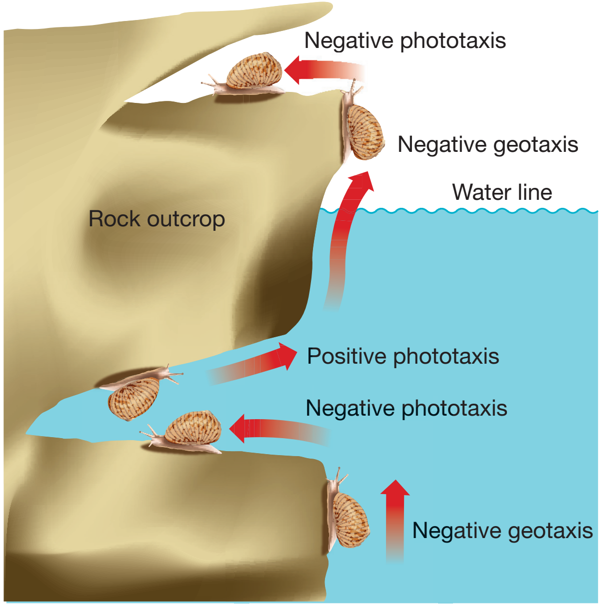


FIG. 16.8 The contribution of behavioral responses of the high-intertidal gastropod *Littorina neritoides* to the regulation of its vertical position on rocky shores. (After Newell, 1979)

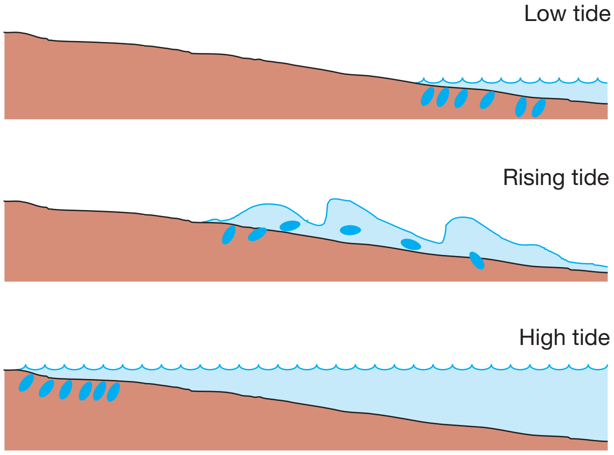


FIG. 16.9 Vertical beach migration of swash riders, such as the mole crab *Emerita* and the beach clam *Donax variabilis*. Note that animals seek sediments that are neither too dry nor too wave washed.

crab *Emerita* (*E. analoga* on the west coast of the United States and *E. talpoida* on the east coast) and several species of the wedge clam *Donax* have adopted the strategy of behaving as **swash riders**, leaving the sediment as they feel the pressure of an approaching wave (**Figure 16.9**). They then ride the wave to a higher position in the intertidal zone and rapidly burrow. When the tide falls, they reverse the process, which guarantees that they will always be located in a moist but not excessively wave-swept level of the beach. As the waves wash back down the beach, the mole crab extends its feathery second antennae, which trap phytoplankton. The mole crab has a streamlined shape and special digging appendages (**Figure 16.10**).

FIG. 16.10 The streamlined shape of the mole crab *Emerita talpoida* allows the animal to burrow into the sand rapidly. (Photograph by Jeffrey Levinton)

Wave Shock

- **Wave shock is a major factor determining the distribution and morphology of intertidal organisms.**

The impact of waves and the material that they carry (sand, pebbles, logs) are important in selecting morphological adaptations to intertidal life. We need only visit a rocky shore on a stormy day to witness the tremendous energy that is focused on the shoreline. Waves may rip organisms from the rocks, erode large volumes of sand, or propel a variety of projectiles to the shore.

Breaking waves can damage rocky-shore organisms in the following ways:

1. *Abrasion.* Particles in suspension or floating debris scrape delicate structures. Water turbulence may whip seaweeds and other erect organisms against rocks.
2. *Pressure drag.* The hydrostatic pressure exerted by breaking waves can crush or damage delicate and compressible structures, such as gas-filled bladders of seaweeds. Most intertidal organisms are liquid filled and, therefore, are relatively incompressible. Larger epifauna will experience greater pressure drag (see discussion in Chapter 6 on limpet size and wave pressure drag).
3. *Acceleration.* Water exerts a directional force against intertidal organisms. Larger organisms may also experience acceleration as their large mass is carried along by waves. Acceleration might also cause ripping of holdfasts or snapping of byssal threads of mussels.

- **Force transducers can be used to measure the force of wave shock.**

Organisms living in wave-swept coasts experience dynamically changing forces as waves collapse upon them. Organisms that project into the water will likely experience strong pressure drag, which is the difference of force upstream and downstream of the organism (see Chapter 6). To measure these forces, one needs to implant **force transducers**, which can measure force along the plane of the rocky surface and perpendicular to the rock. A force transducer is a beam that bends when water impinges on it. As the beam bends, the electrical resistance of a metal band on the beam changes, which causes a change in the voltage, which is proportional to force.

On a wave-swept rocky shore in Washington State, Mark Denny (1985) estimated pressures on a model of a limpet averaging about 0.6 N (N is a newton, a unit of force), but often reaching 3 N. Equally important was the unpredictability of the time of maximum force or the direction. Wave forces can dislodge a number of intertidal organisms and also cause cessations of movement by limpets and snails. Single organisms that project from the rock surface are more at risk than those living among other organisms. For example, when mussels are packed together into dense beds, the entire mussel bed can dissipate the wave along its surface, reducing the force on each individual. Mussels forming such beds are **foundation species**, and strongly affect the structure and physical conditions of associated species.

- **Phenotypically plastic changes in form can reduce the risk of wave shock, but there are often trade-offs with other biological functions.**

While intertidal animals may be vulnerable to being torn from a surface or smashed by wave forces, many species have plastic responses that may reduce mortality. As mentioned, species living on wave-exposed coasts may have thickened skeletons and reduced delicate projecting spines. Barnacles experience increased drag even on the microscale and have feeding appendages and even penises that are shorter or thickened at the base. Emily Carrington (2002) found that mussels in the intertidal of Rhode Island were especially stressed in October, when food was low and water temperatures were still high. Because of this, fall storms were capable of rapidly dislodging large numbers of mussels from intertidal rocks (**Figure 16.11**). The mussels increase byssal thread production in winter, which increases the total attachment strength of the mussel to rocks. Seaweeds may be smaller in stature in open exposed coasts, which reduces drag, and more delicate and longer in protected waters. Larger seaweeds may bend over in a wave-swept surf zone, which reduces drag. But the very size of larger seaweeds causes the mass to accelerate, which can break off the thallus at the stipe.

These plastic responses, however, may come at a cost. The increase of production of byssal threads is physiologically costly to mussels and influences reserves available for somatic growth and gamete production. Seaweeds that grow to smaller sizes in open coasts may survive better, but they also produce fewer reproductive structures and there is, therefore, a trade-off of response to wave action and reproductive output.

CAUSES OF ZONATION

- **Zonation results from preferential larval settlement and adult movement, differential physiological tolerance, and biological interactions such as competition and predation.**

(a)

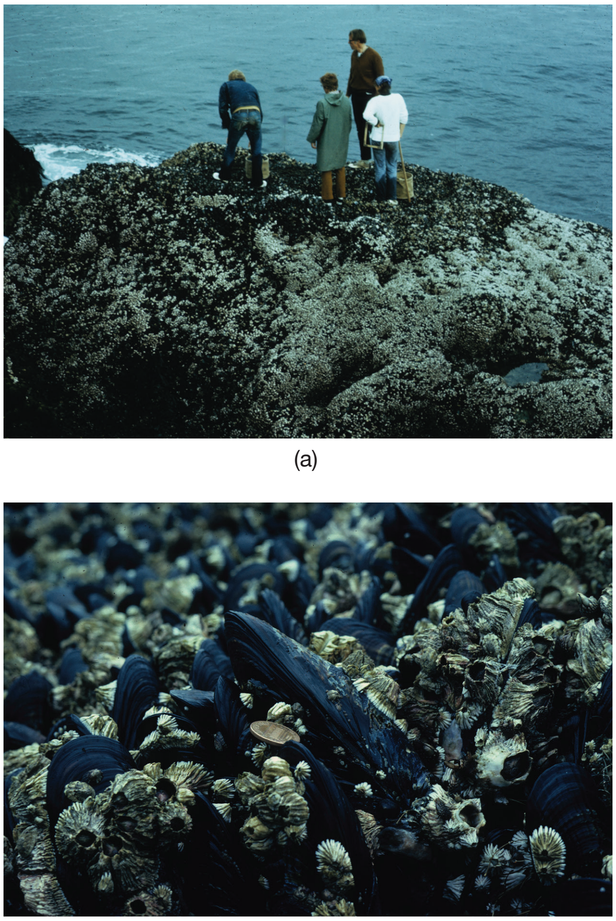
(b)

FIG. 16.11 Mussel dislodgement. The mussel *Mytilus edulis* changes its attachment strength to deal with seasonal changes in water currents and secretes more threads so that it can resist winter storms. But in early fall, it does not have sufficient reserves to attach very well. (a) Mussels in October 3, 2001. (b) Bare space on October 21, 2001, after mussels were stripped from a rock because of fall wave action. (Photographs by Emily Carrington)

Having examined the important physical factors in the intertidal gradient, we can ask the question: What causes zonation? The remarkably similar patterns of species vertical ranges, combined with the sharp boundaries between zones, seem to suggest that zonation can be explained with few factors.

Several major factors combine to form zones.

1. *Physiological tolerance.* Species found higher on the shoreline are generally more tolerant of desiccation, reduced feeding time, reduced access to oxygen, and extreme temperature.
2. *Larval and adult preference.* To some degree, larvae of sessile animals are able to locate the tidal height suitable for adults of their own species. Larvae of the common European Atlantic higher-intertidal barnacle *Chthamalus stellatus* settle in the high shore, although they also settle somewhat lower. Gregariousness (settling in groups, on adults of the same species) also causes


(a)

(b)

FIG. 16.12 (a) Intertidal rocks are often completely covered by organisms. This rock, on Tatoosh Island, Washington, is covered by barnacles (light) and mussels (dark). (b) Close-up of a mussel-dominated rock. (Photographs by Jeffrey Levinton)

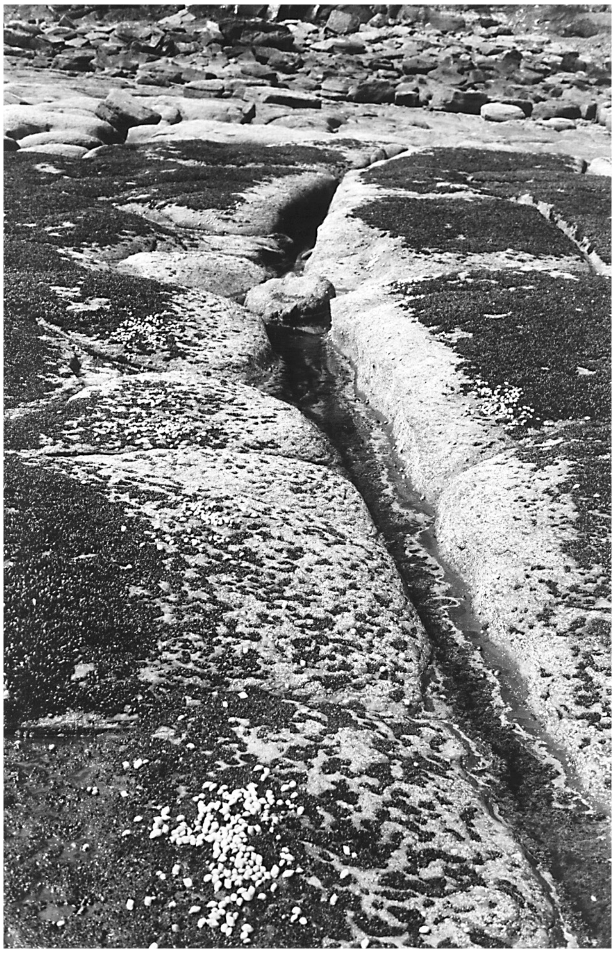


FIG. 16.13 Predation line on rocky shores of England. Below this line (adjacent to the crack in the rock), the gastropod *Nucella lapillus* (white spots) can clear the rocks of its prey, the mussel *Mytilus edulis* (dark-colored areas). (Photograph courtesy of Raymond Seed)

preferential settlement on the "correct" level of the shore. In eastern Australia, larvae of the barnacle *Hexaminius popeiana* settle preferentially on adults of their own species (Coates and McKillup, 1995). If adults are transplanted above the typical shore level at which the adults usually live, the larvae settle there preferentially as well. Survival of recruits, however, is much lower than within the normal tidal level where the adults usually live. Mobile animals can adjust their tidal height by a combination of responses to light, gravity, and moisture, as discussed earlier.

3. *Competition.* Intertidal habitats, particularly rocky shores, may be severely space limited (**Figure 16.12**). Species capable of overgrowing or undercutting others may come to dominate that level of the shore in which they can do well physiologically. Mussels, for example, can usually move by forming and detaching byssal threads. They can climb on top and smother competitors.
4. *Predation.* Predators are often strongly limited by the time of immersion because carnivores such as sea stars and snails must be moist as they move to locate, seize, and ingest prey. This requirement usually limits predation to the lower part of the shore and creates a refuge from predation above a certain shore height, where predators do not have enough time to capture prey. **Figure 16.13** shows a rocky-shore mussel bed on the coast of England. Dog whelks (*Nucella lapillus*) come out of moist lower-intertidal cracks during the rising tide and prey upon mussels. They must return to the cracks when the tide withdraws. Mussel beds on the outer Pacific coast, dominated by *Mytilus californianus*, often have a similar sharp lower limit, which is controlled by the carnivorous sea star *Pisaster ochraceus*. Robert Paine removed sea stars for over a decade and found that the mussel bed gradually extended lower in the tide zone.

Interspecific Competition

- **Field experiments show the importance of interspecific competition for space on rocky shores.**

Field experiments were crucial in understanding the cause of zonation. On rocky shores of both the American and northern European sides of the North Atlantic, one often sees the zonation pictured in **Figure 16.14**. In the highest

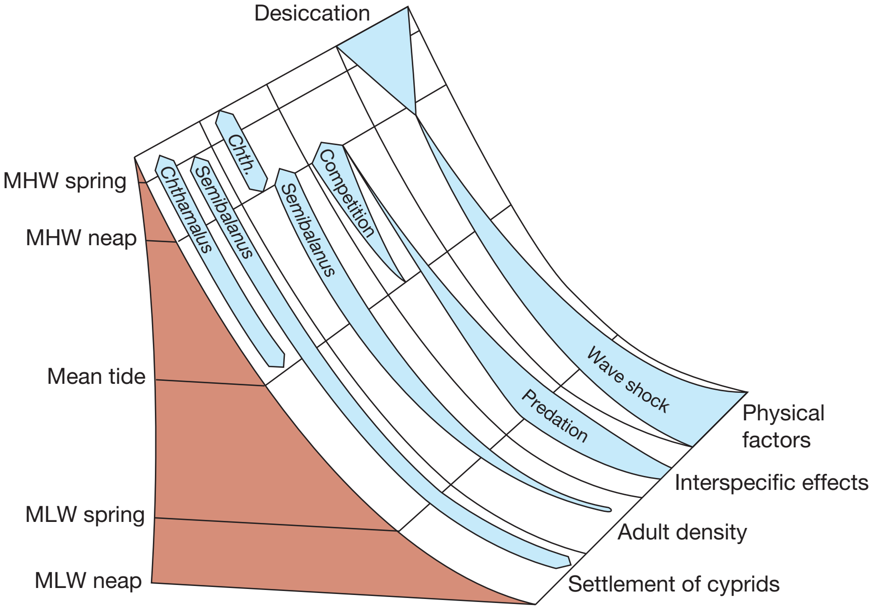


FIG. 16.14 Distribution on rocky shores of Scotland of adult and newly settled larvae of the barnacles *Semibalanus balanoides* and *Chthamalus stellatus*. Width of the bars indicates the relative effects of principal limiting factors. MHW, mean high water; MLW, mean low water. (Modified after Connell, 1961)

part of the shore, adults of the barnacle *Chthamalus stellatus* (*C. fragilis* in New England) dominate available space down to the approximate level of mean high tide. Below, adults of the white barnacle *Semibalanus balanoides* usually dominate. At the level of mean low water, however, barnacles are usually rare. What explains the distribution?

Joseph Connell (1961) studied this problem on a protected rocky shore in Scotland by selective removals of hypothesized competitors and by caging selected areas to exclude the common predatory gastropod, the dog whelk *Nucella lapillus*. First he considered larval recruitment. Cyprids of *Chthamalus* tended to settle high on the shore, but they also settled well within the range in which adults of the same species were rare. *Semibalanus* cyprids recruited in large numbers throughout the intertidal but failed to do very well above mean high water. Hence, there was a substantial area of overlap of larval recruitment, although differential larval recruitment explains some of the difference in adult vertical distribution.

Connell transplanted rocks downward with newly settled *Chthamalus* and found that these barnacles were rapidly overgrown and undercut by recruited *Semibalanus*, which are much faster growing, even causing intraspecific mortality. Above high water at neap tide, *Chthamalus* survival was greater, but the *Semibalanus* there died, owing to their poor survival in the dry reaches of the upper intertidal (**Figure 16.14**).

These experimental results show that the lower limit of *Chthamalus* on the shore is regulated by competition with *Semibalanus*, whereas the upper limit of *Semibalanus* is probably controlled by desiccation. The upper limit of the *Chthamalus* zone is also controlled by desiccation. Predation by the drilling gastropod *Nucella lapillus* controls the lower limit of *Semibalanus*. These results led to the generalization that **the upper limit of an intertidal species is regulated by physical factors, whereas the lower limit is regulated by biological factors** (e.g., competition).

Seaweed zonation may also be strongly controlled by interspecific interactions. On New England's protected rocky shores, the mid-intertidal is dominated by species of the brown seaweed *Fucus*, whereas the lower shore is usually covered by the Irish moss *Chondrus crispus*. Jane Lubchenco (1980) used experimental manipulations to show that the removal of the common herbivore periwinkle *Littorina littorea* and Irish moss resulted in complete coverage of the low shore by the normally mid-intertidal *Fucus* sp.[1] If the herbivore snails were left in place, *Fucus* sp. did not colonize the lower shore so successfully. In this case, the herbivore was functioning as a predator, much as the carnivorous gastropod *Nucella lapillus* functioned in the barnacle example mentioned earlier.

- **Climate change may tip the balance of biological interactions toward changes in intertidal community structure.**

Competitive success on rocky shores involves the ability to overgrow a competitor combined with physiological tolerance to desiccation. The superiority of *Chthamalus* on the upper shore depends on its tolerance of stress relative to other species. Changes in climate would therefore interact with preexisting differences in adaptations to temperature and desiccation stress. A particularly severely cold winter in 1962–1963 in the United Kingdom caused extensive mortality in generally warm-adapted marine species. One surprise was a very high intertidal barnacle, noted for its resistance to heat. It showed no mortality, perhaps because of its general physiological resistance to conditions on the

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[1] When a genus, for example, *Fucus*, is named as *Fucus* sp., we are not sure of the exact species identity.

high shore, which frequently involve cold as much as heat. In the past few decades, coastal waters have been increasing in temperature in this part of Europe and a number of lower-latitude species have been expanding north, including two species of warm-water barnacles (Hiscock et al., 2004). As we have discussed, competition between barnacle species can be intense, so what role will global warming play in reorganizing competitive outcomes in rocky intertidal communities?

Cape Cod is a latitudinal thermal threshold in eastern North America. Nearest the mainland, a canal connects the cold waters of northern Cape Cod Bay with the relatively warmer waters south of Cape Cod. South of the Cape, the barnacles *Semibalanus balanoides* and *Chthamalus fragilis* interact, much as Connell described interactions in Scotland between *S. balanoides* and *C. stellatus*. But in the north side of the Cape, waters are simply too cold for *Chthamalus*. David Wethey (2002) studied interactions between these two species along this special northern frontier. On the south side of Cape Cod, *Semibalanus balanoides* could not outcompete *Chthamalus fragilis* in the highest intertidal, which was too hot for survival. But on the northern end of the canal, the water and air temperatures were sufficiently colder to allow *S. balanoides* to outcompete *C. fragilis*, right to the top of the intertidal zone. Wethey was able to prove that the northern limit of *C. fragilis* was determined by competition as much as climate. He transplanted *Chthamalus* on plates to a locale 80 km to the north of the northern part of the Cape Cod Canal. Adults survived quite well in the absence of *Semibalanus*, which proves that the limit is not just controlled by temperature but by an interaction effect with interspecific competition.

It is interesting to speculate how regional warming, which is well documented in marine waters in this region, will affect range extensions. *Chthamalus fragilis* will probably extend northward, as will many other species by a variety of mechanisms. Some evidence shows that the northern limit of the fiddler crab *Uca pugilator* at Cape Cod is determined by larval survival. Increase of temperature may allow a range extension of this and all other similarly limited species. This may cause a reorganization of species interactions in Cape Cod Bay, just north of Cape Cod.

Predation and Interspecific Competition

- **Predation (or herbivory) may ameliorate the dominance achieved by competition and may strongly affect species composition and species richness.**

The importance of predation has also been demonstrated through field experiments. Robert Paine studied this effect on west coast American rocky shores by removing the carnivorous sea star *Pisaster ochraceus* (**Figure 16.15**). The mussel *Mytilus californianus* soon came to dominate. Such experiments suggest a common effect: **Predation delays the competitive displacement of competitively inferior species by the competitive dominant.** On North Atlantic rocky shores, the dog whelk *Nucella lapillus* preys in the lower intertidal upon the competitive dominant barnacle *Semibalanus balanoides*. In waters of Great Britain, this predation opens up space for colonization by the competitively inferior *Chthamalus stellatus*. This general effect has also been observed among seaweed competitors: That is, competition is reduced by the introduction of grazers such as urchins and snails. On New England shores, snail and sea star predation on mussels permits the Irish moss *Chondrus crispus* to dominate lower-intertidal shores. Mussels tend to dominate available space on more exposed headlands where predators are eliminated owing to wave shock.

FIG. 16.15 The sea star *Pisaster ochraceus* is a top predator on eastern Pacific rocky shores. This sea star was turned over while attacking a mussel, *Mytilus californianus*. (Photograph by Jeffrey Levinton)

Species such as sea stars that prevent the monopolization of a habitat by preying on most potential competitors are known as **keystone species**. These species exert **top-down control** on ecosystems.

Like dog whelks, the sea star *Pisaster ochraceus* is limited by moisture and ascends with the rising tide to attack the lower edge of the mussel bed. At the time of low tide, sea stars can be seen on rocks below the mussel bed (**Figure 16.16**). Paine removed sea stars for many years, and the mussel bed gradually moved downward, as sea stars failed to remove the lowest level of mussels.

Although the sea star *Pisaster ochraceus* is a keystone species with respect to species attached directly to rocks, one must remember that the interstices of the mussel bed may contain large numbers of smaller animal species, such as polychaetes, barnacles, and smaller gastropods. Sea star predation may remove the competitive dominant and increase the number of coexisting large-bodied species attached to rocks; but by removing the mussel bed, it also acts in the same manner as clear-cutting a terrestrial forest—namely, causing the disappearance of many smaller dependent animal species.

Strong interactions come not only from animal predators but also from herbivores. On rocky shores, limpets are especially important in the mid-intertidal zone because they are very effective grazers of diatoms attached to rocks, coralline algae, and seaweeds. Simple removal experiments are very informative. Under normal circumstances, limpet-covered rocks are quite barren. However, Betty Nicotri (1977) removed limpets from the intertidal zone of San Juan Islands, Washington, and soon observed the development of a lush cover of diatoms. Limpet grazing has also been found to inhibit the growth of seaweeds on rocky shores in many regions of the world. Finally, limpets affect strongly the distribution of barnacles because the limpets bulldoze aside and ingest newly settled cyprid larvae. On rocks dense with limpets, it is common to observe (**Figure 16.17**) only a few very large barnacles that managed to survive the limpets (and other sources of mortality).

Predation may be so intense that the competitive dominant is rather rare. For example, several species of turf-forming coralline algae compete for space in the lower-intertidal zone of the outer coast of Washington. Experimental combinations of species produced a surprise: The dominant competitor was rather rare in the natural community. In a sense, the basis for its competitive superiority was the key to its population downfall. It grew rapidly enough to displace other competitively inferior species, but this also made it the favorite food of some common grazing chitons and limpets. As a result, the relatively slower growing and less preferred algal species dominated and occupied most of the space, which was monopolized by coralline algae (Paine, 1990). This result leads to some interesting conclusions. First, the complete monopolization of a resource does not necessarily indicate that predation is unimportant. Second, competition cannot be divorced from predation.

■ Spatial heterogeneity may strongly affect the pattern and intensity of predation on rocky shores.

We have discussed the decreasing effectiveness of mobile carnivores such as sea stars in the higher part of the shore. But even at the same level in the intertidal zone, spatial heterogeneity can strongly influence local patterns of predation. Cracks retain moisture, and many mobile carnivores spend the time of low tide there, with no need to retreat to the lowest part of the tide zone. It stands to reason, therefore, that prey items within easy reach of the cracks and pools will be taken with great frequency. In the intertidal zone of the west coast of the United States, species of the genus *Nucella* drill a variety of barnacle and mussel species.

FIG. 16.16 Mussel bed near Bamfield, British Columbia, showing abundant purple and orange sea stars *Pisaster ochraceus* below a *Mytilus californianus* mussel bed. (Photograph by Jeffrey Levinton)

FIG. 16.17 Limpets on a mid-intertidal rocky shore, San Juan Islands, Washington. Note the unoccupied space with sparse large adult barnacles, caused by intense limpet grazing, which consumes the diatoms but also bulldozes aside most newly settled barnacle larvae. (Photograph by Jeffrey Levinton)

They are often found abundantly at the edges of mussel beds and can stay in these relatively moist areas during low tide. When the tide rises, they move from these protected edge habitats out on the rocks to prey on barnacles and smaller mussels. If a large patch is opened by a storm, however, the snails tend not to move across a large area of open rock. Thus, barnacles and mussels settling in the middle of the patch may occupy a refuge from predation.

While rock cracks and pools are relatively permanent, biological refuges such as mussel beds and seaweeds provide shelter and protection from desiccation and need not be permanent. Anthony J. Underwood (1999) was surveying a rocky shore in New South Wales, Australia, when a severe storm hit in 1974. Before the storm, large patches of the seaweed *Hormosira banksii* covered the rocks, and the carnivorous drilling gastropod *Morula marginalba* survived desiccation at low tide by retreating to the wet shelter of the seaweed canopy (**Figure 16.18**). Barnacle mortality was very high near and within the seaweeds, which was explained mostly by snail predation. In some cases seaweeds whip back and forth, scraping barnacle-settling larvae from the rocks, but that was not the case in this study. The seaweeds indirectly affected the barnacles by positively enhancing the local abundance of the snail. The storm, therefore, set a new pattern for predation interactions by removing the shelter for a major predator. It took about 5 years for the strongly disturbed patches of *Hormosira* to recover fully. We explore this further later when we discuss the issue of the scale of disturbance.

- **Mobile predators can often detect newly recruited sessile benthos and may form strong aggregations and feed on new recruits.**

As we have stressed, larval recruitment is not homogeneous, either between sites or from one year to the next. Predators, such as sea stars, drilling snails, and crabs, would alternately be overwhelmed by food and starved if they did not attempt to find spatially concentrated new sources of food. Such concentrations are liable to develop in sites where larval recruitment was very high; perhaps the water flow was high and brought settling larvae to a given location. It is quite common to see abundant predators where recruitment is high. On rocky shores of Maine, where springtime is a wet, bone-chilling affair, large herds of the drilling snail *Nucella lapillus* move along on rock surfaces

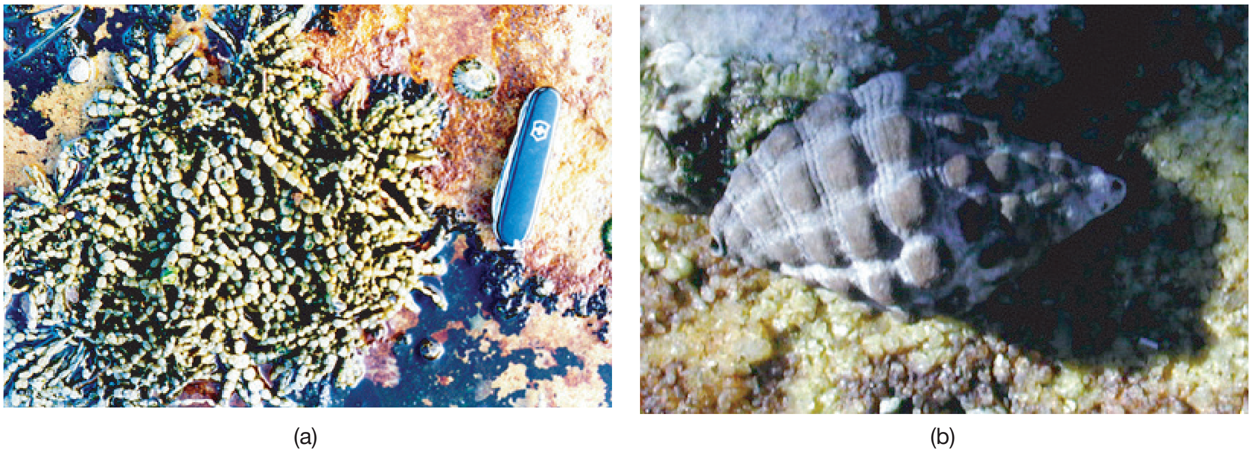
(a)
(b)

FIG. 16.18 (a) The seaweed *Hormosira banksii* forms a canopy under which snails hide and keep moist at low tide. (b) The gastropod *Morula marginalba* is a major predator of invertebrates on rocky shores of southeastern Australia. This snail, in the process of consuming a barnacle, is about 1.5 cm long. (Photographs by Jeffrey Levinton)