizable and best-known
extant brachiopod group. They are found in virtually every
marine environment, but are most common in the cooler,
nutrient-rich waters of mid to high latitudes. Most reports
of terebratulides inhabiting the intertidal refer to the Pacific
Northwest, but they should be found elsewhere in similar
environments. The most common intertidal terebratulide
in the United States and Canada is *Terebratula transversa*,
which is very common from Puget Sound and further
north. *Terebratula* is morphologically quite plastic, in part
because of the tight spaces in which it lives. Commonly,
they are pink, more broad than long, and have longitudi-
nal ribs. They attach with their pedicle, which allows
them to alter their orientation, depending on flow charac-
teristics. They live approximately 10–15 years, and little is
known of their reproductive behavior. Typically, terebratu-
lides are gregarious, so their spatial distribution is patchy.
They are commonly attached to one another and, in turn,
encrusted by bryozoans and annelids. Terebratulide preda-
tors include drilling gastropods, decapod crustaceans,
and indiscriminate browsers such as regular echinoids and
asteroids. It is not unusual to encounter *Terebratula* whose
shells exhibit signs of repaired damage.

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BRITTLE STARS

Sea stars and sea urchins are distinctive, easily recognized,
and frequently encountered members of tidepool and rocky
shore communities. Just as distinctive and easily recognized,
brittle stars are the largest and most diverse of the major
groups of echinoderms, yet they are rarely seen by casual
observers. They usually are active at night and hide under
rocks during the day. Most people will not find brittle stars
unless they turn over rocks; and turning rocks is discour-
aged because it is destructive to habitat. In addition to under
rocks in tidepools, brittle stars are very commonly found on
the sea floor, often in very deep water. Brittle stars are very
colorful and highly variable; some are luminescent.

IDENTIFICATION, CLASSIFICATION, AND
FOSSIL RECORD

It is easy to distinguish brittle stars from other sorts of sea
stars. The body is a central disk with five distinct long, thin,
and flexible arms. The madreporite, or sieve plate, through
which water enters the water vascular system is usually
present, but it is on the oral surface instead of the aboral
surface as in sea stars and sea urchins. Brittle stars also lack
an anus and must consume food and expel wastes through
the mouth on the underside of the central disk.

Brittle stars are members of the Ophiuroidea, the sister group of the Asteroidea (the conspicuous and
familiar starfish or sea stars). Ophiuroideans comprise
about 2000 species and are divided into two groups.
The Ophiurina are the brittle stars and the serpent stars,
which evolved from within the paraphyletic Eurylina
(basket stars) (see Fig. 1).

FURTHER READING

*See also the following articles*
Bryozoans / Phoronids

FIGURE 1 The evolutionary relationships of brittle stars. Adapted from
Smith et al. (2004).
The fossil record for brittle stars is lengthy, extending back 490 million years to the Early Ordovician. During most of this long fossil history, the diversity of brittle stars has been relatively stable and much lower than current biodiversity. The relatively scant fossil record may be due to the delicate nature of brittle stars, exacerbated by low likelihood of fossilization in the habitats they may have occupied.

**ECOLOGY, REPRODUCTION AND BEHAVIOR**

Brittle stars feed on benthic detritus and small animals, either dead or living. Feeding is accomplished in different ways. Large food is moved toward the mouth by the arms. Smaller food particles can be aggregated by flagella, the action of spines, tube feet, and arms, and then transported toward the mouth for ingestion.

Little is known of the enemies of brittle stars. Most echinoderms avoid predation because they are spiny. In addition, brittle stars are photophobic and secretive in tidepools. Thus, natural observations of brittle stars are rare.

Many brittle stars are viviparous, retaining eggs inside the body and giving birth to tiny complete organisms. Among echinoderms, only the ophiuroids possess bursae—sacs inside the body that open onto the oral surface. Gonads line the walls of these five pairs of bursae (one pair for each leg), and gametes are released through genital slits into the water. Some brittle stars brood their young within these bursae.

Asteroid sea stars, sea urchins, and sea cucumbers are all slow-moving and sluggish. Brittle stars and their close relatives can be fast-moving in comparison. The arms of brittle and serpent stars are capable of only lateral, snakelike movements; basket stars can also move their arms vertically. Using these rapid arm movements, brittle stars are able to avoid predation by escaping. The arms of brittle stars lack an ambulacral groove and include numerous articulated ossicles called vertebrae. Covered by plates, muscles connect the vertebrae. Arms of brittle stars are easily lost or shed when attacked but are regenerated more rapidly than in other sea stars. The water vascular system functions in locomotion and respiration. This system of tubes and vessels is lined with ciliated cells and filled with water. Tube feet lack suckers and do not help in locomotion.

**SEE ALSO THE FOLLOWING ARTICLES**

Echinoderms / Sea Cucumbers / Sea Stars / Sea Urchins

**FURTHER READING**


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**BRYOZOANS**

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Bryozoans are a group of sessile, colonial invertebrates that collect food particles with a retractable crown of ciliated tentacles called a lophophore (Figs. 1, 2). Bryozoans live in both marine and freshwater environments. In benthic communities, bryozoans may have important roles as competitors for space, as items of prey, and as habitat for a variety of protists, plants and animals.

**ECOLOGY**

Bryozoans grow on a wide variety of natural substrates, including rock, shell, and wood. Some species grow on brown or red macroalgae or some seagrasses. Other species grow on other invertebrates such as ascidians, gastropods, bivalves, barnacles, and other bryozoan colonies. In addition, many bryozoans will readily settle and grow on synthetic substrates such as glass, solid plastics, and plastic foam. Typically a biofilm, consisting of a matrix of
microorganisms and their secretions, is usually required for bryozoan larval settlement. The larvae of some species, such as *Bugula neritina*, have been shown to preferentially settle adjacent to one another.

As members of benthic communities, bryozoans have been demonstrated to play important roles as competitors for space and as food for other organisms. Bryozoans compete for space with many other benthic organisms such as hydroids, ascidians, algae, and even other bryozoans. Some bryozoans, such as *Membranipora membranacea*, may almost completely cover fronds of kelp and will grow over other organisms that have settled on the frond. As prey items, bryozoans have been observed to be eaten by predators such as nudibranchs, caprellids, sea urchins, and fish. One nudibranch predator, *Doridella* (Fig. 3), has been shown to induce the gymnolaemate *Membranipora membranacea* to grow spines as a potential defense.

**SYSTEMATICS**

Traditionally, bryozoans have been grouped with phoronids and brachiopods into the Lophophorata based on morphological characters. Additional phylogenetic analyses using DNA sequences have suggested that the lophophorate phyla do not represent a monophyletic group and may be part of a larger group of animals that also includes the annelids and molluscs, called the Lophotrochozoa. Within the phylum Bryozoa, taxa have been organized into three classes: the Phylactolaemata, Gymnolaemata, and Stenolaemata. All phylactolaemates live in freshwater. The majority of the living marine taxa and a few freshwater species have been placed within the Ctenostomata and Cheilostomata, the two orders of the Gymnolaemata. Lastly, the Stenolaemata has only one remaining extant order, the Tubuliporata, that contains exclusively marine species. The separation of marine bryozoans into the Gymnolaemata and Stenolaemata is based on differences in zoid morphology and reproductive biology, including embryology and larval structure. Phylogenetic relationships both within and between classes of bryozoans remain largely unresolved.

**COLONY STRUCTURE**

Bryozoans may form colonies that are flat sheets, thick mats, creeping or erect stolons (stemlike filaments), or arborescent (treelike). Differences among colony growth forms have been proposed to be associated with adaptations for increasing feeding efficiency, structural rigidity, growth and regeneration, integration among members of a colony, and defenses against predation. Bryozoan colonies consist of numerous asexually budded individuals, or zooids (see Figs. 1, 2). Zooids are small (usually less than 1 mm long) and are typically cylindrical or boxlike in shape. Zooids in a phylactolaemate colony share a common body cavity, but gymnolaemate and stenolaemate zooids are largely separated from one another by partitions or septa. Gymnolaemate zooids are interconnected through the funicular system, a vascular-tissue homologue that serves as a circulatory system (see Fig. 1). In stenolaemates, small pores in the septa between zooids may allow for adjacent zooids to communicate with one another, including the sharing of nutrients. Polymorphism is common within bryozoan colonies, and zooids may be specialized for feeding, sexual reproduction, attachment of the colony to a substrate, or colony defense. The fundamental unit of a colony is the feeding individual, or autozooid. All other zooid types are called heterozooids. Hetero zooids
are typically derived by modifying autozooid body plans, usually resulting in anatomically incomplete zooids that are incapable of feeding. Consequently, nutrition for heterozooids must be provided by autozooids through connections between heterozooids and autozooids.

ZOOID STRUCTURE
The anatomy of an autozooid is organized into two functional subunits: the polypide and cystid. The polypide includes the lophophore, the U-shaped digestive tract and its musculature, the cerebral ganglion, and the tentacle sheath (see Figs. 1, 2). The tentacle sheath represents the protrusible portion of the body wall, which encloses the tentacles when the lophophore is retracted inside of the zooid. The cystid is the nonprotrusible portion of the body wall and consists of cellular and noncellular components. The cellular portion of the cystid is composed of an outer epidermal layer and a thin underlying mesodermal layer. The noncellular components of the cystid are secreted by the epidermal layer and form the zooecium or exoskeleton of the body wall. The zooecium consists of a thin mucopolysaccharide cuticle and a thicker matrix that may be gelatinous, chitinous, calcareous, or a combination of these substances. Increases in the calcification of zooecium and increases in the anatomical complexity of the frontal surface of zooids of different species have been proposed to be adaptations to predation.

During asexual budding, each new individual is formed first by the growth of the cystid of an existing zooid. The two typical patterns for budding process are intrazooidal, in which one zooid must complete its growth and development before budding new individuals, and zooidal, in which buds continually grow outward from the colony and new individuals become separated from one another by the construction of interior transverse walls. The process of zooidal budding unites the connection between colony growth and the development of individual zooids. Zooidal budding has been proposed as an adaptation for growth and regeneration. In both intrazooidal and zooidal budding, a localized thickening of the cystid of the developing zooid invaginates as a two-layered vesicle (epidermis and coelomic lining) and differentiates as the polypide of the new individual. In many species, the polypide periodically degenerates to form a “brown body” and a new polypide is regenerated from the cystid.

THE LOPHOPHORE AND FEEDING
The lophophore is the crown of tentacles that surround the mouth. The lophophores of phylactolaemates are horseshoe-shaped, whereas the lophophores of gymnolaemates and stenolaemates are circular. Tentacle number (typically between 8 and 35) and length vary among species and are frequently used as taxonomic characters. In addition, tentacle number has been correlated with lophophore size among species. Species with lophophores that have longer and more numerous tentacles capture more particles per unit time than species with lophophores that have shorter and less numerous tentacles.

The structure of tentacles is similar among bryozoans. Each tentacle contains a portion of the body cavity within the lophophore and has one frontal and two lateral tracts of cilia on its surface. The beat of the lateral cilia generate currents that bring water into the top of the lophophore and out between the bases of the tentacles. Water currents may transport food particles toward the mouth. Alternatively, food particles also may be transported to the mouth by the lateral and frontal ciliary tracts, a process that involves reversals in the effective stroke of the lateral cilia when they contact food particles.

Bryozoan zooids extend their lophophores by increasing the hydrostatic pressure within the main body cavity, or coelom, through muscular contraction. However, because of differences in zooid anatomy and degree of calcification, the mechanism by which hydrostatic pressure is increased within the body cavity varies among the three classes. The increase in hydrostatic pressure is due to the contraction of circular muscles in phylactolaemates and of parietal muscles in gymnolaemates, producing a deformation or change in shape of the body wall (see Fig. 1). In stenolaemates, the heavy calcification of the zooid prevents the deformation of the body wall by muscle contraction. Instead, stenolaemates are able to increase the hydrostatic pressure within their body cavities by redistributing fluid from a distal compartment (outer exosaccal cavity) to a proximal compartment (inner exosaccal cavity). These two compartments represent spaces that are pseudo-coels, since they are located between the epidermal and mesodermal (membranous sac) layers of the cystid (see Fig. 2). In all bryozoan groups, the lophophore is retracted through the contraction of retractor muscles coordinated with the relaxation of the muscles that increase the hydrostatic pressure within the main body cavity.

REPRODUCTION AND DEVELOPMENT
Although variation in zooid sexuality exists among species, bryozoan colonies are typically hermaphroditic, containing individuals that may function as males, females, or both. Within a colony, zooids may remain sterile or function only as males, only as females, or as both males and females. Depending on the species, hermaphroditic zooids
may produce sperm and eggs during the same reproductive period (simultaneous hermaphrodites), produce sperm before producing eggs (protandrous hermaphrodites), or produce eggs before producing sperm (protogynous hermaphrodites). Phylactolaemate zooids are exclusively hermaphroditic. Gymnolaemate and stenolaemate colonies are usually mosaics of sterile, sexually immature, and either hermaphroditic or male or female individuals. Sexual dimorphism is common, and both the cystid and polypide may become modified to support sexual reproduction.

In gymnolaemates, most autozooids become sexually mature and are commonly hermaphroditic. In contrast, stenolaemate colonies are typically composed of mostly sterile autozooids, some male autozooids, and only a few female heterozooids called gonozooids. Fully developed stenolaemate gonozooids are much larger than either male or sterile autozooids. In some species, the gonozooid may include space that is actually external to the zooids. The actual brooding volume in all stenolaemate gonozooids is many times larger than any autozooid of the colony. Developing gonozooids may initially have a polypide, but they lose it as they grow and become sexually reproductive.

Internal fertilization has been reported for all three classes of bryozoans, although the process has been best described for gymnolaemates. In gymnolaemates, sperm are released through the tips of the tentacles and are transferred through the water column between functional male and female zooids of the same or different colonies. After entering maternal zooids, sperm fuse with eggs before they complete meiosis, usually while eggs are still primary oocytes. Typically, sperm–egg fusion occurs either within the ovary, while eggs are at early stages of development, or within the body cavity shortly after eggs have been ovulated. In stenolaemates, male zooids also release sperm into the water column through the tentacles. However, the exact timing of sperm–egg fusion is still uncertain in stenolaemates, but it appears likely to be while eggs are still inside of the ovary (intraovarian).

The development of gymnolaemate embryos usually begins after fertilized eggs have been spawned to a location outside of the maternal body cavity. The nature of the external location varies depending on whether the species freely spawns eggs into the water column or retains them. When gymnolaemates retain their eggs, embryos are most often brooded in either specialized chambers called ovi-cells or ooeica (see Fig. 1), invaginations of the body wall called embryo sacs, or spaces that form between the external body wall of the retracted polypides, called the introvert. The only known exception to this pattern of external development is Epistomia bursia, in which fertilized eggs are brooded within the ovary rather than being spawned to an external location.

Three modes of development have been described for gymnolaemate bryozoans. In a few gymnolaemate species, maternal individuals produce many small, yolk-poor eggs within a reproductive season, which are spawned directly into the water column, where they grow and develop into feeding, or planktotrophic, larvae. In contrast, most gymnolaemates produce one large, yolk-rich egg at a time that they brood, releasing a nonfeeding, or lecithotrophic, larva that is about the same size as the original fertilized egg. These species often brood several embryos sequentially during a reproductive season. There are a few species in which individual zooids simultaneously brood several embryos at one time (e.g., Alcyonium gelatinosum). The last developmental mode occurs in several genera, such as Bugula and Celloporella, in which the larvae are maternotrophic. In these species, maternal individuals produce one small egg at a time and supply their brooded embryo with nutrients through a simple placental system. Consequently, maternotrophic larvae are much larger in size than the fertilized egg cell from which they develop.

Stenolaemates have a very specialized reproductive biology called polyembryony. Polyembryony is a reproductive process in which a single zygote is cloned through a budding process to produce 100 or more genetically identical individuals. Early development of a single fertilized egg within a stenolaemate gonozooid establishes a large, multicellular primary embryo. The primary embryo increases in size and buds secondary embryos from lobate extensions. These secondary embryos may develop into larvae or may themselves bud to produce tertiary embryos that develop into larvae. As gonozooids lack a functional polypide, the nutrition to support polyembryony is thought to be supplied by the autozooids surrounding the gonozooid.

Larval forms differ among the three bryozoan classes. Gymnolaemates have the greatest larval diversity, with cyphonautes (shelled, feeding), pseudocyphonautes (shelled, nonfeeding), and coronate (nonshelled, nonfeeding) forms. The cyphonautes larva has been considered to represent the ancestral larval form for the group, since it contains a functional digestive tract. The cyphonautes larva of Membranipora membranacea uses a unique feeding mechanism in which cilia, arranged similarly to those on an adult tentacle, sieve particles from the water.

The free-swimming larval period varies from about four weeks for cyphonautes larvae to several hours for nonfeeding gymnolaemate larvae to under an hour for stenolaemate larvae. Settlement of bryozoan larvae is often associated with changes in the response of larvae to light and gravity.
Initially after their release, larvae typically move toward light (positive phototaxis) and away from the pull of gravity (negative geotaxis). At the time of settlement, larvae either move away from light (negative phototaxis) or no longer use light as a cue to orient their movement (neutral phototaxis) and swim toward the pull of gravity (positive geotaxis). Permanent attachment of bryozoan larvae to substrates occurs through the outward unfolding or eversion of an epidermal layer, called the internal sac, that was tucked up inside the larva, followed by the secretion of an adhesive.

In bryozoans, metamorphosis of the larva results in the formation of an ancestrula, the first member of a new colony. During their evolution, all bryozoans have apparently shifted the development of some adult characteristics into earlier life history stages, a phenomenon called heterochrony. One adult characteristic that has been shifted into larval stages is the ability of the cystid to form all other parts of the zooid. Consequently, all of the structures of the ancestrula, including the digestive tract, are formed from only epidermis, which is derived from ectoderm, and mesoderm. In phylactolaemates, many portions of the ancestrula, including the polypide, are preformed before the larva is released by the maternal zooid. In gymnolaemates and stenolaemates, the formation of an ancestrula requires extensive rearrangements of larval tissues to form an initial cystid from cells contained within invaginations (inward folds) of larval epidermis, and undifferentiated mesodermal cells within the larva.

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BUOYANCY

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An organism’s position in the water column, whether holding station on the bottom or swimming and floating at the water surface, depends first on the balance of vertical forces of weight acting downward counteracted by hydrostatic upthrust acting upwards. These forces alone are insufficient to fully regulate position, except at the bottom of the water column or floating at the surface. Animals control position within the water column using hydrodynamic forces generated by body and limb motions.

CONTROLLING LOCATION IN THE WATER COLUMN

Two hydrostatic forces interact with body density to determine the net weight of an organism in water. Gravity acts on body mass, resulting in the downward force of weight (Fig. 1A). This is counteracted by upthrust, equal to the weight of water displaced by the body volume (Archimedes’s principle). Density (mass/volume) of tissues depends on amounts of materials such as fat, bone, and, in plants, cellulose. For example, densities of fish carcases range from 1060 to 1090 kg m⁻³. The density of seawater is typically about 1024 kg m⁻³. As a result, organisms usually are negatively buoyant, with a positive net weight in water, and tend to sink to the bottom unless an additional force, lift, is created to offset that weight (Fig. 1B).

Hydrostatic lift is generated by incorporating low-density materials into the body, increasing upthrust without a commensurate increase in mass. Gas has a density around 1.2 kg m⁻³ and is commonly held in various structures such as lungs in marine iguanas, birds, and...
However, gases follow the gas laws, according to which the volume varies directly with temperature and inversely with pressure. As a result, volume decreases by half for every doubling of pressure. Small differences in depth near the surface result in large pressure changes and hence volume changes, promoting instability. Some fishes, notably young stages of elasmobranchs in tidepools, avoid this problem by using a different low-density inclusion, lipid, accumulated in organs such as the liver, or in muscle. Lipids have densities around 850 to 930 kg m⁻³, so that more of this material is needed to achieve a given density compared to a gas inclusion. Marine algae avoid potential effects of density changes near the surface by hyperinflating their gas bladders, ensuring that their fronds float.

Hydrostatic forces used for buoyancy are not self-correcting. That is, an organism with a gas inclusion does not return automatically to a position or posture when disturbed by inevitable external forces. As a result, all animals supplement or even replace hydrostatic lift with hydrodynamic lift (see Fig. 1B). Hydrodynamic lift is created during swimming when water flows over the body and appendages, such as fins and legs.

CONTROLLING LOCATION IN CURRENTS

Special challenges are faced by tidepool animals when they are exposed to high currents. Organisms then control their positions to avoid being swept away, by interacting with the bottom in various ways. The principles can be illustrated for a sculpin holding position on the bottom in a flow. It still experiences the same hydrostatic forces as a fish in the water column (see Fig. 1C). In addition, current creates a drag force on the body, tending to push it downstream. Drag is resisted by friction with the bottom. Friction depends on the weight of the fish in water and a friction coefficient related to the roughness of both the bottom and the fish. However, flow over the body also creates hydrodynamic lift, which reduces the weight in water, hence also decreasing friction. The ability of a fish to remain in position therefore depends on maximizing both weight in water and friction and minimizing both hydrodynamic lift and drag.

Drag is reduced by a low profile, typical of limpet and mussel shells (Figs. 2C, F), flatfish such as dabs, and the bodies of many crabs (Fig. 2D). The lift force is minimized by a small body and fin area, as in cottids and blennies. The body must have sufficient volume for internal organs. As a result, a low profile with low drag is unavoidable without spreading out the body, increasing its area and hence lift. Conversely, compacting the volume and reducing lift increases drag.

The resulting inability to simultaneously minimize drag and lift are overcome by numerous adaptations. Many of these increase friction. Animals exposed to high currents often increase the proportion of heavier tissues in the body, especially the skeleton, to increase density and hence the weight in water and friction. This occurs in the skeleton of benthic bony fishes such as cottids, the shells of molluscs, the exoskeleton of lobsters and crabs, and bony ossicles in the arms of starfishes (Fig. 2E). The friction coefficient is very large for systems attached to the bottom, for example in the byssal threads of bivalves (Fig. 2F) and the holdfasts of algae (Fig. 2G). Other ways of increasing friction coefficients are through body roughness, especially scales of fishes, and behaviors such as grasping the bottom by the foot of molluscs, appendages such as the legs of crabs, the tube-feet on the ventral surface of starfish, and the fins of fishes. Hydrodynamic lift can be reduced by behaviors that create flow beneath the body, decreasing the current difference across the body.
body. Some fish angle their paired fins upward, and crabs angle the body upward, to direct lift toward the ground. This adds to weight in water, increasing friction.

When currents overwhelm these mechanisms, animals living in the water column or on the bottom resort to avoiding flow. The forces sculpting habitats such as tide-pools erode substrate and create numerous shelters for flow avoidance by animals.

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