

# *Natural Disturbance and the Dynamics of Marine Benthic Communities*

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All marine communities, past and present, experience biological or physical disturbance. However, it was not until the publication of Dayton's (1971) classic monograph, "Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community," that disturbance began to be appreciated as one of the key processes that structures marine communities. During the decade prior to Dayton's study most experimental studies of marine communities focused on the roles of biological interactions such as competition, predation, and herbivory in determining species' distributions and abundances (see references in Connell 1972, 1974; Paine 1977). Although a number of these studies demonstrated that the strengths of such interactions were affected by variation in the physical environment, only near the extremes of environmental gradients were physical stresses considered to play a primary role in determining community structure. There was a clear tendency to emphasize the importance of biological interactions over physical processes, especially among intertidal studies of this period. This emphasis was a byproduct of a concerted effort by numerous investigators to test the long-standing dogma that the structure of intertidal communities was primarily the product of variation in the mechanical and physiological tolerances of the component species to gradients and thresholds in the physical environment (e.g., Colman 1933; Doty 1946). Sanders (1968, p. 267) took this early view to its extreme when he declared, "...all rocky intertidal assemblages, independent of latitude, especially at higher intertidal levels, must be considered predominantly physically regulated communities, and the adaptations are primarily to the physical environment and the biological interactions are poorly developed."

By the time of Dayton's study, the structure of intertidal communities was well known to vary predictably along gradients of wave exposure (Lewis 1964), and transplantation experiments (e.g., Hatton 1938; Harger 1970) had demonstrated the role of wave action as an environmental factor limiting the horizontal distributions of individual species. By highlighting the direct and indirect effects of disturbance in structuring the community as a whole, Dayton's investigation moved the field a giant step forward. In particular, he demonstrated the complementary roles of wave shock and battering by drift logs in renewing primary space. By provisioning open space, a key limiting resource for many species in the community, these disturbances initiated local recolonization and affected the strength and outcome of interspecific competition. The effects of these agents of physical disturbance were spatially and temporally variable, but nonetheless of primary importance across the intertidal zone, not just at the limits of species' distributions.

In the nearly 30 years since the publication of Dayton's monograph, we have learned a lot about natural disturbance in marine communities. This chapter will discuss the role of natural disturbance in structuring marine communities, including its interaction with other processes. For example, through its influence on the species composition and three-dimensional structure of an assemblage and on the physiological state of component individuals, competition can influence the assemblage's susceptibility to disturbance. Reciprocally, by freeing limiting resources from the control of residents, disturbance can alter the rate and outcome of competition and the likelihood that competitors will coexist locally or regionally. Further, characteristics of the disturbance and of the affected patches of habitat can influence the rate and trajectory of succession, in

which competitive interactions often play a large role. The spatiotemporal relationships of a series of disturbances affect the structure of the resulting mosaic of successional stages as well as the persistence of competitively inferior "fugitive" species (Hutchinson 1951) within the landscape.

The vast majority of observational and experimental studies of disturbance in marine systems have examined its effects on assemblages of organisms that are sessile or sedentary as adults. This emphasis undoubtedly reflects the relative ease with which the impact of disturbance can be observed and studied in such assemblages, as compared to those comprised of mobile species. Studies of the effects of disturbance on assemblages that live on hard substrata have focused primarily on the larger sessile species that represent the bulk of the biomass, cover, and three-dimensional structure of the assemblage—organisms such as mussels, corals, kelps, and seagrasses. These "structural" species (*sensu* Huston 1994) provide food or habitat for "interstitial" species including mobile organisms (e.g., Orth 1977; Suchanek 1979, 1992; Orth et al. 1984; Summerson and Peterson 1984; Dean and Connell 1987a, b, c; Seed 1996; Connell et al. 1997; Jones and Syms 1998). Therefore, the effects of disturbance on "structural" species may percolate throughout the community. Although most of the examples and much of the conceptual framework presented here concerns the effects of disturbance on assemblages of sessile or sedentary organisms, I devote a separate section to the effects of disturbance on assemblages of mobile species. The chapter focuses on assemblages that live on or in natural substrates as opposed to artificial surfaces (e.g., fouling panels) or containers (e.g., trays or boxes of sediment).

I will examine (1) the features of individuals and assemblages that influence disturbance regimes, (2) the interacting effects of disturbance characteristics and biological processes on patterns of recolonization and subsequent changes in the assemblage, and (3) the effect of disturbance on the persistence and coexistence of species. The chapter ends with a discussion of promising directions for future research.

## DEFINITIONS OF TERMS

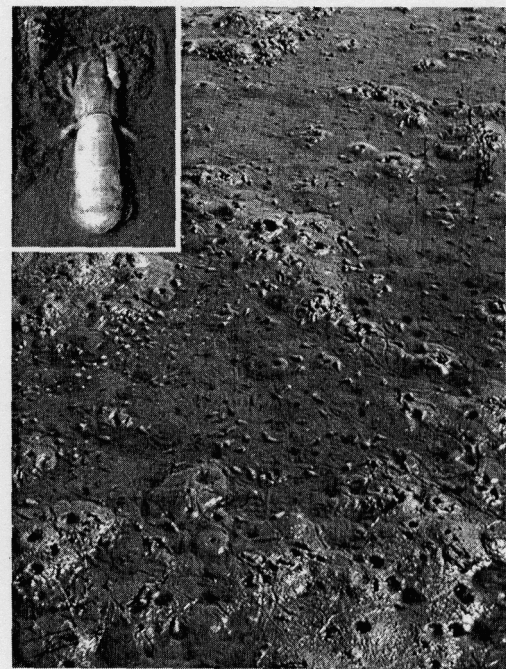
### *Disturbance*

At the outset, I need to be clear about what I mean by *disturbance* in this chapter. The term has been used rather loosely in the ecological literature (Rykiel 1985). Sometimes, it refers to the external agent or force that causes damage or mortality. In other cases, it refers to the damage or mortality itself, that is, the effect of some external agent or force. I prefer the latter interpretation, and that is the way I use the term here. Even when referring to disturbance as an effect on an ecological system, authors differ in how broadly they apply the term. In some papers, disturbance refers to damage (removal of biomass) or mortality caused by any physical or biological phe-

nomenon, and the adjectives *physical* and *biological* distinguish the nature of the causative agent.

Interpreted most broadly, biological disturbance includes partial or complete consumption of prey by predators or grazers, the deaths of parasitized hosts, harmful alterations of the environment caused by activities of animals (e.g., bioturbation: the reworking and resuspension of soft sediments by feeding and burrowing infauna, Figure 4.1) or movements of plants (e.g., algal whiplash), and the displacement of mobile, space-holding prey due to behavioral escape from predators. Dayton (1975) described a clear case of the latter phenomenon in tide pools on the outer coast of Washington State: large numbers of sea urchins "stampeded" away from a sea star predator, thereby creating open, ungrazed space for algal colonization within tide pools. Biological disturbance also includes inadvertent mortality, damage, or displacement suffered by nonprey species as an indirect result of foraging or other behaviors of consumers. For example, a variety of vertebrate and invertebrate predators in soft-sediment environments displace sediment and nonprey species as they excavate in search of prey (Table 4.1, Figure 4.2a). Likewise, seals inadvertently crush and abrade intertidal invertebrates and algae when they haul out of the water to rest onshore (Boal 1980; Figure 4.2b).

I agree with McGuinness (1987a, p. 417) that applying the term *disturbance* in an umbrella fashion to all sources of damage and mortality including predation, herbivory, and parasitism has little heuristic value and often muddles discus-



**Figure 4.1** Bioturbation by the burrowing ghost shrimp, *Callinassa californiensis*, on a mudflat in Bolinas Lagoon, California. (Photos by the author.)

**TABLE 4.1** Kinds of natural disturbance in marine benthic communities.

Agent of disturbance	Direct impacts on organisms or substrate	Habitat or assemblage	Examples
<b>PHYSICAL DISTURBANCE</b>			
Storm waves and currents	Sessile organisms detached or broken; mobile animals displaced, may be injured/ killed	Emergent rocky shore	Jones and Demetropoulos 1968, Seed 1969, Dayton 1971, 1973, 1975, Harger and Landenberger 1971, Paine 1974, Grant 1977, Lubchenco and Menge 1978, Suchanek 1978, Menge 1979, Underwood 1980, 1998, 1999, Paine and Levin 1981, Paine and Suchanek 1983, Sousa 1984, Denny et al 1985, Barry 1989, Vadas et al. 1990, 1992.
		Tide pool	Dethier 1984, Benedetti-Cecchi and Cinelli 1996
		Mangrove prop root epifauna	Bingham and Young 1995
		Coral reef	Stoddart 1963, 1969, 1974, Connell 1973, 1978, 1979, Highsmith et al. 1980, Pearson 1981, Kaufman 1983, Walsh 1983, Porter et al. 1981, Woodley et al 1981, Knowlton et al 1981, Rogers et al. 1982, Dollar 1982, Hughes 1989, Bouchon et al. 1991, Dollar and Tribble 1993, Scoffin 1993, Liddell and Ohlhorst 1994, Wulff 1995, Connell et al. 1997
		Kelp forest	Rosenthal et al. 1974, Barrales and Lobban 1975, Dayton and Tegner 1984, Dayton 1985, Ebeling et al. 1985, Kennelly 1987a, b, Tegner and Dayton 1987, Witman 1987, Seymour et al 1989, Dayton et al. 1992,
		Boulder field	Osman 1977, Lieberman et al. 1979, Sousa 1979a, b, Davis and Wilce 1987, McGuinness 1987a, b
		Soft sediment	Eagle 1975, Rees et al. 1977, Yeo and Risk 1979, Oliver et al. 1980, Hogue 1982, Moverley et al. 1986, Posey et al. 1996, Okey 1997
		Seagrass beds	Thomas et al. 1961, Patriquin 1975, Birch and Birch 1984, Kirkman 1985, Williams 1988, Kirkman and Kuo 1990, Bouchon et al. 1991, vanTussenbroek 1994, Preen et al. 1995, Reusch and Chapman 1995, Valiela et al. 1998, Bell et al. 1999, Ramage and Schiel 1999
		Salt marsh	Guntenspergen et al. 1995
		Wave or current-borne marine or terrigenous sediment	Organisms abraded or buried and smothered
Subtidal hard substrate	Airoldi et al. 1996, Airoldi and Cinelli 1997, Airoldi and Virgilio 1998, Airoldi 1998		
Kelp forest	Dayton et al. 1989, Seymouret al. 1989		
Seagrass bed	Onuf and Quammen 1983, Onuf 1987, Preen et al. 1995, Duarte et al. 1997, Bell et al. 1999		
Coral reefs	Hodgson 1990, Rogers 1990, Cortés 1993, Umar et al. 1998, Wesseling et al. 1999		
Soft sediment	Peterson 1985, Onuf and Quammen 1983		

TABLE 4.1 *continued*

Agent of disturbance	Direct impacts on organisms $\alpha$ substrate	Habitat or assemblage	Examples
Wave or current-borne cobbles	Organisms abraded, crushed, or detached	Salt marsh	Onuf 1987, Rejmanek et al. 1988, Zedler et al. 1992, Guntenspergen et al. 1995, Nyman et al. 1995, Allison 1996
		Mangrove forest	Ellison 1998
		Emergent rocky shore	Lubchenco and Menge 1978, Sousa 1979b, Wethey 1979, Robles 1982, Underwood 1998
Drifting logs	Organisms abraded, crushed, or detached	Tide pool	Dethier 1984, Benedetti-Cecchi and Cinelli 1996, van Tamelen 1996
		Kelp forest	Dayton et al. 1989, Seymour et al. 1989
		Emergent rocky shore	Dayton 1971, Sousa 1984
Ice	Organisms abraded, crushed, or detached; sediments and associated organisms excavated and displaced	<b>Tide</b> pool	Dethier 1984
		Coral reef flat	J. Cubit, pers comm
		Salt marsh	Seliskar and Gallagher 1983
		Emergent rocky shore	Stephenson and Stephenson 1954, 1972, Schwenke 1971, Keats et al. 1985, Wethey 1985, Minchinton and Scheibling 1991, Åberg 1992 a, b, McCook and Chapman 1997, Minchinton et al. 1997, Pugh and Davenport 1997
		Subtidal hard substrate	Slattery and Bockus 1997, Barnes 1999
		Seagrass bed	Short 1983, Robertson and Mann 1984
Exfoliation or fracture of rock surface and displacement by strong flow	Substrate removed along with attached organisms	Soft sediment	Dayton et al. 1970, Gordon and Desplanque 1983, Wilson 1988, Lenihan and Oliver 1995, Gutt et al. 1996, Conlan et al. 1998, Sahade et al. 1998
		Salt marsh	Redfield 1972, Richard 1978, Bertness and Grosholz 1985, Roberts and Robertson 1986, Hardwick-Witman 1985
		Emergent rocky shore	Frank 1965, DeVogelaere 1991
Tectonic activity that uplifts substrate	Organisms experience increased or permanent aerial exposure with associated desiccation, heat, and UV stress	Kelp bed	Ebeling et al 1985, Dayton et al. 1989
		Emergent <b>rocky</b> shore	Haven 1971, Johansen 1971, Castilla 1988
		Seagrass bed	Johansen 1971
Landslide	Organisms abraded, crushed, or buried and smothered	Coral reef	Stoddart 1972, Cortés 1993
		Emergent rocky shore	Garwood et al 1979
Sediment slumps on subtidal slopes	Organisms displaced or buried and smothered	Subtidal hard substrate	Grange and Singleton 1988, Van Dissen et al 1994, Smith and Witman 1999
		Hard substrate	Slattery and Bockus 1997
Lava flow or volcanic ash	Organisms injured/killed by hot lava or smothered under ash	Soft sediment	VanBlaricom 1978, Oliver et al. 1980, Okey 1997
		Emergent rocky shore	Townsley et al. 1962
		Subtidal hard substrate	Gulliksen et al. 1980
		Seagrass bed	M. Fortes, pers. comm. in Short and Wyllie-Echeverria 1996
		Coral reef	Grigg and Maragos 1974

TABLE 4.1 *continued*

Agent of disturbance	Direct impacts on organisms or substrate	Habitat or assemblage	Examples
Extended aerial exposure	Organisms injured/killed by desiccation, heat, or UV radiation	Emergent rocky shore	Lewis 1954, Hodgkin 1960, Connell 1961, Frank 1965, Sutherland 1970, Ottaway 1973, 1979, Wolcott 1973, Branch 1975, Emerson and Zedler 1978, Menge 1978, Suchanek 1978, Sousa 1979a, Underwood 1980, Seapy and Littler 1982, Taylor and Littler 1982, Tsuchiya 1983, Turner 1983b, Pineda and Escofet 1989
		Coral reef flat	Glynn 1968, 1976, Fishelson 1973, Yamaguchi 1975, Loya 1976, Hay 1981, Fadlallah et al. 1995, Connell et al. 1997
		Seagrass bed	Bell et al. 1999
High water temperature	Organisms injured/killed by cold or freezing	Emergent rocky shore	Crisp 1964, Connell 1970, Dayton 1971, Paine 1974, Brosnan 1994, Carroll and Highsmith 1996,
		Seagrass bed	R. Thom and C. Simenstad, pers. comm. in Short and Wyllie-Echeverria 1996
	Organisms injured/killed by heat	Mangroves	Lugo and Patterson-Zucca 1977
		Tide pools Kelp forest	Hodgkin 1959, Dethier 1984 Tegner and Dayton 1987
Low water temperature	Organisms injured/killed by bleaching: loss of symbiotic zooxanthellae (others stressors may be involved)	Coral reef	Brown and Suharsono 1990, Glynn 1990, 1993, Williams and Bunkley-Williams 1990, Glynn and Colgan 1992, Gleason 1993, Jones et al. 1997, Wilkinson et al. 1999
		Coral reef	Davis 1982, Porter et al. 1982, Bohnsack 1983, Lassig 1983
Freshwater flooding	Organisms injured/ killed by osmotic stress or prolonged submergence with anoxia	Subtidal <b>hard</b> substrate	Andrews 1973
		Mangrove prop root epifauna	Goodbody 1961, Farnsworth and Ellison 1996
		Coral reef	Jokiel et al. 1993
		<b>Soft</b> sediment	Thomas and White 1969, Peterson 1975, Moverley et al. 1986, Onuf 1987, Nordby and Zedler 1991
		Salt <b>marsh</b>	Zedler 1983, Zedler et al. 1986, 1992, Guntenspergen et al. 1995
High soil salinity	Organisms injured/ killed by osmotic stress	Mangrove forest	Forbes and Cyrus 1992
		Salt marsh	Zedler et al 1992
Anoxia	Organisms injured/ killed by metabolic stress	Soft sediment	Boesch et al. 1976, Kitching et al. 1976, Santos and Simon 1980a, b, Boesch and Rabalais 1991, Pihl et al. 1991, 1992, Breitbart 1992, Breitbart et al. 1994, 1997, Diaz and Rosenberg 1995
Fire	Organisms injured/ killed by heat	Mangrove fishes	Bouchon et al. 1994
		Salt marsh	Nyman and Chabreck 1995
Lightning strikes	Organisms injured/ killed by heat and cavitation	Mangrove forest	Pajmans and Rollet 1977, Smith 1992, Smith et al. 1994, Sousa and Mitchell 1999, Sherman et al. 2000
Storm-related high winds and surge	Plants defoliated, uprooted, or trunks snapped	Mangrove forest	Craighead and Gilbert 1962, Jiménez et al 1985, Bouchon et al. 1991, McGuinness 1992, Roth 1992, Smith et al. 1994, Imbert et al. 1996
		Salt marsh	Chabreck and Palmisano 1973

TABLE 4.1 *continued*

Agent of disturbance	Direct impacts on organisms or substrate	Habitat or assemblage	Examples
Hail	Trees defoliated; branches and trunks injured/killed by impact	Mangrove forest	Houston 1999
<b>BIOLOGICAL DISTURBANCE</b>			
Accumulations of living or dead plant material (i.e., seasonal algal mats, deposits of drifting detached algae or seagrass, or stranded salt marsh wrack)	Organisms buried and smothered or shaded	Soft sediment	Thrush 1986a, Everett 1991, 1994, Gamenick et al. 1996, Thiel et al. 1998
		Seagrass bed	Holmquist 1997
		Salt marsh	Reidenbaugh and Banta 1980, Hartman et al. 1983, Bertness and Ellison 1987, Ellison 1987, Hartman 1988, Bertness 1991, Bertness et al. 1992a, Guntenspergen et al. 1995, Valiela and Rietsma 1995, Brewer and Bertness 1996, Brewer et al. 1998, Pennings and Richards 1998, see Pennings and Bertness, this volume.
Algal whiplash	Organisms abraded; newly settled/recruited especially vulnerable	Emergent rocky shore	Hawkins 1983, Dayton 1975, Benedetti-Cecchi and Cinelli 1992, Vadas et al. 1992
Bioturbation: sediment reworking and resuspension by infaunal burrowers	Organisms buried and suffocated, or sediment load interferes with feeding	Soft sediment	Rhoads and Young 1970, Aller and Dodge 1974, Gray 1974, Rhoads 1974, Myers 1977, Brenchley 1981, Wilson 1981, Rhoads and Boyer 1982, Thayer 1983, Posey 1986, Brey 1991, Everett 1991, Hall 1994, Dahlgren et al. 1999
		Seagrass bed	Philippart 1994, Grant 1983, Short and Wyllie-Echeverria 1996, Suchanek 1983, Harrison 1987
Sediment excavation and redistribution by foraging predators	Organisms displaced, uprooted, or buried and suffocated	Soft sediment	<b>rays:</b> Reidenauer and Thistle 1981, Sherman et al. 1983, VanBlaricom 1982, Everett 1991, Thrush et al. 1991; <b>crabs:</b> Woodin 1978, 1981, Thrush 1986b, Findlay et al. 1990, Warwick et al. 1990, Hall et al. 1991, 1993, Commito et al. 1995; <b>sea turtles:</b> Preen 1996; <b>whales:</b> Nerini and Oliver 1983, Johnson and Nelson 1984, Oliver and Kvitek 1984, Oliver and Slattery 1985; <b>walrus:</b> Oliver et al. 1985; <b>sea otters:</b> Hines and Loughlin 1980, Kvitek et al. 1988; <b>ducks and gulls:</b> Savidge and Taghon 1988, Cadée 1990; <b>bony fishes:</b> Summers 1980, Billheimer and Coull 1988, Raffaelli et al. 1990
		Seagrass bed, especially margins	<b>rays:</b> Orth 1975, Grant 1983, Valentine et al. 1994, Townsend and Fonseca 1998; <b>crabs:</b> Valentine et al. 1994, Townsend and Fonseca 1998
Red tide	Organisms suffocated	Soft sediment	Simon and Dauer 1977

sions and models of the phenomenon. In this chapter, I use the term *disturbance* in a more restricted way to mean damage, displacement, or mortality caused by physical agents or incidentally by biotic agents. Such incidental biological disturbance might be caused, for example, by actions of animals other than actual ingestion of prey, by wave-induced algal whiplashing of the substrate, or by burial under plant debris. I readily acknowledge, however, that in some cases, such as

disturbance of soft-sediment assemblages by foraging predators, it will be difficult, if not impossible, to determine unambiguously whether an observed reduction in abundance of a resident population was due to predation as opposed to displacement, emigration, or smothering.

How much damage or mortality must these agents cause before we consider it a disturbance? My interest here is with the population and community-level effects of disturbance,

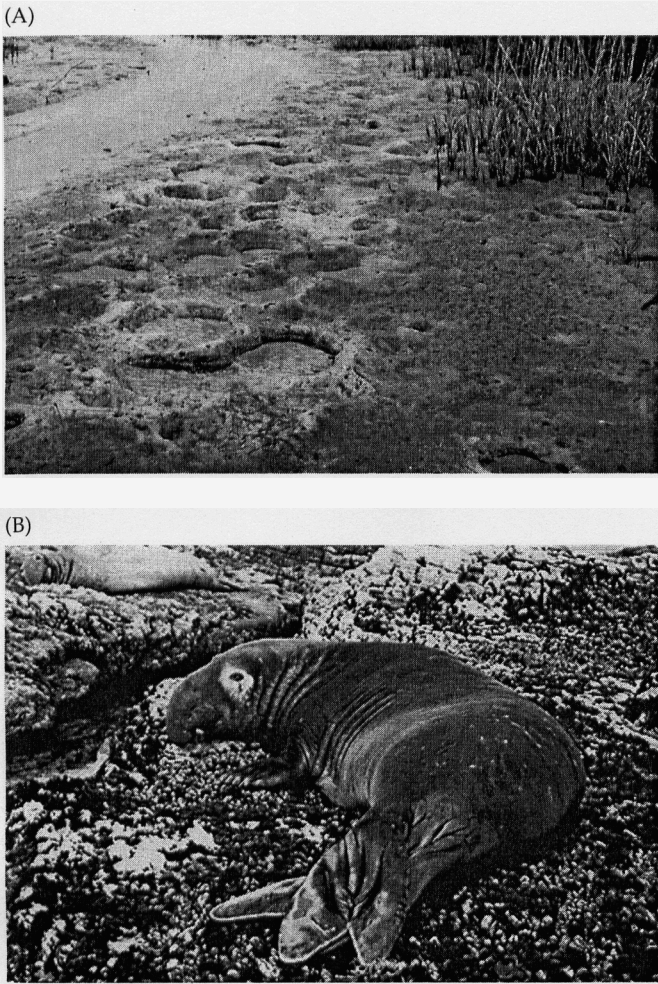


Figure 4.2 (A) Pits made by foraging rays on a mudflat on the Gulf coast of Florida; (B) Elephant seal hauled out onto mussel beds at Año Nuevo Island, California. (Photos by the author.)

so an event that does not alter population size or community structure, even though causing physiological or mechanical stress to individuals, would not constitute a disturbance. Only when an organism's tolerance is exceeded, resulting in its death or a sufficient loss of biomass that the recruitment or survival of other individuals is affected, has a disturbance occurred. My use of the terms *stress* and *disturbance* is consistent with Grime's (1977) definitions: A stress reduces an organism's potential for growth whereas a disturbance removes biomass. From a population dynamics perspective, the removal of even a single individual constitutes a disturbance, albeit small and probably inconsequential to overall dynamics. In other words, a disturbance has occurred when a force: (1) kills one or more resident organisms, or (2) damages them sufficiently to indirectly affect the abundance of other organisms, either positively by enhancing opportunities for recruitment, or negatively, by disrupting positive intra- or interspecific interactions.

### Disturbance Regime

Individual disturbances vary in their size, severity (degree or amount of damage), and duration. The regime of disturbance at a site is characterized by particular distributions of each of these characteristics, as well as a spatiotemporal pattern of occurrence of each type of disturbance. The term *intensity* is sometimes used synonymously with *severity* (e.g., Sousa 1985; Huston 1994; Connell et al. 1997); that is, an intense disturbance is one that does a lot of damage. However, following Sousa (1984), I will use the term *intensity* to mean the strength of the disturbing force. This follows its definition in physics, as the magnitude of force or energy applied per unit area or volume (*Webster's New Universal Unabridged Dictionary* 1983).

Disturbances range in duration from discrete, short-term events that last for a small fraction of the average life span of the affected species to events that exert their impact over much longer periods, sometimes generations. Connell et al. (1997) referred to disturbances near the extremes of this continuum as "acute" and "chronic," respectively. At some point, as the frequency of acute disturbance increases, the interval between them becomes so short that little if any recovery can occur. At that point, their cumulative effect is identical to that of a single chronic disturbance of similar severity (Chapman and Johnson 1990, p. 113). Note that other authors have defined these terms differently. For example, Westman and O'Leary (1986) used them to denote different severities rather than durations of disturbance, that is, a chronic disturbance reduces biomass partially whereas an acute disturbance removes all biomass. I will use these terms according to Connell et al. (1997).

The frequency and predictability of disturbance are key temporal components of the disturbance regime. Frequency refers to the number of disturbances that occur over an interval of time and can be quantified for a particular point in space or across a larger region (see discussion of spatial scales that follows). The recurrence or return interval is the inverse of local disturbance frequency; it is the average time between disturbances at a particular point in space. The predictability of disturbance is inversely related to the variance in the time between disturbances at a particular location. See Sousa (1984) for details concerning these and other measures of temporal variation in the occurrence of disturbance.

### Types of Disturbed Patches

When I refer to a disturbed "patch," I mean a contiguous area or volume in which resident organisms have been disturbed, as defined earlier. Sousa (1985) and Connell and Keough (1985) distinguished two types of habitat patches created by disturbance: (a) patches within continuous habitat, that are bounded by living organisms that were unaffected by the event that damaged or **killed** the original residents of the patch (Type 1), and (b) patches that are isolated from occupied sites (Type 2). Subsequently, Holt et al. (1995) referred to these two types of patches as "embedded" and "isolated," respectively. In this chapter, I have adopted Holt et al.'s more descriptive

names for the two patch types. Patches of space cleared in continuous mussel or algal beds are examples of embedded patches, whereas disturbances that clear the surfaces of more insular substrates such as boulders or bivalve shells create isolated patches. **An** entirely new substrate that results from a lava flow or landslide could be viewed, at least initially, as a large isolated patch. As discussed in detail later, this distinction has important implications for the mode and rate of patch colonization and for regional population dynamics.

### Spatial Scales

How disturbance affects marine communities depends on multiple processes operating across a range of spatial scales. **As** shorthand, I will often refer to "local" and "regional" scales. By "local" scale, I mean within a patch of disturbed habitat, whereas "regional" scale means an area that encompasses more than one patch of disturbed habitat.

## EFFECTS OF DISTURBANCE ON RESOURCE AVAILABILITY AND ENVIRONMENTAL QUALITY

Disturbances often free up limiting resources for exploitation by regenerating survivors and individuals that newly recruit to the disturbed area or by organisms living in its immediate vicinity. In marine benthic assemblages, disturbances most often renew space (usually two-dimensional on hard substrata and three-dimensional in soft sediments) and those resources acquired by organisms while holding space (e.g., nutrients, light, benthic, or suspended food). In some instances, the production or passive accumulation of a limited resource is enhanced by the environmental conditions created by disturbance, increasing its local availability beyond what was present prior to the disturbance or in surrounding undisturbed areas. For example, colonizing infauna feed on organic detritus that differentially accumulates in ray and whale feeding pits (VanBlaricom 1982; Oliver and Slattery 1985). In mangrove forests, soil concentrations of plant-available N can be twice as high within lightning-created canopy gaps (Figure 4.3) where plant uptake is less and warm and sunlit conditions stimulate microbial decomposition, than in the undisturbed, shaded understory (W. Sousa, unpublished data for newly created gaps at Punta Galeta, Panama;  $N = 6$ , paired  $t = 4.05$ ,  $P = 0.01$ ). Disturbances may also make available entirely new kinds of resources. For example, scavenging amphipods feed on wounded infauna left behind in whale or walrus feeding pits (Oliver et al 1985; Oliver and Slattery 1985). Regardless of the mechanism, this increase in resource availability following disturbance often enhances recruitment and growth. Disturbance may also enhance recruitment of particular species by reducing the density and local impact of their natural enemies.

On the other hand, disturbance can increase rates of subsequent mortality by reducing the ameliorating effect of residents on the physical environment or by refuges from consumers. Particularly severe disturbances can irreversibly change or destroy part or all of the habitat. the ex-



Figure 4.3 Lightning-created canopy gap in mangrove forest on Punta Galeta, Panama. (Photo by the author.)

treme, a site may become uninhabitable to prior occupants and their offspring. Such disturbance-caused changes in environmental quality can occur either rapidly or gradually. For example, when storm waves broke away a short section of the exposed reef crest on Heron Island, Australia, drainage patterns of the ebbing tide were immediately altered, lethally exposing hundreds of meters of reef crest corals to the air during low tide (Figure 4.4; Connell et al. 1997). Similarly, sudden vertical displacement of substrata by tectonic activity (Haven 1971; Johansen 1971; Stoddart 1972; Castilla 1988; Cortés 1993) has irreversible effects on the local environment. Gradual unidirectional changes in the physical environment can have similar effects over longer time scales. At first, a change in environmental conditions may alter absolute and relative rates of growth, reproduction, and recruitment. In turn, these changes may affect population density and rates



Figure 4.4 Exposed reef crest on Heron Island, Great Barrier Reef, Australia, killed by exposure following storm-caused alterations *in* drainage of ebbing tidal flow. (Photo by the author.)



and outcomes of biological interactions. As environment conditions continue to change, the levels of one or more physical factors may exceed the physiological tolerances of the affected organisms, directly causing mortality, that is, the stress produces a disturbance. Conditions may have changed to such a degree that juveniles of species that comprised the assemblage on the site prior to the environmental shift cannot reestablish populations. Instances of persistent, large-scale hypoxia, which are increasing in frequency in shallow coastal and estuarine areas due to human-caused eutrophication, fit this scenario (Diaz and Rosenberg 1995). Similarly, gradual warming of nearshore waters appears to have been responsible for marked latitudinal shifts in the species composition of intertidal assemblages in Britain (Southward et al. 1995) and California (Barry et al. 1995; Sagarin et al. 1999). The extent to which these water temperature-related shifts in distribution are driven by increased rates of mortality (i.e., disturbance) of those species that have declined in abundance versus changes in rates of reproduction and recruitment is not known.

Natural disturbances that fundamentally and irreversibly alter habitat quality are certainly important, but uncommon on an ecological time scale. This review focuses on the more typical situation in which the species that occupied the affected area prior to disturbance are potentially able to reestablish populations afterward. It is important to recognize, however, that many forms of human-caused disturbance and environmental change cause very long term, and often irreversible changes in environmental conditions—both abiotic and biotic—that dictate the rate and pattern of regeneration. See Steenack and Carleton (this volume) for a detailed discussion of such anthropogenic impacts on marine populations.

## AGENTS AND REGIMES OF NATURAL DISTURBANCE IN MARINE COMMUNITIES

Numerous agents of physical and incidental biological disturbance have been documented from marine communities (Table 4.1). Previous reviews cover in detail the effects of disturbance on specific marine communities including rocky seashores (Sousa 1985), subtidal hard substrata (Connell and Keough 1985), coral reefs (Pearson 1981; Huston 1985; Connell 1997; Jones and Syms 1998), soft sediments (Thistle 1981; Probert 1984; Hall 1994; Hall et al. 1994), and seagrasses (Short and Wyllie-Echeverria 1996). The habitat-specific chapters in this volume update this information. A suite of different disturbance agents may affect any particular assemblage, each with its own spatial and temporal regime. Some are tightly linked in space and time. For example, forces associated with strong water currents apply potentially damaging mechanical stress to organisms, but also often carry sediments or projectiles that may abrade, crush, or break them.

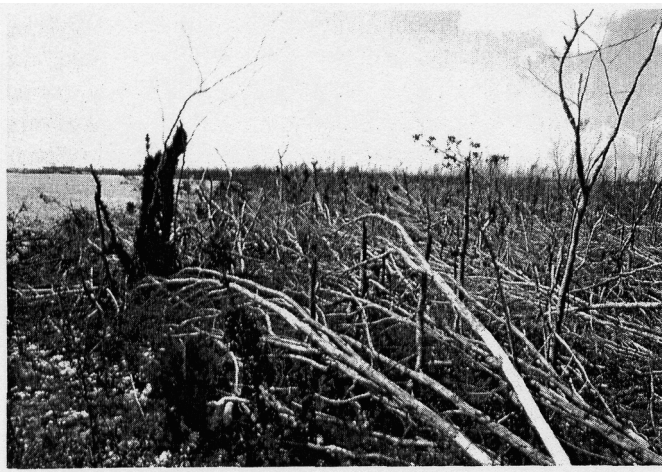
Detailed, quantitative records of natural disturbance regimes in marine habitats are steadily accumulating. Such records are difficult to maintain for more than relatively short periods due to intermittent research funding, the labor-intensive nature of the work, and the limited opportunities for

publishing the results of monitoring programs. Most of those documented in studies listed in Table 4.1 were gathered over the course of a single experimental study, usually conducted at one location and lasting no more than a year or two. Thus, we **know** little about spatial and temporal variation in disturbance regimes within a given habitat. Such short-term records tend, on average, to miss rare, large, and severe disturbance events (Weatherhead 1986; see Connell and Sousa 1983 for a similar conclusion concerning the effect of census record length on estimates of population variability). Although long-term studies are less likely to miss these extreme events, they have tended to focus on the major interannual events (e.g., cyclone damage to reefs, Connell et al. 1997; effects of El Niño-Southern Oscillation (ENSO) associated storms on kelp forests, Dayton et al. 1992), with less attention to smaller-scaled disturbances that occur on the time scale of days, **weeks**, or months.

### *Spatial Variation in Disturbance*

Within a geographic region, the disturbance regime in a particular habitat varies from site to site. For example, Dayton (1971) showed that the risk of being battered by drift logs differed substantially among his rocky intertidal study sites in Puget Sound and on the outer coast of Washington State. The relative importance of different agents of disturbance may also vary among sites as Wethey (1979) found for ice scour and cobble impact, the primary agents of physical disturbance to intertidal barnacle populations in New England. Such spatial variation is the norm and has been well documented in rocky intertidal (e.g., in addition to the studies just cited, Sousa 1979b; Paine and Levin 1981; Dethier 1984; McGuinness 1987a; Farrell 1989), kelp forest (e.g., Foster and Schiel 1985; Seymour et al. 1989), coral reef (e.g., Connell 1978; Aronson and Precht 1995; Connell et al. 1997), salt marsh (e.g., Valiela and Rietsma 1995; Pennings and Bertness, this volume), seagrass (e.g., Kirkman and Kuo 1990; Townsend and Fonseca 1998), and soft-sediment (e.g., Oliver et al. 1980) communities.

Variation in the frequency of particular kinds of disturbance occurs at larger spatial scales as well. For example, winter ice is a common source of disturbance to rocky seashores, salt marshes, and soft-sediment habitats at higher latitudes (see examples in Table 4.1), but with decreasing latitude, the climate warms, and the frequency of ice damage declines to zero. Hurricane winds frequently disturb the canopies of mangrove forests in the central and northern Caribbean region (Figure 4.5; Craighead and Gilbert 1962; Jiménez et al. 1985; Roth 1992; Smith et al. 1994; Imbert et al. 1996), but rarely affect the forests of Panama or South America. Other geographical gradients in the quantity and quality of disturbance can be subtler. For example, in northern marshes along the Atlantic coast of the U. S., wrack deposition that **kills** marsh plants is an important disturbance (Figure 4.6), although its effects are variable among marshes (e.g., Hartman et al. 1983; Hartman 1988; Bertness and Ellison 1987; Valiela and Rietsma 1995; Pennings and Bertness, this

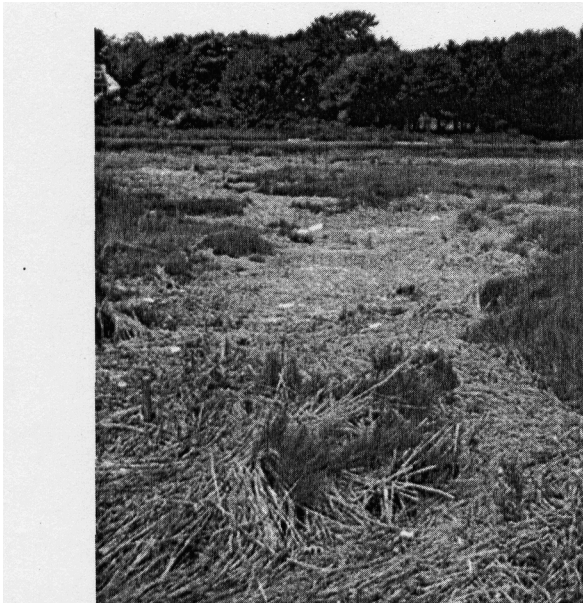


**Figure 4.5** Stands of mangroves killed and defoliated by high winds associated with Hurricane Andrew in 1992, on the shores of Biscayne Bay, Florida. (Photoby the author.)

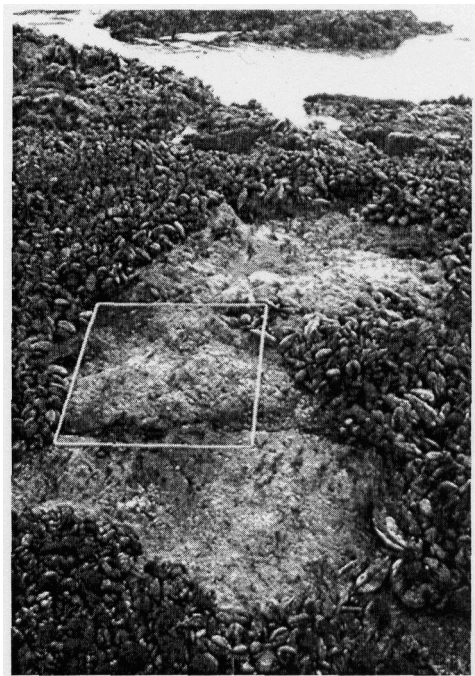
volume). In southern marshes, however, wrack deposits are much lighter, and they may even benefit marsh plants by reducing evaporativewater loss from soils and thereby limiting salt buildup in soils (Pennings and Richards 1998).

#### *Temporal Variation in Disturbance*

The intensities and frequencies of disturbing forces vary in time as well, often seasonally and among years. Numerous studies have documented the seasonaleffects of wave action and storm surge. For example, on the outer coast of Washington State, the mean rate at which patches are cleared in beds of the mussel, *Mytilus californianus*, is more than an order of magnitude greater in winter when large storm waves strike



**Figure 4.6** Accumulations of wrack in the Rumstick Cove salt marsh, Narragansett Bay, Rhode Island. (Photoby J. Levine.)



**Figure 4.7** Patch recently cleared in mussel beds on Bodega Island in central California (quadrant is 0.25 m<sup>2</sup>). (Photoby the author.)

the shore than during summer when waves are much smaller (Figure 4.7; Paine and Levin 1981). Also, the rate of bed disturbance varies 4- to 5-fold among years, depending on the frequency and intensity of storm activity. Wethey (1979, 1985) documented strong seasonality and interannual variability in the physical disturbances that kill intertidal barnacles at Nahant, Massachusetts. Similarly, in southern California, intertidal boulders are much more likely to be moved and overturned in winter when waves are large than in summer when they are small (Figure 4.8; Sousa 1979b). Rates of



**Figure 4.8** Overturned intertidal boulder covered with early successional green algae surrounded by undisturbed boulders dominated by late successional red algae at Ellwood Beach in southern California. (Photo by the author.)

movement are also higher in stormier years. There are, however, some notable exceptions to the seasonal pattern of disturbance in intertidal habitats. In some areas of the world, such as the coast of New South Wales, Australia, rough weather and large storm waves can occur at any time of year with no obvious seasonality in the disturbance they cause (Underwood 1981; McGuinness 1987a).

Disturbance in subtidal, hard substrate habitats is also usually seasonal and variable among years. Kelp forests in southern California are disturbed by strong surge generated by winter storms, which vary in frequency and intensity among years depending on the strength of ENSO conditions (Dayton et al. 1992). Wave action and strong currents associated with cyclones are important agents of disturbance to corals on Heron Island on Australia's Great Barrier Reef (Connell et al. 1997). Cyclonic storms are strongly seasonal in this area (early January to early April), but quite unpredictable in occurrence from year to year. Cyclones passed near the island in 11 out of the 30 study years, but caused significant damage in only 5 of them. Similarly, coral bleaching (Figure 4.9) has most often occurred during the summer or near the end of a protracted warming period associated with ENSO events, but the onset of these conditions is irregular at any one location (Glynn 1993; Jones et al. 1997; Wilkinson et al. 1999).

In soft-sediment environments, the primary agents of disturbance change seasonally. In many areas, lethal hypoxia is a natural phenomenon that regularly develops as the water column becomes sharply stratified during warm summer or autumnal months (e.g., Kitching et al. 1976; Santos and Simon 1980a, b; Diaz and Rosenberg 1995); in other areas, these conditions are aperiodic or persistent. Sediment disturbance by foraging predators (e.g., Woodin 1978, 1981; Reidenauer and Thistle 1981; Van Blaricom 1982; Oliver et al. 1984; Oliver and Slattery 1985; Thrush et al. 1991; Townsend and Fonseca 1998) and bioturbation by infauna (Rhoads 1974) also typically occur in summer or fall when these organisms are most active or abundant on the feeding grounds. In contrast, wave action and strong currents displace and kill infau-

nal populations primarily during the winter storm season (e.g., Eagle 1975; Rees et al. 1977; Yeo and Risk 1979), although cyclones and hurricanes can have important effects, albeit irregularly, at other times of year.

### Spatiotemporal Variation in Disturbance

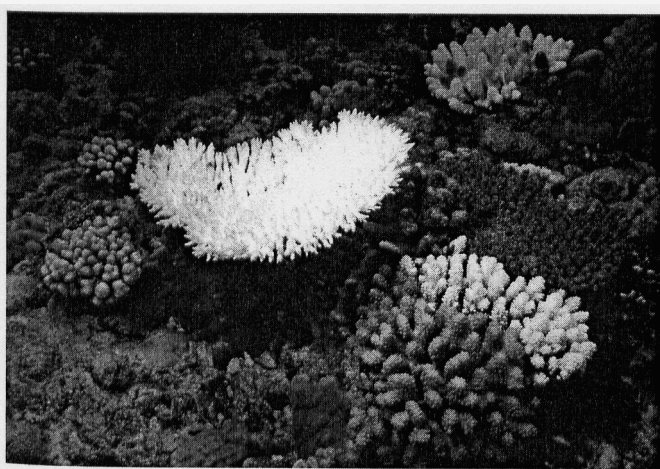
The season of occurrence of a particular kind of disturbance can vary among local sites or geographically. For example, mortality due to heat and desiccation stress at low tide occurs during periods of calm, clear weather when there is little wave splash to ameliorate these harsh conditions. Along the Pacific coast of North America, the seasonal timing of such events depends on local tidal and climatic regimes. In southern California, these stressful 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 (northern California, Oregon, and Washington), daytime low tides and long, desiccating exposures occur in summer (Frank 1965; Sutherland 1970; Dayton 1971; Cubitt 1984). Patterns of intertidal inundation by sand exhibits similar interactions between site and season. Most commonly, sand is deposited in summer, when wave energy and current velocities are low (Hedgepeth 1957; Markham 1973; Daly and Mathieson 1977; Robles 1982; DAntonio 1986), but at certain sites, unique aspects of the local topography and current regime, or proximity to flooding streams and rivers, combine to cause higher deposition of sand or terrigenous sediments in winter (Seapy and Littler 1982; Taylor and Littler 1982; Littler et al. 1983; Turner 1985; DAntonio 1986).

### Variation in Disturbance Size

The sizes of disturbed areas often vary over several orders of magnitude within a given habitat. They range from as small as the space created by the death of a single organism, or part thereof, to in some cases, areas of many square kilometers (e.g., due to hypoxia: Santos and Simon 1980a, b; Boesch and Rabalais 1991; Diaz and Rosenberg 1995; or coral bleaching: Brown and Suharsono 1990; Glynn 1990, 1993; Wilkinson et al. 1999). The size distribution of the disturbed patches created by any particular agent will vary seasonally and among years and sites, reflecting temporal and spatial variation in the intensity of the disturbing force. Paine and Levin (1981) documented such variability in size for patches cleared by wave forces in beds of the mussel, *Mytilus californianus*, on the outer coast of Washington State. Patches created during relatively calm summer months or at protected mainland sites were an order of magnitude smaller than those generated in stormy winter months or at sites receiving heavy wave action. Similarly, I found that the percentage of large intertidal boulders moved by waves was greater in winter months and at the more exposed of my two study sites (Sousa 1979b).

### Correlations among Disturbance Characteristics

Depending on the particular habitat, agent of disturbance, and affected organisms, two or more of the disturbance characteristics (size, severity, and frequency) may be correlated.



**Figure 4.9** Bleached coral colonies on the shallow fore-reef of Moorea, French Polynesia. (Photo by M. Gleason.)

Generally, large severe disturbances occur less frequently and predictably than smaller, less severe ones (Connell and Keough 1985; Sousa 1985). Often, this simply reflects the frequency distribution of storm intensities and severity of damage they cause, but as discussed in the next section, there may be temporal changes in characteristics of individual organisms or assemblages of organisms that affect their vulnerability to disturbance. In such cases, the disturbance regime will be the product of the interaction between the rate and pattern of these “ontogenetic” changes in vulnerability and the timing and intensity of different agents of disturbance.

## SUSCEPTIBILITY OF INDIVIDUALS AND ASSEMBLAGES TO DISTURBANCE

The severity of a disturbance depends on the intensity of the disturbing force, the vulnerability of the target organisms, and in some cases, qualities of the substratum to which the organisms are attached. Vulnerability to disturbance varies with the particular agent of disturbance and with characteristics of affected species, individuals, and assemblages.

### *Characteristics of Species Affect Disturbance Rates*

Species-specific differences in vulnerability are often related to inherent morphological or physiological features, as demonstrated in the following studies from hard substrate and soft-sediment environments. Due to their less robust skeleton and upright growth form, erect branching corals suffer greater damage from wave forces associated with cyclones than massive or encrusting species (Connell 1976, 1978, 1979; Porter et al. 1981; Woodley et al. 1981; Liddell and Ohlhorst 1994; Hughes 1989; Connell et al. 1997). Similarly, vulnerability to damage from storm surge differs among species of erect coral reef sponges, apparently due to differences in the composition of their skeletal fibers (Wulff 1995). Variation in morphological characteristics and physiological tolerances explains interspecific differences in the loss of cover and mortality suffered by rocky intertidal algae and invertebrates due to desiccation, high or low air temperatures, exposure to wave action, or burial and scour by sand or terrigenous sediments (Schonbeck and Norton 1978, 1979; Sousa 1980; Seapy and Littler 1982; Taylor and Littler 1982; Littler et al. 1983; Lüning 1984; D’Antonio 1986; Lüning and Freshwater 1988; Chapman 1995). For similar reasons, salt marsh plant species differ in their response to burial under wrack and soil hypersalinity (Bertness and Ellison 1987; Bertness et al. 1992a; Valiela and Rietsma 1995). Anoxic or hypoxic conditions and associated high concentrations of hydrogen sulfide cause differential mortality among species living in soft-sediment environments (Diaz and Rosenberg 1995; Gamienick et al. 1996). Such conditions can develop beneath dense, seasonal algal mats on intertidal mud flats. Mobile taxa that feed at the sediment-water interface and deeply buried deposit feeders are little affected, but sedentary species that feed at the sediment-water interface, including bivalves and tubicolous suspension feeders, suffer high mortality (Everett 1991, 1994). Species of bivalves with long siphons that can be extended

through the mat survive better than those with short, less-extensible siphons that are unable to penetrate it (Thiel et al. 1998). Peterson (1985) found that different species of bivalves differ in their ability to survive burial under sediments, with deposit feeders surviving better than suspension feeders, and smaller species of deposit feeders surviving better than larger ones.

### *Characteristics of Individual Organisms Affect Disturbance Rates*

The size and shape of an individual organism, and ontogenetic changes in these features, affect its vulnerability to potentially disturbing forces, contributing to variation in disturbance rates within and among species. These effects are very evident when organisms are subjected to the forces associated with flowing water, an important agent of disturbance in marine intertidal and subtidal communities. Organisms living in flow experience drag, lift, and accelerational forces (Koehl 1982, 1984; Denny et al. 1985; Denny 1988, 1995, 1999; Gaylord et al. 1994; Gaylord 2000). As an organism grows, with associated changes in shape and volume, the relative magnitudes of these forces also change. Generally speaking, as an organism grows larger, the hydrodynamic forces impinging on it increase, making adhesive failure or breakage more likely. Ongoing studies are attempting to identify the specific forces that disturb intertidal organisms and determine the degree to which they are responsible for setting an upper limit to the size of organisms living on wave-swept shores. See Denny and Wethey (this volume) for a detailed treatment of the influence of hydrodynamic forces on marine organisms and communities.

Size and shape also affect an organism’s vulnerability to agents of disturbance such as desiccation and extreme air temperatures. In this case, the influence of these morphological traits is often indirect, reflecting the physiological consequences of changing surface-to-volume ratios. Smaller individuals with their greater surface-to-volume ratio are more likely to be killed by environmental extremes because their internal condition is less buffered from rapid or large changes in the external environment. Among intertidal invertebrates, small individuals have been shown to suffer higher mortality than large ones under the same regime of desiccation. Examples include barnacles (Connell 1961), limpets (Wolcott 1973), and sea anemones (Ottaway 1973, 1979; Pineda and Escofet 1989). Similarly, differences in thallus size and shape, by their influence on surface-to-volume ratios, contribute to variation in desiccation resistance within and among species of intertidal algae (Schonbeck and Norton 1979; Dromgoole 1980; Bell 1995). On the other hand, as discussed later, the microclimate experienced by small individuals is often moderated by the presence of larger neighboring organisms that block the wind, cast shade, or retain moisture.

In some cases, smaller size is advantageous in stressful environments. For example, small individuals may be better able than larger ones to escape extremes of the physical environment by moving into cracks and crevices in the substratum (Figure 4.10). When suspension-feeding bivalve popula-



**Figure 4.10** Littorine snails in a rock crevice on Bodega Head in central California—note the greater number of small individuals occupying the refuge. (Photoby the author.)

tions become buried beneath sediment, small individuals suffer less mortality than large ones, because small clams are better able to reestablish their normal vertical feeding positions in the unconsolidated new sediment (Peterson 1985).

#### *Aggregation and Species Interactions Affect Disturbance Rates*

Living in either conspecific or heterospecific groups can alter an individual's risk of being damaged or killed by an agent of disturbance. Whereas living at high density in physically benign habitats often increases the risk of mortality due to competition and, in some cases, disturbance by hydrodynamic forces (see later examples), living at high density often lowers the risk of mortality in physically harsh environments because the presence of neighbors directly or indirectly buffers environmental extremes. For example, at physically stressful higher tidal elevations, the barnacle, *Semibalanus balanoides*, suffers less mortality when living in medium- to high-density aggregations than at low density (Bertness 1989). A dense cover of barnacles shields the rock surface from the sun so that it remains cooler than areas where barnacles are sparser. Because rock temperature is the primary determinant of barnacle tissue temperature, barnacles in dense aggregations experience less thermal stress. Mussels (*Mytilus edulis* and *Guekensia demissa*) and furoid algae (*Fucus distichus* and *Ascophyllum nodosum*) also suffer less mortality from heat and desiccation near the upper limit of their vertical distributions when living at high as compared to low density (Bertness and Leonard 1997). Similarly, rocky intertidal sea anemones (e.g., *Actinia fenebrosa*; Ottaway 1979; *Anthopleura elegantissima*; Pineda and Escofet 1989) and algae on coral reef flats (Hay 1981) survive desiccation better when living in clonal aggregations and turfs, respectively, than as solitary individuals. Heat and desiccation stress are not the only agents of disturbance that can be ameliorated by living in aggregations. In high-latitude salt marshes, mussels (*G. demissa*) living in beds suffer less mortality from winter ice scour than do isolated mussels (Bertness and Grosholz 1985).

Heterospecific associations can also reduce the rate of disturbance in physically stressful habitats. For example, mortality from thermal and desiccation stress is often reduced for intertidal algae that live beneath the canopy of other species (Dayton 1975). Beds of the mussel, *Mytilus californianus*, that become overgrown with algal turfs are less likely to be killed by freezing air temperatures, although algae-covered mussels have lower body weights and suffer modestly higher rates of dislodgment by intense wave action (Brosnan 1994). Reusch and Chapman (1995) demonstrated experimentally that mussels (*Mytilus edulis*) living within stands of eelgrass (*Zostera marina*) were less likely to be dislodged during storms of moderate intensity than mussels living without eelgrass neighbors. However, eelgrass afforded mussels no measurable protection from dislodgement during intense storms. There was no evidence of a reciprocal effect: the presence versus absence of mussels made no difference to the storm damage suffered by patches of eelgrass.

The presence of other species may also afford protection from agents of biological disturbance. For example, infaunal invertebrates that live amongst dense seagrass (e.g., Orth 1977; Orth et al. 1984; Summerson and Peterson 1984; Townsend and Fonseca 1998) or large worm tubes (Woodin 1978) suffer lower mortality from the activities of foraging crabs or rays than those that inhabit areas of the bottom where seagrasses or worm tubes are sparse or absent. High densities of seagrass stems and rhizomes or worm tubes interfere with the movement and foraging behaviors of these epifaunal predators, creating refugia not only from predation but also from the negative effects of being displaced or buried as crabs and rays excavate or otherwise disturb surface sediments while searching for food or simply moving about the bottom.

In other instances, an increase in the local density of organisms and associated effects of competition on the morphology or physiology of individuals, and, in some cases, on the three-dimensional structure of the assemblage increases the per capita risk of mortality due to disturbance. For example, when barnacles settle densely at lower tidal heights and experience little predation, they soon grow to fill the available space. The ensuing competition forces neighboring individuals to coalesce and form hummocks of weakly attached, elongate individuals (Figure 4.11; Bames and Powell 1950; Connell 1961; Menge 1976; Grant 1977; Bertness 1989; Bertness et al. 1998). These hummocks of barnacles are more easily torn loose by wave action than are isolated individuals of the conical or columnar form that develops under less-crowded conditions. Similarly, although mussels living in beds may experience a lower per capita risk of dislodgement by wave forces as compared to isolated mussels (Bell and Gosline 1997), as mussel beds become older and multilayered, the risk of massive dislodgment and patch formation increases (Harger and Landenberger 1971; Paine 1974; Paine and Levin 1981). Multilayered beds of the mussel, *Mytilus californianus*, have a higher profile than single-layered beds, exhibit areas of hummocking where groups of densely packed individuals have been lifted away from the substratum, and a higher proportion of their members are attached by byssal threads to other mussels



**Figure 4.11** Hummocked barnacles—unstable elongate individuals at center have been removed by wave action. (Photo by the author.)

rather than to the rock surface. Lift, generated by the pressure difference between the slow-moving water in the interstices within the bed and the fast-moving water within waves that break over it, detaches individual mussels (Denny 1987). Once a few mussels have been removed, the features of multilayered beds just described make it likely that sections of the "fabric" of the bed will begin flapping in flow and be peeled away from the substratum forming a bare patch. Thus, up to a point, mussels reduce their risk of being disturbed by wave forces by living in beds, but once the bed becomes deeply layered, the risk of massive dislodgment increases.

Similarly, algae that grow in aggregations may face a greater risk of disturbance than isolated individuals. For example, in dense kelp beds, broken, as well as intact, plants frequently become entangled with neighbors (e.g., *Macrocystis pyrifera*, Rosenthal et al. 1974; Dayton et al. 1984; Seymour et al. 1989; Dayton et al. 1992; *Nereocystis luetkeana*, Koehl and Wainwright 1977). When these clumps of tangled thalli are subjected to a current, the holdfasts and stipes of intact members of the tangle experience increased drag, compared to untangled individuals. As a result, holdfasts of entangled intact plants can be ripped from the substratum, or their stipes broken (Figure 4.12). By comparison, kelp plants growing in sparser beds are less likely to become entangled with their neighbors and experience a lower rate of this kind of disturbance.

Populations that have experienced a history of competition for food may suffer higher rates of mortality (i.e., disturbance) following severe environmental conditions than populations that have not. For example, when buried under sediment, suspension-feeding clams that had been maintained at high densities suffered nearly twice the mortality of clams that had been growing at low density over the same period of time (Peterson and Black 1988). The former showed clear symptoms of competitive stress prior to the addition of sediment, including lower shell growth and gonadal weight, and higher mortality than low-density controls. Apparently, competition among



**Figure 4.12** Entangled, detached kelp plants washed onto a beach in California following a large winter storm. (Photo by M. Foster.)

clams for suspended food when growing at high density compromises their ability to survive the physiological stresses associated with burial under sediment. Peterson (1985) documented similar density-dependent mortality of suspension-feeding bivalve following a natural sedimentation event.

Heterospecific associations can increase the risk of disturbance. For example, heavily epiphytized macroalgae are more likely to be detached or broken by hydrodynamic forces than nonepiphytized individuals (Menge 1975; Sousa 1979a; DAntonio 1985). Likewise, subtidal mussels that have been overgrown by kelp plants are much more susceptible to being torn loose by storm surge than mussels that are free of kelp; by reducing kelp cover, urchin grazing indirectly increases mussel survival (Witman 1987).

Partial predation, herbivory, and parasitism can also indirectly increase the mortality caused by a potentially disturbing force. For example, wounds from grazing or boring organisms increase the risk of breakage because the force is imposed on a smaller cross-sectional area, that is, the mechanical stress is increased (Black 1976; Koehl and Wainwright 1977; Santelices et al. 1980; Tegner et al. 1995). Likewise, animal parasites may reduce the physiological tolerance of their host to environmental extremes, and thereby increase the mortality they cause. For example, the salt marsh snail, *Cerithidea californica*, is much more likely to be killed by low oxygen conditions if it is infected with larval digenetic trematodes than if it is uninfected (Sousa and Gleason 1989).

#### *Effects of Species Diversity and Composition on Disturbance Rates*

So far, I have discussed how individual and population-level characteristics and pair-wise species interactions can affect the rate of disturbance. The frequency and severity of disturbance also varies among assemblages differing in species composition and diversity. In most cases, these assemblage-level differences seem to reflect characteristics of their domi-

nant species, but there have been very few marine studies that have explicitly addressed the question of whether there are higher-order properties that cause multispecies assemblages to differ in their resistance to potentially disturbing forces. In other words, does the aggregate response of a multi-species assemblage to a disturbing force, in terms of lost cover or biomass, differ from what would be the sum of independent responses by the member species?

Two studies conducted with assemblages of intertidal macroalgae have tested for such higher-order effects. I experimentally disturbed intertidal boulders that supported different successional stages (see Figure 4.8) by overturning them for different lengths of time, effectively manipulating the intensity of disturbance (Sousa 1980). These successional stages differed in species composition and diversity. I measured both the severity of damage (i.e., loss of percent cover) and the pattern of regeneration after the boulders were righted. In terms of resistance to disturbance, our present focus, differences among the assemblages in the amount of cover lost at a given intensity of disturbance were entirely explained by physiological and life history characteristics of the component species. Early successional assemblages suffered the greatest loss of cover for a given length of overturning because they were dominated by the ephemeral, sheetlike, green alga *Ulva* sp., which is particularly vulnerable to abrasion and shading. Late successional assemblages, dominated by the perennial red alga, *Gigartina canaliculata*, suffered the least damage, because this species has a tougher, more elastic thallus and is shade tolerant. Middle successional assemblages, being a diverse mixture of these two species plus several other perennial red algae, were intermediate in their resistance to damage. Diversity per se had no additional influence on the amount of cover lost to disturbance.

The second study, by Allison (1997), tested the effects of species diversity and composition on the resistance and resilience of a high intertidal, algal-dominated assemblage to an experimental heat treatment. He selectively weeded plots to create macroalgal assemblages that differed in diversity and species composition, then exposed them to a heat lamp for 90 minutes. Changes in algal cover over the first month following the heat treatment were considered a measure of the resistance of the experimental assemblages to change. Allison found that differences in pretreatment cover and biomass explained the greatest proportion of the variance among plots with respect to resistance; the greater the cover and biomass prior to heat treatment, the greater the loss of cover and biomass in response to the treatment. Similar to my result (Sousa 1980), most of the significant effects of the diversity manipulation on resistance to damage were parsimoniously explained by characteristics of the component populations, rather than by some higher-order effect of species diversity per se. For example, higher diversity treatments, especially those dominated by fucoids, suffered greater loss than lower diversity treatments because, on average, the diverse plots had greater cover and biomass than the low diversity plots, that is, they had more to lose.

Differences in the vulnerability of different successional stages to disturbance can dictate the temporal patterning of disturbance in a habitat. Fairly predictable cycles of disturbance may result if later stages are more vulnerable than earlier ones. For example, on the outer coast of Washington State, where patches are cleared in beds of the mussel, *Mytilus californianus*, by a combination of wave forces and the impact of drifting logs (see Figure 4.7; Dayton 1971; Paine 1974; Suchanek 1978, 1979, 1981; Paine and Levin 1981), succession proceeds through a series of stages dominated in turn by diatoms, macroalgae, barnacles, and finally, back to mussels. Mussel beds, particularly older multilayered ones, are more likely to be dislodged by wave action than are earlier successional stands of macroalgae or barnacles. Thus, the rate at which species are replaced during succession, in this case by hierarchical interspecific competition, will control, to some degree, the frequency of disturbance. The complete successional sequence from diatoms to mussels takes a minimum of 7–8 years, and this is approximately the interval between successive disturbances of the same patch of space at the most exposed sites (Paine and Levin 1981). The recurrence interval is longer at less-exposed sites.

The frequency of disturbance need not always be influenced by the successional state of the assemblage. In intertidal boulder fields, I studied (see Figure 4.8; Sousa 1979a, b, 1980) the sessile organisms that grew on the upper surfaces of the boulders consisted mostly of short, turflike macroalgae and barnacles. Successional variation in the composition of these assemblages probably has little, if any influence on the probability that wave forces would overturn a boulder. Similarly the occurrence of landslides and lava flows that kill benthic organisms are unaffected by the abundance, size or age of their victims.

### Substrates Affect Disturbance Rates

Characteristics of the substrate itself can influence the disturbance regime. Barnes and Topinka (1969) showed that the force required to detach the alga *Fucus* from the test of a barnacle is less than that necessary to remove it from the rock surface itself. In some cases, the adhesive strength of an organism exceeds that of other organisms to which it is attached, or the breaking stress of the rock itself. When the rock or host organism breaks, the attached individual is carried away (Dayton 1973; Denny et al. 1985; Witman 1987; Bell and Gosline 1997).

## REGENERATION OF SESSILE ASSEMBLAGES FOLLOWING DISTURBANCE

### Environmental Alterations That Affect Regeneration

As discussed by Connell et al. (1997), disturbances not only kill or damage resident organisms, but also directly or indirectly alter the biological or physical environment of survivors and individuals that recruit to the affected area following the event. These alterations of the environment can

strongly influence subsequent patterns of recolonization and succession. Direct changes to the physical environment include alterations of the substrate and local topography, which in turn affect currents, light levels, and sedimentation rates. Direct impacts on the biological environment include changes in the abundance and distribution of associated species that potentially interact with the residents. The biological environment will be indirectly modified by disturbances that alter the local abundance of spatial refuges, food, or nutrients available to resident species or others that interact with them, or the supply of propagules.

### *Life History and Mode of Reestablishment*

There are four mechanisms by which populations become reestablished in a patch of disturbed substrate or sediment: (1) vegetative regrowth of survivors within the patch; (2) recruitment from propagules that survive the disturbance (e.g., seed banks in salt marshes: Hopkins and Parker 1984; Hutchings and Russell 1989; Ungar and Woodell 1993, 1996; Baldwin et al. 1996; Baldwin and Mendelssohn 1998; Staniforth et al. 1998; seagrass beds: Inglis 2000; banks of microscopic juvenile stages of algae on rocky seashores: Santelices et al. 1995; Blanchette 1996; Worm et al. 1999; Edwards 2000); (3) lateral inward encroachment by juveniles or adults from the surrounding undisturbed assemblage, by vegetative spreading, active movement, or passive transport in flow; and (4) recruitment from dispersing propagules including spores, larvae, or fragments capable of attaching to the substrate and growing vegetatively. Of the four, the role of seed and spore banks is the least well documented. The relative contributions of these different modes of recolonization depend in part on the severity of the initial disturbance, as does the rate of recovery. Following disturbances that cause low to moderate levels of damage, vegetative propagation is often the predominant mechanism of recovery for populations of species that are able to survive their injuries and regrow (e.g., red algal turfs, fucoid algae, crustose and rhizoidal species: Dayton 1975; Lubchenco and Menge 1978; Lubchenco 1980; Sousa 1980; Dethier 1984; Williams 1988; McCook and Chapman 1992; Airoidi 1998; Scrosati 1998; Underwood 1998; Umar et al. 1998; corals: Connell 1973; Highsmith et al. 1980; Tunnicliffe 1981; Highsmith 1982; Fong and Lirman 1995; Smith and Hughes 1999; salt marsh plants: Allison 1995, 1996; Bertness and Ellison 1987; Baldwin and Mendelssohn 1998; seagrasses: Patriquin 1975; Short 1983; Turner 1983a, b, 1985; Kirkman 1985; Williams 1988, 1990; Kirkman and Kuo 1990; Rollon et al. 1998; Bell et al. 1999; Ramage and Schiel 1999; Rasheed 1999). If vegetative regrowth is sufficiently robust, it may even preempt the space and inhibit propagule settlement or juvenile recruitment (Denley and Underwood 1979; Sousa 1979a; Connell et al. 1997; Osman and Whitlatch 1995a, b). As the severity of disturbance increases, the fragments of clonal species that remain are so small or damaged that they cannot reestablish or survive, and their populations can only regenerate via colonists from outside the patch. For example, on coral reefs, the stronger the disturbance, the less vegetative

recovery, because surviving fragments are badly scoured and suffer delayed mortality (Knowlton et al. 1981).

For nonclonal invertebrates (e.g., mussels, barnacles, some tunicates, and most infaunal species) and many kelps, disturbance is an all-or-none phenomenon. Lacking the ability for somatic regeneration, such solitary organisms (*sensu* Jackson 1977a) are either killed or displaced (i.e., disturbed), or left intact and in place (i.e., not disturbed). For example, patches newly cleared in continuous mussel beds or stands of barnacles are initially devoid of living macroorganisms (Paine and Levin 1981), leaving no opportunity for vegetative regeneration. When recolonization is completely dependent on propagules arriving from outside the patch, recovery will generally be slower than in situations where vegetative regeneration plays a substantial role in regeneration (Connell and Slatyer 1977, see later examples).

### *Severity of Initial Damage*

Only the most severe disturbances remove all resident individuals from the affected area. Such events are relatively rare. More typically, some resident organisms are killed or displaced, but others either sustain injuries from which they recover or escape harm altogether (Foster and Sousa 1985; Malanson 1984). As discussed in the last section, the capacity for vegetative regrowth is a critical life history feature that often affects the rate and course of succession. Given how common this situation is, it is surprising how few experimental studies have explicitly compared the response of assemblages to different severities of disturbance. One would expect assemblages to recover more quickly and with greater fidelity from disturbances of low to moderate severity as compared to those that kill most or all of the residents.

This prediction held true for the boulder field algal assemblage that I experimentally disturbed in the manner described earlier (Sousa 1980). Regardless of successional stage, assemblages growing on the upper surface of boulders that were overturned for shorter periods recovered more rapidly and completely than those that suffered greater damage from longer periods of overturning. Other studies that have manipulated the severity of disturbance include De Vogelaere's (1991) of an intertidal algal-invertebrate assemblage, Underwood's (1998) of stands of the intertidal fucoid alga, *Hormosira banksii*, and Airoidi's (1998) of a red algal turf-dominated assemblage in the shallow subtidal. These studies experimentally mimicked partial disturbance to compare its effects on successional dynamics to those of complete clearing. Partial disturbance consisted of superficially removing macroalgal and/or invertebrate cover, leaving behind live algal holdfasts and crusts. All living cover, including holdfasts and crusts, was removed from the complete disturbance plots. All three studies found that the severity of experimental disturbance affected the rate and pattern of recolonization. Assemblages that developed in partially disturbed plots converged more rapidly with those in unmanipulated control plots, in terms of species composition and extent of algal and invertebrate cover, than did completely cleared plots. De Vo-



gelaere and Airoidi observed that completely cleared plots underwent a longer succession, the stages of which were characterized by species that never became common in the partially cleared plots. Underwood found that grazers had a greater impact on *Hormosira* recolonization in the complete than partial removal plots.

Kennelly (1987b) examined, with a series of field manipulations, the effects on understory algae and invertebrates of different severities of disturbance to the canopy of an *Ecklonia*-dominated kelp forest. The extent to which the kelp canopy was thinned and the degree to which the kelp plants were removed (fronds only, fronds and stipes only or entire plant including holdfast) had significant effects on the understory assemblage. Individual species differed in their responses to the treatments, and there was considerable heterogeneity among replicates due to variation either in propagule availability or postsettlement survival.

I know of only one study that has experimentally investigated the effect of disturbances of differing severity on marsh communities. Baldwin and Mendelssohn (1998) applied three severities of disturbance to replicate plots in two different kinds of oligohaline marsh, one dominated by *Spartina patens* and the other by *Sagittaria lancifolia*. The treatments were (1) no disturbance, (2) nonlethal clipping of aboveground vegetation, and (3) application of a lethal herbicide. In both vegetation types, plants in the nonlethal disturbance plots quickly resprouted vegetatively, reestablishing assemblages similar in composition to unmanipulated controls. The lethal disturbances, however, produced marked shifts in the composition of the vegetation that persisted throughout the two-year study. Plots that experienced lethal disturbance were recolonized entirely by recruitment of seedlings, in some cases from a buried seed bank. Individual species responded differently to the treatment, but the abundances of a number of annual and perennial species that are uncommon in the undisturbed marsh were clearly enhanced by the removal of the dominant, perennial clonal species, *Spartina* and *Sagittaria*.

Most experimental studies of disturbance in marine communities have applied a single level of disturbance—complete removal of resident organisms. The studies just discussed highlight the importance of examining the effects of a more realistic range of disturbance severities in future studies. Results from completely cleared plots may not represent conditions following a typical disturbance.

### *Patch Characteristics That Affect Recolonization and Succession*

Characteristics of a disturbed patch and of the area surrounding it can have a variety of direct and indirect effects on the rate and pattern of recolonization. These characteristics include patch type, size, shape, surface characteristics, location, and time of creation.

**PATCH TYPE.** The relative contributions of the four modes of reestablishment (see "Life History and Mode of Reestablishment") differ with patch type. Embedded patches are bound-

ed by a living assemblage, so all four means of colonization are possible, whereas lateral encroachment of individuals from surrounding areas cannot occur in isolated patches.

**PATCH SIZE AND SHAPE.** Recolonization of a disturbed patch can be affected directly or indirectly by its size and shape. The influence of these features often varies with patch type. Next, I discuss the most conspicuous and well studied of these effects. See Sousa (1984, 1985) for a more complete treatment.

A direct effect of patch size is its influence on the number and species composition of colonizing propagules. Larger clearings would be expected, all else being equal, to receive a greater total number of colonists per unit time than smaller ones. In the process, large clearings "sample" a greater proportion of the pool of available propagules than do small patches, affording species whose propagules are less well represented in the pool a greater opportunity to recruit. This effect is more likely to be observed in disturbed isolated than embedded patches because the former have no neighboring organisms to exert either positive or negative effects on recolonization, and colonization is primarily by dispersing propagules. In such systems, if the dominant competitors produce fewer propagules or disperse them less broadly than competitively inferior species, this direct effect of patch size on colonization rates and resulting differences in species interactions within patches can generate marked spatial variation in the composition of the assemblage among patches. Small patches, to which weakly dispersing, dominant competitors recruit less often, will serve as refuges for inferior competitors, which will often be competitively excluded from large patches.

To my knowledge, this "propagule sampling" effect has yet to be demonstrated in a real system of disturbed patches, but the scenario fits well with the dynamics of invertebrate assemblages that grow on the shells of the bivalve *Pinna*, which protrude from the soft sediments in which they live, forming small, discrete isolated patches. These assemblages are comprised of small, determinate sheetlike bryozoans and solitary organisms, including serpulids. In contrast, assemblages on nearby pier pilings (which could be considered large isolated patches) are dominated by indeterminate, sheetlike, colonial tunicates that are competitively dominant over the forms that characterize the *Pinna* assemblages (Kay and Keough 1981). Keough (1984) experimentally confirmed the mechanisms generating these patterns. He also presented evidence that competitively inferior species such as bryozoans and serpulids settle preferentially in small, isolated patches where they experience less competition, whereas larvae of competitively superior tunicates prefer larger substrates that allow greater colony size and higher reproductive output. Keough attributed the evolution of these differences in settlement preference to the distinct selection regimes experienced by individuals that recruit to the different types of patches. Other studies have documented very similar differential distributions of invertebrate life forms among insular patches of subtidal hard substrate that differ in size (Jackson

1977b; Karlson 1978). Rates of recruitment to isolated patches will also be affected by interactions between flow and various features of the insular substrate, especially the shape and thickness of its edges (Mullineaux and Garland 1993).

The processes that influence recolonization of embedded disturbed patches, which are immediately surrounded by living organisms, may be very different from those just discussed for isolated patches. Organisms that surround an embedded patch can have positive or negative effects on recruitment, and the direction and strength of these effects will vary not only with patch size and shape, but with characteristics of these neighbors (e.g., their size, morphology, or feeding biology) and the prevailing environmental conditions (e.g., during exposure to air at low tide versus submerged in flowing water). In these situations, indirect effects of patch size can overwhelm the direct effect previously described. For example, because small patches have a greater ratio of edge to internal area, the number of reproductive adults near the patch will often be greater per unit patch area than for large patches. For species whose propagules do not disperse far, settling in greatest numbers close to the adult, this may result in a denser settlement and more rapid recruitment to small patches than large ones, opposite to the prediction for isolated patches. Even animals whose larvae travel long distances, but are attracted to settle gregariously near conspecific adults, may do so more densely in small versus large embedded patches of the same shape. In this case, the stimulus for settlement is locally enhanced in smaller patches because of the greater numbers of nearby adults per unit area of patch. The latter result was obtained in two experimental field studies of intertidal invertebrates whose larvae are chemically stimulated to settle near adults, the barnacle, *Chthamalus anisopoma* (Raimondi 1990) and the tubeworm, *Galeolaria caespitosa* (Minchinton 1997). Similarly, Navarrete and Castilla (1990) found that the mussel, *Perumytilus purpuratus*, recruited only to the walls of adult barnacles, and never to bare rock. Consequently, smaller clearings in stands of barnacles, which have a higher ratio of perimeter recruitment sites to internal area, were more rapidly colonized and dominated by mussels than larger clearings.

Variation in the supply of propagules to embedded disturbances of different size may or may not result in correlated differences in settlement and recruitment, depending on the effects of neighboring organisms on these processes. For example, the very feature that could promote an enhanced supply of propagules to smaller embedded clearings, namely a high edge-to-area ratio, can indirectly make the internal environment of such clearings inimical to settlement or recruitment. The smaller the clearing, the more completely organism living along its edge may shade or whiplash its surface, deplete the local supply of nutrients and suspended food, or ingest dispersing propagules (e.g., Young and Gotelli 1988). The strength of these effects will depend on numerous details of the particular situation, including mainstream flow dynamics, height and morphology of the surrounding organisms, and the topography of the surrounding substrate (Abel-

son and Denny 1997). On the other hand, especially at mid and upper levels of rocky intertidal shores, the presence of neighboring organisms often ameliorate the harsh physical conditions that usually develop during low tide following the removal of cover. In summer, the surface of the rock within clearings in intertidal assemblages receives higher levels of solar radiation and airflow, which cause higher air and substrate temperatures and lower humidity, compared to the surrounding undisturbed sites. However, in winter at high latitudes, the opposite may occur: Organisms that colonize clearings will be exposed to colder air temperatures and greater risk of freezing than those in the surrounding assemblage where the canopy provides insulation. The buffering effect of neighboring organisms on the internal environment of the patch will be greater in smaller patches because the neighboring canopy will cover or cast shade on a greater proportion of their internal area.

Another very important consequence of the greater edge-to-area ratio of smaller embedded patches is that they are more rapidly filled than larger patches by vegetative ingrowth of clonal organisms or immigration of mobile or attached, but semimobile, solitary organisms that live on the perimeter of the disturbed area or in the area surrounding it (e.g., mussels: Suchanek 1979; Paine and Levin 1981; Sousa 1984; De Vogelaere 1991; Littorin and Gilek 1999; colonial invertebrates: Kay and Keough 1981; Palumbi and Jackson 1982; Connell and Keough 1985; algae: Dye 1993; salt marsh plants: Bertness and Ellison 1987; Ellison 1987; Hartman 1988; infaunal invertebrates: Smith and Brumsickle 1989). Conversely, recruitment from dispersed larvae, spores, or seeds generally makes a greater contribution to recolonization of large patches. What constitutes a small versus large embedded patch in any particular system depends on the mobility of the species in the assemblage. The greater the mobility of potential postlarval and adult colonizers, the larger the disturbed patch must be before larval settlement makes a significant contribution.

Experimental studies examining the effect of patch size on recolonization following disturbance have been conducted in a variety of marine habitats. All have created embedded clearings of different sizes, in some cases crossed with manipulations of other variables. By far, the greatest number of such studies has been conducted in rocky intertidal or subtidal habitats. Many of these have demonstrated differential recruitment or growth of species among experimental clearings differing in area. As discussed earlier, differences in settlement rate as a function of patch size, explain some of these results (e.g., barnacles: Jernakoff 1983; Raimondi 1990; tubeworms: Minchinton 1997; mussels: Navarrete and Castilla 1990), but in other cases, it is uncertain which of the previously discussed mechanisms or others were responsible for the observed patterns. Variation in desiccation stress or intensity of algal whiplash, the former more important in large clearings and the latter in small, has been suggested as the cause of differential success of various algal species and barnacles among experimental clearings of different size (Sousa 1984;

Kim and DeWreede 1996). By comparison, Airoidi (1998) found that clearing size had little effect on the recovery of a subtidal turf-dominated algal assemblage, where neither desiccation stress nor algal whiplash occurs. **On** the other hand, in a taller stature, fucoid-dominated algal assemblage, also in the subtidal, shading or some form of adult interference caused the density of recruits to be lower in smaller clearings and on the edges, as compared to centers, of larger ones (Emmerson and Collings 1998).

Another indirect mechanism by which the size of a disturbed patch has been demonstrated to affect recolonization and subsequent succession on rocky seashores is through its interaction with herbivory. This interaction has been most convincingly documented for disturbance-generated clearings in beds of the mussel, *Mytilus californianus*, on Pacific Northwest shores. Small clearings often support higher densities of limpets than large ones (Suchanek 1978, 1979; Paine and Levin 1981). Furthermore, during the early stages of succession in larger patches, limpet grazing is restricted to a 10 to 20 cm-wide browse zone on the perimeter of the patch, resulting in a nearly algal-free halo around the edge of the clearing (Figure 4.13; also see photos in Dayton 1973; Suchanek 1978, 1979; Sousa 1984). It had been hypothesized that this pattern occurs because beds of mussels surrounding a cleared patch afford limpets and other small grazers a refuge from wave shock, desiccation stress, and possibly predation. Because small clearings have a greater ratio of edge-to-area, they are accessible to a greater number of these grazers per unit area. The consequence of this spatially restricted

foraging is that the total area of small patches is subject to relatively intense grazing, whereas the centers of large patches experience little grazing and therefore develop a more extensive cover of algae. By simultaneously manipulating clearing size and access to herbivores, I confirmed that this interaction between patch size and herbivory produced marked differences in succession between experimental clearings of two different sizes at a mussel-dominated site in northern California (Sousa 1984). Several other studies that have monitored recolonization in experimental clearings of different size, but did not manipulate herbivores, nonetheless observed patterns that were entirely consistent with an interaction between patch size and herbivory. The studies were conducted in a high-intertidal algal-barnacle assemblage in Oregon (Farrell 1989), a midintertidal assemblage dominated by mussels, barnacles, and coralline algae in central California (De Voelaele 1991), and a low-intertidal coralline-dominated assemblage in southern Africa (Dye 1993). In each case, one or more species of molluscan herbivore developed higher densities in small than large clearings and near the edges as compared to the centers of the larger clearings. The species composition and successional dynamics of the sessile assemblage that developed in the clearings of different size varied in a predictable fashion with their respective herbivore densities. In contrast, Benedetti-Cecchi and Cinelli (1993, 1994, 1996) found little consistency in the effect of clearing size on patterns of colonization and succession in three intertidal habitats on the west coast of Italy: low intertidal sandstone platforms dominated by coralline algae, midintertidal mixed-species algal assemblages, and algal-dominated tide pools. In the midintertidal and tide pool habitats, where an herbivore exclusion treatment was crossed with the clearing size manipulation, limpets recruited in higher densities to the smaller control clearings, and their grazing may have contributed to the lower algal cover that developed in those plots, but the interaction between clearing size and herbivore exclusion was not statistically significant. Nor did they detect a difference in species composition or abundance in the center versus edges of clearings that might be attributable to limpets foraging inward from the periphery. Benedetti-Cecchi and Cinelli suggested the alternative explanation that some factor other than limpet grazing was responsible for the lower algal cover in small plots and that limpets were simply responding to the availability of space free of fast-growing algae that might otherwise exclude them from the substratum. Similarly Worm and Chapman (1998) found no evidence that a grazing-patch size interaction affected recruitment of *Fucus evanescens* to clearings in a dense turf of the red alga, *Chondrus crispus*.

Few experimental manipulations of disturbed patch size have been conducted in other marine habitats. Shumway and Bertness (1994) found that mechanisms of succession differed markedly between experimental clearings of different size in a New England salt marsh that were intended to mimic bare patches created by wrack deposition. The soil in the large clearings became highly saline due to evaporation, whereas

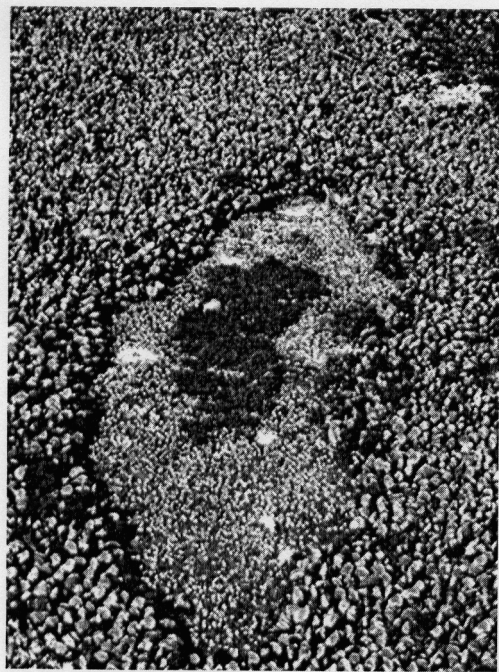


Figure 4.13 Patch cleared in intertidal mussel beds showing central stand of early successional algae surrounded by peripheral grazed halo on Tatoosh Island, Washington. (Photo by the author.)

soil salinity in small clearings differed little from that under undisturbed vegetation. As a result, large patches were colonized almost exclusively by seedlings of a highly salt-tolerant species, *Salicornia europaea*. Once established, this species ameliorated the extreme salt levels by shading the soil, thereby reducing evaporation, and allowing less salt tolerant, but competitively superior species, to establish. In other words, facilitation was initially the primary mode of succession in large patches. In small patches, the dominant perennial species could invade from the outset and competitive interactions dictated patterns of succession. Working in the same study site, Ellison (1987) found that seedlings of *Salicornia europaea* that recruited to areas from which competitors had been removed suffered much higher levels of herbivory by a chrysomelid beetle than seedlings that recruited beneath an intact canopy. Ellison suggested that the beetles might more easily locate the seedlings in open disturbed sites. If this were the case, one would predict that rates of herbivory might differ among patches of different size, possibly in the opposite fashion to the common pattern on intertidal shores. That is, *Salicornia* plants might suffer greater damage in large than small clearings.

It has proved very challenging to conduct similar experiments examining the recolonization of disturbed patches in soft-sediment environments because of the technical difficulties of defaunating the sediment without completely altering its structure. Early studies of recolonization patterns in soft sediments attempted to circumvent this problem by deploying trays or cups of defaunated sediments (e.g., McCall 1977) as a mimic of the intact seafloor. Smith and Brumsickle (1989) demonstrated that this technique introduces a serious bias, selectively excluding postlarval immigrants from the surrounding undisturbed sediment. As discussed later, Smith and Brumsickle's experiments and other studies (VanBlaricom 1982; Bell and Devlin 1983; Levin 1984; Oliver and Slatery 1985; Savidge and Taghon 1988; Frid 1989; Emerson and Grant 1991; Thrush et al. 1991, 1992; Günther 1992; Hall et al. 1994; Shull 1997) have shown that postlarval immigration by juveniles and adults plays a large role in the colonization process and affects subsequent patterns of community development. To study the effect of disturbed patch size on recolonization, Smith and Brumsickle (1989) collected replicates of two different sizes of cores of intact sediment, defaunated them by freezing, and returned them to their original positions, flush with the undisturbed sediment surface. The small cores were colonized more rapidly than the large cores, with higher accumulation rates of total fauna, species, and individuals in the five dominant taxa. The relative contributions of different modes of colonization also differed with core size. The proportion of colonists that were postlarval immigrants was nearly twice as high in the small cores as the large ones. Conversely, larval recruits constituted a greater proportion of the individuals colonizing large cores. Further, successional patterns differed markedly between core sizes, probably as a consequence of the differences in mode of colonization. The authors attributed these differences to the same indirect ef-

fects of patch geometry that can affect recolonization of disturbed patches in the rocky intertidal. The greater edge-to-area ratio of smaller patches affords relatively greater access to postlarval immigrants. Conversely, as disturbance size increases, so does the contribution of larval recruitment (e.g., Santos and Simon 1980a; Levin 1984; Butman 1987; Günther 1992), although recruitment by postlarvae and adults may continue to contribute significantly to recolonization of large disturbances in high-energy environments (i.e., intertidal sand flats) where waves or strong currents erode sediments and disperse the resident infauna widely (e.g., Emerson and Grant 1991; Commito et al. 1995; Thrush et al. 1996).

Thrush et al. (1996) created disturbance patches of three sizes in an intertidal sand flat habitat by "smothering" the sediment in place. They found that small patches recovered more rapidly from disturbance than large ones and attributed the difference to the greater instability of sediment in the large patches where tube-building polychaetes that stabilize sediments were slower to colonize. These tube builders dominated the assemblage that surrounded the experimentally defaunated patches.

Scale dependency in the patterns and processes of infaunal response to disturbance is receiving increased theoretical attention (Zajac and Whitlatch 1985, 1991; Whitlatch et al. 1998; Zajac et al. 1998). A major goal of this work is to generate specific predictions about the relative contributions of larval recruitment versus postlarval juvenile and adult immigration (by crawling, burrowing, or passive transport by currents) to the recolonization of disturbed patches (Günther 1992). Specifically how do these relative contributions change as a function of size and other characteristics of a disturbed area, and what consequences do these differences have for rates, patterns, and variability of succession? Most of our current understanding of this phenomenon is based on experimental studies conducted at spatial scales of generally less than 1 m<sup>2</sup> (Hall et al. 1994). Our knowledge of infaunal responses to larger-scale disturbances comes largely from fortuitous observations.

The effects of patch shape on recolonization and succession following a disturbance have rarely been studied in marine benthic communities. In fact, very few studies have quantified this feature of disturbed patches (e.g., Paine and Levin 1981). One might predict that the effect of shape would often be a simple extension of the size-related, edge-to-area ratio effects described earlier. These would be enhanced in more irregularly shaped patches where this ratio is greater. Indeed, Raimondi (1990) observed denser barnacle recruitment in rectangular than square clearings of the same size, consistent with the hypothesis that a higher ratio of patch edge to area enhances recruitment of gregariously settling organisms. Generalizations concerning the effect of disturbance shape on recovery from disturbance await additional observational and experimental studies of its influence, independent of disturbance size and severity. In some instances, patch size and shape may be correlated, as Paine and Levin (1981) found for clearings in intertidal mussel beds: the length/width ratio increased with clearing size. Clearly,

however, the perimeter to area ratio of disturbed patches strongly influences, both directly and indirectly, patterns and processes of recolonization in a wide variety of benthic marine habitats.

**PATCH SURFACE CHARACTERISTICS.** The composition, rugosity, topography, and orientation of the substratum can strongly influence patterns of recolonization and succession, either directly or indirectly. Although these effects have been little studied in the context of natural disturbance events, experimental investigations suggest that variation in such characteristics among disturbed patches could account for a substantial amount of spatial heterogeneity in assemblage structure. Field (e.g., Connell 1961; Foster 1975; Harlin and Lindbergh 1977; Wethey 1986; Chabot and Bourget 1988; Morse et al. 1988; Raimondi 1990; Vadas et al. 1990) and laboratory studies (e.g., Crisp 1974, 1976; Norton and Fetter 1981; Norton 1983; Morse et al. 1988) have demonstrated the influence of small-scale surface heterogeneity, and its interaction with flow, on the settlement and/or recruitment of algae and invertebrates to hard substrata. The composition of the rock itself, and its influence on environmental conditions at the rock surface, can also affect these processes (e.g., McGuinness and Underwood 1986; Raimondi 1988a; Bavestrello et al. 2000; see Caffey 1982 for an exception).

Similarly, the course of succession in soft sediments can vary with sediment type (Zajac and Whitlatch (1982a, b), the properties of which are often further modified by the activities of colonizing infauna (e.g., Rhoads and Young 1970; Gray 1974; Rhoads 1974; Rhoads and Boyer 1982; Thayer 1983; Probert 1984; Hall 1994). The settlement of larvae onto soft sediments and the passive transport of larvae, postlarvae, and adults across them, are also strongly affected by surface topography including the presence of biogenic structures, such as worm tubes, and their interaction with flow (Eckman 1983; Eckman et al. 1981; Butman 1987; Snelgrove and Butman 1994). This and other effects of tube builders, including their influence on sediment stability, can exert a strong influence on successional dynamics following disturbance in soft-sediment habitats (Gallagher et al. 1983; Whitlatch and Zajac 1985; Noji and Noji 1991; Thrush et al. 1996).

Invertebrate larvae are often attracted to, or repelled from, potential settlement sites by chemical cues released by conspecifics, other species, or the substrate itself (Crisp 1974, 1976; Meadows and Campbell 1972; Butman 1987; Chabot and Bourget 1988; Raimondi 1988b; Morse et al. 1988; Chia 1989; Woodin 1986, 1991; Pawlik 1992). Disturbed patches on hard substrates or in soft sediments may differ in the kinds and strengths of positive or negative cues they provide to dispersing larvae (see examples in "Patch size and shape").

Recolonization of disturbed sites may also be affected by larger-scale variation in surface topography such as cracks and crevices in rocks, which may provide protection from physical hazards such as desiccation and hydrodynamic forces. Such heterogeneity in the rock surface may also afford prey species a refuge from grazers or predators (e.g., Brock

1979; Menge and Lubchenco 1981; Lubchenco 1983; Hixon and Brostoff 1985). In some cases, however, consumers themselves escape stressful physical conditions or their own predators by living in crevices, concentrating their foraging in the immediate vicinity. In this case, colonists might be at greater risk in patches with a greater degree of substrate heterogeneity (Menge 1976, 1978; Levings and Garrity 1983; Fairweather et al. 1984; McGuinness and Underwood 1986). Variation in surface characteristics is likely to be greater among small patches than large ones because the former "sample" a smaller portion of the underlying substratum. For just the opposite reason, within-patch variation in such characteristics should be greater for large than small patches.

**PATCH LOCATION.** The location of a disturbed patch can markedly affect the rate and pattern of its recolonization. It does so in two fundamental ways, by determining (1) the availability of propagules and (2) the physical and biological characteristics of the environment in which recolonization and succession will take place. For species whose propagules are not dispersed far from the parent, proximity of the patch to a source of propagules can strongly affect patterns of recolonization and succession. Experiments and observations suggest that short-distance dispersal is an important source of small-scale, spatial variation in recruitment of some species of intertidal and subtidal algae (Dayton 1973; Paine 1979; Sousa 1984; Reed et al. 1988; Farrell 1989; Kendrick and Walker 1991, 1995; Kim and DeWreede 1996; Allison 1997; Johnson and Brawley 1998; Stiger and Payri 1999; but see Menge et al. 1993), seagrasses (Orth et al. 1994), subtidal epifauna (Grosberg 1987; Keough and Chernoff 1987; Davis and Butler 1989; Stoner 1990; Hurlbut 1992; Osman and Whitlatch 1998; Uriz et al. 1998; Smith and Witman 1999), and soft-sediment bivalves that brood (Commito et al. 1995). Other taxa for which larval dispersal is quite limited or nonexistent include corals with brooded planula larvae (Harrison and Wallace 1990), crustaceans that brood, and gastropods with direct development. Distance from source should affect the contribution of such organisms to the recolonization of disturbed patches.

Even though distance from source may be unimportant to the colonization of species whose propagules disperse long distances, the availability of their propagules will often vary among patches created in different locations. The supply of such propagules to a particular location will be affected by flow patterns, physical and biological barriers, the timing of release, and larval behavior and can strongly affect rates of settlement and recruitment (e.g., Hruby and Norton 1979; Caffey 1985; Gaines and Roughgarden 1985, 1987; Gaines et al. 1985; Butman 1987; Young and Chia 1987; Raimondi 1990; Gaines and Bertness 1991, 1992; Minchinton and Scheibling 1991; Bertness et al. 1992b; Hurlbut 1992; Sanford et al. 1994; Hills and Thomason 1996; Harris et al. 1998; Leonard et al. 1998; Todd 1998; Underwood and Keough, this volume; Morgan, this volume).

Patches created in different locations will also differ in the composition of the assemblages that surround them. This

will obviously affect the rate and pattern of colonization by vegetative ingrowth or lateral movement of neighboring adults. As discussed earlier, if filter-feeders are a major component of the organisms that surround a patch, they may intercept and consume larvae or spores before they ever reach the patch.

The physical and biological environment of the patch's location affects all aspects of its repopulation, including the survival and growth of settling propagules, recruits, and adults. The degrees to which species differ in their tolerances of these conditions will determine their success at colonizing and growing to maturity within the disturbed patch.

**TIME OF PATCH CREATION.** The timing of disturbance can affect both the rate and course of recolonization and succession. Timing is important for at least two reasons. First, the availability of propagules is temporally variable, often having a strong seasonal component. All else being equal, recruitment of a species will be most enhanced by disturbances that create space during periods when its propagules are available in greatest numbers. Second, characteristics of the physical and biological environment that affect the recruitment, survival, and growth of colonists and survivors also vary in time. Temporal variation in these conditions affects the performance of individuals that recruit from settled propagules, as well as those that spread into the disturbed patch from its edges, or vegetatively regenerate from surviving fragments. Variation in rates and patterns of recolonization and succession related to the timing of disturbance has been clearly demonstrated by experiments in rocky intertidal communities (e.g., Paine 1977; Emerson and Zedler 1978; Sousa 1979a; Hawkins 1981; Benedetti-Cecchi and Cinelli 1993, 1994, 1996; Blanchette 1996; Kim and DeWreede 1996; Airoidi 1998; Chapman and Underwood 1998). In a number of these studies, however, differences in the early stages of succession among plots cleared at different times disappeared over time as the later successional stages converged to the composition and structure of the undisturbed assemblage of long-lived animals and plants that surrounded the plots. Thus, in these intertidal assemblages, differences in the timing of disturbance affected the rate and trajectory of succession, but not its endpoint.

Studies of the effects of time of disturbance on recolonization and succession in subtidal habitats are rare. Kennelly (1987a) studied the effect of temporal variation in disturbance on successional patterns in an *Ecklonia radiata* kelp forest. The season in which he experimentally removed stipes and fronds from the study plots had a large effect on the rate and pattern of algal recruitment and succession. If the clearings were made in winter, when the kelp recruits, *Ecklonia* reestablished a canopy relatively quickly. In contrast, summer, autumn, and spring clearings developed an extensive cover of turf algae, which subsequently inhibited kelp recruitment. This turf persisted over the next year, but was gradually being invaded and shaded out by kelp that recruited on the edges of the plots. Therefore, as is typical of intertidal systems, differences in the time of disturbance in subtidal kelp

forests have a sizeable effect on the structure and species composition of early and middle successional stages as a result of temporal differences in propagule availability. Over time, however, these differences disappear as the assemblages converge toward their predisturbance state. The timing of disturbance also affects the demography of giant kelp (*Macrocystis pyrifera*) populations along the southern coast of California. Tegner et al. (1997) followed the fates of two cohorts of this species that had established in the same kelp bed after two severe storms that occurred in different years. The environmental conditions that followed these disturbances were dramatically different, which in turn led to very different fates for the two kelp cohorts.

As for subtidal hard substrate habitats, the effects of disturbance timing have seldom been examined for soft-sediment infaunal assemblages. Nevertheless, the few studies that have documented recolonization patterns in plots of defaunated sediment deployed at different times of year have seen large effects of the timing of simulated disturbance on infaunal succession (e.g., Zajac and Whitlatch 1982a, b; Ford et al. 1999).

#### *Mechanisms of Succession Following a Disturbance*

Succession, the sequence of species replacements that follow the initial recolonization of a disturbed patch, can proceed by a variety of mechanisms. Succession is driven by differences in species' reproductive biology, growth rates, competitive abilities, vulnerabilities to natural enemies and extremes of the physical environment (i.e., longevity), and their direct and indirect interaction with patch characteristics discussed earlier (Sousa 1985). Connell and Slatyer (1977) summarized the evidence for three alternative models of successional species replacement: facilitation, tolerance, and inhibition. Under the facilitation model, early successional species modify the environment so that it is more suitable for later successional species to establish and grow, while making the site less suitable for the local recruitment of conspecifics. According to the tolerance model, the presence of early successional species has little influence, positive or negative, on the recruitment and growth of later successional species. However, late species are more efficient at exploiting limited resources and competitively exclude the early species. The inhibition model predicts that early successional species can preempt resources and resist the establishment of late successional species as long as they remain healthy and undamaged. In most cases, this inhibition is transient. Successional replacement occurs because late species replace early species by outliving them, gradually accumulating as early species succumb to physical stress or attacks of natural enemies.

Although a number of authors have criticized the Connell-Slatyer models for oversimplifying successional processes in a variety of ways and for being phenomenological rather than mechanistic (Dean and Hurd 1980; Day and Osman 1981; Turner 1983a; Quinn and Dunham 1983; Breitburg 1985; Pickett et al. 1987; Walker and Chapin 1987; McCook 1994), there is no question that by clearly differentiating the alterna-

tive mechanisms in a testable form, Connell and Slatyer reinvigorated experimental research on successional patterns and processes. A comprehensive review of these studies is beyond the scope of this chapter, but they clearly demonstrate the diversity of mechanisms that drive successional sequences in marine communities (e.g., Sousa 1979a; Dean and Hurd 1980; Day and Osman 1981; Zajac and Whitlatch 1982b; Gallagher et al. 1983; Lubchenco 1983; Turner 1983a, b; Breitburg 1985; Foster and Sousa 1985; Whitlatch and Zajac 1985; van Tameelen 1987; Johnson and Mann 1988; Williams 1990; Bertness 1991; Farrell 1991; McCook and Chapman 1991, 1997; Bertness and Shumway 1993; Wootton 1993; Shumway and Bertness 1994; Benedetti-Cecchi and Cinelli 1996; Hixon and Brostoff 1996; Berlow 1997; Kim 1997). There is good evidence for all three models, operating either alone or in concert within a given successional sequence. Facilitation tends to occur most frequently in physically stressful environments where stress-tolerant, early colonists may ameliorate the extreme conditions, or in areas of high consumer pressure where positive associations with other species may provide defense against natural enemies (Bertness and Callaway 1994; Bertness and Leonard 1997). In areas with more moderate physical conditions or consumer densities, the tolerance and inhibition mechanisms of succession predominate. Many, if not most, interspecific interactions involve simultaneous and directly opposing positive and negative effects (Callaway 1995; Holmgren et al. 1997), the relative importance and net outcome of which vary with environmental conditions.

Farrell (1991) extended the Connell-Slatyer models with a set of predictions of how different patterns of damage or mortality by consumers would affect the rate of species replacement under the three Connell-Slatyer models of succession. Sousa and Connell (1992) found generally good agreement between Farrell's predictions and the results of experimental studies of the influence of marine grazers on algal succession.

### *Effects of Species Diversity and Composition on Recovery from Disturbance*

The experimental perturbation studies of Sousa (1980) and Allison (1997) not only examined how the species diversity and composition of an intertidal algal assemblage affected its resistance to a potentially disturbing force, as described earlier, but also how these features influenced its rate of recovery (i.e., resilience). In my study, the rate and pattern of recovery varied with the intensity and severity of damage and among assemblages of differing succession age. The latter effect was entirely attributable to differences in the life history characteristics of the component species, including their capacity for vegetative regeneration and rates of recruitment and growth from propagules. The diversity of the assemblage did not explain any additional variation in the response of the assemblage to disturbance. Allison (1997) found that rate of recovery to the reference state was affected by both the initial diversity of the assemblage and the intensity of the heat treat-

ment. However, as in my study, the effect of diversity on the assemblage's response to disturbance appeared to be "strongly contingent on the characteristics of the stress and the characteristics of the removed species" (Allison 1997, p. 136), and not a simple function of the number of species in the assemblage. Thus, as with resistance to disturbance, there is no evidence from these studies that higher-order effects of the diversity of species within a trophic level influence the process of recovery from disturbance.

### *Complex and Historically Contingent Interactions Precipitated by Disturbance*

Many of the examples I have discussed thus far concern the effects of disturbance on particular species or pair-wise species interactions. There are a number of examples of disturbances that catalyze a series of cascading interactions that can dramatically affect community structure. Here, I describe some striking examples.

Disturbances can initiate trophic cascades. During a five-year monitoring study of a *Macrocystis pyrifera* forest off the coast of southern California, Ebeling et al. (1985) documented the effects of two unusually severe winter storms on kelp forest structure and dynamics. The study forest grew on an isolated shale outcrop, and in the summer of 1979 a large surface canopy of *Macrocystis* covered the reef. The first storm hit in February of 1980; the powerful surge stripped the entire *Macrocystis* canopy from the reef. Most understory kelp survived to regrow new blades the following spring, and *Mucrocystis* sporophytes recruited to open space. This regeneration was cut short, as large numbers of adult sea urchins emerged from refuges in cracks and crevices to forage for food. Elimination of the *Macrocystis* canopy had cut off the supply of drift kelp, the urchins' preferred food. By the fall of 1980, urchins had removed all the newly recruited kelp plants and much of the understory kelp that had regrown vegetatively after the storm. Similar dynamics have since been observed in other southern California kelp forests following large ENSO associated storms (Tegner and Dayton 1987; Dayton et al. 1992). The reef remained in this barren state until the spring of 1983, when strong surge from another intense storm swept sea urchins off the exposed part of the reef. By June of 1983, sporophytes of *Macrocystis* and understory kelps had recruited densely on the reef, and within a few months formed an extensive canopy. The insular nature of the reef, which was bounded by area of sand bottom, precluded its recolonization by adult urchins from other areas. Larval sea urchins did settle onto the reef in large numbers after the second storm, but these small urchins were unable to control the expanding kelp population (Breitburg 1996). Once a canopy of large invulnerable plants was reestablished, urchins returned to feeding on drift kelp, coexisting with the mature plants.

In addition to their direct effects on kelp populations, urchins apparently had an indirect negative effect on the abundance of surfperch on the reef. Prior to the first storm, these fish fed on small crustaceans that live within the algal

turf that seasonally covered more than 15% of the rock surface. Stands of understory kelps provided an essential refuge for young-of-the-year of five species of surfperch from predation by adult surfperch and kelp bass. Following the storm, as urchins grazed away the turf and understory kelp, surfperch densities declined sharply and young-of-the-year perch disappeared entirely from the reef (Ebeling and Laur 1985; Ebeling et al. 1985). In addition, adult surfperch altered their foraging patterns in response to the loss of kelp canopy (Stouder 1987). Surfperch populations were recovering in spring/summer of 1983 as the algal turf and kelps redeveloped on the reef following removal of urchins by the second storm.

This example not only demonstrates how the strength and effects of trophic interactions can be modified by disturbance, but also that the same agent and intensity of disturbance can have dramatically different effects depending on the state of the community. That state is determined, in part, by the community's history of disturbance. The coral reefs of Jamaica provide another case of a system's prior history of disturbance dictating its response to subsequent perturbations. Hughes (1989) documented how selective mortality of corals caused by a previous storm indirectly determined the outcome of competition between algae and corals following the mass mortality of sea urchins by disease. Hughes and Connell (1999) discuss the interactive effects of recurrent disturbances on Australian and Jamaican reefs.

Another example comes from coral reefs in the eastern Pacific that were strongly impacted by the intense 1982–83 ENSO (Glynn and Colgan 1992). Sea surface warming associated with this event caused extensive reef coral bleaching and up to 70–95% mortality of corals on reefs in Costa Rica, Panama, Colombia, and Ecuador. In addition to the direct mortality due to bleaching, this disturbance indirectly altered trophic interactions on the reefs in a way that magnified coral mortality. Glynn (1990) quantified the latter effect on Uva Island in the Gulf of Chiriqui, on the Pacific coast of Panama, where bleaching killed 96% of the corals. As *Pocillopora* colonies died, the small crustacean “guards” that normally shelter in living colonies of this species disappeared. These crustaceans defend their host colonies from attack by the sea star corallivore, *Acanthaster planchi*, and generally reduce the impact of this predator on the reef. With the loss of the guards, predation rates on surviving corals increased, adding to the disturbance's already strong direct negative effects.

## RESPONSES OF MOBILE ANIMALS TO DISTURBANCE

Compared to sessile organisms, the responses of mobile marine animals to disturbance have been little studied, except in soft-sediment assemblages where the dispersal of postlarval stages and adults plays such an integral role in the recolonization of disturbed sediments (see earlier discussion). I believe there are two major reasons for the comparative inattention to the responses of mobile animals to disturbance (Sousa 1984).

First, their responses are often less easily observed and quantified than those of sessile species, and certainly more difficult to study experimentally. Second, for much of the past three decades, mobile animals, especially vertebrates, have been the “posterchildren” for competition-based, equilibrium theories of community organization (Wiens 1977; Karr and Freemark 1985). If mobile animal populations are considered fundamentally equilibrial in nature, then disturbances are relegated to the category of exceptional events that temporarily obscure our view of the “true” regulatory processes. As such, there is little reason to study their effects in detail. In recent years, a far more balanced vision of the myriad processes that affect populations of mobile animals has taken root, with increasing numbers of studies of the direct and indirect effects of disturbance on assemblages of mobile animals.

Extreme environmental conditions and physical forces can directly kill appreciable numbers of mobile marine animals. For example, cold temperatures and large storm waves have been observed to kill coral reef fishes (Bohnsack 1983; Lassig 1983); juveniles appear to be especially vulnerable to wave surge (Bouchon et al. 1994). Anoxic conditions that developed after a hurricane killed large numbers of mangrove fishes (Bouchon et al. 1994). As described earlier, strong, bottom surge from large storm waves and associated scour by sand and rocks decimated sea urchin populations on a subtidal reef in southern California (Ebeling et al. 1985; see also Dayton et al. 1989). Heavy sedimentation and low salinity conditions following winter storms extirpated a large sand dollar population from a California coastal lagoon (Onuf 1987). Hypoxic water kills benthic fishes, especially newly recruited individuals, which are less able to avoid these conditions by moving to better oxygenated shallow sites, as Breitburg (1992) showed for the naked goby, *Gobiosoma bosc*, in Chesapeake Bay. Even nonlethal hypoxic conditions can affect the survival of larval fish by increasing or decreasing their risk of being consumed by predators (Breitburg et al. 1994, 1997). Predation by sea nettles, which are less sensitive to the debilitating effects of low oxygen concentration than larval gobies, increased, whereas predation by juvenile striped bass, which are more sensitive to hypoxia than goby larvae, decreased. Pihl et al. (1992), also working in Chesapeake Bay, observed similar increases in predation by mobile fish and crustaceans on benthic invertebrate prey that became incapacitated during periods of hypoxia.

Mobile animals can behaviorally avoid potentially lethal environmental stresses, an option not available to sessile species. Whether they are successful or not depends on the rapidity with which harsh conditions develop and their intensity, as well as the mobility of the organisms in question. Sea anemones (*Anthopleura elegantissima*) avoid lethal levels of heat and desiccation by moving to more shaded and wet microhabitats (Pineda and Escofet 1989). Juvenile and adult fishes and crustaceans escape potentially lethal hypoxic conditions in deeper water by migrating inshore where dissolved oxygen concentrations are higher, then they recolonize deeper sites after hypoxic conditions have dissipated (Loesch



1960; Kramer 1987; Pihl et al. 1991; Breitburg 1992; Diaz and Rosenberg 1995).

Physical disturbances also cause short- and long-term changes in the habitat that can have major indirect effects on populations of mobile animals. Changes in the physical and biogenic structure of the habitat often lead to reductions in the abundance of particular mobile animals or changes in species composition. One example is the indirect effect of storms on kelp bed surfperch populations described earlier (Ebeling and Laur 1985; Ebeling et al. 1985; Stouder 1987). In a comparable *Ecklonia radiata* kelp forest, Syms and Jones (1999) studied the response of a guild of demersal blennies to experimental removal of the kelp plants from plots of three different sizes. They observed significant effects of canopy removal and plot size on the persistence and resilience of resident populations, with the assemblages in small plots showing greater variability in both characteristics. Some of this variability was attributed to greater edge effects in the small plots, particularly with respect to the movement of fish in and out of the plots.

Similarly, disturbance-induced changes in the three-dimensional structure of coral reefs can affect the structure of associated fish assemblages (e.g., Kaufman 1983; Walsh 1983; reviewed by Jones and Syms 1998). A wide range of species-specific responses has been documented to such changes in habitat structure, many negative, but some positive. However, there have been few well-designed tests of alternative explanations for these responses, so the mechanisms underlying them are poorly understood. Syms (1998) attempted such a test by applying three levels of physical disturbance to 10 x 10 m plots on the fringing reef at Lizard Island on Australia's Great Barrier Reef. However, none of the fish groups he monitored responded very strongly to disturbance at that spatial scale; most of the variation among experimental plots was explained by larger scale spatial heterogeneity across the study reef. Syms highlighted the need for future studies to examine the responses of reef fish to habitat disturbance over a range of spatial scales.

Changes in habitat structure due to disturbance within coastal lagoons can also exert negative indirect effects on mobile species. As a result of unusually heavy rains associated with large storms in 1978 and 1980, large quantities of fine sediment were deposited in Mugu Lagoon in southern California. These deposits reduced the low-tide volume of the lagoon and eliminated most of the previously extensive cover of eel grass, *Zostera marina*. Probably for lack of sufficient habitat, rather than direct mortality from sedimentation or lowered salinity, the total density of water column fishes declined by almost 50% and species richness by more than 30% between 1977 and 1981 (Onuf and Quammen 1983). There were also marked shifts in spatial distributions of species as they aggregated in surviving areas of preferred habitat.

Disturbance to structural species can also indirectly affect interactions involving mobile predators and their sessile prey. For example, on a rocky shore in New South Wales, Australia, where intense storm waves removed large portions of a previ-

ously extensive canopy of the fucoid alga *Hormosira banksii*, the barnacle *Chamaesipho tasmanica* recruited heavily to the cleared patches. The barnacle had been absent beneath the intact canopy prior to the disturbance and remained so beneath undisturbed fucoid canopies. Experiments demonstrated that this spatial variation in barnacle abundance resulted from a reduction in the foraging efficiency (but not numbers) of predatory whelks (*Morula marginalba*) in areas where shelter afforded by the algal canopy had been eliminated.

As described in "Patch Characteristics That Affect Recolonization and Succession," the responses of mobile consumers to various characteristics of disturbed patches can strongly affect the rate and pattern of recolonization and succession. Interactions between patch size and grazing intensity are especially notable (e.g., Sousa 1984). More generally, mobile consumers can strongly affect the recovery of sessile populations from disturbance, and spatial and temporal variation in their influence can generate substantial and sometimes persistent heterogeneity in the abundance and age structure of populations of sessile prey species (e.g., Knowlton et al. 1990; Carroll and Highsmith 1996). The rate at which consumers recolonize disturbed areas and the life stage with which they do so (e.g., as larvae versus juveniles or adults) affect the degree to which they can limit the recruitment and growth of prey populations and thus the relative importance of predation versus competition during colonization (Breitburg 1996). The strength of these effects depends on the functional response of the consumer and the absolute and relative sizes and growth rates of consumers and prey.

The impact of consumers on prey populations within a disturbed patch will also vary with the location of the patch because the density and foraging efficiency of consumers varies spatially with environmental conditions. For example, on rocky shores, some predators forage less efficiently in wave-swept environments (Menge 1978; Lubchenco and Menge 1978), and grazers are generally less abundant at sites where sediment scour is common (Robles 1982; D'Antonio 1986). Consequently, the influence of these consumers on patch colonization by sessile species is likely to be less in such areas. In Caribbean mangrove forests, species of large, herbivorous crabs that feed on mangrove propagules are abundant in the low intertidal, but rare at higher tidal levels where detritivorous species predominate. Consequently, rates of crab predation on mangrove propagules that disperse into lightning-created canopy gaps decrease with increasing tidal elevation (Sousa and Mitchell 1999).

In some instances, disturbance of sessile assemblages improves conditions for mobile species and results in a net increase in their abundance. For example, in the intertidal boulder fields where I worked, limpet density was inversely related to boulder size; that is, the highest densities were found on small boulders (Sousa 1985). This pattern 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 large boulders (Sousa 1979a). In addition, limpets prefer to graze on microscopic

algae or immature thalli of macroalgae (Nicotri 1977) that are more abundant on frequently disturbed substrata. In contrast, the upper surfaces of rarely disturbed large boulders are covered with larger, turflike perennial algae that are not consumed by limpets. These turfs occupy space and trap sediment, making the substratum uninhabitable to limpets. Dense stands of macroalgae, particularly at mid- and low intertidal, commonly outcompete limpets for space (e.g., Dixon 1978; Sousa 1979a, 1984; Underwood and Jemakoff 1981; Benedetti-Cecchi and Cinelli 1993). The consequence of this interaction is that the surfaces of small boulders are more intensively grazed by limpets than the surfaces of large boulders.

Finally, the sessile organisms that comprise each stage of succession following a disturbance differ in many characteristics critical to the survival, growth, and reproduction of mobile animals that live amongst them. These features include species composition, structural complexity, secondary chemistry, microclimate, and the quantity and quality of the food and shelter they provide. Consequently, the composition of mobile animal assemblages often changes with the successional stage of the sessile assemblage. In the most thorough study of its kind in marine environments, Dean and Connell (1987a, b, c) documented these changes for the early, middle, and late seral stages of the boulder field algal assemblage that I studied (Sousa 1979a, b, 1980) in southern California. Altogether, they collected 214 animal species belonging to 12 phyla from these algal assemblages, the majority of them mobile. Species richness, diversity, composition, and trophic structure varied among the stages, as well as seasonally within each stage. Using lab and field experiments, Dean and Connell demonstrated that a variety of processes contributed to the patterns and that different mechanisms were important for different species. The primary mechanisms determining associations of animal species with seral stages appeared to be active habitat selection and differential predation by fishes.

## EFFECTS OF DISTURBANCE ON LOCAL AND REGIONAL POPULATION PERSISTENCE AND SPECIES DIVERSITY

### *Persistence of Populations*

The immediate effect of disturbance is to reduce biomass and abundance, but its net effect in many benthic assemblages is to increase the local abundances of numerous species that would be less abundant or absent altogether in the absence of disturbance. It does so by freeing up resources held by prior occupants of the disturbed area or by generating new resources. Some of these species are strict fugitives, meaning that in the absence of disturbance they would be driven regionally extinct by competitive exclusion or some other mechanism of successional replacement (Hutchinson 1951). They persist by colonizing newly disturbed sites via dispersal of propagules from older ones. For other species, disturbance leads to increases in local abundance, but their persistence does not depend on it. A portion of the population of such a species permanently occu-

pies a part of the habitat that provides refuge from their competitors, while taking advantage of habitatwide opportunities for recruitment afforded by disturbance. In areas outside of this refuge, where the species faces competition, it may persist as a true fugitive or in a source-sink relationship with the portion of the population that lives in the refuge (Shmida and Ellner 1984; Holt 1985; Pulliam 1988).

The local and regional dynamics of fugitive populations reflect the interplay of life history traits, species interactions, and the regime of disturbance. For a fugitive species to persist, disturbances must generate colonizable space within the dispersal distance of extant local populations and before those populations go extinct. Paine's (1979, 1988) long-term study of populations of the sea palm, *Postelsia palmaeformis* (Figure 4.14), on Tatoosh Island off the coast of Washington State, provides one of the clearest examples of a fugitive species that requires a specific frequency and quantity (percent of space cleared) of disturbance to persist. At this and other sites, sea palm sporophytes recruit primarily to wave-generated clearings in beds of the mussel, *Mytilus californianus* (Dayton 1973; Blanchette 1996). During a 10-year period, Paine monitored the abundance of this annual plant at 26 sites, with varying regimes of mussel bed disturbance. Sea palm populations persisted for all 10 years at the 7 sites that regularly experienced high levels of disturbance. Sea palms were absent from the other 19 sites where either the frequency of disturbance or the quantity of open space it generated was lower. Paine was able to establish populations of sea palms at the latter sites, and these persisted for at least two generations. This ruled out the possibility that sites lacking sea palm populations were simply unsuitable for their establishment. At sites where *Postelsia* naturally persisted, the subpopulations of sea palms within any particular clearing eventually go extinct due primarily to competition for space with mussels and turflike algae. In fact, local populations go extinct rather precipitously as their density falls below about

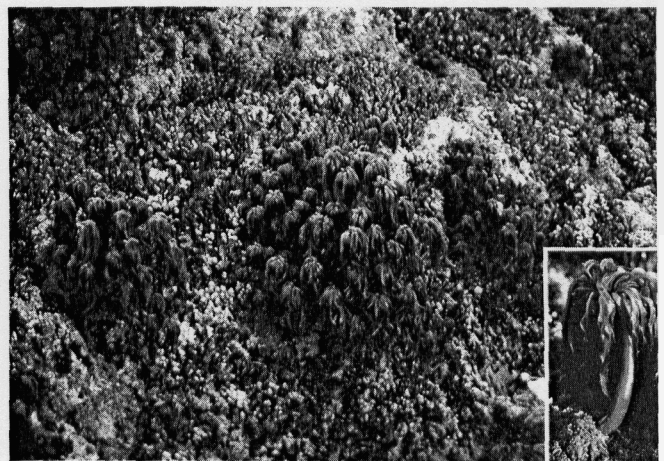


Figure 4.14 Stands of the sea palm, *Postelsia palmaeformis*, surrounded by mussel beds on Bodega Head in central California. (Larger photo by author; inset photo by A. De Vogelaere.)

30 plants per m<sup>2</sup>. Apparently, this density of plants produces insufficient spores to compensate for losses to grazers and competition. The dispersal distance of sea palm spores is very limited, only about 1–3 m from a stand of adult plants (Dayton 1973; Paine 1979, 1988). Therefore, the persistence of sea palm populations at a particular site requires that, within the time it takes for local subpopulations to go extinct, there be adequate dispersal of spores to open space created within 1–3 m of an extant stand. Regional extinction will occur if the average disturbance rate is too low or the interval between disturbances too long to ensure this. Establishment of new populations beyond the short range of spores dispersed from intact stands may occur when detached, but buoyant and fertile sporophytes are transported by currents to remote sites where they strand and deposit spores (Paine 1988).

Other species clearly benefit from disturbance, although their persistence does not depend on it. For example, recruitment of the sabellid polychaete, *Phragmatopoma californica*, which forms aggregations in intertidal and shallow subtidal habitats from central California to Panama, is greatly enhanced by wave disturbance (Barry 1989). Individual worms live in tubes constructed of cemented sand grains; larvae settle gregariously and their tubes become fused together into dense honeycomblike aggregations that grow to be as much as 50 cm thick and may cover many square meters of hard substratum. These aggregations persist for several months to years, but are eventually broken apart by wave forces or water-borne projectiles. When the tubes break open, large numbers of eggs are spawned, which are then fertilized in the water column. Larvae are competent to settle and metamorphose into the adult stage 2–8 weeks later, but can delay settlement and remain in the plankton for several months. The aggregations are most commonly disturbed during winter storms. As a result, *Phragmatopoma* larvae are most abundant in the plankton during winter and spring, which is also the period of heaviest settlement. Barry (1989) found that the level of *Phragmatopoma* recruitment on an intertidal reef in southern California was highly correlated with estimated wave power 2.5 to 5 months earlier, with the highest correlation at a 5-month lag interval. There was large interannual variability in *Phragmatopoma* recruitment over the nearly four years that Barry monitored it; years with the most recruitment were those with the greatest storm activity.

Several studies have demonstrated the strong effects of different disturbance regimes on the demography of affected populations. These include Åberg's (1992a, b) elegant analysis of the demographics of populations of the fucoid alga, *Ascophyllum nodosum*, under different regimes of ice scouring, and Wethey's (1985) innovative use of historical weather records to build a population projection model for populations of the intertidal barnacle, *Semibalanus balanoides*, at Nahant, Massachusetts. One of the predictions from Wethey's model was that species that lived exclusively in the zone affected by sea ice scouring would have gone extinct under the regime of sea ice Occurrence that has existed in New England during the past 300 years. This result may explain the absence from New Eng-

land shores of large, long-lived species with delayed reproduction that are common at mid- to low intertidal zones elsewhere in the world where sea ice does not form.

My previous discussion of the role of disturbance in promoting the persistence of fugitive species leads directly to a major question in community ecology: how does disturbance affect species diversity in natural communities? This question has been tackled in a variety of ways: with correlation analyses, experimental field studies, and theoretical models. The effect of disturbance on species diversity, that is, the coexistence of species, is intimately tied to changes in diversity over the course of succession. Species diversity within a disturbed patch is low immediately after a moderate to severe disturbance that has killed many or all of the residents. As species reestablish populations within the patch, diversity rises, in terms of both species richness and evenness. In many, if not most, benthic marine assemblages (exceptions discussed later), diversity is maximal at some intermediate stage of succession, declining thereafter as one or a few species come to dominate the assemblage and effectively block the recruitment of other species (see references on succession cited earlier). At that point, generally referred to as the climax stage, successional replacement of species ceases, and the dominants maintain their populations by recruitment from propagules or vegetative propagation.

Hierarchical interspecific competition is one process that commonly causes the decline in species diversity late in succession. In these cases, later successional species are better competitors for the increasingly limited resources available as populations build up within the patch (i.e., the tolerance succession model of Connell and Slatyer 1977). Competition is not, however, the only mechanism that can produce this decline. The late successional dominants may be species that have simply outlived others that recruited earlier to the patch by being better defended against natural enemies or environmental stresses (i.e., the inhibition succession model of Connell and Slatyer 1977; Sousa 1979a). As vulnerable species succumb to these sources of mortality, the defended species secure the space or other resources they held. By virtue of their longevity, defended species will retain these resources for long periods, and thereby prevent other species from invading.

Given this form of successional trajectory in species diversity, under what conditions will disturbance maintain high diversity? The answer to this question depends on the spatial scale of interest (Collins and Glenn 1997): local (within a patch) or regional (among patches). Under certain conditions, disturbance can maintain a persistently diverse assemblage within an area equivalent to the size of a single disturbed patch of space. However, even when disturbance cannot prevent a small number of species from monopolizing individual patches of space, asynchronous disturbances can maintain regional diversity by transforming the landscape into a mosaic of different successional stages that vary in species composition. I will now discuss, in turn, the potentially diversifying effects of disturbance at these two spatial scales.

### Maintenance of Local Species Diversity

Disturbance can maintain local diversity in at least two ways. Connell (1978) coined the terms *compensatory mortality* and *intermediate disturbance* for these hypothesized mechanisms. According to the compensatory mortality hypothesis (CMH), local diversity will be maintained if the potential late successional dominant suffers a disproportionately higher rate of damage or mortality from disturbance than the species that it would otherwise exclude from the patch. If such disturbance is chronic, this diverse condition may be a fairly stable condition, but in many cases, disturbance rates vary in time, so the assemblage will likely seesaw back and forth over a range of diversity. As long as the rate of disturbance is moderately greater than the rate of exclusion and recruitment of the inferior competitor is sufficient, diversity within a patch will be maintained at a higher level than if the patch were never disturbed.

The intermediate disturbance hypothesis (IDH) embodies a second mechanism by which disturbance can maintain local diversity. In this case, the effects of disturbance are non-selective, but nonetheless promote local diversity by renewing resources, such as space, at a rate sufficient to allow continued recruitment and persistence of species that would otherwise be driven locally extinct by interactions with late successional dominants. On the other hand, disturbance must not occur so often, or with such severity, that many species are eliminated. As the name of the hypothesis implies, disturbance must occur at some intermediate frequency or severity that allows species to accumulate within the patch, but prevents one or a few of them from monopolizing its resources. In other words, as in the case of intermittent compensatory mortality, the assemblage within the patch is maintained in a nonequilibrium state, and assuming sufficient dispersal, local coexistence of species is insured.

These thumbnail sketches of the two mechanisms oversimplify the conditions under which each of them will maintain local diversity. These conditions have been explored with a number of graphical and mathematical models that differ in their basic structures and assumptions. Before I discuss their general conclusions, I will briefly describe the different ways in which these models have explored the effects of disturbance on local diversity and the roles of various processes in mediating these effects. Huston (1979, 1994) presented graphical predictions of how the growth rates of competitors influence the rate of competitive exclusion, and therefore the level of disturbance necessary to maintain diversity. Graphical models by Petraitis et al. (1989) and Collins and Glenn (1997) examined how the interplay of life history traits, competitive ability, and disturbance determines local species richness through their influence on species' immigration and extinction rates. Caswell and Cohen (1991) developed a Markov chain model to study the effects of disturbance on the dynamics of 2–3 interacting species in a spatially subdivided habitat, in which the patches are linked by random dispersal (i.e., no neighborhood effects). By numerical simulation, they investigated the interacting effects of different rates of distur-

bance and competitive exclusion, mechanisms of succession, and transitive vs. intransitive competitive interactions on local and regional diversity within the metapopulation. Disturbance was indiscriminate in this model: A disturbance eliminates all species and returns the patch to an empty state. More recently, Dial and Roughgarden (1998) explored the conditions for disturbance-enhanced diversity with a two-species extension of an earlier one-species model by Roughgarden and Iwasa (1986). These models explicitly incorporate the dynamics of two demographic stages that are common to the life histories of many species of marine organisms—space-limited adults and pelagic propagules. The Dial and Roughgarden model examines the effects on species coexistence of varying relative rates of adult survival, reproduction, propagule survival; and settlement. It assumes that higher rates of disturbance produce higher levels of adult mortality, and that higher rates of propagule settlement lead to greater numbers of adults. Dial and Roughgarden investigated a number of different scenarios including cases in which: (1) the subordinate competitor is neither more resistant to disturbance, nor a better colonizer than the dominant competitor; (2) the subordinate is superior to the dominant in both respects; (3) the subordinate is a better colonizer, but more susceptible to disturbance; and (4) the subordinate is more resistant to disturbance, but a poor colonizer.

The general conclusion of all five of these models is the same: Intermediate rates of disturbance will maintain local diversity under certain conditions. In specifying these conditions, recent theory has added critical details and therefore predictive power to the original, simple graphical presentation of the IDH (Connell 1978). One feature that clearly enhances the diversifying effects of disturbance is the existence of particular trade-offs in the life histories of the interacting species. Disturbance is more likely to maintain diversity if subordinate competitors are better than dominant competitors at colonizing the open space created by disturbance. Disturbance-mediated coexistence is also more easily realized when dominant competitors are less resistant to disturbance, as in the CMH. Only when subordinate competitors are both more susceptible to disturbance and weaker colonizers than the dominant competitor is it impossible for disturbance to maintain diversity. For all other combinations of traits (Cases 2–4), some intermediate level of disturbance, contingent on the rate of propagule settlement, will act to maintain diversity. Dial and Roughgarden's (1998) model also predicts an "intermediate recruitment effect" in these situations. That is, at a given level of disturbance, coexistence will only occur at intermediate rates of recruitment. Only the subordinate competitor persists when the overall recruitment rate is low, the species coexist when recruitment rates are intermediate, and the superior competitor dominates when recruitment rates are high. Their model also predicts that positive covariation between disturbance and overall rates of recruitment reduces the diversifying influence of disturbance because open space is more rapidly filled, reducing the opportunity for the subordinate species to recruit. On the other hand, negative covari-

ance between disturbance and recruitment rates is predicted to intensify the diversifying effect of disturbance. The Dial and Roughgarden model (1998) makes the explicit assumption that benthic populations are recruitment-limited: Higher settlement rates result in higher adult densities. If instead, the density of adults of some or all of the interacting species were limited by post-recruitment biotic interactions, the predictions might be different. This question seems ripe for theoretical exploration.

The level of disturbance necessary to maintain local diversity, and the degree to which diversity will be enhanced, are also predicted to vary with the rate of competitive exclusion, transitivity of species interactions, frequency of positive interspecific interactions, and model of succession (Karlson and Buss 1984; Huston 1979, 1994; Sebens 1987; Caswell and Cohen 1991; Hacker and Gaines 1997). Higher levels of disturbance are required to ensure local species coexistence with more asymmetrical competitive interactions and higher rates of competitive displacement. The rate of competitive exclusion tends to be slower when competitive interactions are nontransitive (e.g., in the three-species case:  $A > B > C$ , but  $C > A$ ) as compared to transitive or hierarchical ( $A > B > C$ , and  $A > C$ ) so that less disturbance is necessary to maintain diversity when nontransitive interactions predominate. Similarly, positive interactions, particularly those that ameliorate harsh physical conditions, are predicted to increase the range of disturbance rates over which species can coexist, and increase the peak levels of diversity maintained by intermediate levels of disturbance. Predictions from the Caswell and Cohen model (1991) concerning the effects of different successional mechanisms on disturbance-mediated coexistence depend on the colonization rates of earlier versus later successional species. Under the tolerance model, hierarchical competition drives successional replacements, and intermediate levels of indiscriminate disturbance will enhance diversity as long as the early successional species is the better colonizer. Intermediate levels of indiscriminate disturbance also enhance diversity when succession is driven by facilitation, but neither the degree of enhancement nor the frequency of disturbance that maximizes diversity are greatly affected by absolute or relative rates of dispersal. The prediction for a strict inhibition model, in which the first species to colonize an open patch excludes all others until removed by disturbance, is that diversity will only be maximized at intermediate rates of indiscriminate disturbance when the dispersal rates of early and late species are equal. Regardless of the successional model, the higher the rate of competitive exclusion, the greater the rate of disturbance must be to maintain diversity.

In many respects, existing models have explored only the tip of a very large iceberg of factors that dictate the effects of disturbance on natural populations and communities. These include many of the features I have discussed here, including the spatially and temporally explicit nature of recruitment, variation in the severity of damage and opportunity for vegetative recovery, and the myriad consequences of variation in patch size. In addition, Petraitis et al. (1989) identify some po-

tentially important effects of correlations among disturbance characteristics such as size, severity, and frequency that merit more theoretical attention. The effects of some of these interactions among disturbance characteristics have been explored in verbal and graphical models of the effects of disturbance on regional species diversity described in the next section.

Empirical studies that unambiguously demonstrate the diversifying influence of disturbance on local diversity are not as numerous as one might expect, given the attention that this phenomenon receives. Correlational studies relating coral species richness to surrogate measures of disturbance frequency, such as percent living cover or topographic complexity, suggest that intermediate frequencies of storm-induced disturbance are responsible for high diversity in some areas on coral reefs (e.g., the hump-shaped relationships reported by Connell 1978 and Aronson and Precht 1995). However, projected dynamics from a matrix model of the probabilities of species replacements estimated from Connell's long-term permanent plots (Tanner et al. 1994) indicated that the IDH did not fully predict successional changes in species diversity following disturbance by cyclones. Patterns at a wave-protected, shallow subtidal site were generally in accord with the hypothesis; diversity peaked some time after cyclone disturbance, then declined, as a few species competitively dominated the assemblage during the subsequent storm-free interval. In some areas, however, such as the reef flat, diversity remained high long after a cyclone because other sources of mortality ensured that some space was always available for colonization by competitively inferior species. These additional agents of mortality included exposure to air at low tide, which damages erect fast-growing corals disproportionately. Storm damage can also be compensatory, as it often falls most heavily on faster-growing branching corals that are competitively dominant in subtidal areas of the reef in the absence of wave damage (Connell 1976, 1978, 1979; Porter et al. 1981; Woodley et al. 1981; Hughes 1989). Rogers (1993) critically evaluated observational evidence for the IDH in the literature on the effects of hurricanes on coral reefs. Patterns of species diversity and evenness in shallow-water coral assemblages are generally consistent with the predictions of the IDH, but deeper water assemblages tend to be diverse despite a generally lower disturbance rate.

My study of the effects of disturbance in algal-dominated intertidal boulder fields in southern California (Sousa 1979a, b) remains one of the only studies that has experimentally tested the IDH in a marine habitat. At the site where I worked, wave action that overturns boulders is the predominant agent of disturbance. As I described earlier, when a boulder is overturned, the organisms on what was formerly its top surface are damaged or killed. The longer it remains overturned, the greater the mortality, and therefore the greater the amount of open space that becomes available when the boulder is righted. 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 aver-

age, the most diverse assemblage of organisms (Sousa 1979b). The interval between disturbances of small boulders is short, so relatively few species have time to establish populations on their surfaces. On large boulders, which are rarely disturbed, succession proceeds without interruption, resulting in domination of the cover by a single species of long-lived, turflike algae. I was able to confirm that the rate of disturbance rather than substratum size was responsible for these patterns by experimentally stabilizing small boulders and monitoring succession on their surfaces as compared to nonstabilized boulders of the same size. The trajectory of succession on the stabilized small boulders was identical to that on larger, more stable boulders. Observations of diversity patterns in subtidal boulder or cobble fields (Osman 1977; Davis and Wilce 1987) suggest that the same process maintains diversity there. However, McGuinness (1984, 1987a, b) found little support for the mechanism in intertidal boulder fields on the coast of New South Wales, Australia. At his sites, wave disturbances as well as sand burial were important, but only the assemblages on the undersides of low intertidal boulders exhibited patterns of diversity with respect to boulder size that were consistent with the IDH. Other intertidal habitats in which disturbance has been shown to enhance or maintain diversity of sessile species include tide pools (Dethier 1984) and salt marshes (Bertness and Ellison 1987; Ellison 1987; Bertness et al. 1992a; Brewer et al. 1997, 1998; but see Valiela and Reitsma 1995).

The foregoing discussion of the diversifying influence of disturbance on local diversity presumes that the diversity of an assemblage of species that colonizes a disturbed patch of habitat rises, then falls over the course of an uninterrupted succession. This is not a universal pattern. For example, in some seagrass beds, diversity seems to monotonically increase over time to some maximum set by the regional species pool (Williams 1990). In these cases, the climax state is a mixture of coexisting species that live interspersed throughout the bed. Williams (1990) hypothesized that these species coexist at equilibrium by partitioning nutrients and light within a three-dimensional habitat in the manner of Tilman's (1982, 1985) resource ratio hypothesis. Similarly, experimental exclusion of predators (and by inference, elimination of disturbance in general) from assemblages of soft-sediment infauna, often does not result in a decline in diversity, a common outcome of similar experiments in rocky intertidal habitats where one or a few competitively superior species usually exclude the others (Peterson 1979). Instead, both the total density of organisms and species richness increases when predators are excluded. Peterson (1979) suggested that competitive exclusion is rare in soft-sediment environments because interference competition by crushing or overgrowth, both common mechanisms on hard substrates, is uncommon among inhabitants of soft sediments. In addition, the low metabolic rates of infaunal organisms make exclusion by exploitation competition ineffective or extremely slow. Further, the three-dimensional nature of soft-sediment habitats allows resource partitioning, and negative adult-larval interactions may keep densities below carry-

ing capacity. Furthermore, as Frid and Townsend (1989) have argued, rapid recolonization of disturbed sites by highly mobile juvenile and adult life stages from surrounding areas, which is typical of many soft-sediment assemblages (see earlier references) will often preclude an increase in local diversity by larval recruitment (e.g., Thrush et al. 1991).

A hump-shaped relationship between diversity and time since the last disturbance also may not obtain in physiologically stressful habitats. For example, Brewer et al. (1997, 1998) did not observe a decline in species richness in the late stages of patch succession in the more stressful low intertidal areas of a New England salt marsh, where soil salinity is high and redox potential low. Instead, species richness increased monotonically in these areas following experimental removal of the vegetation. Edaphic conditions in newly cleared patches in the low marsh are particularly severe, and they can only be colonized by vegetatively spreading, salt-tolerant species. However, as the cover of these species increases, the harsh conditions are ameliorated, facilitating the recruitment of less tolerant species; hence, the increase in species richness. Thus, in the low marsh, positive interactions were more important than competition in determining species richness, which never overshot predisturbance levels. In contrast, the trajectory of species richness during succession in areas cleared of vegetation in the less stressful high marsh did exhibit an intermediate peak. Late in succession, competitively dominant clonal perennial excluded annual fugitive species.

In such cases where diversity increases monotonically during succession, disturbance will not enhance or maintain local (i.e., within-patch) species diversity. It can only reduce diversity. Nevertheless, disturbance will generate spatial heterogeneity in assemblage structure among patches disturbed at different times in the past (Thrush 1991; Hall et al. 1994). Furthermore, even if there is an overall decline in diversity in response to disturbance, it may still mediate interactions within certain suites or guilds of species, and for these the intermediate disturbance hypothesis could apply. For example, recent soft-sediment mesocosm experiments have shown that intermediate levels of biological disturbance by heart urchins (*Bryopsis lyrifera*) and bivalves (*Abra alba* and *Nuculoma tenuis*) result in more diverse assemblages (both locally and regionally) of meiobenthic nematodes and macrofauna (Widdicombe and Austen 1998, 1999; Austen et al. 1998). The precise mechanisms producing this response were not identified, but both bioturbation and predation were probably involved.

### *Maintenance of Regional Species Diversity*

Certain regimes of disturbance can maintain regional diversity among a collection of disturbed patches, even when they do not maintain it locally within the patches. In essence, this is the fugitive species case extended to multiple species. For example, at Paine and Levin's (1981) midintertidal, mussel-dominated sites on Tatoosh Island, the organisms occupying any particular area of substratum are disturbed, at most, every 7-8 years. As discussed earlier, this interval is to a large extent determined by changes in the intrinsic vulnerability of

the assemblage to disturbance over the course of succession. A 7–8 year interval between disturbances is sufficiently long that a large number of species is able to establish in a newly cleared patch of open substratum. For a time, within-patch diversity increases as species accumulate. However, this frequency of disturbance is too low to maintain high diversity within the patch. Over 7–8 years, lateral encroachment of adult mussels or recruitment of larval mussels will close all but the largest patches. In the process, the diversity of the assemblage within the patch declines as species are competitively excluded. Eventually, all species other than mussels that occupy primary space will be driven locally extinct. Nevertheless, localized disturbances to the mussel beds can enhance regional diversity by creating opportunities for colonization in areas that mussels will inevitably come to dominate. Asynchronous, localized disturbances transform the assemblage into a mosaic of different successional stages. Theory (e.g., Hastings 1980; Abugov 1982; Caswell and Cohen 1991) indicates that regional diversity is generally enhanced by intermediate rates of disturbance (i.e., area or number of patches cleared per unit of time). When the average rate at which individual patches are disturbed is either high or low, regional diversity will be less than when patches are disturbed at some intermediate rate. This is because at high average disturbance rates, early successional species dominate most patches, whereas at low average rates, late successional species do. The position along an axis of disturbance rate at which regional diversity will be maximal varies with all the same features that affect disturbance-mediated patterns of local diversity (see earlier discussion).

In addition, regional diversity will be affected by the average size and severity of disturbances and how synchronously they occur. Assuming that large disturbed patches favor colonizing or early successional species, and small patches favor competitive or late successional species, Miller (1982) made the following predictions about the effects of average patch size on regional diversity. At a low average disturbance rate, competitive exclusion within patches is likely, so regional diversity will be higher if the mean size of cleared patches is large, thus favoring the continued persistence of colonizing species. Conversely, when the average rate of disturbance is high, regional diversity will be greater when the areas disturbed are small, as this will insure the continued persistence of competitive species. Malanson (1984) has taken this model one step further, by incorporating the effects of disturbance severity (he uses the term *intensity*). He noted that for many disturbances, size and severity are indirectly correlated with frequency, so that severity of disturbance can be substituted for disturbance size in Miller's model. In other words, when the average rate of disturbance is high, regional diversity will be maximized when the average severity of damage is low, favoring competitive species, which should be better able to survive the disturbance or reestablish populations at lower levels of resource availability. When the average rate of disturbance is low, regional diversity will be enhanced by severe disturbances that free up more resources for colonizing

species. Malanson makes a number of other predictions from his graphical model, including the prediction that regional diversity will be maximal under disturbance regimes characterized by either (1) infrequent, large, and severe disturbances, or (2) frequent, small, and low-severity disturbances.

Abugov (1982) has examined how the phasing of disturbance might affect regional diversity. Disturbances are in phase when they occur synchronously and are unphased if the probability of each occurrence is independent of any other. In the simplest case, as phasing increases, so does the proportion of colonizing species in the assemblage. So, one would predict that an increase in the phasing of disturbances will decrease regional diversity when colonizing species predominate, but increase it when competitively dominant species occupy most of the space. More complicated patterns are also possible if one allows for changes in the relative competitive and dispersal abilities of the species. To my knowledge, none of the predictions from these models have been formally tested in marine communities.

## CONCLUSIONS

Dayton (1971) concluded that the intertidal community he studied was "characterized by continuous physical and biological disturbance, an abundance of free space, and a large number of species which utilize this same potentially limiting resource." He wondered whether his system was a special case because its features differed so strikingly from those predicted by the paradigm that dominated community ecology at the time—that natural assemblages are primarily structured by interspecific competition. We now know that his observations were not unusual. Disturbance is an integral part of the environmental template (Southwood 1977) of every marine habitat. In the nearly 30 years since Dayton's paper, regimes of disturbance and its effects on community structure and dynamics have been studied in most marine benthic environments, and we have a much better understanding of the ways in which its effects interact with numerous biological and physical processes. Debates over whether marine communities are biologically accommodated or physically controlled have been replaced by a more balanced appreciation of the critical roles played by both kinds of processes. Disturbances, particularly multiple events that occur in rapid succession (Paine et al. 1998), are now recognized as prime initiators of shifts in community structure between alternate compositional states (e.g., Knowlton et al. 1990; Knowlton 1992; Hughes 1994; Petraitis and Latham 1999), which may or may not be persistent (Connell and Sousa 1983). Such shifts are increasingly likely as the rate and severity of anthropogenic disturbance increase worldwide.

So many factors affect the impact of disturbance agents on natural communities and subsequent patterns of succession, that sweeping generalizations are difficult (and probably unwise) to make. Nonetheless, several common patterns emerge from the body of benthic disturbance literature I have reviewed here:

1. The frequency, areal extent, and severity of a particular kind of disturbance vary spatially and usually have a strong seasonal component. Disturbance characteristics are often correlated: Large, severe disturbances occur less frequently and predictably than small, less-severe ones.
2. The impact of a disturbance agent depends on its dynamic properties as well as those of the affected organisms. Ontogenetic changes in organisms and successional changes in the three-dimensional structure and species composition of their assemblages alter their susceptibility to disturbance and thus its temporal and spatial patterning and severity. Substantial progress is being made in developing biomechanics-based models of these phenomena.
3. The influence of intra- and interspecific aggregation on vulnerability to disturbance appears to vary in a predictable manner along gradient of environment harshness. In physically harsh areas, aggregation often lowers the risk of disturbance (i.e., death due to physiological stress) by ameliorating potentially lethal environmental conditions. In contrast, high-density populations living in physiologically more benign conditions may suffer higher rates of disturbance because morphological or physiological changes caused by competition make them more vulnerable to other agents of disturbance (e.g., wave impact, sedimentation). On the other hand, members of dense aggregations living in benign environments may be at lower risk of disturbance from biological agents.

The effects of intimate interspecific associations such as epiphytism and parasitism on disturbance rates have been less studied. The effects of epiphytes appear to parallel those of aggregation in general: Epiphytes reduce their host's risk of mortality in harsh environments, but can increase the risk under physiologically benign conditions. Parasitism often tends to act synergistically with other agents of physiological stress to increase rates of mortality under physically harsh conditions, causing less mortality when environmental conditions are favorable.

4. Whether diversity begets stability is an old, but still vital question in ecology. To date, there have been only two studies that have directly addressed this question in marine benthic environments, and both were conducted on rocky seashores. Neither lends strong support to the hypothesis that the diversity of an assemblage affects its resistance or recovery from disturbance in a manner that differs from the aggregate responses of its component populations. With so few studies, and these conducted in but a single habitat, it is impossible to generalize about higher-order effects of benthic diversity on disturbance regimes or recovery from disturbance.
5. The severity of a disturbance, and therefore the extent to which survivors contribute to recolonization, strongly affects both the rates and patterns of succession. Yet,

most experimental studies of succession have imposed a single level of unnaturally severe disturbance: complete removal of residents.

6. The size and shape of disturbed patches seem to be broadly important to patterns and rates of recolonization in marine benthic assemblages. The effects of patch size and shape are often related to the corresponding change in perimeter to area ratio, which mediates the influence of neighboring sessile and mobile species, both competitors and consumers, and the flux of resources and propagules.
7. We tend to focus on the effects of individual disturbances, but each assemblage has a history of disturbance, and we know from a handful of studies that history can dictate the present state of the system and how it will respond to a new event.
8. The interplay between life history and disturbance characteristics accounts for a substantial amount of spatiotemporal variation in population demography and community structure. It transforms many marine landscapes into mosaics comprised of habitat patches that differ in the time since they were last disturbed, and hence the structure and species composition of the assemblages that occupy them. As in terrestrial systems, the persistence of some species within such landscapes depends on a particular frequency and quantity of disturbance. If either the amount of resource renewed by disturbance is too low, or the interval between disturbances is too long, such populations will go extinct. Other species that exploit disturbances, but do not necessarily depend on them for persistence, will decline in numbers.
9. Considerable observational and some experimental evidence indicates that intermediate levels of indiscriminate disturbance and disturbance that causes differential (i.e., compensatory) mortality of, or damage to, dominant competitors enhances or maintains local and regional species diversity in a variety of assemblages of sessile marine organisms. These assemblages include those of rocky seashores, subtidal hard substrates, coral reefs, and less-physiologically stressful areas within salt marshes. These are systems in which diversity peaks at a middle stage of succession, declining later in succession as one or a few species come to dominate the assemblage. Intermediate frequencies of disturbance maintain the assemblage in an earlier, more diverse stage of succession, whereas compensatory mortality or damage prevents competitive exclusion from occurring. In contrast, such a diversifying effect of disturbance has rarely been observed or experimentally demonstrated in seagrass beds or assemblages of soft-sediment infauna. These are systems in which diversity often rises monotonically following disturbance, peaking late in succession. It has been suggested in the case of seagrasses that the three-dimensional distribution of light and nutrient resources affords greater opportunity for coexis-



tence by resource partitioning, although the same should be true for salt marsh plants. Infauna coexistence may similarly be enhanced by the three-dimensional distribution of living space. In addition, the unstable nature of the sediment substrate precludes certain forms of interference competition that are common mechanisms of competitive exclusion on hard substrates. Further, disturbances in soft sediments are often so rapidly colonized by postlarvae and adults **transported** by currents from surrounding areas that there is little opportunity for new, nonresident species to establish. In physically harsh portions of salt marshes, the stressful conditions prevent the establishment of species other than those that occupied the site prior to disturbance.

Frankly, however, such generalizations are premature, as very few studies have directly manipulated disturbance rates in any benthic community. In fact, recent manipulative studies using mesocosms show that intermediate rates of bioturbation can enhance the diversity of certain assemblages of soft-sediment infauna.

## FUTURE RESEARCH DIRECTIONS

I have already mentioned a number of patterns and questions that beg additional investigation. Without being exclusive, I see several additional directions for novel and useful future research on the role of disturbance in marine benthic communities.

### *Spatially Explicit Studies of Disturbance in Benthic Landscapes*

Most of the empirical work on disturbance in marine communities has focused on the local or within-patch scale, asking questions about the effects of disturbance and disturbed patch characteristics, life history features, and species interactions on recolonization, succession, and local diversity. As a result, we know a lot about the responses of species to different kinds of disturbance, and the postdisturbance dynamics of populations and assemblages within individual patches of disturbed habitat. But as I discussed earlier, populations occupy landscapes comprised of mosaics of patches, so their dynamics are the product of processes operating within collections of patches connected by varying amounts of migration. How does the regime of disturbance, species life history characteristics, dispersal, and interspecific interactions affect the aggregate dynamics of the subpopulations living in different patches? In other words, how are metapopulation and metacommunity dynamics linked to the spatiotemporal regime of disturbance? Answering this question requires a spatially explicit approach that integrates the demography of patches and their internal dynamics with their arrangement in space. For some species with long-distance dispersal of propagules, the arrangement of patches within a particular landscape may matter little to their dynamics, but for many species with more limited dispersal, the spatial relationships

of newly disturbed sites and older "source" patches will matter. Paine's (1979, 1988) studies of subdivided populations of the sea palm, *Postelsia palmaeformis*, provide a clear example of a system where a spatially explicit metapopulation model would be necessary for predicting dynamics. Paine and Levin's (1981; see also Levin and Paine 1974) model of disturbance-generated patches in mussel beds describes the dynamics of patch age and size distributions, but takes no account of the spatial relationships of patches because colonists are assumed to come from a large bath of broadly dispersing propagules, the composition of which is unrelated to the local abundance of adults. For situations in which patch colonization is a local phenomenon, the descendants of their model, in particular, recent spatially explicit simulation models of the patch dynamics of grassland disturbance (Wu and Levin 1994; Moloney and Levin 1996) could be adapted to marine systems. The latter models clearly demonstrate that spatial and temporal autocorrelation of disturbances play as great a role in determining landscape-scaled dynamics as the rate and intensity of disturbance.

### *Disturbance and Biological Invasions*

There is substantial evidence that disturbance, both natural and anthropogenic, can promote the invasion of nonindigenous species into terrestrial and freshwater habitats (e.g., Hobbs and Huenneke 1992; Moyle and Light 1996; D'Antonio et al. 1999). In turn, these terrestrial invaders often differ qualitatively from native species in traits that affect their susceptibility to disturbance. Their presence can **thus** alter the natural regime of disturbance or introduce entirely new forms of disturbance (Mack and D'Antonio 1998). On the other hand, there are also clear examples of terrestrial, nonindigenous invasions that were facilitated by anthropogenic suppression of natural disturbance.

Such phenomena are very poorly documented in marine communities, despite a general impression in the literature that disturbance promotes invasion into marine habitats as well (Cohen and Carlton 1998). Most introductions of nonindigenous marine species are effected by accidental or intentional introductions of immature stages (e.g., larvae in ballast water) or adults (e.g., salt marsh plants used in restoration efforts) **by** humans (Carlton and Geller 1993; Ruiz et al. 1997). These invaders often establish in portions of habitats that are relatively underutilized by native species and not especially disturbed. Examples include invasion by cordgrass, *Spartina spp.*, onto mudflats along the Pacific coast of the United States where there are no native marsh plant competitors and few herbivores (Daehler and Strong 1996), and the establishment of the desiccation-tolerant, introduced snail, *Azetella myosotis*, in the semiterrestrial zone of Pacific Northwest marshes from which the two common native species of marsh snails are **ex**-cluded by the dry conditions (Berman and Carlton 1991).

Clear-cut cases of disturbance promoting the establishment of nonindigenous species are few. Nichols et al. (1999) observed that populations of the introduced clam, *Potamocor-*

*bula amurensis*, rapidly increased to dominate the benthos in northern San Francisco Bay following the near extirpation of native assemblages by a major flood. Reusch and Williams (1999) found that an introduced mussel, *Musculista senhousia*, grew best and most densely in native eelgrass (*Zostera marina*) beds that had been fragmented by disturbance, as compared to continuous undisturbed beds in which suspended food was less available due to slower flow rates. Meng et al. (1994) observed an increased rate of invasion by nonindigenous fish species into the Sacramento-San Joaquin estuary in California following the reduction by a major flood of already drought-stressed populations of native fishes.

Obviously, there is insufficient information to make any generalizations concerning the relationship between nonindigenous invasions and disturbance in marine benthic habitats. Given the remarkable rate at which nonindigenous species are being dispersed around the world by humans, it is imperative that we move from anecdotal impression to rigorous investigation of this relationship.

### *Effects of Patch Size and Shape*

Our ability to predict the effects of disturbance on community composition and dynamics would greatly benefit from more experimental work on the direct and indirect effects of patch size and shape and the mechanisms that generate them. These characteristics, particularly as they affect the perimeter to area ratio of disturbed patches, appear to be generally important to successional dynamics in marine habitats. Patch shape is rarely measured in studies of disturbance, and its effects have been much less thoroughly investigated than patch size. Most studies of the effects of patch size and shape have been conducted on very small scales, usually less than a square meter. Where logistics and ethics allow, comparable studies at larger scales could provide valuable information on the scaling of such edge effects that might aid predictions concerning the effects of large-scale anthropogenic disturbance and habitat fragmentation.

### *Effects of Disturbance Severity*

Much of our understanding of the processes of recolonization and succession following disturbance comes from experimental studies of the most severe level of disturbance: complete removal of the resident organisms and sterilization of the substrate. A more general picture of these processes will come from future studies that examine patterns and mechanisms of recovery from a range of severities of damage.

### *Effects of Correlations among Disturbance Characteristics*

We know that the size, severity, and frequency of disturbance covary, but such correlations are seldom quantified, and their effects on population and assemblage dynamics are rarely studied. Theory predicts that patterns of regional species diversity will be strongly influenced by the pattern of covariation among disturbance characteristics. Studies of these relationships, especially when coupled with the development of

spatially explicit patch models, described earlier, should be very fruitful.

### *Effects of Species Diversity on Susceptibility to, and Recovery from, Disturbance*

As discussed earlier, we know very little about the independent influence of species diversity on rates of disturbance and recovery. Existing studies suggest subtle effects, if any. However, ongoing declines in the biodiversity of numerous marine habitats in response to human activities make rigorous experimental investigations of these relationships all the more urgent.

### *Long-Term Records of Disturbance Regimes*

There is a pressing need for the collection of long-term records of natural disturbance regimes. Such records can provide a baseline against which we can objectively measure the effects of global climate change. As the frequency and intensity of storms or the density and distribution of agents of biological disturbance change in response to a changing climate, so too will the regimes of disturbance in many marine benthic habitats. It is critical to document not only changes in mean values of disturbance characteristics (e.g., frequency, size, and severity), but also in their variances. As discussed earlier, variation in the time interval between disturbances, for example, can greatly affect the abundance and persistence of species. Ideally, such studies should pay equal attention to small, "everyday" disturbances and larger "unusual" ones, and document the regime of disturbance at multiple sites to quantify the full range of natural variation in disturbance regimes.

Such long-term records will also provide detailed histories of the disturbances experienced by particular assemblages and a better understanding of the nature and mechanisms by which the response of a system to disturbance is contingent on how it was affected by, and responded to, past disturbances.

### *Interactions among Disturbances Occurring on Different Spatial and Temporal Scales*

Every marine habitat is affected by multiple agents of disturbance. These agents exert their effects at different spatial and temporal scales. Do these effects interact and how? An example from Florida mangrove forests suggests that there can be important interactions between disturbances that occur at different spatial scales. In 1992, Hurricane Andrew caused extensive damage and mortality of mangroves in south Florida; particularly hard hit were stands of *Rhizophora mangle*, a species that lacks the capacity to resprout from adventitious meristems. However, in the midst of these swaths of dead or dying adult trees were small, dense patches of surviving juvenile trees, which were flexible enough to escape wind damage. These patches of young trees had established within canopy gaps, up to 1000 m<sup>2</sup> in area, caused by lightning strikes that had formed months or years prior the hurricane. In this case, the prior occurrence of small-scale disturbance in the form of lightning gaps provided opportunities for recruit-

ment of young trees whose offspring will eventually internally repopulate the much larger areas damaged or destroyed by the hurricane (Smith et al. 1994). Undoubtedly similar phenomena await discovery in other marine habitats.

### Direct and Indirect Effects of Disturbance on "Interstitial" Species

Disturbance to "structural" species has been well studied, but the secondary effects on so-called "interstitial" species that live amongst them, including mobile species, are less well documented, including the patterns and processes by which their populations recover following a disturbance. Anthropogenic disturbances such as blast fishing on reefs and bottom trawling drastically reduce structural complexity of the affected assemblage. The reestablishment of habitat complexity during succession and the associated recovery of populations of organisms that require it **beg** additional study.

### Can the Findings of Relatively Small-scale Studies of Natural Disturbance Meaningfully Inform Investigations of Anthropogenic Disturbance?

Anthropogenic disturbances often occur over larger spatial scales than natural disturbances and are usually more severe (e.g., fishing with bottom trawls and dredges), frequent (e.g., damage from anchors, and dynamite and poison fishing on coral reefs, bait and clam diggers on mud and sand flats, foot traffic on rocky seashores), and chronic in their impact. They may also differ qualitatively from natural forms of disturbance (e.g., chemical pollution), and as noted previously, some forms of anthropogenic disturbance dramatically reduce the structural complexity of the habitat. Predicting the response of marine communities to anthropogenic damage from information on their responses to natural disturbance is complicated by these multivariate differences. It is often not

just a simple matter of scaling up from small to larger disturbed areas. Nevertheless, if we know enough about the natural history of the affected systems, we should be able to make sound and testable predictions about the consequences of a particular change in a disturbance regime. As yet, concepts emerging from basic studies of disturbance ecology have had little influence on investigations of anthropogenic disturbances such as bottom trawling or blast fishing on reefs (but see Watling and Norse 1998). Such studies are still in an early descriptive phase; concepts and predictions should **develop** in time. With the rate of anthropogenic disturbance ever increasing, there is, unfortunately, no shortage of work to be done in this area.

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