

# Chapter 7

## Disturbance and Patch Dynamics on Rocky Intertidal Shores

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### I. INTRODUCTION

The zonation of animal and plant populations with tidal height is one of the most cosmopolitan and often-studied features of rocky intertidal shores (Lewis, 1964; Stephenson and Stephenson, 1972). Physiological stress due to exposure and bio-

logical interactions such as predation (or grazing) and interspecific competition constrain organisms to live within characteristic, if somewhat fluctuating, vertical limits on the seashore (see, e.g., Connell, 1961a, 1972; Paine, 1974; Schonbeck and Norton, 1978, 1980; Lubchenco, 1980; Underwood, 1980; Robles and Cubit, 1981). Within these distributional limits, populations are subjected to a variety of natural disturbances. Selective pressures associated with different regimes of disturbance have probably been important in the evolution of the diverse life histories exhibited by intertidal organisms (see, e.g., Suchanek, 1981). That disturbance is common in this habitat does not negate the fact that biological processes such as larval settlement, interspecific competition, and predation are also important determinants of community structure (Connell, 1972; Paine, 1977; Underwood and Denley, 1984). In fact, the interplay between disturbance and these biological processes accounts for much of the organization and spatial patterning of intertidal assemblages.

This chapter deals primarily with the effects of natural disturbance on the assemblages of sessile algae and invertebrates that occupy the surfaces of intertidal rocks. Space for attachment and/or resources associated with open substrates (e.g., light, access to suspended food) are usually the prime limiting requisites. Not surprisingly, species that are poor competitors for primary space [colonizable rocky substratum including that encrusted by some coralline algae; *sensu* Dayton, (1971) and Paine, (1974)] commonly exhibit facultative epizoisism or epiphytism. Here, I consider only the dynamics of assemblages occupying primary space. Organisms secure space by overgrowing or laterally crushing their neighbors, by spreading vegetatively into open space, or by growing from settled propagules (zygotes, spores, or larvae). Propagules are often unable to invade occupied surfaces (see, e.g., Sousa, 1979a; Dayton, 1973; Denley and Underwood, 1979; Paine, 1979) and depend on disturbances to create the open space required for colonization. Since the damage caused by most disturbances is localized, primary space is often provided as more or less discrete patches. Various attributes of a newly created patch—for example, its size, shape, and location—can affect its colonization and ensuing biological interactions. Thus, localized disturbances transform an assemblage of sessile organisms into a mosaic of patches varying in such characteristics as size and age (time since last disturbed) and, consequently, in species composition.

While the majority of the examples in this chapter are drawn from studies of temperate rocky shores, this does not imply that disturbance is uncommon on seashores at other latitudes. This bias merely reflects the geographical distribution of research activity.

The term “disturbance” has been used rather loosely in the ecological literature. Some authors (see, e.g., Dayton, 1971) apply it to any mechanism that renews the limiting space resource but distinguish between disturbances of physical versus biological origin. The latter are referred to as “biological disturbances” and encompass everything from singular acts of predation that free space occupied by the prey individuals killed (or displaced via behavioral escape from the vicinity of the predator) to nonpredatory acts (e.g., hauling-out behavior of pinnipeds: Boal, 1980)

that inadvertently kill or displace other organisms. Similarly, the foraging or territorial defense behavior of motile consumers sometimes causes mortality of non-prey species (e.g., bulldozing of sessile species by limpets: Dayton, 1971; Stimson, 1973; Choat, 1977). This chapter will focus primarily on the effects of physical disturbance.

Physical disturbances to intertidal assemblages include burial under sand or terrigenous sediments and associated scouring (Markham, 1973; Daly and Mathieson, 1977; Robles, 1982; Seapy and Littler, 1982; Taylor and Littler, 1982; Littler *et al.*, 1983), overturning of unstable substrata by wave action (Sousa, 1979b), exfoliation of the rock surface (Frank, 1965), impact and abrasion by large water-borne objects (see, e.g., logs: Dayton, 1971; Dethier, 1984; Sousa, 1984; J. Cubit, on intertidal reef flats in Panama: personal communication; cobble: Lubchenco and Menge, 1978; Sousa, 1979b; Wethey, 1979; Robles, 1982; Dethier, 1984; D. Lindberg, personal communication; ice: Stephenson and Stephenson, 1954, 1972; Dayton *et al.*, 1970; Schwenke, 1971; Wethey, 1979), and stresses associated with wave action that detach organisms from the rock surface (Jones and Demetropoulos, 1968; Seed, 1969; Harger and Landenberger, 1971; Paine, 1974; Grant, 1977; Lubchenco and Menge, 1978; Suchanek, 1978; Menge, 1979; Underwood, 1980; Paine and Levin, 1981; Paine and Suchanek, 1983; Dethier, 1984; Sousa, 1984). Climatic extremes experienced during prolonged low tides can also act as physical disturbances. For example, low (Crisp, 1964; Connell, 1970; Dayton, 1971; Paine, 1974) or high air temperatures with associated desiccation stress (Lewis, 1954; Hodgkin, 1960; Connell, 1961b; Frank, 1965; Glynn, 1968, 1976; Sutherland, 1970; Branch, 1975; Emerson and Zedler, 1978; Suchanek, 1978; Sousa, 1979b; Underwood, 1980; Hay, 1981; Seapy and Littler, 1982; Taylor and Littler, 1982; Tsuchiya, 1983) also kill or defoliate algae and cause mortality of sessile and mobile invertebrates. With notable exceptions (see, e.g., Seapy and Littler, 1982), few studies have quantified the amount of colonizable space generated by such severe climatic events or documented subsequent patterns of recolonization.

Very extensive areas of open space are occasionally generated by large-scale earth movements such as landslides (Garwood *et al.*, 1979), lava flows (Townesley *et al.*, 1962; see also Grigg and Maragos 1974, Fig. 1), and uplifting by earthquakes (Haven, 1971; Johansen, 1971). For obvious reasons, studies of the effects of such phenomena on intertidal communities are rare. J. Cubit and S. Garrity (personal communication) are presently documenting patterns of succession along the Pacific coast of Panama on shorelines newly created by landslides resulting from an earthquake in 1976 (Garwood *et al.*, 1979). Haven (1971) and Johansen (1971) studied the effects of uplifting by the Alaskan earthquake of 1964 on intertidal invertebrate and algal assemblages, respectively. They examined patterns of mortality and changes in zonation caused by vertical displacement of portions of the shore. Lebednik (1973) conducted a similar study of changes in algal zonation on an intertidal rocky bench uplifted by underground nuclear testing on Amchitka Island, Alaska. The remainder of this chapter explores the effects of the more common, smaller-scale disturbances described above.

## II. KINDS OF OPEN SPACE PRODUCED BY DISTURBANCE

Disturbances can generate at least two very different kinds of open space: (a) patches within occupied sites, and (b) patches isolated from occupied sites (hereafter referred to as types 1 and 2, respectively). The extent of the damage and the physical dimensions of the rock surface will determine whether a disturbance generates type 1 or type 2 patches.

Patches of bare space cleared in mussel or algal beds are examples of the first kind of patch. The space opened up by the disturbance (e.g., wave impact or log battering) is smaller than the area of continuous occupied substratum so that the open space is bounded by living organisms (this is, in fact, how the patch is discerned). The overturning of a boulder by wave action also frees space for colonization. When this event clears the entire surface of the boulder, the area of the damage is identical to that of the substratum. The resulting patch of open space is not contiguous with the occupied substratum (except when boulders come into direct contact) and is an example of the second kind of patch. Type 2 patches are more characteristic of systems in which areas of continuous substrata are relatively small (e.g., boulder fields). However, even a relatively large section of shoreline bounded by surge channels or sand beaches may become a large isolated patch if it is subjected to a large disturbance over its entire surface. Paine and Levin (1981, p. 161) described such a situation on shores dominated by mussel beds. Conversely, small type 1 patches may be generated in the cover of sessile organisms on a boulder if, for example, the boulder is overturned only briefly or is struck by wave-borne cobbles or logs (Sousa, 1979a, 1980).

A similar dichotomy in patch types applies to subtidal assemblages of sessile invertebrates (Connell and Keough, Chapter 8, this volume). As discussed below, this distinction has important implications for the mode of patch colonization and for regional population dynamics.

## III. CHARACTERISTICS OF THE DISTURBANCE REGIME

While physical disturbances have been recognized as having an important influence on intertidal community structure for more than a decade (Dayton, 1971), surprisingly few studies have gathered quantitative information concerning regimes of natural disturbance in rocky intertidal habitats. The effects of disturbances vary in areal extent, intensity, and frequency. These features of the disturbance regime often influence subsequent patterns of secondary succession within disturbance-generated patches of open space.

### A. Areal Extent

The patches of open space created by physical disturbances vary in size. Some are quite small, as when a single plant or animal is removed from the substratum. At

the opposite extreme, some disturbances (e.g., sand inundation) may denude large sections of seashore. To my knowledge, only two studies have documented the size distributions of such patches. Paine and Levin (1981) have shown that the size distribution of storm-generated clearings in mussel beds on the outer coast of Washington State is well approximated by a lognormal distribution. The mean patch area was found to vary with the season, year, and site, reflecting the temporal and spatial variation in wave stress. Patches born in the relatively calm summer months tended to be smaller (range of means at four sites: 103–652 cm<sup>2</sup>) than those produced in the winter (162–6374 cm<sup>2</sup>), when wave energy was greater. Patches at relatively protected mainland sites on the Olympic Peninsula were about an order of magnitude smaller than those on nearby Tatoosh Island, which receives heavy wave action.

The precise mechanism by which patches are created in mussel beds and the factors that determine the size of a patch at birth are unknown (see Paine and Levin, 1981, pp. 150–151). There is also some disagreement as to whether the exposed edges of extant clearings are more likely to experience subsequent disruption (resulting in an expansion of the patch area) than are intact portions of the mussel bed. Dayton (1971) inferred from occasional observations made at three outer coast sites that some patches expanded in area by an average of 24–4884% (low to high exposure sites, respectively) over a 24-month period following initial disruption of the bed. Such a situation would be analogous to the phenomenon of wave-regenerated balsam fir (*Abies balsamea*) forests at high altitudes in the northeastern United States (Sprugel, 1976; Sprugel and Bormann, 1981). However, Paine and Levin (1981) found that patch size in mussel beds is generally fixed at birth and suggested that coalescence of several small neighboring patches into one large one may give the false impression (particularly if observations are only occasional) that patches grow in size by erosion along their edges. No other studies have measured the size distributions of type 1 patches on the seashore.

The size distributions of type 2 patches are determined by the dimensions of the discrete substrata. For example, when a boulder is overturned by waves and remains so for some months (Sousa, 1980), the algae and sessile invertebrates on what was formerly its top surface are killed. If subsequent wave action rights the boulder, a discrete patch of open space becomes available for colonization. The size distribution of such patches is identical to that of the population of boulders that has experienced disturbance of this intensity.

I have shown (Sousa, 1979b) that the size of boulders overturned by waves varies with season and site. The percentage of large boulders moved by waves was greater in winter months and at the more exposed of my two study sites. Casual observations over the past 8 years indicate tremendous annual variation in the size of boulders moved by storm waves, a reflection of annual variation in the intensity of storms. On the mainland near Santa Barbara and on San Nicholas Island in southern California, S. Swarbrick, R. Dean, and D. Lindberg observed (personal communication) the horizontal displacement of entire boulder fields following an unusually severe storm in the winter of 1983.

## B. Intensity

Landslides, lava flows, geological uplifting, and smaller-scale exfoliation or fracture of a rock face produce surfaces that are biologically sterile, but such events are rare. The more common forces of disturbance in the intertidal zone (listed earlier) cause variable amounts of damage to attached organisms. At maximal intensity, they remove all macroscopic organisms, leaving only microorganisms on the rock surface. The existence of surviving dormant propagules of macroorganisms (e.g., algal spores) analogous to buried dormant seeds in terrestrial soils (Kivilaan and Bandurski, 1973; Marks, 1974; Harper, 1977; Gross, 1980; Gross and Werner, 1982) remains an interesting possibility that has yet to be rigorously verified in the field. Less intense disturbances often leave survivors with repairable injuries. This is especially true for some species of macroalgae that possess a remarkable ability to regenerate from small surviving fragments or crusts persisting within cracks or crevices in the rock surface (Dayton, 1975; Lubchenco and Menge, 1978; Lubchenco, 1980; Sousa, 1980; Dethier, 1984). In contrast, the effects of disturbance on the predominantly solitary intertidal invertebrate fauna (as opposed to colonial ones: Jackson, 1977a; Connell and Keough, Chapter 8, this volume) tend to be all or none. That is, either an individual is removed from the rock surface or it is unaffected altogether (except possibly indirectly due to changes in the composition and abundance of its neighbors or natural enemies). As a result, patches created in monospecific stands of mussels or barnacles are usually devoid of living macroorganisms at birth (Paine and Levin, 1981; W. Sousa, personal observation).

The degree of damage caused by a disturbing force depends on (a) the magnitude of the force, (b) physiological and morphological characteristics of the organisms in question, and (c) the nature of the substratum to which the organisms are attached. A stronger disturbing force is more likely to cause intensive damage; however, an organism's size and shape affect the magnitude of the force it encounters. Intertidal organisms on wave-swept shores experience drag, lift, and accelerational forces due to the moving water (Koehl, 1977, 1982; Denny *et al.*, 1985). As an organism grows larger, the drag and lift forces it experiences (due to instantaneous nonaccelerating water flow) increase. If, however, the organism grows isometrically (i.e., with constant shape), these increased forces associated with large size are distributed over a proportionately larger area (that projected in the direction of flow), and the stress (force/area) resisted by the attachment or support structures remains constant. If this were the case, the organism would be no more likely to be detached by drag and lift forces when it becomes large than when it was small. However, this situation is sometimes unrealistic. Not all intertidal organisms maintain a constant shape as they grow. It is my subjective impression that the basal holdfast area (or cross-sectional area of the stipe) of many algae becomes proportionately smaller (compared to the area exposed to flow) as the plant grows. Morphological measurements made by Santelices *et al.* (1980) indicate that this is true of the brown algae *Lessonia nigrescens* and *Durvillaea antarctica*, which inhabit the low intertidal zone of central Chile. Thus, the stress on the holdfast (or stipe)

due to drag and lift probably increases with size. More importantly, water flow in the intertidal is not steady but alternately moves toward and away from shore and thus is periodically accelerating. Breaking waves and associated eddies also induce large accelerations in the flow. Therefore, in addition to drag and lift, an attached intertidal organism experiences a force termed the "acceleration reaction." In accelerating flow, the magnitude of this force increases with the organism's volume (rather than the projected area), so that the organism experiences increased stress as it grows larger even if growth is isometric. Stress increases with size to some maximum level, the breaking stress, that the organism's tissues or adhesive material can sustain, at which point the organism is partially or completely removed from the rock surface. Wounds caused by grazing or boring organisms are likely sites of breakage (Black, 1976; Koehl and Wainwright, 1977; Santelices *et al.*, 1980) since the stress is imposed on a smaller cross-sectional area. In short, the larger an organism is, the more likely it will be damaged or killed by wave action of a given magnitude. However, the influence of neighboring organisms on the wave forces an individual plant or animal experiences must also be considered. The forces impinging on an isolated individual may be very different from those acting on an individual that is surrounded by organisms of equal or greater stature. To my knowledge, the latter phenomenon has yet to be investigated in detail.

It is not surprising that those organisms that do attain large sizes on the seashore, such as some species of macroalgae, exhibit morphological traits that serve to reduce the hydrodynamic forces acting on them (Koehl, 1979, 1982; Denny *et al.*, 1985). Regardless, overgrowth by epizoid or epiphytic organisms may increase the forces acting on a host and thus increase the likelihood that it will be dislodged during heavy wave action (Menge, 1975; Sousa, 1979a).

Similar considerations may apply to groups of sessile organisms. Assemblages can become more vulnerable to disruption as their individual members increase in size and number. Two examples illustrate this point. Following an initial dense settlement in an area with few predators, newly recruited individuals of the barnacle *Balanus balanoides* often grow to fill the available space. The ensuing competition for space forces neighboring barnacles to coalesce and form hummocks of weakly attached, elongate individuals (Barnes and Powell, 1950; Connell, 1961b; Menge, 1976; Grant, 1977). Such hummocks of barnacles are more easily torn loose by wave action than are individuals of the conical or columnar form that develops under less crowded conditions. Similarly, as beds of the mussel *Mytilus californianus* exhaust the available primary space, continued recruitment from the plankton causes them to become multilayered. Multilayered beds have a higher profile than single-layered ones, and a higher proportion of individuals in the former are attached by byssal threads to neighboring mussels rather than to the rock surface. This makes multilayered beds less stable and more subject to disruption by wave forces than single-layered beds (Paine, 1974; Paine and Levin, 1981).

In some situations, the opposite relationship between individual size and the likelihood of disturbance may pertain. Small individuals may succumb more rapidly than large individuals to physiologically stressful conditions such as low or high

temperatures, desiccation, and so on, presumably due to their greater surface-to-volume ratio (see, e.g., Connell, 1961b; Wolcott, 1973). However, in many instances, the microclimate that a small individual experiences may be moderated by the presence of neighboring organisms that block the flow of air, cast shade, or retain moisture. Small organisms can also more easily seek refuge from extremes of the physical environment within cracks and crevices in the rock surface than can large organisms.

There are likely to be species-specific differences in vulnerability to particular kinds and magnitudes of disturbing forces. My own experiments (Sousa, 1980) demonstrated that macroalgal species differ in the degree of damage they suffer when the substrate to which they are attached is overturned by waves. Similarly, there are marked differences in the responses (i.e., amount of cover lost) of intertidal plants and animals to aerial exposure and burial under sand or terrigenous sediments (Seapy and Littler, 1982; Taylor and Littler, 1982; Littler *et al.*, 1983). Littler and Littler (1980) found that under the same regime of wave exposure, some species of macroalgae suffer greater loss of tissue than others.

The nature of the substratum to which an organism is attached may also influence the vulnerability of the organism to wave forces. Barnes and Topinka (1969) showed that the force required to detach the alga *Fucus* is less if the plant is growing on the test of a barnacle than if it is attached directly to the rock surface. In some cases, the adhesive strength of an organism may exceed that of other organisms to which it is attached or the breaking stress of the rock surface itself. When the rock or host organism breaks, the attached individual is carried away (Dayton, 1973; Denny *et al.*, 1985).

### C. Frequency and Seasonality

The frequency of disturbance determines the interval of time over which recolonization can occur. Some kinds of disturbance such as landslides are rare, while others such as wave shear occur frequently. The precise frequency of a particular kind of disturbance is determined (a) by temporal variation in the strength of the force that creates the disturbance and (b) by the "intrinsic vulnerability" of the organisms or substratum (if movable, as in the case of boulders) to which a force of given magnitude is applied.

The magnitudes of forces capable of disturbing intertidal assemblages vary in time; in most cases, they are highly seasonal. Mortality due to heat and/or desiccation stress at low tide occurs during periods of calm, clear weather when there is little wave splash to ameliorate the harsh conditions of exposure. The seasonal timing of such events will depend on the local tidal and climatic regime. For example, in southern California, these conditions occur in winter, when extreme low tides shift into daylight hours and frequently coincide with hot and dry Santa Ana wind conditions (Sousa, 1979a; Seapy and Littler, 1982). At more northern latitudes on the same coast (northern California, Oregon, and Washington), daytime



low tides and long exposures occur in summer, as does the mortality caused by desiccation stress (Frank, 1965; Sutherland, 1970; Dayton, 1971; Cubit, 1984).

Wave energy is maximal in winter along most temperate coasts, causing marked seasonality in related disturbances. The mean rate at which patches are cleared in beds of the mussel *M. californianus* on the outer coast of Washington State (measured as the percentage of the bed cleared per month) is more than an order of magnitude greater in winter than in summer (Paine and Levin, 1981). Similarly, the probability that a boulder will be disturbed by wave action is much higher in winter (Sousa, 1979b). In any season, not unexpectedly, this probability decreases with the size (i.e., mass) of a boulder, an intrinsic property of the substrate. As mentioned earlier, the frequency of disturbance varies among years and sites in both of the above systems.

Wethey (1979) documented marked seasonality in the physical disturbances of *B. balanoides* populations on the shore at Nahant, Massachusetts. Scour by floating ice and loose cobbles causes extensive mortality in winter. Ice scour was most damaging to barnacle populations at wave-exposed sites in the mid-intertidal zone, while the impact of cobbles was greatest at wave-protected areas during periods of high winds. Mortality from both sources varied considerably among the three winters of the study. Wethey estimated from weather records that cobble-related mortality in wave-protected areas on the Massachusetts coast has been important every 3–5 years since 1630. Heavy mortality from ice damage at wave-exposed sites has probably occurred once every 10 years in the high intertidal zone and once every 4 years in the mid-intertidal zone over the past 360 years.

Assemblages of organisms living in tide pools may also experience seasonal disturbances; the seasonal likelihood of disturbance varies with the height of the pool (Dethier, 1984). The occupants of high pools tend to be disturbed by heat stress in summer, while those of low pools are disturbed primarily in winter by strong wave forces and the impact of wave-driven logs or cobbles. On average, the inhabitants of a tide pool on the coast of Washington State experience a disturbance (loss of >10% cover within 6 months due to an exogenous factor) every 1.5 years.

Some forms of disturbance such as sand inundation occur exclusively in one season. Most commonly, sand is deposited in summer, when wave energy and current velocities are low (Hedgpeth, 1957; Markham, 1973; Daly and Mathieson, 1977; Robles, 1982), but at certain sites, unique aspects of the local topography and current regime combine to cause deposition only in the winter (Taylor and Littler, 1982; Littler *et al.*, 1983). During the major period of sand intrusion, the degree of deposition may vary in a regular fashion with the tide as well as irregularly with storm activity. Local topographic features (e.g., channels and outcrops) can induce substantial small-scale spatial variation in both the depth and the frequency of sand burial. The deposition of terrigenous sediments carried to the sea by flooded streams and rivers is also highly seasonal and varies in degree from year to year. Seapy and Littler (1982) studied the effects of such an inundation by fine sediments following heavy rains on Santa Cruz Island off the coast of southern California.

In some regions of the world, annual patterns of storm-related mortality are unlikely to be strongly seasonal. For example, on the coast of New South Wales, Australia, rough weather and large storm waves can occur at any time of the year with no obvious seasonality (Underwood, 1981).

The frequency of disturbance, like its intensity, may be influenced by temporal changes in the intrinsic vulnerability of the target organisms. As discussed earlier, such changes occur during ontogeny. As an organism grows, its vulnerability to some disturbing forces (e.g., the drag and accelerational forces associated with flowing water) may increase, while its susceptibility to other stresses (e.g., desiccation) may decrease because of a smaller surface-to-volume ratio. The frequency of disturbance may therefore be linked to the growth rate of an organism. When wave forces are the major disturbing agent, a high rate of individual growth could increase the frequency of disturbance, all else being equal. The opposite might be true in the case of desiccation stress.

The phenomenon of variability in intrinsic vulnerability may operate at the community level as well. As succession proceeds, the vulnerability of the assemblage to disturbance may change, due in some cases to changes in individual as well as group morphology. For example, recolonization of patches cleared in mussel beds on the outer coast of Washington State proceeds through a series of stages: diatoms → macroalgae → barnacles → mussels (Dayton, 1971; Paine, 1974; Paine and Levin, 1981). Beds of mussels, particularly older multilayered ones, are more likely to be dislodged by wave action than are stands of macroalgae or barnacles. Thus, the probability that a patch of clear space will be created depends on the successional age of the assemblage occupying the space. The rate of successional species replacements will therefore control, to some degree, the frequency of disturbance. After a patch of open space has been generated in a bed of *M. californianus*, a minimum of 7–8 years elapse before the same area can be subjected to another major disturbance (Paine and Levin, 1981). This was the shortest rotation period observed; intervals between successive disturbances were longer at less exposed sites. The apparent cyclic vulnerability of some intertidal assemblages to disruption by waves seems analogous to cycles of inflammability controlled by the rate of accumulation of combustible plant material, characteristic of some terrestrial plant communities (White, 1979; Horn, 1981b; Minnich, 1983). It should be noted as well that in some instances the vulnerability of an assemblage to a particular kind of disturbing force may decrease with successional age (Sousa, 1980) if the species characteristic of later successional stages are more resistant to the force than are those of early stages.

The frequency of disturbance need not always be influenced by the successional state of the assemblage. In the boulder fields I studied, the short sessile cover (mostly turflike macroalgae) probably had little influence on the probability that a rock would be disturbed by wave action. On the other hand, in similar habitats supporting larger organisms, the forces associated with waves that act on such individuals may increase the probability that the underlying mobile substratum will be displaced (see, e.g., Schwenke, 1971, p. 1116). If such large species are typical

of later successional stages, the frequency of disturbance will, as discussed above, be influenced by the rate at which succession proceeds.

#### D. Correlations among Characteristics of the Disturbance Regime

The preceding discussion alludes to several important correlations among the individual characteristics of the areal extent, intensity, and frequency of disturbance. In boulder field habitats, all three are linked. When a boulder is overturned by wave action, the organisms on what was formerly its top surface begin to suffer damage and may eventually be killed by a combination of sea urchin grazing, anoxia, light levels below compensation intensity, crushing, and abrasion (Sousa, 1980). The longer a boulder remains overturned, the greater is the mortality of the attached organisms. Since a greater force is required to overturn a large boulder than a small one, and since large winter storms that generate such forces occur less frequently than small storms, large boulders are less likely to be overturned than small boulders. For the same reason, when a large boulder is overturned, it remains turned for a longer period of time than a small boulder. When righted, the former top surface of a large boulder is usually devoid of living macroorganisms. Therefore, in the boulder field system of type 2 patches, large clearings (overturned large boulders) are the least frequent and contain the fewest survivors (they are subject to the most intense disturbances).

There are also interactive effects among some characteristics of the disturbance regimes in more continuous intertidal habitats where type 1 patches predominate. The largest clearings in beds of *M. californianus* are created by forceful winter storm waves (Paine and Levin, 1981) and are therefore less frequent than small clearings that can be produced by waves of lesser magnitude in any season, though most commonly in winter. In mussel beds, unlike boulder fields, the intensity of disturbance does not vary among patches. This is a consequence of both the solitary habit of mussels and the way in which a disturbed patch is operationally identified. A patch exists only when a sufficient number of mussels has been removed to reveal the primary substratum, so by definition there are no "survivors" in a newly created patch regardless of its size or how frequently it is redisturbed. The same is true of patches in assemblages of other solitary species such as barnacles. If, however, one measured the intensity of disturbance as the number of resident organisms removed per unit area, rather than the number that survived within a patch, a three-way interaction among the disturbance characteristics would be expected. Infrequent large storms would affect large areas and cause intense damage. As discussed earlier, the frequency of disturbance might be mediated by temporal changes in the intrinsic vulnerability of the assemblage.

Unlike mussels or barnacles, many species of marine algae are capable of regenerating from small portions of thalli that survive within a patch. Rather than the all-or-none response to disturbance exhibited by solitary invertebrates, the intensity of disturbance to stands of such algae can vary from slight tissue damage to com-

plete mortality. This being the case, I would expect that in assemblages of algae capable of vegetative regeneration, all three characteristics of disturbance would interact in the manner described earlier.

#### IV. MODES OF PATCH COLONIZATION

A patch of open space is colonized (a) by dispersed propagules such as spores or larvae and/or (b) by vegetatively propagating macroalgae and attached but semi-mobile solitary invertebrates (e.g., mussels and sea anemones) that encroach inward from its perimeter. Drifting fragments of macroalgae may sometimes become established within a patch (Sousa, 1979a), but this method of colonization seems far more significant for corals (Highsmith, 1982; Connell and Keough, Chapter 8, this volume). One reason is that coral fragments are much denser in water than are pieces of algae. The former sink to the bottom and can become lodged in a position suitable for attachment and growth. It is much more difficult for a drifting algal fragment to attach firmly to the newly exposed surface of a rock. Colonization by drifting algal fragments will not be considered further.

Rates of colonization by dispersed propagules and vegetative encroachment will depend on a variety of patch characteristics as briefly described in the following sections.

##### A. Patch Type

Earlier, I distinguished between patches that are formed within occupied areas (type 1) and those that are isolated from occupied areas (type 2). Type 1 patches can potentially be colonized either by water-borne propagules or by vegetative encroachment. The relative importance of these modes of colonization will depend on other characteristics of the patch including its location, size, and shape. Type 2 patches can be colonized only by water-borne propagules. Space within both kinds of patches can be filled by vegetative regrowth of surviving algal fragments if the disturbance is not too intense.

##### B. Patch Location

The location of a patch can greatly influence the mode and rate of colonization. Colonization by vegetative ingrowth from the perimeter (or the analogous inward spreading of attached but mobile individuals) is unimportant for most type 1 patches cleared in the midst of nonmobile solitary species such as barnacles or furoid algae. Only the smallest such patches can be filled by the lateral growth of neighboring solitary organisms. The contribution of water-borne propagules to patch colonization may, in some cases, depend on the proximity of the patch to a source of dispersing propagules (i.e., reproductively mature individuals). Several studies

(Dayton, 1973; Paine, 1979; Sousa, 1984) provide evidence of relatively short-range dispersal (i.e., a few meters or less) by the propagules (spores or zygotes) of some species of intertidal macroalgae.

A patch's position with respect to various environmental gradients (tidal height, wave exposure, current velocity, degree of insolation) can directly affect colonization rates (see, e.g., Denley and Underwood, 1979). Those species constrained to live within a particular range of tidal heights will, quite obviously, become important occupants only of patches created in that zone.

### C. Patch Surface Characteristics

Variation in the composition and rugosity of the rock surface among patches may also cause spatial variation in patterns and rates of patch colonization. A number of field (see, e.g., Connell, 1961b; Harlin and Lindbergh, 1977) and laboratory studies (see, e.g., Crisp, 1974; Norton and Fetter, 1981) have demonstrated the influence of relatively small-scale surface texture on the settlement and/or recruitment of algae and sessile invertebrates. Larger-scale heterogeneity in surface texture such as cracks and crevices may affect settlement as well as enhance recruitment by providing refuge from consumers (see, e.g., Lubchenco, 1983, also references cited earlier). On the other hand, at upper tidal levels, consumers themselves may be constrained by physical exposure to forage only over the substratum immediately adjacent to such crevices in the rock surface (see, e.g., Menge, 1976, 1978a; Levings and Garrity, 1983). The type of rock on which the patch occurs may influence the settlement and/or recruitment of some species (Nienhuis, 1969; den Hartog, 1972) but not others (Caffey, 1982). Variation in surface characteristics is likely to be greater among small patches than large ones because the former "sample" a smaller portion of the substratum.

### D. Patch Size and Shape

The size of a disturbance-generated clearing may affect colonization in a variety of ways. Simply as a consequence of greater area alone, large patches would be expected to sample a greater proportion of the pool of available spores and larvae, and might therefore support a greater number of species. In my own study of algal succession in the low intertidal in southern California (Sousa, 1979a), at least two of the algal species that became abundant on 225-cm<sup>2</sup> concrete settling surfaces were nearly absent from smaller 100-cm<sup>2</sup> clearings that were created in monocultures of the dominant alga. However, this result could be attributed to differences other than size between the two kinds of patches. The smaller patches were more spatially isolated from adult plants of these species than were the large patches. In addition, the small patches were surrounded by a dense algal turf that may have harbored small grazers (e.g., amphipods or polychaetes) that preferentially fed on recruits of the two species. The turf surrounding the small patches may have also altered the internal physical environment of these patches in such a way as to

discourage their recruitment. Finally, the type of substrata, one being of concrete and the other of natural sandstone, may have caused different patterns of colonization. This explanation seems unlikely, however, since patterns of recruitment on small (163 cm<sup>2</sup>), experimentally stabilized sandstone boulders placed closer to the concrete blocks, were very similar to those seen on the larger artificial surfaces.

More recently (Sousa, 1984), I documented the patterns of succession within clearings of two sizes in mussel beds. The abundance of only one out of the eight common species of macroalgae that colonized the patches was influenced by the size of the patch per se. This species, the red alga *Endocladia*, colonized patches of both sizes but became more abundant in the larger ones. Again, it is impossible to say whether this resulted from the effect of sampling area alone or from some difference in the internal physical environments of the patches (e.g., humidity, insolation, patterns of water flow) to which this particular species was sensitive. To my knowledge, neither of these effects has been explicitly investigated in intertidal habitats.

Few studies have investigated whether the larvae of intertidal invertebrates can actively select a patch of bare space in which to settle based on its size alone. In the study just described, the size of a patch had no direct effect on recruitment by the mussel *Mytilus edulis*. In contrast, Jernakoff (1983) found that the barnacle *Tesseropora rosea* settled more densely in small (25 cm<sup>2</sup>) clearings in beds of algae than in large (200 cm<sup>2</sup>) ones. The mechanism causing this pattern was not identified.

Differences in the biological environments of patches varying in size have been examined to a limited degree. As discussed in Section V, several studies have demonstrated differences in the density of consumers, especially herbivores, in patches of different size, as well as the effects of this interaction on within-patch dynamics.

Perhaps the most obvious influence of patch size on colonization derives not from the size of a patch per se but from the manner in which the ratio of patch perimeter length to area changes with patch size. This effect is probably most important for type 1 patches cleared in assemblages of species that are able to invade by lateral movement of individuals or by vegetative ingrowth of clones. The rate at which clearings in mussel beds are filled by the lateral encroachment of adults is affected by a variety of features of the patch environment [e.g., depth of the surrounding bed, angle of the substratum (Paine and Levin, 1981)]. All else being equal (including patch shape), however, smaller patches have a greater ratio of edge to area and are therefore closed by the lateral encroachment of mussels at a correspondingly higher rate (Paine and Levin, 1981; Sousa, 1984). Very large clearings in mussel beds are recolonized primarily by settlement of larvae from the plankton. Vegetative encroachment is also an important means of securing space for some turf-forming species of macroalgae (Sousa, 1979a; Sousa *et al.*, 1981), and I would expect the result described above for mussel beds to obtain in patches of different sizes cleared in stands of these species. Connell and Keough (Chapter 8, this volume) and Miller (1982) describe examples of similar phenomena in assemblages of subtidal colonial invertebrates and terrestrial plants, respectively.

The rate of colonization by propagules may also vary with patch size. The number of nearby adults per unit patch area may be greater for small patches than for large patches, and may result in a greater density of settling propagules and more rapid colonization of small patches. This would be important only if these propagules are not dispersed very far from the parent organisms. On the other hand, the recruitment and growth of plants and animals in clearings within stands of erect macroalgae are more likely to be negatively influenced (e.g., through shading, whiplash, competition for nutrients) by the surrounding adult plants when clearings are small than when they are large (Sousa, 1979a). Also, as Connell and Keough (Chapter 8, this volume) suggest, colonization of small patches will be more negatively influenced by the presence of neighboring assemblages of suspension-feeding invertebrates that prey on settling propagules.

The relationship between perimeter length and patch area may also influence the pattern of colonization of isolated discrete patches (type 2). The roughly laminar flow of water over the surface of such patches will often be disrupted at their edges by the formation of turbulent eddies (Hoerner, 1965; Evans, 1968; Foster, 1975; Munteanu and Maly, 1981). Water velocity is slower in these eddies than in the region of more laminar flow near the center of the patch. This slower-moving water may trap spores and larvae and thus enhance their settlement along patch edges (Foster, 1975; Munteanu and Maly, 1981; W. Sousa, personal observation). Once settled, these individuals could enjoy higher rates of growth and/or survival than organisms living in more central areas of the patch because the eddies might concentrate the particulate foods of suspension feeders or make food capture easier. Eddies also reduce the thickness of the boundary layer. The increased water circulation close to the substratum due to the reduction of the boundary layer may enhance rates of nutrient renewal and waste removal for small, newly settled individuals on the edge of the patch. Since a greater percentage of the internal area of a small patch is likely to be influenced by such turbulent patterns of water flow, small patches may be disproportionately colonized by species that benefit from turbulence created at the edges. If the species whose recruitment is enhanced by this "edge effect" is also capable of vegetatively spreading into the center of a patch, it may dominate small patches at an even faster rate (Schoener and Schoener, 1981).

The influence of patch shape on colonization is likely a simple extension of the above arguments. The more circular a type 1 patch of given area, the lower its ratio of perimeter length to area will be, and the more slowly it will be filled by invasion along its perimeter. Predictions concerning rates of colonization of isolated discrete patches (type 2) that differ in shape will be dictated by the extent to which edge-induced turbulence disproportionately enhances colonization of patches with a high perimeter length-to-area ratio.

### **E. Time of Patch Creation**

The time at which a patch is created by disturbance may determine, to some degree, the course of succession because the propagules of certain species are only

seasonally available to colonize (see, e.g., Connell, 1961a,b; Dayton, 1971; Paine, 1977, 1979; Emerson and Zedler, 1978; Denley and Underwood, 1979; Sousa, 1979a; Hawkins, 1981; Suchanek, 1981). Several studies (Paine, 1977; Emerson and Zedler, 1978; Hawkins, 1981) have found that the early successional algal colonists were very different in experimental clearings made in different seasons. In theory, such initial differences might influence subsequent colonization so as to cause large differences in the composition of later successional stages between patches created in different seasons. There is, however, little evidence that this occurs in intertidal communities. Patches created in different seasons eventually come to be dominated by the same long-lived dominant animal or plant species (Paine, 1977; Sousa, 1979a; Hawkins, 1981), although the rate of successional species replacement varies because recruitment and growth are seasonal.

The abundance of a species will be most enhanced by disturbances that create space during periods of time when its propagules are available for settlement. However, any temporal or spatial variation in the distribution and abundance of propagules in the water column will enhance variation in rates of settlement and recruitment among similar patches (Connell, 1961a; Lewis and Bowman, 1975; Bowman and Lewis, 1977; Hruby and Norton, 1979; Caffey, 1982; Hawkins and Hartnoll, 1982; Salman, 1982).

## V. RESPONSES OF MOBILE CONSUMERS TO PATCH CHARACTERISTICS

Within-patch dynamics are influenced by a variety of biotic interactions (Thompson, Chapter 14, this volume). In some systems, the abundance of consumer species within patches and their influence on the composition of the patch assemblage vary predictably with the size of the patch. This phenomenon has been observed in both type 1 and type 2 patches.

Several investigations have found that small patches in beds of the mussel *M. californianus* support higher densities of grazers (especially limpets) than do large patches (Suchanek, 1978, 1979; Paine and Levin, 1979; Sousa, 1984). It has been hypothesized that this pattern occurs because the bed of mussels surrounding a patch serves as a refuge for small grazers from wave shock, desiccation stress, and predation. The observation that grazing by these organisms is largely restricted to a 10- to 20-cm browse zone around the perimeter of the patch (see photos in Dayton, 1973; Suchanek, 1978, 1979; Sousa, 1984) is circumstantial evidence that the beds provide some sort of protection. The consequence of this spatially restricted foraging is that the total area of small patches is subject to relatively intense grazing, while the centers of large patches experience little grazing and therefore develop a more extensive cover of algae. The assemblages of algae that developed within small and large experimental patches differed markedly in composition (Sousa, 1984). The assemblage in small patches consisted of grazer-resistant but apparently competitively inferior species, whereas that in large patches included grazer-vul-



nerable but competitively superior species. The abundance of the mussel *M. edulis* in the experimental clearings was also affected by the interaction between grazing and patch size (Sousa, 1984). The density of *M. edulis* was lowest in small patches from which the green alga *Ulva*, a preferred substratum for the settlement of the mussel, was rapidly removed by grazing. Small mussels may also have been bulldozed off the rock surface by limpets. Similarly, Hawkins (1981) observed that green algae grew only in the centers of cleared areas in stands of barnacles, and attributed this pattern to the grazing forays of small snails (*Littorina*) that apparently refuged among the barnacle tests. Presumably, larger clearings in stands of barnacles would develop a more extensive algal cover than small clearings. Menge (1978b) has shown that predation by the gastropod *Thais* is more intense under a canopy of algae where physical conditions are benign than in the open where conditions are harsher. One could infer that snails consume more prey in small clearings in a stand of algae than in large clearings. This phenomenon is likely to be observed in any system of type 1 patches where natural enemies prefer, or are forced, to live largely within the phase(s) of the community mosaic that surrounds the patch, while their prey occupy the interior of the patch.

The opposite pattern of natural enemies preferring the conditions of the patch interior to those of the neighboring assemblage was demonstrated by Underwood *et al.* (1983). In natural populations, most individuals of the limpet *Cellana tramoserica* are found in clearings free of barnacles. When confined with fences to areas with varying degrees of barnacle cover, limpets suffered greater weight loss and mortality as the density of barnacles increased. The negative influence of barnacle cover was stronger when limpets were enclosed in areas dominated by the larger of the two species of barnacles tested. In a separate experiment, adult limpets were transplanted into unfenced plots in which clearings of different sizes had been created in the barnacle cover. The total cleared area in each plot was equal. Within 2 days, 67–69% of the limpets had emigrated from the plots containing small clearings (mean area = 37–39 cm<sup>2</sup>), while only 3–27% had left the plots with large clearings (mean area = 177–200 cm<sup>2</sup>). Almost all limpets (88–94%) emigrated from control plots in which barnacle cover was not manipulated. The rate of emigration was higher from plots dominated by the larger species of barnacle. In other words, limpets exhibited a behavioral avoidance of areas in which only small patches of bare substratum were available. This avoidance was presumably related to the increased cost of foraging in such areas. The net effect might be that small clearings in stands of barnacles are less intensively grazed by *Cellana* than are large clearings. Interestingly, another species of limpet living on the same shore, *Patelloida latistrigata*, recruited equally well at all barnacle densities, and its adults survived better in the presence of barnacles (Creese, 1982; Underwood *et al.*, 1983). The impact of grazing by this species might be greater in small clearings than in large ones, since its density increases with barnacle density (Creese, 1982).

I documented (Sousa, 1977) an interaction between the size of type 2 patches and the density of consumer species in intertidal boulder fields. The density of limpets was considerably higher on small boulders than on large ones (Fig. 1). The cause of

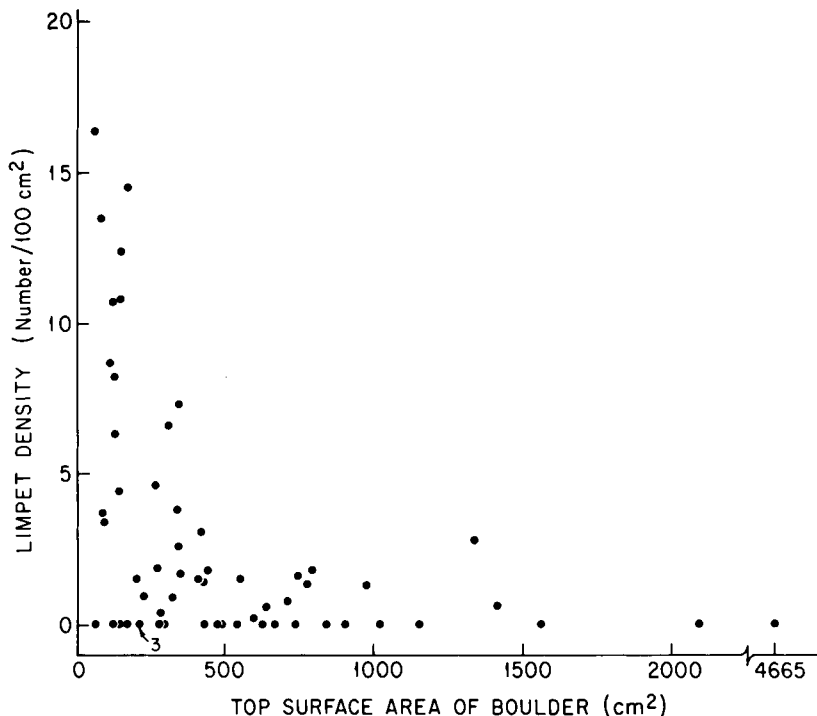


Fig. 1. Density of limpets (*Notoacmea fenestrata*, *Collisella strigatella*, and *Collisella scabra*) on 60 randomly selected boulders of different sizes sampled at Ellwood, California, on July 16, 1974. (See Sousa, 1979a,b, for details.)

this pattern was not investigated but is probably explained by the fact that small boulders are more frequently disturbed by wave action and therefore have more open space for limpet attachment and grazing than do large boulders (see Table 2 in Sousa, 1979b). In addition, limpets prefer to graze on microscopic algae or immature thalli of macroalgae (Nicotri, 1977). These would be more available on more frequently disturbed substrata. The upper surfaces of rarely disturbed large boulders are covered with larger perennial macroalgae. These plants, which are not grazed by limpets, trap sediment or otherwise fill the space, making the rock surface uninhabitable to limpets. A number of studies present evidence that dense stands of macroalgae, particularly in the middle and low intertidal zones, outcompete limpets for space (Dixon, 1978; Sousa, 1979a; Underwood and Jernakoff, 1981; Sousa, 1984). The net effect of this pattern of limpet distribution is that small boulders are more intensively grazed by limpets than are large boulders.

The impact of consumers on prey populations within a patch will also vary with the location of the patch. Herbivores and predators often forage less effectively and/or are least abundant in areas exposed to strong wave action (Menge 1976, 1978a,b; Lubchenco and Menge, 1978; J. F. Quinn, 1979) or shifting sediments

(Robles, 1982). Consequently, their influence on patch colonization by sessile species is likely to be less in such areas. The demography and abundance of populations of mobile consumers may also vary with the composition of sessile organisms among which they live. For example, the density, rate of recruitment, and size distribution of limpet (*Patella vulgata*) populations differ in areas dominated by mussels versus barnacles at the same tidal height (Lewis and Bowman, 1975). Therefore, if a significant proportion of the consumers that forage within a patch come from surrounding occupied areas, identical patches created within different background assemblages may experience different levels of consumer pressure.

## VI. WITHIN-PATCH DYNAMICS

A sequence of species replacements follows the initial colonization of a newly created patch of open space. In its general features, the sequence will be characteristic of the particular tidal height, regime of wave exposure, and geographical locale, all of which will determine the pool of species available to colonize the patch. Patterns of species replacement in various regions of the world are documented in many of the references cited earlier. Any of several mechanisms of replacement may operate at each step in the successional sequence (Connell and Slatyer, 1977; Sousa, 1979a). However, regardless of the mechanisms operating, the sequence of successional replacement tends to be deterministic and usually leads to the monopolization of space within the patch by one or a few competitively dominant and/or long-lived species (see e.g., Paine, 1966, 1974; Dayton, 1971, 1975; Lubchenco and Menge, 1978; Sousa, 1979a; Paine and Levin, 1981). Unless some mechanism (see below) acts to prevent local dominance, populations of species characteristic of earlier stages of succession become locally extinct.

The time to extinction from a patch of those species characteristic of earlier stages of succession will depend on (a) the mode of colonization by the late successional, dominant species, (b) the kind of patch (type 1 versus 2), and (c) the size and shape of the patch. If the late successional species can invade open space both by vegetative encroachment from the borders of the patch and by recruitment of planktonic propagules, dominance will be attained more rapidly than if space becomes occupied primarily through recruitment from the plankton. However, in type 2 patches, even if the late successional dominant is capable of spreading vegetatively or by lateral movement of individuals into open space, the initial colonization must be by dispersed propagules. Consequently, in this situation, dominance of patches will occur more slowly and populations of early successional species will persist longer in type 2 patches than in comparable type 1 patches.

Along a continuous rocky shore, the local extinction and successional replacement of early colonists will be most rapid in small type 1 patches shaped irregularly and created within stands of late successional dominants that are able to fill the patch rapidly by lateral encroachment. Populations of early successional species

will be more persistent in larger, more circular patches (with a smaller ratio of perimeter length to area) since the rate of encroachment by the dominant species will be slower.

Small patches will also be dominated more quickly than large ones when the late successional dominant disperses its propagules only a short distance. In large patches whose radii exceed the dispersal distance of the late successional species, dominance will develop only gradually as colonists spread slowly inward from the border over several generations. No such spatial gradient in settlement will occur in small patches whose radii are short relative to the dispersal distance of the dominant. Propagules will be deposited relatively uniformly and densely throughout such patches, and successional replacement will be relatively rapid.

The opposite relationship between patch size and rates of successional replacement has been hypothesized for systems of type 2 patches in subtidal epifaunal assemblages (Jackson, 1977b; Karlson, 1978; Kay and Keough, 1981; Keough, 1984b; Connell and Keough, Chapter 8, this volume). Early colonists may persist longer in small rather than in large type 2 patches. This could occur if, as often appears to be the case (see, e.g., Sousa, 1979a), the late successional dominant produces fewer propagules and/or disperses them more seasonally than do the species characteristic of earlier stages. Since small patches "sample" less of the available pool of spores and larvae than do large patches, this alone will cause late successional species to be underrepresented in some small patches. Successional replacement of earlier colonists in such patches will be slow and may not occur at all if late successional species have very limited powers of dispersal. In systems of discrete substrata, one might expect a strong selective advantage to accrue to individuals of an early successional species whose propagules selectively settle in smaller patches (Keough, 1984b; Connell and Keough, Chapter 8, this volume). To my knowledge, this phenomenon has not been studied on rocky intertidal shores.

The replacement of a species within a patch may not always be gradual. It may disappear precipitously as the density of its population falls below some lower threshold level necessary for local replacement. For example, populations of the annual brown alga *Postelsia palmaeformis* within open patches in mussel beds rarely persist at densities below 20–30 plants per square meter (Paine, 1979). Apparently, this density of plants produces insufficient spores to compensate for losses to grazers and to competition with the coralline algae-dominated understory and/or adjacent mussels.

Several mechanisms may act to prevent local extinction and thus maintain a diverse assemblage within a patch. The mechanisms most commonly documented to maintain local diversity in intertidal assemblages are compensatory mortality and intermediate disturbance (Connell, 1978). The first of these mechanisms refers to the situation in which the potential late successional dominant suffers a disproportionate rate of mortality from causes largely unrelated to its interaction with earlier successional species. Selective predation by the starfish *Pisaster* on the competitively dominant mussel *Mytilus californianus* is a classic example (Paine, 1966, 1974). Local diversity will also be maintained if populations within a patch are

repeatedly disturbed at intermediate frequencies and intensities. These intermediate scales of disturbance allow species to accumulate within the patch but prevent domination by a few competitively dominant and/or long-lived species. This relationship between frequency of disturbance and diversity within a patch can be readily observed in those boulder field habitats where wave forces are the predominant source of disturbance. Boulders of intermediate size (or mass) are overturned by wave action more frequently than large boulders and less frequently than small boulders. As a result, boulders of intermediate size support, on average, the most diverse assemblage of sessile organisms (Sousa, 1979b). Intermediate frequencies and intensities of biological and physical disturbance also maintain diversity in tidepool assemblages (Paine and Vadas, 1969; Lubchenco, 1978; Dethier, 1984).

At mid-intertidal levels on the outer coast of Washington State, an assemblage of organisms occupying a particular area of substratum is disturbed at most once every 7–8 years (Paine and Levin, 1981). This interval is sufficiently long that a large number of species is able to colonize a newly created patch of open substratum. For a time, the diversity of the assemblage within the patch increases as these species accumulate. However, the frequency of disturbance is too low to maintain this state of high diversity. The interval between disturbances is long enough that all but the very largest of clearings will be closed by lateral encroachment of adult mussels or by larval recruitment of mussels from the plankton. The diversity of the assemblage within the patch will gradually decline as species are competitively excluded. Eventually all species that occupy primary space other than mussels will be driven locally extinct. Therefore, while localized disturbance enhances the regional diversity of sessile organisms by creating opportunities for colonization in an area that mussels can potentially dominate, rates of disturbance at the sites studied by Paine and Levin (1981) are too low to maintain a persistently diverse assemblage on any one area of substratum.

## VII. REGIONAL PERSISTENCE OF FUGITIVE SPECIES

In situations where no mechanism is effective in maintaining local diversity, species other than the late successional dominant(s) that are restricted to live within a particular range of tidal heights can only persist in that zone as true fugitive species (Hutchinson, 1951). Fugitive species persist as members of the assemblage by dispersing their offspring into space newly cleared by disturbance with suitable conditions for recruitment, growth, and reproduction. Other species may have broader distributional boundaries that include relatively exclusive refugia outside the zone in question. Although disturbance is not strictly required for the persistence of the latter species in the community, the exploitation of the additional space created by disturbance will enhance the size of their populations within the region.

As suggested by earlier comments, the regional dynamics and abundance of a species on the seashore reflects the interplay of that species' life history and the regime of disturbance. For a fugitive species to persist, disturbances must generate

colonizable space within the dispersal range of extant populations and within the period of time it takes for those populations to go extinct. Dispersal distance and the time to local extinction are, to some degree, functions of the life history of the particular species as well as local population density. Paine's (1979) long-term study of the sea palm *Postelsia* provides one of the clearest examples of an intertidal species that requires a specific frequency and quantity (percentage of space cleared) of disturbance to persist. During a 10-year period, populations of the plant were monitored at 26 sites on Tatoosh Island off the coast of Washington State. The regimes of wave-induced disturbance of mussel beds varied among the sites. Populations of sea palms, which recruit primarily to clearings within the beds (Dayton, 1973), were present in all 10 years at the 7 sites that had high levels of regular disturbance. Sea palms were absent from the other 19 sites where either the frequency of disturbance or the quantity of open space generated by disturbance was lower. The experimental establishment and persistence (for at least two generations) of populations of sea palms at the latter sites ruled out the possibility that sites lacking natural populations were simply unsuitable for their establishment. At sites where populations were naturally persistent, the subpopulation within any particular clearing was doomed to local extinction due primarily to competition with a variety of sessile organisms, including mussels and coralline algae. The regional persistence of populations at such sites depended upon adequate dispersal of spores to new clearings within about 1.5 m (the approximate dispersal distance) of extant stands. At other locations along the Washington coast, individual stands of sea palms seem to persist longer than they do on Tatoosh Island. P. Dayton (personal communication) monitored 15–20 stands of *Postelsia* on Waadah Island from 1965–1974. All of the stands, with the exception of 3 that had been experimentally manipulated, persisted through the 9 years of observation. Reasons for the greater persistence of stands at the latter site have not been investigated. Competition for space with other sessile organisms may have been less intense on Waadah than on Tatoosh. In addition, the stands Dayton observed may have been sufficiently dense that enough open space was generated each fall and winter, when detached adult plants carried away overgrown competitors (Dayton, 1973), to ensure repopulation of the patches of substratum for many generations. According to Paine's (1979) calculations, stands of sea palms on Tatoosh rarely reach densities at which this mechanism could maintain a local population for more than a few years. A detailed comparative study of *Postelsia* populations at these and other sites might reveal the causes of variation in local dynamics.

The observation that many species of algae and invertebrates on the Pacific coast of North America disperse their propagules in winter provides circumstantial evidence that the open space generated by disturbance is important to the persistence of some intertidal populations. Winter is the season in which disturbance is most prevalent and open space for recruitment is most available (Sousa, 1979a; Paine and Levin, 1981; Suchanek, 1981, and references therein).

Not all cleared space is of equal quality in promoting the persistence of, or enhancing the abundance of, a particular species. For example, as discussed earlier, small clearings in mussel beds are closed more quickly by lateral encroachment of

adult mussels and are also subjected to more intense grazing than are large patches. Therefore, species that are vulnerable to grazing will have a low probability of becoming established in small patches (Suchanek, 1979; Sousa, 1984). Even if some individuals are successful in recruiting to such patches and grow to an invulnerable size, competitive exclusion by mussels will be relatively rapid. Regional populations of species that are vulnerable to grazing will be smaller, in proportion to the total area cleared, on shores where the patches are small than on shores where disturbances generate large clearings. On the other hand, populations of grazer-resistant species that lose in competition with grazer-vulnerable species may become established more successfully and persist longer in relatively small patches where the abundance of grazer-vulnerable species is low. This seems to occur in spite of the faster rate at which small patches are closed by mussels (Sousa, 1984). The expectation is that grazer-resistant species will be disproportionately more abundant on shores characterized by small-scale disturbances.

Similar considerations regarding the effect of patch quality on the regional abundance and persistence of populations apply to intertidal boulder fields. Boulders smaller than a certain size are disturbed so frequently that populations of most perennial species cannot become established on their surfaces (Sousa, 1979b). The sparse cover on these boulders is dominated by highly vagile and fast-growing early successional species. All else equal, the regional abundance of perennial species should be less in fields where the mean size of boulders is small than in fields where the mean size is large. The opposite pattern would be predicted for populations of early successional species.

## VIII. CONCLUDING REMARKS

Nearly a half-century of experimentation and quantitative observation has yielded considerable information concerning the role of biological interactions in structuring rocky intertidal communities. Only recently, however, have the effects of disturbance on the local and regional dynamics of intertidal assemblages and on the evolution of life histories been recognized as potentially important. Consequently, much of the available data gathered from this habitat cannot be used to test the predictions made in this chapter. It is my hope that the ideas presented herein will serve as a useful guide for future studies as to the kinds of data needed to elucidate the effects of natural disturbance, including its interplay with biological processes. By viewing intertidal assemblages as mosaics of patches generated by disturbance, we can better understand their dynamics and comparison with communities of terrestrial plants discussed in other chapters of this volume will be facilitated.

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