

Chapter 14

Disruption, Succession and Stochasticity

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Ecological disruptions play an important role in generating spatial and temporal patterns of species occurrence and coexistence. Disruptions are particularly obvious in marine benthic communities, where the scale of disruption and recovery can be particularly amenable to experimental investigation and quantification.

14.1 Definitions

Disruptions can be defined as interference with the orderly course of a process. Several different general mechanisms can be considered as ecological disruptions. Perhaps the most discussed is the concept of disturbance. Two general perspectives of disturbance have emerged in the literature. A view generally taken by terrestrial ecologists is that disturbance is a pulsed perturbation from an equilibrium state (White and Pickett 1985). This definition follows more closely the dictionary definition of disturbance, and is similar to the idea of ecological disruption. Implicit in this definition is that an identifiable equilibrium state of a system exists, and that the system tends to converge to that equilibrium state in the absence of disturbance.

A second definition of disturbance is a physical process that removes living biomass from an ecosystem (Sousa 1984b). This definition requires neither that an equilibrium reference point be identified, nor that the system must reach the equilibrium point in the absence of disturbance, and it avoids the difficulty of identifying whether a perturbation is pulsed or not, which depends largely on the temporal perspective adopted by an investigator. Additionally, this definition enables empirical quantification through demographic analysis of known individuals in conjunction with detailed measurements of the physical environment, or observations of signs associated with a physical process (e.g., impressions left by ice scour, changed orientation of boulders, spatial patterning of mortality, characteristic patterns of body part remnants). Experimental studies can also be implemented in which investigators impose (e.g., Petraitis and Dudgeon 1999), or in some cases remove (e.g., Sousa 1979b), mortality patterns on the system to infer effects of disturbance. For these reasons, we will consider disturbance a physical process that removes living biomass from an ecosystem, and use this definition for the remainder of the chapter.

14.1.1 Anthropogenic Versus Natural Disturbance

Another perspective on disturbance makes a distinction between perceived origins. Disturbance can be considered anthropogenic (derived from human activity) or “natural” (derived without human intervention). In some cases, making this distinction leads to a fundamental conflict between the perturbation-based vs. mortality-based definitions described above; “natural” disturbance, when viewed over a sufficiently long timescale, may be considered as a chronic process, whereas anthropogenic changes may be considered a recent novel event. Hence, a human activity (e.g., building a breakwater) may be considered a disturbance that moves a system from a prior equilibrium, by reducing a process (e.g., wave impact) considered a disturbance in the mortality-based framework.

14.1.2 Physical Disturbance Versus Consumers

By focusing on physical processes as drivers of disturbance, we are explicitly excluding consumer–resource interactions as a type of disturbance. A key difference between the two is that negative feedback is expected between consumers and their resources, but not for disturbance; eating prey contributes to increased fitness of the consumer, thereby increasing consumer pressure, whereas the physical processes creating disturbance are generally unaffected by the populations they impact. However, under some circumstances, it may be practical to treat consumer–resource interactions as another source of disturbance (e.g., Menge and Sutherland 1976). For instance, the two processes would be similar when the effects of prey on consumers are weak, such as when consumers are extreme generalists, when pronounced interference interactions strongly regulate predator populations, or when dispersal scales of predators are much greater than the scale of the study. Several models, however, propose that the relative importance of predation and disturbance will be observable at different ends of a stress gradient (Menge and Sutherland 1976).

Organisms are more clearly agents of disturbance when they are ecosystem engineers (Jones et al. 1994) with activities changing the physical environment in ways that kill other organisms. For example, basking pinnipeds or human visitors crush intertidal organisms as they move across the shoreline, or kick past a reef while diving (Hawkins and Roberts 1993; Keough and Quinn 1998). In other cases, physical disturbance is closely linked to the feeding mechanism employed by the predator while foraging, such as rays, sea otters, and gray whales that burrow, dig, or turn over rocks while foraging, smothering or crushing non-prey species in the process (Oliver and Slattery 1985), and species such as gulls that actively rip algae from the rocks while searching for hiding prey, or building nests. Canopy algae can also be a source of disturbance through abrasion or “whiplash” as they are moved around by water motion, and dislodge or kill other organisms (Dayton 1971). In all these cases, there is no clear benefit for the individual species creating the mortality.

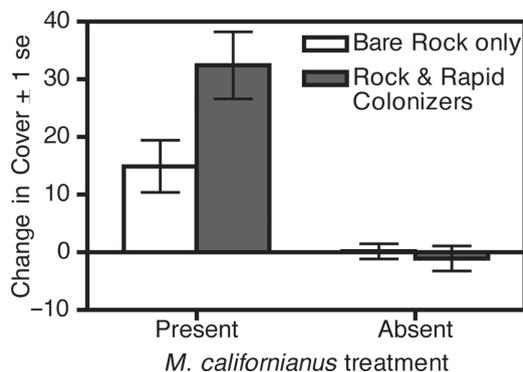


Fig. 14.1 Effect of wave disturbance on rocky intertidal plots with the dominant mussel *Mytilus californianus* present, and on immediately adjacent experimental plots where all *M. californianus* were chronically removed (see Wootton 2004). Experimental plots were dominated by coralline algae (*Corallina vancouveriensis*), acorn barnacles (*Semibalanus cariosus*), and goose barnacles (*Pollicipes polymerus*). Data are change in (%) cover of bare rock, or of bare rock and species that rapidly colonize bare rock (ephemeral algae and *Balanus glandula*) in plots between censuses spanning a disturbance event. Strong disturbance mortality of mussels is not reflected in mortality of other species in the same area

Aside from biotic sources of disturbance, numerous physical mechanisms commonly create disturbances in marine environments (reviewed in Sousa 1984b, 2001).

A critical aspect of disturbance that is sometimes ignored is that, within the same area and at the same time, the disturbance agent may affect species or individuals differentially. This is distinct from the abilities of different species to recover in specific disturbance regimes. For example, wave disturbance can strongly impact populations of large mussels, yet leave other species essentially intact (Fig. 14.1), and typhoons more strongly affect mature, highly developed coral reefs (Connell et al. 1997). This feature can have profound impacts on ecosystems by introducing species differences that may facilitate coexistence (Wootton 1998), affect recovery patterns (Connell and Slatyer 1977), and contribute to spatial patterning (Wootton 2001). On a practical level, broad gradients of disturbance assumed in many theoretical treatments (e.g., Connell 1978) may be difficult to identify empirically, because they do not act uniformly on all species. Thus, the observed responses to disturbance might in part reflect the fact that some species or types of individuals are not really disturbed, instead of reflecting their ability to better recover from disturbance.

14.1.3 Other Ecological Disruptions

Although disturbance is most often considered within the broader topic of environmental disruptions, other ecological processes might also be considered disruptions. Changes in environmental stress can generally cause disruptions. If disturbance is

defined as a physical process that induces mortality, then stress can be defined as a physical process that reduces physiological performance without immediately causing death, although it may do so when combined with other factors such as food limitation over longer time frames (e.g., Wootton 1998). In some cases, disturbance and stress may have the same general effects on ecosystems, particularly when stress operates in a density-independent manner on organisms (e.g., by changing metabolic rates). Stress impacts may differ fundamentally, however, if they change physiological rates in ways that alter interactions among species. For example, high temperatures could rapidly kill predators by preventing these from maintaining water balance, or could change physiological rates at which predators capture and digest food, fundamentally altering interactions with their prey. Because the latter alters feedbacks within the food web, its consequences could be quite different than those of simple reductions in abundance of the predator.

Changes in water flow regimes are another ecological disruption of particular relevance to marine systems. There has been much recent interest in this topic, as models suggest that global warming may substantially alter large-scale ocean currents and storm patterns (IPCC 2001; ACIA 2004). Some aspects of water flow are easily related to disturbance and stress concepts: changes in storm intensity may alter wave disturbance, and changes in water temperatures associated with different currents can affect physiological stress levels and some types of disturbance (e.g., the prevalence of ice scour or freeze events). Changes in water movement can also disrupt key marine processes in ways that are less easily linked to direct mortality or physiological performance, because of its central role in material transport. Disruption of current and upwelling patterns may change the rate of recruitment of organisms to different areas (Farrell et al. 1991), gene flow, or the aggregation and delivery of nutrients and food resources to local shorelines (Bustamante et al. 1995; Menge et al. 1997).

14.1.4 Stochasticity

If disruption can be defined as interference in the orderly course of a process, then it is also relevant to consider the concept of stochasticity. Stochasticity can be defined as a process lacking any particular order or plan—hence, it underlies the concept of disruption. There is an emerging body of theoretical literature on stochastic processes and their implications that may help to understand the role of disruptions in marine systems. Stochasticity arises from two fundamental sources (Lande 1993). First, demographic stochasticity and related concepts (e.g., genetic drift) arise as a sampling phenomenon involving a limited number of discrete events, analogous to flipping a coin. For example, the annual probability of survival by sea otters is some fractional value between 0 and 1, but an individual sea otter either lives or dies. A similar situation holds for the probability of a physical event occurring (e.g., a volcanic eruption, or a tsunami). Although such stochasticity may not usually be important to ecosystems, because it is a factor only when the event is rare, in some instances, such as in the examples provided, the impacts of rare

components are sufficiently strong that their variability can serve as an important disruption. Second, environmental stochasticity arises from variation over time in factors external to a system, which cause deviations from mean values of parameters such as demographic rates, interaction strengths among species, and supply rates of recruits and nutrients. Because it is externally derived, environmental stochasticity is typically expected to be independent of local system conditions. The perception of environmental stochasticity depends on the scale with which a system is viewed. The source of stochasticity can be spatially external to the system, such as physical forcing by large-scale climatic processes or movement of organisms from other spatial locales, or from changes in local abiotic or biotic conditions that have not been included in the conceptualization of the system. Hence, changing the spatial scale, and the suite of variables considered as a system can affect the perceptions of the role of stochastic processes.

More generally, it is important to appreciate that the scale of observation affects the perception of disruptions, and how they are studied. A seemingly persistent set of conditions in ecological time (e.g., present sea-level conditions, chronic nutrient runoff) may be perceived as pulsed disruptions over geological time. Similarly, wave disturbances, mudslides or lava flows represent massive unpredictable disturbances at local spatial scales (<km), but are regular features of the seascape at larger scales (e.g., >100s km). Hence, perceptions of the same system viewed at different scales may vary radically, with small-scale studies characterizing a system as being in a highly stochastic non-equilibrium state, whereas large-scale observation suggests that the same system is in a highly deterministic equilibrium state (De Angelis and Waterhouse 1987; Petraitis et al. 1989). The study of disruptions, particularly disturbances, has taken two polar perspectives on the problem, which have both contributed to our understanding of ecological communities: disruptions as unique events, and disruptions as chronically occurring processes. In the next sections we review these two perspectives.

14.2 Disruptions as Unique Events

Disruptions are most notable when they occur as intense events that wreak large-scale destruction on a system, such as hurricanes, earthquakes, landslides, volcanic eruptions, or ice ages. Frequently, these events have recurrence times on the scale of a human lifespan or longer, and hence draw particular attention because they are unusual situations. Such circumstances naturally lead to treating disturbances as unique events that introduce a historical aspect to the compositions of communities and ecosystem processes, resulting in a focus on the patterns and mechanisms of recovery from the disruption back to “normal” conditions. These issues underpin one of the earliest conceptual pillars of ecology, the study of ecological succession and ecosystem development (Cowles 1899; Gleason 1926; Clements 1936), and provide an important basic touchstone for considering the restoration of ecosystems following human disruption.

Succession has a variety of definitions. The narrow view of succession suggests that it is a highly deterministic pattern of species replacements following a disturbance event. A broader view defines succession as a non-random pattern of species replacement following disturbance. Although early investigators clearly appreciated that stochastic elements were present during recovery from disturbance (Cowles 1899), adoption of the narrow view of succession led to intense debate between advocates (e.g., Clements 1936), who tended to view patterns at large spatial scales, and detractors, who were impressed by the variable patterns they observed at local scales (e.g., Gleason 1926). Intensive study of recovery patterns now indicate that the broader view is compatible with both perspectives in the debate, as patterns of recovery are not strongly deterministic, but are clearly not random either (Paine and Levin 1981). In benthic marine systems, unpredictable recruitment from the plankton, and priority effects arising from indeterminate growth of many marine species generate an element of stochasticity in the recovery, while differences in life history traits, tolerances to physical conditions, and responses to interactions with other species lend some predictability to the recovery.

Given that recovery patterns are non-random, what are the mechanisms important in succession? One organizing framework for shedding light on this question was proposed by Connell and Slatyer (1977), who advanced a trichotomy of scenarios based on the relationship between species characteristic of early and later stages of succession. They noted that three qualitative relationships were possible: early species could have positive (facilitation), negligible (tolerance), or negative (inhibition) effects on later-stage species, and these relationships serve to identify mechanisms that are important in recovery from disturbance. This clear qualitative contrast also serves as a framework that enables succession to be readily probed with field experiments, a feature that benthic ecologists have used advantageously. Multiple patterns of recovery have been documented in marine systems, and any successional sequence may contain elements of multiple mechanisms (e.g., facilitation at one stage, inhibition at another).

Facilitation embodies the classical view of succession, and implies that beneficial interactions play a key role in disturbance recovery. For this reason, facilitation is often expected when physical conditions are harsh in the aftermath of a disturbance, where early species have both a high physiological tolerance to stress, and are capable of modifying the environment when present. For example, barnacles can be important for facilitating establishment of mussels and algae on rocky shores (e.g., Johnson 1992; Berlow 1999).

Tolerance patterns of succession imply an important role of life history differences in dispersal, growth, maturation, and reproductive rates among species, as neither negative nor positive effects of early species on later species are detectable. Many marine species exhibit distinct differences in life history characteristics (Thorson 1950), ranging from benthic diatoms that have lifecycles on the order of days, to brown algae, bivalves, and corals that take several years to mature, and have distinct annual reproductive cycles. Hence, it would not be surprising if, for instance, the early dominance of diatoms in many benthic successional sequences arises primarily from their fast lifecycle. Nevertheless, direct evidence for tolerance

succession is scant in marine benthic systems. It is uncertain why this should be, and further study of this mechanism is required. One possible explanation is that recruitment in many species is dependent on transport via ocean currents, which may be highly unpredictable, thereby disrupting any clear successional pattern based on life history differences.

Inhibitory effects of early species on later-stage species in succession present a quandary: how can succession proceed to later species under these conditions? One solution to this problem is that other mortality factors may differentially affect early compared to later-stage species. For example, consumers may differentially prefer feeding upon early-stage species, releasing later species from inhibition. Consumers can be particularly effective at promoting succession following disturbance, because of a natural tendency for predator populations to lag behind prey populations over time. Their subsequent arrival and population increase may then release later species from inhibition, creating a non-random pattern of species replacements over time. Connell and Slatyer (1977) noted that inhibitory interactions are common among sessile organisms in general, and suggested that this mechanism of succession might be more common than previously suspected, because studies of succession often do not consider recovery patterns of mobile consumers following disturbance. Experimental studies, in which populations of early species were reduced and in which populations of consumers that feed on early species were reduced, have now demonstrated that inhibition patterns of succession occur frequently in marine benthic systems. Examples include grazers removing rapidly growing ephemeral algae, and favoring more resistant perennial algae (Sousa 1979a; Lubchenco 1983), and predators removing earlier-colonizing animals that inhibit later species (Wootton 2002).

Although understanding the relationship between early and later successional species has proven fruitful, other conceptual frameworks may also aid in identifying key mechanisms operating during recovery from disturbance. For example, if different phases in the recovery are characterized by dominance of different species, it may be profitable to ask what processes are important in the rise to dominance of particular species. This involves first colonization (life history traits, physical transport mechanisms) and then establishment (competition, facilitation, physical stress) processes, and the demise from dominance of species, which generally involves changes in mortality regimes, or recruitment failure (Farrell 1991; Wootton 2002). This rise-demise perspective identifies a richer suite of mechanisms that may be important in recovery from disturbance than does the Connell-Slatyer framework, and further emphasizes that key mechanisms may vary throughout the recovery process.

14.3 Disruption as a Chronically Recurring Process

When ecosystems are observed over sufficiently long time periods, even large intense disruptions occur multiple times. Given such observations, ecologists have more recently started asking how different disturbance regimes can affect community and

ecosystem characteristics. In taking this perspective, it is useful to identify general characteristics of disruptions to understand their consequences better. Disruptions introduce at least three features to ecosystem structure and dynamics. First, adding disruptions generally leads to increases in average mortality experienced by organisms within the system, which can alter population dynamics and long-term persistence of interacting species by altering the potential equilibrium points of the system (Wootton 1998). Second, disruptions are usually pulsed events; hence, they add temporal variability to the system, which makes it less likely that ecosystems will strictly attain an equilibrium condition (Connell 1978; Huston 1979). Third, disruptions are generally limited in aerial extent; hence, they introduce spatial variability into the landscape, which can affect population viability and species coexistence (Paine and Levin 1981; Petraitis et al. 1989; Chesson 2000). A related approach to understanding disruptions involves characterizing their intensity (related to average mortality and spatial extent) and frequency (related to temporal variability; Sousa 1984a). The generality of these categorizations is scale-dependent, as a frequent disturbance event from the perspective of a long-lived organism, such as a seagull, might be quite different from that of a species with rapid population turnover, such as an amphipod.

The effects of recurring disturbance are most extensively explored in the intermediate disturbance hypothesis (IDH; Dayton 1971; Horn 1975; Connell 1978). This theory posits that species diversity is maximized at intermediate disturbance levels, with high disturbance eliminating species, and low-disturbance situations being characterized by high competitive exclusion. Benthic marine systems have played an important role in generating and experimentally testing aspects of the hypothesis. Observations of rocky intertidal areas disturbed by waves and floating logs revealed that species that would otherwise be displaced via competition persisted in these areas (Dayton 1971; Paine and Levin 1981). Long-term studies of Australian coral reefs emphasized the recurrent nature of tropical storm disturbances on shorelines, and identified unimodal relationships between coral diversity and time since disturbance (Connell 1978). Experiments and observations in coastal boulder fields supported the intermediate disturbance hypothesis by documenting increasing disturbance rates via rolling by waves with decreasing rock size, maximal richness of sessile species on intermediate-sized rocks, and increases in richness when small rocks were experimentally stabilized (Sousa 1979b).

Although empirical patterns in benthic marine communities support the IDH, more detailed studies are needed to fully understand the phenomenon, and when it occurs. Specifically, what mechanisms and components of disturbance are responsible for the patterns? Initially, an emphasis was placed on the introduction by disturbance of non-equilibrium conditions (Connell 1978; Huston 1979). Recent theoretical analyses indicate, however, that simply introducing stochastic non-equilibrium conditions while holding other components of disturbance constant either does not affect species coexistence, or reduces it, because the risk of stochastic extinction increases (Wootton 1998; Chesson 2000). In contrast, increases in average mortality rates by disturbance can promote species coexistence under some conditions. In general, disturbance needs to act more strongly on competitively dominant

species to promote coexistence, which tends to equalize the fitness of different species, and its effectiveness also requires that a stabilizing mechanism be present, such as differentiation in resource use, external immigration, or disturbance effects that are density-dependent. The introduction of spatial heterogeneity by disturbance provides perhaps the most powerful mechanism for promoting coexistence, both by creating temporary refuges from dominant species in space if tradeoffs between colonization and competitive dominance exist, and by promoting spatial heterogeneity among sessile species, which can enable niche differentiation by species that use the sessile species as habitat. Detailed empirical studies are needed to evaluate which of these mechanisms are most important in natural communities.

Although good empirical support for the IDH exists from communities of sessile marine species, there are likely to be many situations where the theory does not hold. For example, the IDH is based on the assumption that systems are organized by inter-specific competition, but there is ample evidence that consumer-resource interactions and positive interactions play important roles in marine ecosystems (Paine 1994; Bertness and Leonard 1997). Theoretical analysis indicates that in multi-trophic situations, the IDH often does not hold, particularly for mobile animals, and that it is highly dependent on where in the food web disturbance has its strongest effects (Wootton 1998). These results may explain why the best evidence for the IDH comes from studies of sessile species, but more extensive study of disturbance in a food web context is required.

Further understanding of the implications of disturbance on species diversity may come from distinguishing between its causes and effects, and considering potential feedbacks related to disturbance. For example, species may interfere with each other in a manner that is relevant only in the presence of disturbance. In benthic marine systems, cracks in the rock often provide refuges from disturbance caused by strong wave shear, scouring debris, and desiccation. As the space available in these cracks can be limited, increasing abundance may prevent all population members from taking refuge in these cracks, thereby increasing mortality at high densities in the presence of disturbance, and creating negative density dependence. Density of organisms may also affect susceptibility to wave disturbance by affecting adhesion ability or drag coefficients. In cases where density limits attachment area or strength, negative density or biomass dependence may arise. For example, as barnacles or mussels become abundant, the area of rock on which they can attach remains the same, but attachment area per unit biomass declines, making it easier for wave dislodgement to occur. Not all interactions confer increased susceptibility to disturbance, however. For example, increases in sessile species density can increase water trapping, reduce evaporation, and increase the boundary layer, thereby reducing disturbance from desiccation, salinity stress, and waves, and lowering the chances of species loss to disturbance (Palumbi 1985; Bertness and Shumway 1993).

Aside from affecting overall mortality levels, disturbances are a key component in generating large-scale landscape pattern. In many cases, spatial heterogeneity is created from spatially restricted intense physical conditions, such as when multiple waves converge on a local area, or a piece of floating log impacts the shore. In other cases, landscape patterning arises from the interplay of physical factors promoting

disturbance, and interactions among organisms. For example, when organisms attach to each other and one individual is disturbed, the disturbance can be transmitted to neighbors, creating a locally enlarged area of disturbance that is dependent on organism density (Wootton 2001). Locally propagated disturbances may also arise in marine systems when organisms change the local hydrodynamic or physical environment, thereby increasing susceptibility of their neighbors to disturbance when they are removed (Paine and Levin 1981). Such localized processes can introduce density dependence into disturbance impacts, and create spatial patterning that self-organizes in predictable ways (Wootton 2001).

Ecological disruptions in general can also play an important role in shaping marine ecosystems in the presence of strong non-linear interactions among organisms. In such situations, multiple basins of attraction may exist to which the ecosystem tends to converge depending on initial conditions. Strong differences in body size or other traits among individuals of a species, coupled with strong trait-based shifts in species interactions can generate such non-linearities. Disruptions play an essential role in these situations by shifting the system from one basin of attraction to another, which can create strong spatial heterogeneity and facilitate coexistence (Wilson 1992). Within marine ecosystems, strong individual variation within species is the norm as a result of indeterminate growth and variation in larval-adult life forms, which may favor the existence of multiple basins of attraction (Berlow and Navarrete 1997). Although demonstrating regime shifts between alternative stable states is difficult, because of the long-term studies and experiments required (Connell and Sousa 1983; Bertness et al. 2002), several situations from marine systems suggest that they may occur. In South Africa, spiny lobsters once dominated nearshore benthic communities, but were reduced to low populations following anoxia events linked to harbor construction. Associated with the decline, predatory snails were released from lobster predation, and increased to become dominant species in the system. Following this ecological disruption, managers attempted to reestablish lobster dominance by releasing adults, but this program failed when the snails at high abundance were able to quickly overwhelm and eat their former predators (Barkai and McQuaid 1988). Another possible example occurs in New England rocky intertidal shores, where disturbance by ice and other sources creates patches of bare space on the rocks. Here, the community dominance of the area appears to depend on whether mussels or rockweed colonize the area first; established mussel beds abrade rockweed, and harbor grazers that prevent establishment of the seaweed, whereas rockweed “whiplashes” the rocks and harbors mussel predators, inhibiting the establishment of small mussels (Petraitis and Dudgeon 1999, 2005). Further research is needed into these types of disruption-induced regime shifts, as they may be very hard to predict a priori.

In summary, disruptions play an important role in shaping the patterns of ecosystems, and understanding their impacts is critical to developing appropriate responses to human impacts on the environment. Marine benthic communities have provided key insights into the mechanisms associated with disruptions and recovery, and are likely to play an important role in future investigations, because of their experimental tractability and relatively rapid dynamics through time.

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