their mathematical equations a large number of variables influencing larval dispersal, such as oceanography (current direction/speed, presence of eddies/complex flow fields), larval duration, mortality in the plankton, and larval competency duration. Estimating dispersal outcomes using models can be particularly valuable to determine the relative importance of these variables on dispersal outcomes.

Some models assume that larvae act as passively floating particles despite the knowledge that larvae can exhibit complex behavior (such as vertical migration and swimming). Estimating dispersal using models relies upon the acceptance of a number of assumptions about the parameter values of variables influencing dispersal.

SEE ALSO THE FOLLOWING ARTICLES

Genetic Variation, Measurement of / Larval Settlement, Mechanics of / Monitoring: Techniques

FURTHER READING

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DISTURBANCE

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The term "disturbance" refers to the displacement, damage, or death of organisms caused by an external physical force or condition or incidentally by a biological entity. Physiological or mechanical stress that does not result in tissue loss or death would not be considered a disturbance, although such stress is a common precursor to disturbance. The force or condition that causes disturbance is referred to as the agent of disturbance. Disturbance affects the structure and dynamics of intertidal populations and communities in a variety of ways. By displacing, damaging, or killing resident organisms, disturbance may (1) free up limiting resources, particularly space, for exploitation by colonists or survivors and thereby reset the successional state of the assemblage, (2) promote or hinder the coexistence of competitors, and (3) disrupt or enhance the influence of positive interspecific interactions. The nature and consequences of these effects depend on characteristics of both the disturbance regime and the affected organisms and assemblages.

COMMON AGENTS OF DISTURBANCE ON ROCKY SEASHORES

Common agents of physical disturbance on rocky seashores include wave forces; impact or abrasion by waveborne objects such as cobbles, logs, or ice; extremes of air or water temperature; and desiccation associated with long periods of exposure at low tide. Abrasion by suspended sand or burial under deposited sand is an important agent of disturbance in areas where sandy beaches are contiguous with areas of hard substrate.

Biological entities also cause disturbance on rocky seashores. Biological disturbance occurs when organisms (other than targeted prey) are damaged, displaced, or killed by activities of animals or by algal fronds whiplashing rock surfaces. Examples of disturbance caused by animals include the bulldozing of sessile invertebrates or algae from the interior of territories maintained by limpets (Fig. 1) and the crushing and abrasion of invertebrates and algae by seals as they haul out onto emergent rocks to rest. Some authors also refer to the negative impacts of predation, herbivory, and parasitism as biological disturbance. It is, however, useful to distinguish between these trophic interactions and the phenomena just described, because the patterns and consequences of the two can be quite different.

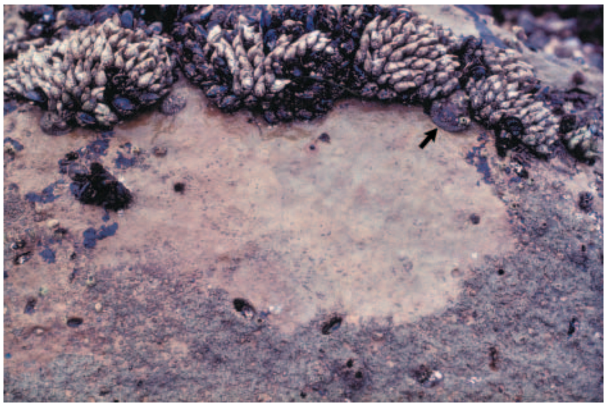

FIGURE 1 Defended territory of an owl limpet *(Lottia gigantea)*. The limpet (at arrow) has bulldozed barnacles, smaller limpets, and other sessile space competitors from its territory (lighter-colored central area). This behavior maintains open space, promoting the recruitment of diatoms and early successional algae on which the owl limpet grazes. Photograph by the author.

Some agents of disturbance permanently alter physical characteristics of the habitat, thereby causing irreversible changes in community structure. Examples include lava flows that cross the intertidal zone and sudden vertical displacement of the shore by seismic activity. Such events are less common than less severe forms of disturbance from which intertidal populations are able to regenerate.

CHARACTERISTICS OF DISTURBANCE

Defining Features

To study the effects of disturbance and compare them among different habitats, it is important to adopt a common set of terms and metrics for describing and quantifying its characteristics. Disturbances can differ in a variety of ways, including their severity (i.e., degree of damage caused) and size (i.e., areal extent). They also vary in duration; some are discrete, short-term events that last for a fraction of the life time of an organism ("acute" disturbances), while others exert their impact over much longer periods ("chronic" disturbances). A floating log crushing a stand of barnacles would be considered an acute disturbance. Cobbles battering and abrading the sides of a tidepool or surge channel on every rising tide would represent a chronic disturbance to most macroscopic organisms. These defining features of a disturbance (severity, size, and duration) strongly influence the rate and mechanisms by which the affected population or community regenerates.

The Regime of Disturbance

Seashores vary in the sizes, severities, and durations of disturbance they experience. The distributions of one or more of these characteristics often differ in mean or variance among shores or sections of a shore. The disturbance regime is described by these distributions of disturbance properties, together with the spatial and temporal patterning of their occurrence. Frequency and predictability of disturbance are especially important temporal components of the disturbance regime. Frequency refers to the number of disturbances that occur over an interval of time. The predictability of disturbance is inversely related to the variation in time between successive events. The more regular a disturbance, the more predictable it is. This patterning of disturbance has an important effect on the abundance and persistence of intertidal populations and, thus, the species composition and diversity of intertidal communities (see "The Impact of Disturbance," later in this article).

Spatial and temporal variation in the regime of disturbance is a key source of heterogeneity in intertidal environments. Within a geographic region, some sites suffer more damage from drift logs, ice scour, the impact of cobbles, or wave forces than others. At larger spatial scales, the importance of ice damage or heat stress varies with latitude. The intensities and frequencies of disturbing forces vary in time as well; strong seasonal variation in disturbance rates is typical in most regions. More biomass is lost and open space generated during months when large storm waves or floating ice is common. For example, on the outer coast of the state of Washington, the mean rate at which bare patches are cleared in beds of the mussel *Mytilus californianus* is more than an order of magnitude greater in the winter, when large storm waves strike the shore, than during the summer, when waves are much smaller. Similarly, in southern California intertidal boulder fields, boulders are more likely to be overturned during stormy winter months than in the summer, when wave energy is low. Ice scour is obviously a very seasonal phenomenon at temperate latitudes. Large interannual variation in disturbance rates has been documented in all these systems.

Interactions between Properties of Organisms or Populations and Disturbing Forces

The regime of disturbance is determined not only by the patterning and intensity of external agents of disturbance (e.g., wave forces, fluctuations in air or water temperatures) but also by intrinsic variation in the susceptibility of the target organisms. Consider, for example, the forces associated with breaking waves on the seashore. As a wave breaks against the shore, intertidal organisms in the path of the flowing water experience drag, lift, and accelerational forces. An organism's size, shape, and flexibility influence the absolute and relative strengths of these forces. The first two forces, drag and lift, result from the unequal pressures that develop on different sides of an organism as water flows past it. In the case of drag, greater pressure develops on the upstream side of the organism than downstream in the turbulent wake; the net force tends to push the organism in the direction of flow. All else equal, the force of drag increases with the size of an organism, or more specifically, the area of the organism that is projected in the direction of flow. Organisms that are inherently more streamlined in shape, or are flexible enough to assume a streamlined shape in flow, will experience less drag than those that have a fixed shape and a relatively larger area projected into flow. Organisms in flow may also experience a vertical force that tends to lift them off the substrate. A net upward force develops because water cannot flow under an attached organism and only slowly around its base, potentially resulting in relatively high pressure beneath it, while pressure above the organism drops because the flow of water is forced to accelerate over it. Size and shape have similar effects on the magnitude of lift as they do on drag. The third kind of hydrodynamic force, accelerational force, develops when flow around an organism is accelerating. In contrast to lift and drag forces, which are proportional to the area exposed to flow, accelerational force is proportional to the volume of fluid displaced by the organism.

Our understanding of the combined impact of these different forces on intertidal organisms is a work in progress, but recent theory and empirical studies are providing insight to the manner in which disturbance from wave forces can limit organism size and density. Generally speaking, as an organism grows larger, the hydrodynamic forces it experiences increase, making adhesive failure or breakage more likely. However, accurate predictions concerning the effects of wave forces on sessile organisms are made more challenging by the fact that neighboring organisms or substrates intercept and modify flow, thereby influencing the forces that target organisms experience. As a result, laboratory measurements on isolated individuals may not translate well to the situation in the field.

An organism's size and shape also affect its susceptibility to damage or death by climatic extremes. Small individuals or organisms have larger surface-to-volume ratios, making them more susceptible to drying out or heating up during prolonged exposures to the air at low tide. This pattern has been documented for common intertidal organisms such as barnacles, limpets, sea anemones, and various species of macroalgae. On the other hand, small individuals are better able to fit into cracks and crevices, where they can escape the extreme conditions. Surrounding organisms of the same or different species can also modify local physical conditions, often retaining moisture, blocking the wind, or insulating against extreme temperatures and thus ameliorating potentially lethal conditions. For example, at higher levels on the shore, where high temperatures and long exposures to the air create highly stressful conditions, the barnacle *Semibalanus balanoides* suffers less mortality when growing at high density than at low or medium density. Dense stands of barnacles shade the rock surface, so that it remains cooler than areas supporting lower barnacle densities, and, as a consequence, barnacles in dense aggregation experience less thermal stress.

Under more benign conditions, high population density and species interactions can increase the likelihood of disturbance by an external force. For example, when barnacles recruit in high numbers to sites with plentiful food, few predators, and moderate physical conditions, they quickly grow to fill the open space. As they come into contact with neighboring individuals, they begin to grow upward instead of expanding at the margin. This process leads to the formation of hummocks of weakly attached, elongate individuals that are more prone to being torn loose by wave forces than are barnacles of the shorter, conical shape characteristic of individuals growing at lower densities. Similarly, as mussel beds *(Mytilus californianus)* develop, individuals coalesce into aggregations that form a single-layer over the rock surface, to which the byssal threads of most individuals are attached. As the mussels grow larger and new individuals recruit to the bed, primary space becomes limiting. The bed gradually becomes multilayered, with an increasing proportion of mussels being attached to the shells of other mussels rather than to the rock itself. Multilayered beds have a higher profile than single-layered beds and develop hummocks, where densely packed individuals have been lifted away from the substratum. As this bed morphology develops, a lifting force is generated by the pressure difference between the water that slowly flows through the interstices of the bed and the rapidly flowing water within waves that break over the top of it. This force pulls weakly attached mussels out of the bed, increasing the roughness of the bed surface. As edges of disrupted sections of the bed are projected into the flow, drag increases, and the fabric-like matrix of mussels begins to flap in flow and to peel away from the substratum, creating patches of cleared space.

This feedback between the growth and development of an assemblage and its vulnerability to one or more agents of disturbance has the potential to generate endogenous cycles of disturbance within some communities. For example, long-term monitoring of *Mytilus californianus* beds at a wave-exposed site on the outer coast of the Pacific Northwest of the United States has shown that any given area of mussel bed is redisturbed by wave forces at an average interval of 7–8 years. This coincides with the duration of succession from bare rock to a mature, multi-layered, wave-vulnerable mussel bed. Thus, it appears that the rate of succession and associated changes in community vulnerability to disturbance strongly influences the disturbance recurrence interval. At less wave-exposed sites, the interval between successive disturbances is longer. This is because succession to a more vulnerable state is slowed by a lower supply of propagules (i.e., lower recruitment), lower concentrations of suspended food and dissolved nutrients (i.e., slower growth), and more stressful abiotic conditions (i.e., more desiccation), and because forceful waves are less frequent.

THE IMPACT OF DISTURBANCE

The impact of disturbance is "in the eye of the beholder." For example, the loss of several fronds from an alga as a result of moderate drag forces can markedly affect its subsequent growth or reproduction but may have little or no effect on the dynamics of its population or the structure of the community in which it lives. In contrast, if intense forces associated with a large wave break an alga's stipe or tear its holdfast from the rock, not only is the individual alga affected, but so are the density and age/size structure of its population. Furthermore, the space opened by the disturbance becomes available for colonization, which is likely to alter assemblage structure.

From a population or community dynamics perspective, a disturbance has occurred when an external force or physiological stress kills one or more resident organisms or damages them sufficiently to indirectly affect the abundance of other organisms in the assemblage. The indirect effect of this damage may be positive or negative. When damage frees up limiting resources, other organisms may benefit. In rocky intertidal habitats, bare space is the most important limiting resource for most sessile and some mobile species (e.g., limpets). It allows for secure attachment, access to resources (light and suspended and benthic food), and room for growth and reproduction. On the other hand, damage to an organism by disturbance may disrupt a mutualistic or predator–prey interaction, adversely impacting nontarget species.

Effects of Disturbance Characteristics on Succession

The severity, size, and location of a disturbance can markedly affect the patterns and mechanisms of regeneration. A very intense, acute disturbance may kill all residents in the affected area, in which case the site can be recolonized only via the settlement and recruitment of juvenile stages (larvae, spores, or zygotes) dispersing in from outside source populations or from the lateral movement of older individuals living just outside the disturbed area. In contrast, reoccupation of open space generated by less severe disturbances can also be from vegetative regrowth of damaged survivors. The relative contribution of vegetative regrowth obviously depends on the growth form of the affected species. Hard-shelled, "unitary" organisms, such as barnacles and mussels, cannot regenerate from severe damage, while "modular" organisms, such as many red and brown macroalgae and clonal invertebrates such as sponges, bryozoans, colonial tunicates, and some species of anemones, are capable of vigorous regrowth from surviving tissues. Generally speaking, a disturbed assemblage will regenerate more rapidly and with greater fidelity to its original composition when reestablishment can occur by vegetative regrowth than when recruits must come from outside the affected area.

Succession is the sequence of species replacements that occurs during recolonization of a disturbed area. Early successional species colonize shortly after a disturbance; characteristically, such species produce many small propagules (e.g., spores or larvae) that are dispersed over large distances. In contrast, the later successional species, which replace earlier colonists, produce fewer, larger propagules that are not dispersed as far from the parent. Because of these life history differences, the size of a disturbed area can influence the rate of successional replacement, particularly following a severe disturbance, in which recruits must come from outside the patch. When the disturbed area is small, both early- and late-arriving species can colonize the entire area, which usually results in a faster sequence of species replacement than occurs in large cleared patches. In contrast, only better-dispersing early successional species may be able to immediately colonize the centers of large disturbances; the more poorly dispersing species that typically dominate later in the sequence must slowly colonize their way into the center over multiple generations. This slow encroachment by late successional species may be by propagule dispersal, vegetative growth, or both.

Disturbance size can also indirectly affect successional dynamics by influencing the impact of consumer species. The influence of selectively grazing limpets on algal succession in patches cleared by disturbance in intertidal mussel beds is a good example. When wave forces or drifting logs create patches of bare space in mussel beds, limpets inhabiting the surrounding intact bed forage only a limited distance (about 10–15 cm) into the patch. Thus, the entire interior of small clearings (<20–30 cm in diameter) will be grazed, while the centers of large clearings remain ungrazed (Fig. 2) until the edges of the mussel bed encroach or a protective canopy of large algae develops in the clearing. Consequently, the centers of large disturbed patches provide temporary refuges for algal species fed on by limpets. This interaction between the size of a disturbed area and grazing pressure affects the rate and pattern of algal recolonization and the species composition of the assemblage that develops. Large clearings develop dense canopies of species whose juvenile stages are vulnerable to

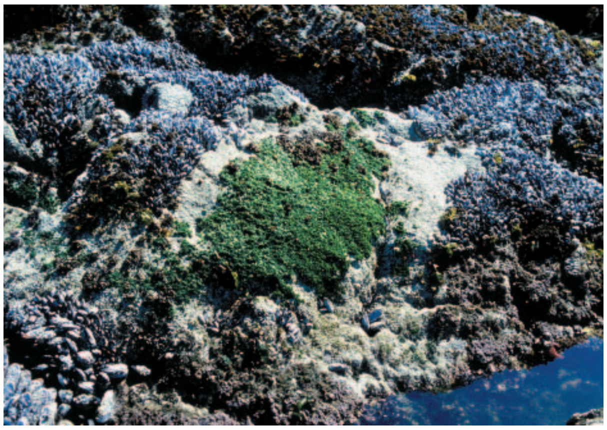

FIGURE 2 Recolonization of a patch of bare space created by wave forces in a bed of the mussel *Mytilus californianus*. A dense turf of the early successional green alga *Ulva* dominates the center of the clearing; the bare zone around the perimeter of the patch is maintained by limpet grazing. Limpets forage only 10–15 cm from the protective environment of the surrounding mussel bed. Photograph by the author.

grazers, whereas small clearings are dominated by algal species that grow as grazer-resistant turfs or crusts.

Effects of Disturbance Characteristics on Population Dynamics

Discussions by non-ecologists of the impact of disturbance in natural communities commonly emphasize the losses resulting from disturbances: Organisms are damaged or killed, and their population density is reduced, sometimes resulting in local extinction. However, as is true for other ecosystems, the abundances of certain intertidal organisms are enhanced by particular regimes of disturbance; in fact, some appear to have evolved a dependence on disturbance for their persistence. Two particularly compelling examples, one an invertebrate and the other an alga, come from seashores along the Pacific coast of North America. Recruitment of the sabellid polychaete worm *Phragmatopoma californica*, which can be found growing in dense aggregations in rocky intertidal (Fig. 3) and shallow subtidal habitats from central California to Panama, is strongly enhanced by disturbance. Larvae of this species settle in dense aggregations on the rock surface. Individual worms live in tubes constructed of cemented sand grains; neighboring tubes fuse to form large, honeycomb-like structures that can be 50 cm thick and cover several square meters of substrate. These aggregations are often disturbed during winter storms by strong wave forces or wave-borne projectiles. When the tubes are broken, large numbers of eggs are spawned and then fertilized in the water column. The larvae are competent to settle 2–8 weeks later, but they can delay settlement and remain in the plankton for several months. A study in southern California found that recruitment of *Phragmatopoma* was highly correlated with wave power measured at the monitored sites 2.5–5 months earlier, with the highest correlation at a 5-month lag interval. In addition, recruitment of the worm was highest during years with the greatest storm activity.

FIGURE 3 Aggregations of the sabellid polychaete worm *Phragmatopoma californica*, growing along the edge of a rocky intertidal bench. Photograph by the author.

Not only are populations of the sea palm *Postelsia palmaeformis* enhanced by a certain regime of space-clearing disturbance, but their persistence may depend on it. This brown alga has an annual life history: The macroscopic sporophyte phase of its life cycle recruits most densely in disturbance-generated clearings in beds of the mussel *Mytilus californianus* (Fig. 4). The mussel is a superior space competitor; as it gradually reoccupies the patch by larval recruitment or the inward movement of edge individuals, fewer and fewer sea palm sporophytes are able to establish each generation. Eventually, the local density of sporophytes falls below that which can produce sufficient gametophyte stages to maintain the population, and the local population goes extinct. For *Postelsia* to persist across

FIGURE 4 Stands of the sea palm *Postelsia palmaeformis*. The clumps of sporophytes occupy patches of cleared space that were opened by wave forces within a bed of the mussel, *Mytilus californianus*. *M. californianus* is the dominant space competitor at this tidal height. Photograph by the author.

an intertidal landscape that is dominated by mussels, new disturbances must create cleared space within the dispersal distance of the alga's spores (roughly 1–3 m from the edge of an adult stand). Its spores must then successfully colonize this open space within the time it takes for the source population to go extinct or fall to such low density that successful dispersal is precluded. Therefore, regional extinction will occur when either the average disturbance rate (area cleared per unit time) is too low or the interval between successive disturbances is too long. The term "fugitive species" has been coined for organisms that, like *Postelsia*, experience frequent population extinction at small spatial scales but nonetheless persist at larger scales by virtue of being able to rapidly establish new populations in recently disturbed sites where resources are plentiful.

Effects of Disturbance Characteristics on Community Structure

LOCAL SCALE

The disturbance regime has a marked influence on the kinds, numbers, and relative abundances of species in a local community. When disturbance is chronic and severe, the time between events is so brief that few if any invertebrates or macroalgae can colonize and grow to maturity; under such conditions the habitat will remain relatively barren, except for rapidly colonizing films of diatoms or persistent, disturbance-resistant crusts of some coralline algal species. When disturbance is slightly less frequent and severe, the assemblage will be dominated by early successional species (e.g., green algae such as *Ulva*) that can colonize and grow rapidly during the short intervals between successive disturbances. As the interval between disturbances increases or their severity declines, a more diverse suite of longer-lived, more slowly colonizing species are able to establish and gradually replace early successional species. Where disturbance is rare, succession is able to continue uninterrupted, leading to dominance of the assemblage by one or a small number of long-lived late successional species and a decline in species diversity. The mechanisms of successional replacement can be several, including competitive exclusion of early by later species or differential resistance of later species to consumers (e.g., predators or grazers) or pathogens. Such observations inspired the Intermediate Disturbance Hypothesis, which predicts that local species diversity will be maximal when disturbance occurs with intermediate frequency and severity. Such a disturbance regime allows both sufficient time for species to accumulate and a sufficient rate of resource renewal to prevent dominance by one or a few late successional species. The community is maintained in a diverse, mid-successional state. The faster the rate of successional replacement, the higher the disturbance rate must be to maintain diversity. The role of intermediate disturbance rates in maintaining rocky intertidal diversity has been most clearly documented in boulder fields, where wave forces overturn the boulders at frequencies inversely related to their size and mass. When a boulder is flipped over, organisms on what was formerly the upper surface are abraded, suffocated, or shaded to death. When the boulder is later righted to it original position, the denuded surface is available for recolonization. Boulders of intermediate size are overturned by storm waves less frequently than smaller boulders but more frequently than large boulders. As a consequence, the algal assemblages on their upper surfaces are maintained in a middle successional stage that is more diverse than the early or late successional stages that characterize the surfaces of smaller and larger boulders, respectively.

An alternative mechanism by which disturbance can maintain high local diversity is called the Compensatory Mortality Hypothesis. If damage or mortality caused by disturbance falls disproportionately on the species that dominates late in succession, it will be prevented from excluding earlier successional species, and diversity will be maintained. In other words, the selective impact of disturbance on the potential dominant compensates for its competitive or other advantage over earlier successional species. Although some selectively feeding intertidal predators have been shown to maintain diversity by this mechanism, there do not appear to be any examples of compensatory mortality caused by physical agents. The increased vulnerability of older, multi-layered *Mytilus* *californianus* beds to wave forces is a possible example. In this case, however, competitive exclusion of earlier successional species has already occurred long before disturbance intercedes, so diversity is not being maintained, strictly speaking.

REGIONAL SCALE

The regime of disturbance also affects the species composition and dynamics of assemblages over larger areas comprising multiple local patches of habitat; this is often referred to as the regional or landscape spatial scale. As describe earlier, the occurrence of disturbance varies in space and time and often transforms rocky intertidal landscapes into mosaics of different successional stages that vary in species composition and diversity as a function of the time since the last disturbance event. This is true of continuous rocky shores (Fig. 5) as well as inherently patchy habitats such as intertidal boulder fields (Fig. 6).

FIGURE 5 Intertidal mosaic of algal- and mussel-dominated patches. These two phases of the mosaic represent, respectively, mid- and late stages of succession following space-clearing wave disturbance. Photograph by the author.

The richness and diversity of species that occupy such a landscape will be highest when the variance in patch age (i.e., time since last disturbed) across the landscape is maximal. Typically, this will occur at sites with intermediate rates of space-clearing disturbance. If the rate is very high, most clearings will be in an early stage of succession, dominated by a small number of rapidly colonizing species. If the rate of disturbance is low, most clearings will be in a late stage of succession, dominated by competitively dominant or consumer-resistant species that have replaced earlier colonists. At intermediate rates of disturbance, most patches will be in a diverse middle successional stage composed of a mixture of surviving earlier colonists and establishing later colonists.

FIGURE 6 Boulders supporting different stages of algal succession following overturning of the substrate by wave forces. The recently disturbed boulder in the center of the photo is covered with the early successional green alga *Ulva*. The surfaces of surrounding, undisturbed boulders are covered with late successional red algae. Photograph by the author.

The regime of disturbance that maximizes species diversity depends on myriad characteristics of the initial disturbance (e.g., distributions of size, shape, and severity), its spatial and temporal pattern of occurrence, and the life histories and other aspects of the biology of the affected organisms and other species that might newly colonize the system from outside. Precise predictions are made all the more challenging because these factors rarely operate independently. Interactive effects are commonplace; some were mentioned earlier, and the interested reader can find a more detailed discussion of these complex but important phenomena in the Further Reading.

Effects of Anthropogenic Disturbance

Rocky intertidal habitats are increasingly affected by various forms of disturbance caused by human activities. Anthropogenic agents of disturbance include increased rates of sedimentation associated with shoreline development or the installation of breakwaters, oil spills, trampling, and harvesting of edible or bait species. Some, such as exposure to oil, are qualitatively novel agents of disturbance for most rocky intertidal communities, to which member species cannot have evolved morphological resistance, physiological tolerance, or compensatory life history attributes. Other kinds of human disturbance, such as trampling and sedimentation, are qualitatively similar to natural agents of disturbance but differ in their patterns of occurrence and severity of effect. They often occur more frequently and at times that do not match the seasonality of comparable natural disturbances. In addition, their impacts are often more severe and chronic. Consequently, we expect the changes resulting from anthropogenic disturbance to be more extreme and persistent than those of natural disturbance events.

SEE ALSO THE FOLLOWING ARTICLES

Biodiversity, Maintenance of / Ice Scour / Projectiles, Effects of / Size and Scaling / Succession / Wave Forces, Measurement of

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