chapter 5

The Ecology and Evolution of Marine Consumer–Prey Interactions

J. Emmett Duffy and Mark E. Hay

Predation is a nearly universal pressure affecting the phenotypes of organisms as well as the organization and functioning of communities and ecosystems. The impacts of consumers (herbivores and predators) on population and community structure are often determined by, or interact with, processes covered in other chapters of this volume (e.g., physical processes, competition, recruitment). To prevent excessive overlap, we minimize focus on these interactions and review selected examples of direct effects of consumers on prey, and of the indirect consequences of these effects for communities and ecosystems. We focus primarily on organism-level interactions between consumers and prey, and on their adaptive responses to one another.

Consumer pressure is intense in many marine ecosystems. In subtidal marine communities such as coral reefs or kelp beds, for example, herbivory is commonly one of the primary forces determining the distribution and abundance of plants, and often the species composition and diversity of the entire community. Indeed, in numerous marine systems, the activity of consumers so dramatically alters local communities that these systems change fundamentally when consumers are removed. For example, herbivorous fishes or sea urchins can remove approximately 100% of daily algal production on shallow coral reefs (Carpenter 1986), with herbivorous fishes sometimes taking more than 150,000 bites/m^2/day (Figure 5.1). These fishes and urchins keep reefs largely devoid of macroalgae and allow corals to flourish by reducing competition from the more rapidly growing seaweeds (Lewis 1986; Miller 1998). As these herbivores severely declined around the Caribbean island of Jamaica due to a combination of overfishing and urchin disease, coral reefs suffered severe overgrowth by seaweeds, and live coral cover declined from more than 50% to less than 5% throughout this entire island nation (Hughes 1994; Figure 5.2). Removing herbivores from these habitats converted species-rich, structurally complex coral reefs into a completely different community dominated by a limited number of seaweeds.

Herbivores have equally dramatic impacts in temperate systems. Numerous ecological and paleontological studies show that subtidal benthic communities in the temperate northeastern Pacific shift from sea urchin–grazed barrens to lush kelp beds depending on the presence or absence of sea otters, which selectively forage on sea urchins and molluscan herbivores, reducing grazer biomass, and allowing kelps to flourish (Estes and Palmisano 1974; Simenstad et al. 1978; Duggins et al. 1989; Estes and Duggins 1995; Estes et al. 1998). Where otters have been removed from kelp communities by hunting or predation, urchin densities increased, urchins drove kelps to local extinction (Figure 5.3), and fishes, kelp-associated invertebrates, and seals or sea lions that feed on kelp-bed fishes also declined dramatically. Because kelp beds normally export organic matter to other nearby communities (Duggins et al. 1989), these adjacent systems and their species (e.g., bivalves to bald eagles) are impacted as well. Thus, in the reef example, grazers increased diversity by removing seaweeds and allowing corals to produce the biogenic structure that enhances reef biodiversity, while in the kelp-bed system grazers directly removed the major biogenic structure (kelps) and caused a decline in biodiversity, productivity, and transport of kelp-derived resources to associated near-shore communities.

Similarly pervasive system-level impacts of consumers have been documented in pelagic communities. A spectacular example is the unwitting manipulation of the subarctic Pacific pelagic zone by release of pink salmon from hatcheries. In (alternating) years when pink salmon are abundant in this region, zooplankton are rarer and phytoplankton more abundant (Shiomoto et al. 1997). These observations of strong top-down control in a pelagic ecosystem lend credence to suggestions that whaling could have allowed large population increases in their prey, krill, with concomitant changes elsewhere in the food web, pushing back to the last century the time when human impacts on consumers began to change the oceans on a very large scale. Indeed, Jackson (1997) has marshaled evidence that human hunting of green turtles, manatees, and other formerly abundant megafauna began to change Caribbean marine ecosystems shortly after Europeans arrived in the region in the sixteenth century. It is clear that current fishing has global-scale impacts because the mean trophic level of animals harvested from the sea is decreasing (Pauly et al. 1998).

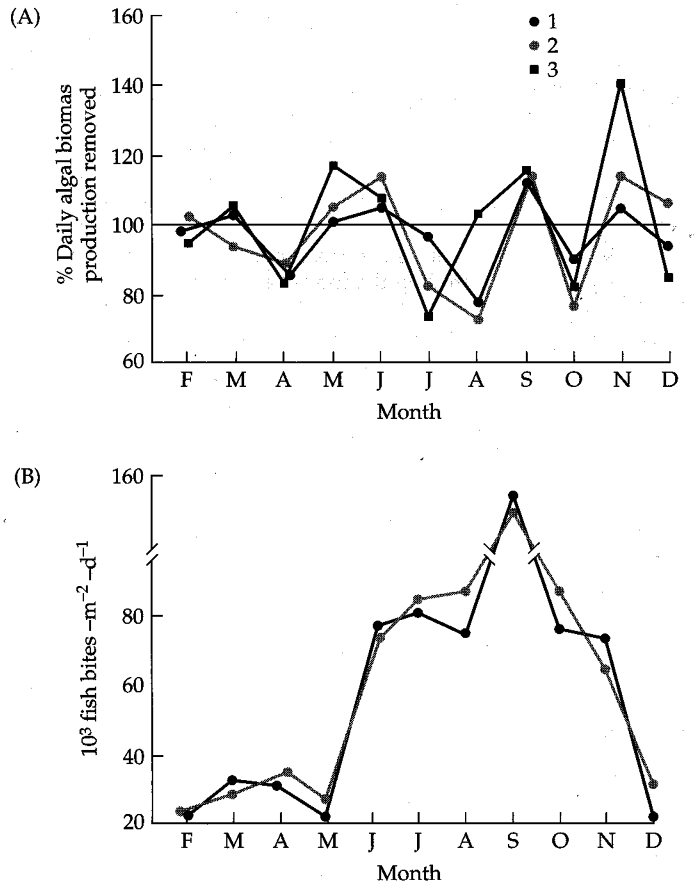

Figure 5.1 (A) Herbivorous fishes and sea urchins consume ~100% of daily algal production on a coral reef. The different curves represent experimental treatments with (1) all herbivores, (2) fishes and mesograzers only, and (3) urchins and mesograzers only. (B) Bite rates by herbivorous fishes throughout the year on a shallow fore-reef in St. Croix, U.S. Virgin Islands. (After Carpenter 1986.)

How Do Prey Deal with Consumer Pressure?

Escapes in Space, Time, or Size

The intensity of consumer pressure common in marine systems should exert strong selection on prey to avoid being eaten. Escape from consumers often entails avoidance in time, in space, or in both time and space. An especially impressive example involves the daily vertical migrations of zooplankton. The pelagic zone offers little structure to shield prey from visually orienting predators so that many zooplankters undertake vertical (in the open ocean) and horizontal (in estuaries) migrations to avoid predators. Indeed, the daily vertical migration of zooplankton and small nekton (e.g., fishes, squids, and shrimps) is one of the most conspicuous biological phenomena of the open oceans. Many such animals forage in food-rich surface waters at night and migrate

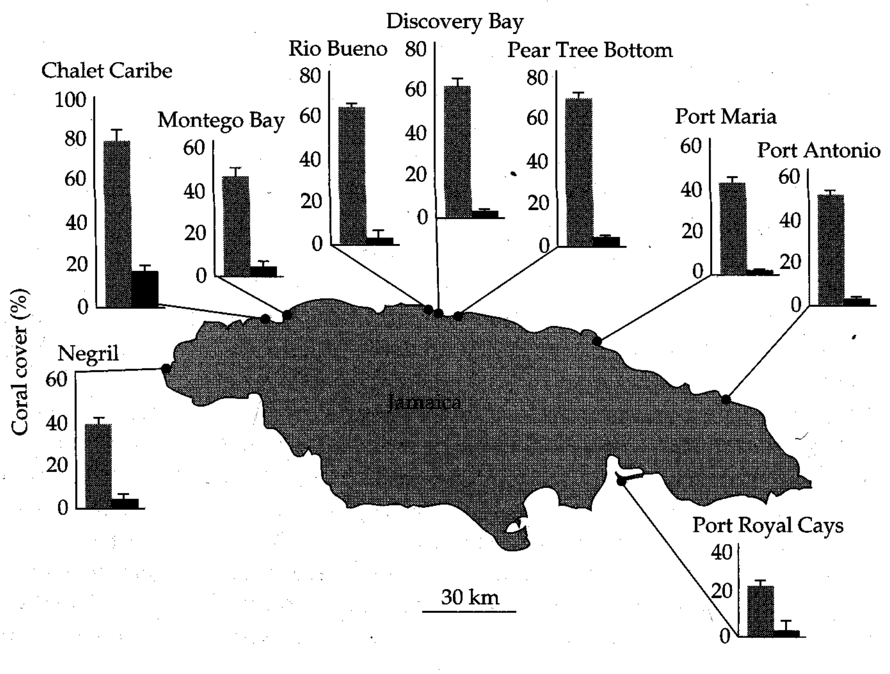

Figure 5.2 Large-scale changes in the cover of live coral at fore-reef sites along >300 km of the Jamaican coastline surveyed in the late 1970s (hatched bars) and the early 1990s (filled bars). (After Hughes 1994.)

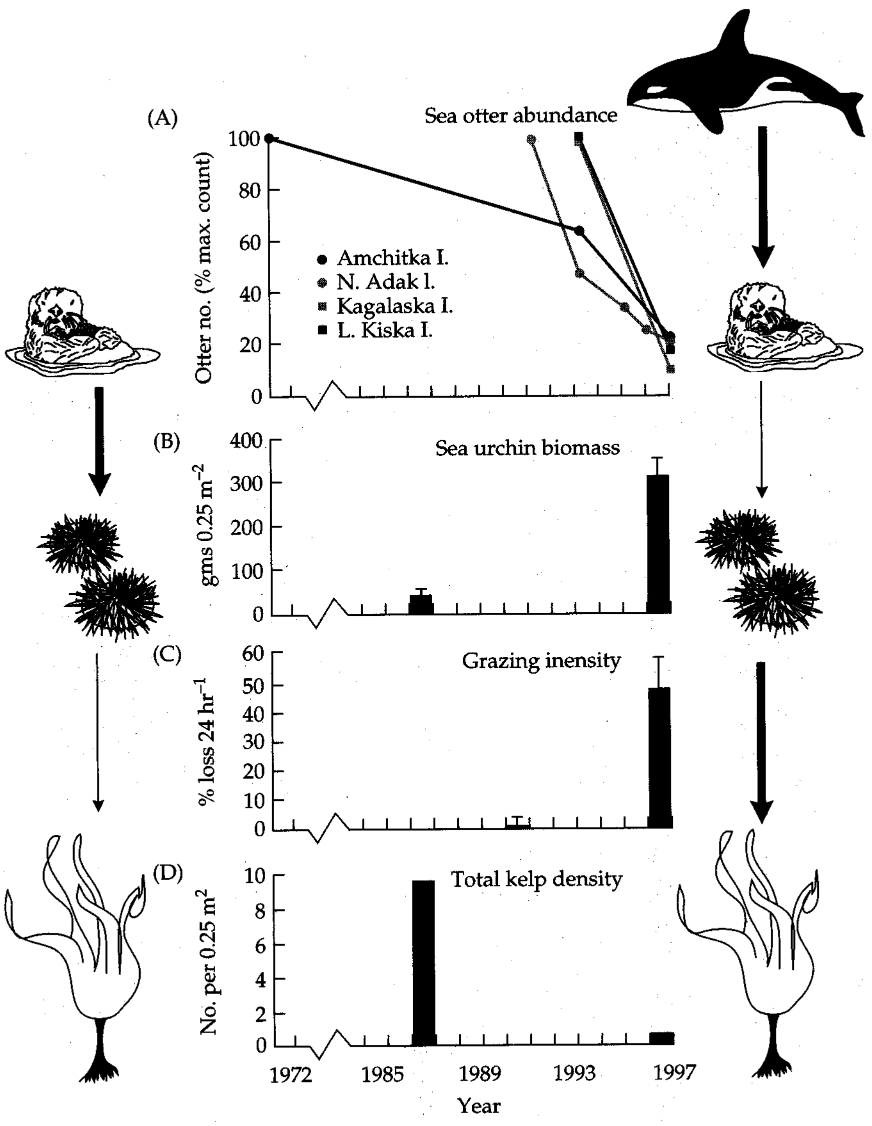

Figure 5.3 A marine trophic cascade extending through four trophic levels. Declines in sea otter abundance at several islands in the Aleutian archipelago (A) were correlated with increased sea urchin abundance (B), and grazing intensity (C), and greatly reduced kelp abundance (D) at Adak island. Sea otters declined concurrently with a sudden increase in killer whale predation on them. The cartoons show the proposed mechanisms controlling the food chain before (left) and after (right) the sea otter decline. Thick and thin arrows represent strong and weak interactions respectively. (After Estes et al. 1998.)

tens to hundreds of meters downward (>800 m in the salp *Salpa aspersa*, Wiebe et al. 1979) into dimmer waters each day during those periods when the visually hunting predators of surface waters are most active. Several observations suggest that this behavior functions primarily to avoid predation. Vertical migrations are more pronounced in large and strongly pigmented species, which are more conspicuous to visual predators (Hays et al. 1994). Vertical migration of copepods can be induced by exposure to predatory fishes in enclosures (Bollens and Frost 1989a). And finally, there are seasonal and interannual correlations between predatory fish abundance and the strength of vertical migration (Bollens and Frost 1989b; Hays 1995). These consumer-induced migrations have important consequences for global ocean biogeochemistry, as the migrants transport materials from the euphotic zone to the deep ocean (Longhurst et al. 1989; Hays et al. 1997).

Planktonic larvae of many estuarine crabs similarly reduce their risk of predation by undertaking large-scale horizontal, rather than vertical, migrations. Field surveys of predator abundance and gut contents showed that fishes that eat crab larvae are predictably more abundant in estuaries than in coastal waters during summer when crab zoeae are released (Morgan 1990). Most estuarine crab species efficiently move their vulnerable larvae out of dangerous estuarine waters by releasing larvae during spring high tides at night; this serves to transport them rapidly to deeper, safer waters without detection by visual predators (Morgan and Christy 1997). As is true of vertically migrating copepods in the open ocean (Hays et al. 1994), species of crab larvae that are more heavily pigmented enter predator-rich waters primarily during darkness, whereas those that are exposed during daylight are more transparent (Morgan and Christy 1997).

Sessile prey that cannot migrate between habitats can still exploit predictable temporal variance in consumer activity to escape in time. Several seaweeds seasonally shift morphologies in ways that minimize losses to herbivores (Lubchenco and Cubit 1980). For example, temperate herbivores are often active primarily during the summer, and several genera of algae have life histories that capitalize on these seasonal changes in grazing pressure. Complex life histories, involving alternation of morphologically distinct generations that differ in growth potential and resistance to herbivores, are common among seaweeds (*Ulothrix, Urospora, Petalonia, Scytosiphon, Bangia*, and *Porphyra* are examples). Upright forms of these species are good competitors but are more susceptible to herbivores and occur primarily during seasons when herbivore activity is low. The less competitive, but more herbivore-resistant, crustose forms dominate during seasons when herbivores are active. Though upright forms normally occur in the field only during winter when herbivore activity is suppressed, these forms persist during the summer if grazers are experimentally excluded (Lubchenco and Cubit 1980).

Some species can also shift morphology very rapidly (within a few days), without the shift being tied to life-cycle stages, and can do so in direct response to the recent history of herbivore activity. Working on a Caribbean reef, Lewis et al. (1987) demonstrated such a dramatic shift in the brown seaweed *Padina jamaicensis*. In areas heavily impacted by grazing fishes, *Padina* grew as an uncalcified turf of small, irregularly branched creeping axes that had a single apical cell and that were closely adherent to the substratum. On areas of the reef where herbivory was slight, *Padina* grew as a calcified, upright, and foliose blade that was generated by meristematic cells along the entire leading edge of the fan-shaped blade. Because of their morphological dissimilarity, these two forms had at times been assigned to separate genera. When herbivorous fishes were excluded from portions of the reef for as little as 96 h, the uncalcified turf form shifted to the calcified upright form. Transplant and caging experiments showed that the upright form grew rapidly, reproduced, and was a superior competitor, but it was highly susceptible to removal by herbivorous fishes. In contrast, the turf form could persist in areas of high herbivore impact, but it did not competitively exclude other reef species, and it was never observed to reproduce sexually.

Seaweeds may also minimize herbivore damage by flushing their new, most palatable growth during periods of predictably low herbivory. An extreme example is the tropical algal genus *Halimeda*, which synchronously produces its youngest, and most nutritious, portions only at night while herbivorous reef fishes are not feeding (Hay et al. 1988, Paul and Van Alstyne 1988). New segments are uncalcified and more nutritious than the rest of the plant, but these young segments are defended with more potent chemical defenses than are present in older segments. During the following day, as the new segments calcify, become more heavily invested with structural defenses, and less valuable nutritionally, concentrations of chemical defenses decrease. Thus, these seaweeds minimize exposure of their newly produced tissues by producing them very rapidly during the night while herbivorous fishes are inactive.

Nonmobile prey also escape consumers by growing in habitats or microhabitats in which consumers are not active. On a microhabitat scale, prey may escape by living in cracks and holes that are inaccessible to consumers. For example, on intertidal rock surfaces of Pacific Panama where consumer pressure is particularly intense, herbivore-resistant algal crusts dominate exposed surfaces while less resistant foliose algae occur primarily, or exclusively, in holes and cracks (Menge et al. 1985). On a larger, between-habitat scale, many seaweeds, corals, and sponges that are physiologically capable of growing on topographically complex, but consumer-rich, reef slopes occur only, or primarily, on topographically simple sand plains or reef flats, or in mangrove or seagrass areas where consumer densities are lower (Randall 1965; Ogden et al. 1973; Hay 1981a, 1984, 1985; Lewis 1986; Littler et al. 1989; Dunlap and Pawlik 1996). Similar escapes also occur on larger spatial scales. Along the Great Barrier Reef of Australia, algal mass is much greater on inshore reefs than on offshore reefs. Although this difference in abundance has commonly been assumed to result from greater availability of nutrients inshore, it now appears to be due primarily to higher grazing on offshore reefs (McCook 1996, 1997; McCook et al. 1997). Finally, on a geographic scale, Bolser and Hay (1996) recently demonstrated that seaweeds from the tropical Caribbean were considerably less palatable to both temperate and tropical herbivores than were seaweeds from the warm temperate western Atlantic. This palatability difference was due primarily to greater chemical defenses among the tropical seaweeds. Thus, it is possible that temperate areas serve as large-scale spatial escapes from tropical consumers. Consistent with this idea, many of the tropical seaweeds that are restricted to unstructured, consumer-poor reef flats or sand plains in the tropics extend into temperate areas and grow well on reefs there; conversely, the herbivore resistant seaweeds that cooccur with consumers on tropical reefs rarely extend very far into temperate areas (Hay 1981a; M. E. Hay pers. obs.).

In contrast to their usually negative impacts on prey, consumers sometimes create spatial refuges for certain types of prey. Reef damselfishes are small aggressive herbivores that establish and vigorously defend gardens of palatable algae upon which they feed. These gardens experience reduced herbivory compared to areas not defended by damselfishes. Some seaweeds depend on these herbivore-created escapes, and algal diversity may be higher in territories than in either caged or uncaged areas outside territories (Hixon and Brostoff 1983, 1996). The algal-dominated territories also serve as refuges for a wide variety of small invertebrates that shelter there (Klumpp et al. 1988).

Finally, prey may also escape in size if they become too large for consumers to handle effectively. Such size-related escapes presumably result from larger individuals being tougher, harder, less nutritious, or more easily recognized as unpalatable. Strictly speaking, this phenomenon is not an escape since consumers detect, but do not significantly damage, the prey. Size-related differences in susceptibility are important, however, since most prey must pass through a juvenile stage that often is more vulnerable to consumers. Even for chemically defended prey that are avoided as adults, newly settled juveniles may be eaten by unselective consumers because they are not recognized, and thus not avoided, at this small size, or because smaller prey are easier to handle or more nutritious. The challenge for many sessile prey, then, is to survive until they reach a size at which they are less vulnerable. For example, kelp sporelings are more vulnerable to herbivores than are larger plants, and the kelp sporelings escape herbivores more often when hidden among filamentous brown algae than when growing on bare rock (Harris et al. 1984). Similarly, small (< 3 cm) *Fucus vesiculosus* plants are more susceptible to grazing snails than are larger plants, and survival of small plants is enhanced by settlement in small cracks or among barnacles where herbivores cannot graze effectively (Lubchenco 1983). In contrast, recruitment and growth of algae can be so great that they swamp the ability of molluscan herbivores to eat the young plants; under these conditions, the plants may quickly reach a refuge in size beyond which they no longer suffer mortality at the normal herbivore densities (Dayton 1975). In extreme cases, algal growth may be heavy enough to alter the habitat in such a way that the area becomes unsuitable for some herbivores (Underwood and Jernakoff 1981). These prey might thus be producing their own spatial escapes, via habitat modification.

Associational Escapes

Communities strongly affected by consumers are often dominated by unpalatable prey. These unpalatable species can create spatial escapes for more palatable species (Hay 1986; Littler et al. 1986; Pfister and Hay 1988). For example, field experiments demonstrated that the palatable red alga *Hypnea musciformis* was quickly eaten by fishes when growing alone, but grew more rapidly than it was consumed when placed in contact with its herbivore-resistant competitor, the brown alga *Sargassum filipendula* (Hay 1986). During the yearly peak in herbivore abundance, *Hypnea* and other palatable seaweeds were found exclusively in association with unpalatable plants, whereas during seasons when herbivores were less active, palatable plants were not strongly associated with unpalatable species. In communities where associational refuges are important, dominance of the community by a few unpalatable species can increase species richness rather than decreasing it, as would be expected if competition were of primary importance (Hay 1986). This occurs because palatable species that would have been eliminated by consumers can persist only in association with their unpalatable competitors. Similarly, on coral reefs, nearly twice as many taxa occurred within 10 cm of the chemically defended brown alga *Stypopodium zonale* than in similar-sized areas away from *Stypopodium* (Littler et al. 1986). As a final example, temperate seaweeds in the genus *Desmarestia* contain sulfuric acid at up to 18% of plant dry mass (Anderson and Velimirov 1982). In South American kelp beds heavily grazed by sea urchins, the palatable kelp *Macrocystis* often cannot colonize unless it invades an area encircled by *Desmarestia* plants; these plants act as "acid brooms," prohibiting urchins from entering the area (Dayton 1985). Associational escapes can thus be effective in a variety of habitats and against very different kinds of consumers.

There are numerous other associations among marine animals that similarly appear to offer protection to one, or both, of the partners. Examples include pomacentrid fishes that live exclusively in association with sea anemones, whose stinging nematocysts protect both species from enemies; hermit crabs that place stinging anemones on their claws and use these as defenses (Vermeij 1983); and shrimps and other animals that live in obligate association with often chemically rich coral-reef sponges (Pawlik 1983; Duffy 1992, 1996) or stony corals (Patton 1976). Interestingly, some such guests return the favor to their host by defending it against its own predators or competitors. For example, several species of crustaceans and polychaetes that associate with the East Pacific coral *Pocillopora damicornis* attack and even kill crown-of-thorns starfish that molest their host coral (Glynn 1980, 1981), increasing survival of the coral host (Glynn 1983). Similarly, some crustaceans form nonobligate associations with various branching corals or coralline algae (Coen 1988; Stachowicz and Hay 1996; Stachowicz and Hay 1999). The crabs receive a topographically complex refuge from fish predators but also protect their host by removing fouling seaweeds and invertebrates. For a few species, these refuges can be made more mobile and carried with them. As an example, in geographic areas where consumers are most active, the juvenile decorator crab *Libinia dubia* selectively decorates with a chemically noxious seaweed that lowers its susceptibility to consumers (Stachowicz and Hay 1999, 2000).

Tolerating Consumers

Some prey can coexist with attacking consumers if being attacked has minimal effects on prey fitness. Such prey can be considered to be tolerant of consumer activity. In a rather extreme example, when the freshwater phytoplankter *Sphaerocystis schroeteri* is consumed by the zooplankter *Daphnia magna*, more than 90% of the *Sphaerocystis* cells are undamaged, and the nutrient enrichment that occurs during gut passage enhances the growth of gut-passed cells by more than 60%, thus more than compensating for the slight damage the grazers do to the algal population (Porter 1976). In situ grazing experiments indicated that densities of this alga increased with increases in grazer density. The alga appeared to rely on grazers as a rich localized source of nutrients.

Some coralline algae show a similar pattern of tolerance to, or even reliance on, their associated herbivores. A recent study by Littler et al. (1995) provides an excellent example. On reef fronts in the Caribbean, the coralline crust *Porolithon pachydermum* is heavily grazed by the chiton *Choneplax lata*, with approximately 50% of the chiton's gut contents being composed of this alga. However, the alga is predictably associated with the chiton, and it grows well and produces reef structure best when the chiton is present. If the herbivorous chiton is removed, the coralline is overgrown by fleshy algae. These fleshy algae attract grazing fishes, and the fishes bite deeply into the substrate, removing not only fleshy algae but the coralline as well. Thus, removal of *Porolithon*'s major herbivore causes bioerosion in excess of production. The coralline is tolerant of chiton grazing, in part because its meristematic region is protected below the depth to which the chiton's radula scrapes algal cells. A somewhat similar example of gastropod and coralline algal interactions in subarctic systems is provided by Steneck (1982).

Consistent with the above studies, the dominant plants in areas most affected by herbivory represent the extreme ends of the spectrum of susceptibility to herbivores—small filamentous forms that are very susceptible (Carpenter 1986; Lewis 1986) and heavily calcified, crustose corallines that are very resistant (Steneck 1986) to herbivores. Both of these forms may depend on herbivores to prevent their exclusion by larger macroalgae (Lewis 1986), even though such reliance may entail loss of the plant's own tissues. Small filamentous algae persist on reefs despite large losses to grazers by growing very rapidly, and by having basal portions that escape herbivores due to the topographic complexity of the substrate (Carpenter 1986; Lewis 1986; Steneck 1988). This strategy of "tolerating" rather than deterring herbivory allows inconspicuous filamentous algae to make up much of the plant biomass on grazed areas of coral reefs. These plants are in fact more productive on a mass-specific basis when they are grazed because cropping prevents self-shading, and herbivore excretion may increase available nutrients (Carpenter 1986, 1988).

In some cases, fitness losses to herbivores may be minimized if ingested propagules remain viable and are dispersed via defecation by the herbivore, a situation reminiscent of seed dispersal by birds and mammals on land (Figure 5.4). For several opportunistic algae exposed to grazing by gastropods, gut passage significantly increases the production of motile spores and the growth rate of sporelings relative to uningested controls (Santelices and Ugarte 1987). In contrast, spores and vegetative portions of late successional plants are rarely resistant to digestion. However, grazing may provide some benefits even for late successional plants. For example, amphipods graze on cystocarps (reproductive structures) of the red alga *Iridaea laminarioides*, releasing spores into the water column when the cystocarps are opened (Buschmann and Santelices 1987). Spores released by amphipods were as viable as naturally released spores, and surprisingly, ungrazed fronds often had cystocarps that remained closed and did not naturally release their spores. The percentage of such unopened cystocarps was significantly greater at sites without amphipods than at sites with high amphipod densities. Although a lower proportion of spores ingested by amphipods germinated compared with uningested spores, those that did germinate had higher growth rates, presumably due to nutrients absorbed by the algal cells during passage through the herbivore gut (Buschmann and Santelices 1987). Gut passage of viable algal propagules has now been documented in a variety of herbivores including fishes, sea urchins, amphipods, and gastropods (Santelices and Ugarte 1987; Paya and Santelices 1989).

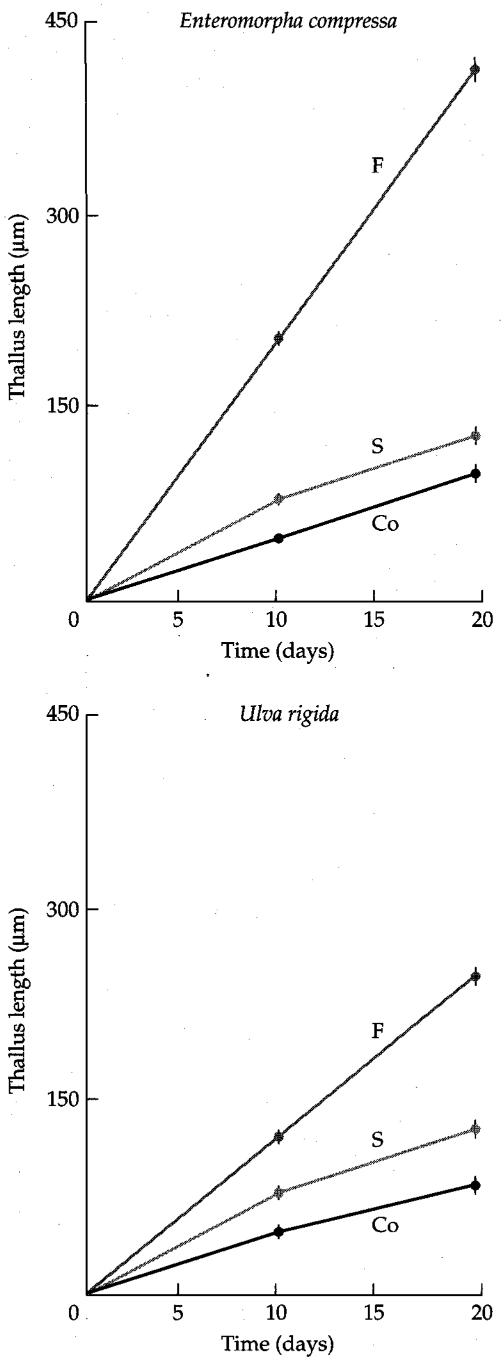

Figure 5.4 In some cases, consumers may benefit their prey. Reproductive propagules of several algal taxa, such as these two green seaweeds, passed intact through the guts of grazing molluscs (F = *Fissurella*, S = *Siphonaria*). Sporelings derived from the gut-passed propagules grew significantly faster than those that had not been passed through a grazer's gut (Co = Control). (After Santelices and Ugarte 1987.)

A final example of a prey adaptation that may involve elements of both escape and tolerance is the mass spawning of reef corals. On the Great Barrier Reef, corals of at least 32 species release gametes synchronously during a brief but predictable period of four to five nights after full moons in late spring, resulting in huge densities of gametes and larvae in the water (Harrison et al. 1984). These authors suggested that one function of this synchronous, rare spawning may be to overwhelm the capacity of potential predators, such that a relatively small proportion of larvae from any individual colony are eaten. An intriguingly similar multispecies mass spawning occurs in some tropical green algae (Clifton 1997).

Deterring Consumers

If prey do not escape or tolerate consumers, they must deter them so that rates of consumption do not exceed rates of production. This deterrence commonly occurs through chemical, structural, or behavioral defenses. In some cases, prey use mixed strategies of defense in which chemical and structural deterrents are combined to form additive or synergistic defenses, with these sometimes varying spatially, seasonally, or even hourly to maximize effectiveness (Hay et al. 1988; Hay et al. 1994; Schupp and Paul 1994; Hay 1996).

MORPHOLOGICAL AND STRUCTURAL DETERRENTS. Armor, spines, and other such morphological elaborations are obvious features of many organisms living in environments where consumer pressure is substantial. Studies of gastropod prey have demonstrated that narrow apertures and various sculptural features such as spines and thickened shells all reduce gastropod vulnerability to predation by crabs and fishes, and that predation-deterrent morphologies, moreover, are much more frequent in habitats and geographic regions where predation is more intense (Vermeij 1976; Zipser and Vermeij 1978; Palmer 1979; Bertness 1981; Bertness and Cunningham 1981; Bertness et al. 1981). Although not confirmed by experiments, similar patterns of covariance between predator activity and frequency of body sculpture are found in marine isopods (Wallerstein and Brusca 1982).

For seaweeds, general models have been proposed that predict how morphology should affect susceptibility to herbivores (Littler and Littler 1980; Steneck and Watling 1982; Littler et al. 1983a,b; Steneck 1983; Steneck and Dethier 1994). In general, microalgae are predicted to be most susceptible to herbivores, with resistance of other algal forms increasing in the following order: filamentous algae, sheetlike algae, coarsely branched algae, leathery or rubbery algae, jointed calcareous algae, and crustose corallines. This prediction is based in part on the decreasing food value expected as seaweeds allocate more production to less digestible structural materials that make them tougher and more difficult to bite. Feeding choices of some molluscs and sea urchins are broadly supportive of the predicted relationship (Steneck and Watling 1982; Littler et al. 1983a,b), but other molluscs diverge from predicted patterns (Padilla 1985), as does feeding by reef fishes (Hay 1984; Lewis 1985). Predictions based on morphology alone are also difficult to evaluate because morphological trends can be confounded by chemical defenses. For example, many calcified tropical seaweeds also produce chemical defenses (Hay 1984; Paul and Hay 1986); thus the low palatability of calcified species could be due to either trait, or to both (Hay et al. 1994; Schupp and Paul 1994).

A few investigations have directly addressed how algal morphology affects susceptibility to herbivores. Steneck and Adey (1976) demonstrated that the encrusting coralline *Lithophyllum congestum* grew as a smooth crust on reef slopes where feeding by herbivorous fishes was intense but produced upright branches when it occurred on the edges of reef flats where fish feeding was reduced. When compared with the crustose form, the form with upright branches had higher growth and reproduction, but it was also much more susceptible to parrotfishes, which excluded the upright form from the reef slope. Similarly, various clonal seaweeds can occur in low-herbivory habitats as loose aggregations that grow rapidly but lose more tissues to herbivorous fishes and sea urchins, whereas in habitats most affected by herbivores, they occur as densely packed colonies of uprights that grow slowly but have lower losses to herbivores (Hay 1981b). The study of *Padina jamaicensis* by Lewis et al. (1987) discussed earlier documented one of the most dramatic cases of altered morphology in response to herbivory. All of these examples indicate that morphological plasticity helps seaweeds persist in areas that are heavily grazed, but that the morphologies that resist herbivory entail a significant cost in terms of growth and reproduction.

CHEMICAL DETERRENTS. Recent reviews of chemical defenses against marine consumers are numerous (e.g., Hay and Fenical 1988, 1996; Hay 1992, 1996; Hay and Steinberg 1992; Steinberg 1992; Paul 1992; Pawlik 1993), so our coverage here will be brief. Sessile marine organisms that do not have physical defenses against consumers (e.g., spines, hard shells) commonly produce unusual chemical compounds (Faulkner 1999 and references therein), termed secondary metabolites because they are not necessary for primary metabolic processes. Several thousand novel secondary metabolites, including terpenes, acetogenins, alkaloids, and polyphenolics, have been described from sponges, ascidians, soft corals, bryozoans, polychaetes, seaweeds, marine microbes, and other benthic and pelagic organisms (Fenical 1993; Faulkner 1999 and his previous reviews cited therein). These diverse metabolites appear to be most common and ecologically important among tropical benthic organisms that are subject to high rates of attack by consumers (Hay and Steinberg 1992; Paul 1992; Pawlik 1993; Faulkner 1994; Bolser and Hay 1996). However, secondary metabolites also play important roles in temperate communities (King 1986; Hay and Steinberg 1992; Steinberg 1992; Woodin et al. 1993; Duffy and Hay 1994; Cronin and Hay 1996a, b; Stachowicz and Hay 1999) and Antarctic benthic communities (McClintock 1994), and potentially in pelagic (Huntley et al. 1986; Shaw et al. 1995; McClintock et al. 1996; Wolfe et al. 1997) communities worldwide.

Experimental investigations in both the field and laboratory have confirmed that many secondary metabolites from seaweeds and benthic invertebrates serve as defenses against consumers (reviewed by Hay and Fenical 1988, 1996; Hay 1991a, 1996, 1997; Hay and Steinberg 1992; Paul 1992; Pawlik 1993; Pawlik et al. 1995). Because consumer pressure in marine systems is often high and because these systems are often more experimentally tractable than terrestrial systems, it has been possible to identify clearly the ecologically important consumers against which compounds should be tested, and often to test compounds in the field against the diverse assemblage of natural consumers that occur there (reviewed by Hay and Steinberg 1992; Hay et al. 1998). Thus, marine investigators can apply purified metabolites at natural concentrations to otherwise palatable foods in the field and determine in a short period of time whether or not the compounds decrease predation under natural field conditions (Hay et al. 1987a; Paul 1987; Hay 1991a; Hay and Steinberg 1992; Pawlik et al. 1995). These types of assays have shown that many marine secondary metabolites function as defenses against consumers, and that potential prey without these defenses are often excluded from habitats where large, generalist consumers such as fishes and sea urchins are common (Hay 1985, 1991a, 1997; Littler et al. 1989; Dunlap and Pawlik 1996).

Spatial patterns in the distribution of marine secondary metabolites over a range of scales also support the general hypothesis that these compounds serve as defenses against consumers. At the geographic scale, for example, there is much evidence that intensity of consumer activity generally increases toward the equator (Jeanne 1979; Bertness at al. 1981; Menge and Lubchenco 1981; Heck and Wilson 1987; Coley and Aide 1990), which should select for better prey defenses at low latitudes. The geographic distribution of morphological defenses in marine invertebrates strongly supports this hypothesis (Palmer 1979; Vermeij and Currey 1980; Bertness et al. 1981). Thus, it has generally been assumed that chemical defenses are also best elaborated and most important in tropical systems (Bakus and Green 1974; Levin and York 1978; Vermeij 1978; Fenical 1980; Gaines and Lubchenco 1982; Faulkner 1984; Hay and Fenical 1988; Coley and Aide 1990; Hay 1991a). Yet there are few critical tests of this assumption. Consistent with this hypothesis, Bolser and Hay (1996) found that tropical seaweeds from reefs in the Bahamas were, on average, about half as palatable to both temperate and tropical sea urchins as were related seaweeds from temperate reefs in North Carolina. Direct assays of chemical extracts from these seaweeds demonstrated that most of the difference was attributable to more deterrent chemical extracts from the tropical plants. Thus, seaweeds from tropical habitats with higher rates of herbivory were less palatable and better defended chemically than were similar seaweeds from temperate locations where herbivory rates are lower. Similarly, salt-marsh plants from southern marshes (Georgia) where herbivore diversity and abundance are greater, were less palatable to both southern and northern herbivores than were plants of the same species from northern (Rhode Island) marshes with lower herbivore diversity and abundance and presumably lower grazing intensity (Pennings et al., in press). Although these latitudinal patterns support the conventional wisdom, it should be emphasized that selection for defenses is imposed by consumers, not geography, as evidenced by the finding that Antarctic invertebrates are often chemically defended from local consumers (McClintock 1994). At smaller spatial scales, between-habitat differences in algal palatability reflect similar patterns of spatial variation in consumer activity (Hay 1984).

Once prey have become chemically defended from most larger consumers, they appear to become targets of evolutionary opportunity for smaller specialist consumers that selectively live on and consume chemically noxious prey (Hay 1992; Hay and Fenical 1996). By associating with or consuming these well-defended prey, the specialist consumers often escape or deter their own predators. For example, the Spanish dancer nudibranch, *Hexabranchus sanguineus*, feeds on sponges that contain oxazole macrolides that deter feeding by reef fishes (Pawlik 1993). The nudibranch slightly alters these compounds and concentrates them in its dorsal mantle and egg masses, where they serve as highly effective defenses against consumers. Small consumers can also lower their susceptibility to their own consumers through simple physical association with noxious prey—they need not sequester defensive metabolites. For example, the tube-building amphipod *Ampithoe longimana* consumes a wide variety of seaweeds, but in coastal North Carolina, it prefers to live on and feed from chemically defended brown algae in the genus *Dicytota* (Hay et al. 1987b; Duffy and Hay 1991b, 1994). The amphipod is relatively resistant to the alga's chemical defenses, while local fishes and sea urchins are strongly deterred (Cronin and Hay 1996a,b). Because local fishes feed on both undefended seaweeds and on amphipods, the amphipods are relatively safe from predation when on *Dicytota* (which the fishes rarely visit) but are much more susceptible when on an alga that is palatable to fishes. During seasons when fishes are feeding most actively, these *Dictyota*-tolerant amphipods increase in abundance, whereas co-occurring amphipod species that do not associate with *Dicytota* and that are not resistant to its chemical defenses are driven to local extinction (Duffy and Hay 1994). Other small herbivores similarly reduce predation by associating with chemically defended algae (Hay et al. 1989, 1990a,b). The role of predator avoidance in the evolution of such associations is especially compelling in associations where the smaller organism specializes on a defended host but does not feed from that host (Sotka et al. 1999; Stachowicz and Hay 1999).

Although chemical defenses against consumers have been studied most extensively in benthic systems, chemical defenses also occur in variety of planktonic organisms, including invertebrate meroplanktonic larvae (Lindquist et al. 1992; Lindquist and Hay 1996), invertebrate holoplankton (Shanks and Graham 1988; McClintock and Janssen 1990), and phytoplankton (Wolfe et al. 1997), suggesting that chemical defenses are pervasive components of marine systems.

CALCIFICATION AS A DETERRENT. Many seaweeds incorporate $CaCO_3$ into their tissues. This calcification could deter herbivores by making seaweeds harder and more difficult to bite or by diminishing their nutritional value due to the addition of indigestible structuring materials (Littler and Littler 1980;

Steneck 1983, 1986; Hay 1984; Duffy and Hay 1990; Targett and Targett 1990; Duffy and Paul 1992; Pennings and Paul 1992; Pitlik and Paul 1997). These suggestions are consistent with findings that $CaCO_3$-producing seaweeds are commonly low-preference foods for reef herbivores (Littler et al. 1983a,b; Hay 1984; Paul and Hay 1986; Steneck 1988). Although calcification undoubtedly prevents some herbivores from feeding on these harder seaweeds (Steneck and Watling 1982), many reef herbivores (e.g., parrotfishes, sea urchins) can easily bite into calcified seaweeds, and several recent investigations (Hay et al. 1994; Schupp and Paul 1994; Meyer and Paul 1995; Pennings et al. 1996) suggest that the $CaCO_3$ in seaweed thalli may actually serve as a chemical, as well as a structural, deterrent.

Pennings and Paul (1992) and Hay et al. (1994) added $CaCO_3$ to artificial foods so as to mimic the presence of $CaCO_3$ in the food without increasing food hardness. Assays with gastropods, fishes, sea urchins, and amphipods indicated that $CaCO_3$ could significantly affect the feeding of some herbivores, even when the $CaCO_3$ had no effect on the nutritional value or toughness of the food (Pennings and Paul 1992; Hay et al. 1994; Schupp and Paul 1994). The study by Schupp and Paul (1994) gave the clearest indication of what mechanisms might produce this effect. Adding $CaCO_3$ to foods significantly decreased the feeding rates of fishes with acid-mediated digestion, but stimulated, or did not affect, feeding by fishes with neutral or more basic guts (also see Hay et al. 1994; Meyer and Paul 1995; Pennings et al. 1996). This suggests that $CaCO_3$ may deter some species through the neutralizing effect that it has in a low-pH gut and possibly because of the large amount of CO_2 that would be released. Thus, $CaCO_3$ may deter some herbivores by increasing plant toughness (Pitlik and Paul 1997), but $CaCO_3$ can also deter consumers in other ways, possibly by functioning as a chemical defense. Schupp and Paul (1994) suggested using the term mineral defense to distinguish this chemical effect from that of $CaCO_3$ serving as a hardening agent or from the chemical effects of bioactive secondary metabolites.

Similar assumptions of defensive function have often been made for the mineral spicules common among sessile invertebrates such as sponges and corals. Experimental studies support this hypothesis for some soft corals and gorgonians (Harvell et al. 1988; Gerhart et al. 1988; Van Alstyne and Paul 1992; Van Alstyne et al. 1992, 1994), whereas predatory fishes are indifferent to sponge spicules when incorporated into realistic artificial foods (Chanas and Pawlik 1995, 1996), and spicules of a soft coral even stimulated feeding by a specialist predator (Wylie and Paul 1989).

THE INTEGRATION OF MULTIPLE DEFENSES. The effectiveness of many structural and chemical defenses is influenced by other prey traits or the environmental and recent historical context in which prey–consumer interactions occur (Duffy and Paul 1992; Cronin and Hay 1996b; Hay 1996). For example, estuarine crab zoeae bear spines that reduce their vulnerability to planktivorous fishes, but the crabs also time larval release and dispersal to minimize encounter with fishes (Morgan 1987, 1989, 1990). Such context-dependency of defenses is likely to be widespread and important but has received little attention.

Many marine prey produce multiple defenses, yet interactions among defensive traits have rarely been assessed. Chemical and mineral defenses (i.e., $CaCO_3$) commonly cooccur in marine algae, for example, and have been demonstrated to function either additively or synergistically to reduce susceptibility to consumers (Hay et al. 1994; Schupp and Paul 1994; Meyer and Paul 1995). As an example, the green alga *Halimeda goreauii* contains both an unusual secondary metabolite and a heavily calcified thallus. When sea urchins were offered a nutritionally valuable food containing the metabolite alone or $CaCO_3$ alone, neither trait had any deterrent effect; when these traits were combined, however, they interacted synergistically to suppress feeding strongly (Hay et al. 1994). This interaction changed when the experiment was repeated using a food of lower quality, indicating that food value, $CaCO_3$, and secondary metabolites interacted to affect sea urchin food choice. Chemical defenses of other reef seaweeds and sponges also can be more effective in foods of lower nutritional quality (Duffy and Paul 1992). Because benthic invertebrates such as sponges, gorgonians, and ascidians commonly produce both defensive secondary metabolites and siliceous or calcified spicules, such interactions could be common in invertebrates as well as seaweeds.

Moreover, the co-occurrence of multiple defenses often appears to be important in defending prey against the broad range of consumers that occur in marine systems. Working with seaweeds, Paul and coworkers have demonstrated numerous instances in which a combination of chemical and $CaCO_3$-based defenses provides protection against a broader range of herbivores than would either trait acting in isolation from the other. In general, feeding by parrotfishes was commonly deterred by chemical, but not $CaCO_3$, defenses, whereas feeding by surgeonfishes was commonly deterred by $CaCO_3$, but not by chemicals (Schupp and Paul 1994; Meyer and Paul 1995; Pennings et al. 1996; Paul 1997).

WHY ISN'T EVERYONE WELL DEFENDED?

Given the effectiveness of defenses such as those discussed above, why are defenses not universal among organisms? The most likely answer is that defenses are generally costly in terms of growth, reproduction, or competitive ability. This conclusion is supported on a broad scale by the generally positive spatial correlation between intensity of predation and frequency of defenses or of low susceptibility to consumers (Hay 1984, 1985, 1991a; Lewis 1986; Bolser and Hay 1996), suggesting that where predation intensity is low, less-defended forms have a competitive advantage over better-defended forms.

The most direct evidence that defenses are costly comes from organisms with phenotypically plastic defensive traits, in which fitness can be compared in better-defended and less-defended morphs of the same genotype, or within the same population. The evolutionary interplay between costs and benefits of defense is illustrated most clearly by inducible defenses, a form of phenotypic plasticity in which a given genotype produces defenses in response to specific cues from a consumer. Induced defenses should be favored when predation is partial, is a reliable predictor of further damage, and when there is sufficient time after an attack (or after detection of the predator) to mount an effective defense (Harvell 1990). Conversely, constitutive (permanent) defenses should be favored where the probability of attack is unpredictable in time and space but high on average, and the prey is unable to mount an effective defense after attack or detection. Since defenses and costs can be measured within individual genotypes in inducible taxa, they provide promising opportunities for examining the tradeoffs involved.

One of the most thoroughly documented marine example of induced defenses involves induction of defensive spines in the bryozoan *Membranipora membranacea* in response to the specialist nudibranch predator *Doridella steinbergae* (Harvell 1984). Focusing on the cues involved in spine induction and how these benefitted the bryozoan, Harvell (1986) found that curved spines were produced only in the presence of the specialist predator, and that spines could be induced by waterborne cues from the predator even without contact. Spines effectively reduced predation; nudibranchs were less than half as successful when spines were present. Lab experiments supported the hypothesis that spine induction entailed a cost: Spined colonies grew significantly less than unspined colonies. When similar assays of cost were conduced in the field, costs for spined colonies were small relative to those predicted from laboratory assays (Harvell 1992), suggesting that the occurrence or magnitude of costs may be context dependent. Other examples of induced defenses, discussed above, include several marine algae that show marked morphological plasticity in the face of consumer pressure, changing their growth form when subjected to grazing (Lubchenco and Cubit 1980; Lewis et al. 1987).

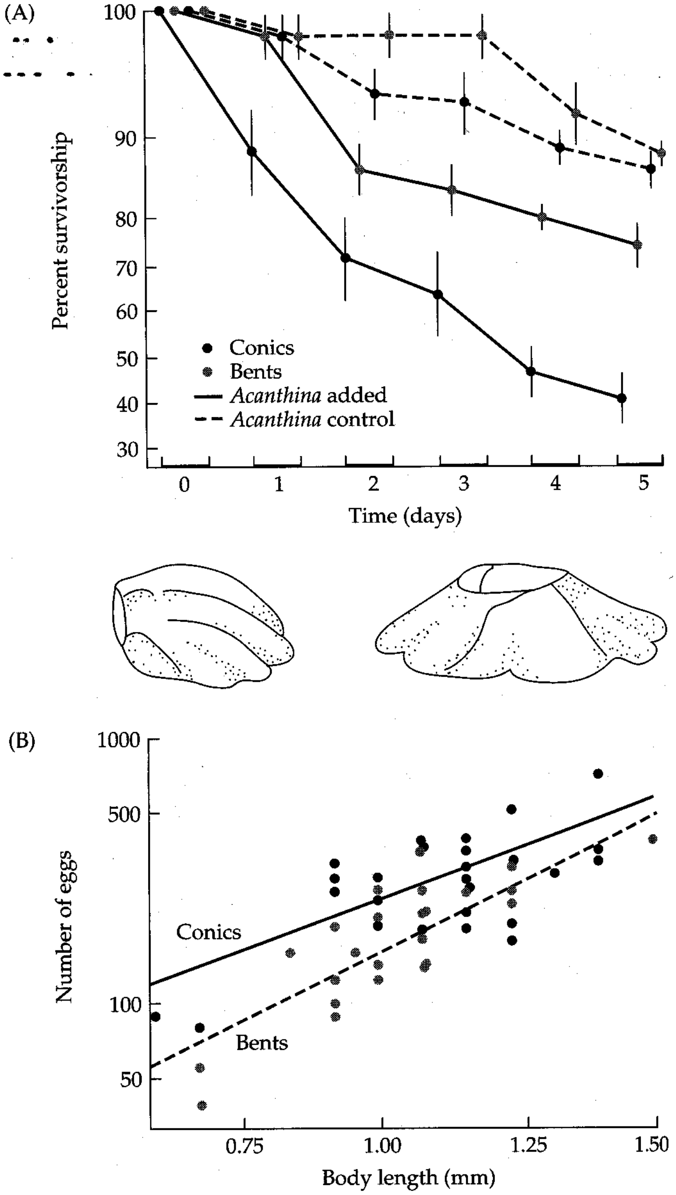

Figure 5.5 The fitness cost of defense in a polymorphic barnacle. (A) Field experiments showed that the bent morph (left) survived better than the conic morph (right) in the presence of the predatory gastropod *Acanthina*. (B) The bent morph, however, pays for this advantage in lower fecundity, and the conic morph predominates in the absence of predators. (After Lively 1986a,b.)

Predator-induced phenotypic plasticity has long been known in a variety of clonally propagating animals and plants. But it has also been demonstrated with increasing frequency in unitary animals. A good example comes from the intertidal acorn barnacle *Chthamalus anisopoma*, which exhibits two co-occurring morphs in the Gulf of California (Figure 5.5); the conic form typical of acorn barnacles and an asymmetric "bent" morph in which the aperture is perpendicular to the base (Lively 1986a,b). Lively's field experiments demonstrated clearly that the bent morph functioned as a defense against predatory gastropods. The bent form survived better than the conic form in the presence of a predatory snail, and field quadrats stocked with predatory snails recruited barnacle populations with substantial proportions of bents, whereas no bents developed in predator-free control quadrats. But the defense was costly; bents grew more slowly and averaged 27% lower fecundity than conics, apparently because the bent morphology constrains available brood volume. Thus bents should be outcompeted by conics in the absence of predation. Other examples of induced defenses in nonclonal organisms include bivalves (Reimer and Tedengren 1996; Leonard et al. 1999), gastropods (Appleton and Palmer 1988; Trussell 1998), and even fishes (Brönmark and Miner 1992). In all of these cases, the predator—or a chemical effluent thereof—induces a switch in the prey individual's developmental pathway, producing a stronger or better-defended adult.

There are also examples of induced chemical defenses in marine algae, but the costs associated with chemical induction are less clear than for those of morphological defenses. Van Alstyne (1988) demonstrated that *Fucus* plants attacked by gastropods increased their levels of phenolics and became less palatable. Similarly, amphipod grazing on the brown alga *Dicytota menstrualis* induced production of defensive diterpenes and reduced susceptibility to future attack (Cronin and Hay 1996b). For some seaweeds, the spatial variation in secondary metabolites among habitats experiencing different levels of herbivory is also suggestive of induction. For example, seaweeds from areas of coral reefs where herbivory is intense often produce more potent and higher concentrations of chemical defenses than plants of the same species from habitats where herbivory is less intense (Paul and Fenical 1986; Paul and Van Alstyne 1988). However, in the green seaweeds *Halimeda*, *Udotea*, and *Caulerpa* that show this pattern, clipping experiments failed to induce increased terpenoid chemical defenses (Paul and Van Alstyne 1992). Clipping or urchin grazing of temperate seaweeds also failed to induce higher levels of phlorotannins in the kelps *Ecklonia* and *Alaria* or in the rockweed *Sargassum* (Pfister 1992; Steinberg 1994, 1995). Thus, the higher levels of constitutive chemical defenses from sites with many herbivores may have been generated by preferential grazing that removed the more susceptible individuals, by local genetic adaptation to strong consumer pressure, or by among-habitat differences in other variables. The frequency of induced defenses in marine algae, and its implications for costs of defense, remain uncertain.

Although induced defenses have received considerable attention in terrestrial systems, their frequency, importance, and consequences are still debated (Baldwin 1990; Tallamy and Raupp 1991; Alder and Karban 1994; Karban and Baldwin 1997). Most terrestrial investigations of induction have focused on insect grazing, whereas most marine investigations have focused on larger herbivores such as fishes and urchins rather than on mesograzers, such as amphipods, that may be more ecologically similar to insects (Hay et al. 1987b). Mesograzers have been considered less important than larger herbivores because of the perception that they remove little seaweed biomass relative to the larger herbivores (see the debate among Bell 1991; Duffy and Hay 1991a; Brawley 1992). Grazing by mesograzers has been inadequately investigated, however, and there are convincing cases of mesograzers having large impacts on seaweed populations (Kangas et al. 1982; Haahtela 1984; Brawley 1992) or even on total community structure (Brawley and Adey 1981; Tegner and Dayton 1987; Duffy and Hay 2000) under certain circumstances, particularly when activity of their predators is low.

Several lines of evidence suggest that mesograzers are the grazers most likely to induce seaweed chemical defenses. First, these consumers feed over temporal and spatial scales that would allow induced responses to benefit the individual prey organism. Second, because mesograzers often are not deterred by constitutive levels of defenses, induction to higher levels may be needed to deter them. The two clear examples of induced chemical defenses in seaweeds (Van Alstyne 1988; Cronin and Hay 1996b) both involve mesograzers (a snail and an amphipod), each of which could graze for long periods on a plant without killing it and could thus be affected by a defense that took days, or weeks, to induce. The nudibranch predator that caused defensive spine induction in bryozoan prey (Harvell 1984, 1986) is also, in essence, a mesograzer. In contrast, fishes and urchins are generally large relative to their prey and are often capable of rapidly killing prey that they find palatable. Thus, to avoid being killed by these larger more mobile consumers, prey organisms may need to be constantly defended rather than inducing defenses following attack. For many chemically defended seaweeds and invertebrates, low concentrations of chemical defenses are generally effective deterrents against fishes and urchins, but are less effective or may even stimulate feeding by mesograzers (Hay et al. 1987b; Hay 1991b, 1992; Van Alstyne and Paul 1992; Pawlik 1993; Duffy and Hay 1994; Hay and Fenical 1996). Thus, constitutive levels of chemical defenses appear to be effective against the larger consumers. It is therefore possible that induction in seaweeds has appeared deceptively uncommon because it rarely occurs in response to clipping or grazing by larger herbivores, whereas it may occur more often in response to mesograzer feeding.

Mechanistic understanding is critical to evaluating induced (and other) defenses, as induction of chemical changes does not always translate to reduced palatability. For example, when the brown alga *Fucus vesiculosus* was grazed by amphipods, the alga's phenolic levels increased by a statistically significant 100% (M. Deal and M. Hay, pers. comm.); however, this had no effect on feeding by the amphipods and did not lead to amphipods choosing ungrazed over grazed plants. Increases of specific chemicals following grazing may occur to minimize microbial invasion of wounds, or for other reasons unrelated to the initial grazer. Some terrestrial studies show that microbes entering plants via insect bites have a much greater effect on chemical induction than does the direct damage done by the insect (Raffa and Smalley 1995); the above example of *Fucus* might involve a similar explanation. Because resistance to consumers can change for reasons other than secondary metabolites, and because concentrations of secondary metabolites can change in response to many factors other than herbivory, studies of induction should assess induction using consumer feeding (e.g., Renaud et al. 1990; Cetrulo and Hay 2000), rather than chemical analyses alone. If feeding is significantly affected, bioassay-guided investigations can then be conducted to determine directly the mechanisms altering resistance.

EVOLUTION OF PREY DEFENSES

The cases discussed above offer compelling evidence that particular phenotypic characters reduce the prey's vulnerability to predation and thus that those features currently serve a defensive function. In many cases it also seems likely that those features evolved for the purpose of reducing predation. The abundance of marine consumers (many of which have recently been depleted from natural systems;

Hughes 1994; Jackson 1997; Dayton et al. 1998) and their intense feeding rates in many ecosystems (e.g., see Figure 5.1) clearly suggest that consumers have exerted strong selection on prey populations and communities. But plausibility and apparent ecological "fit" are not proof that a given defensive trait arose by selection from consumers rather than through fortuitous preadaptation (see Steneck 1992 and Vermeij 1992 as examples). Questions about such historical processes are by their nature more difficult to answer confidently than questions about current ecological processes, and one must generally rely on indirect evidence. A growing body of data supports the conclusion that consumer pressure has commonly driven the evolution of a wide range of prey traits that allows escape, tolerance, or deterrence of consumers. Sources of evidence include direct experimental demonstration of prey evolution, historical or fossil evidence, and comparative data. Nevertheless, several well-known cases of apparent coevolution between marine consumers and prey appear on closer examination to be more complicated, and less convincing, than originally thought. Thus, reconstructing the evolutionary history of consumer–prey interactions must be approached rigorously.

Evolution of Escape Mechanisms

Many prey reduce predation through life history patterns that minimize overlap with predators in time and space, that is, by escaping predators. Life history patterns are molded by a plethora of selection pressures (Stearns 1992), and it is likely that many life history characters evolved in part as responses to selection pressures other than predation. Thus, prey that coexist with consumers may simply be those prey whose existing life histories allowed them to persist in the presence of active consumers. Nonetheless, there are convincing cases of consumers selecting for life history characters that allow prey escape. The strongest evidence for evolution of prey traits in response to predation comes from experimental demonstration that predators cause heritable changes in phenotype that reduce the prey's vulnerability to predation. We know of no marine examples, but such historical time series have been documented experimentally in a small number of other cases, notably the rapid (6–18 generations) adaptive changes in several life history characters of freshwater guppies after their transplantation from predator-rich streams to streams where predators are rare (Reznick et al. 1997). Transplanted guppies showed heritable increases in generation time and body size at maturity, and reduction in fecundity and allocation to reproduction, as predicted by life history theory (Stearns 1992). These changes parallel differences between populations occurring naturally in low- versus high-predation streams (Reznick et al. 1996; Reznick and Bryga 1996), and are expected to influence the prey's odds of escaping from larger generalist predators.

Comparative data suggest that the life histories and behaviors of many pelagic organisms are adapted to escape predation. In the upper oceans, for example, most zooplankton are very small and transparent, presumably as an adaptation to escape detection by visually hunting predators (Hobson and Chess 1976; Hamner 1995). The dispersal patterns of estuarine crab larvae also appear adapted to escape predators (Morgan 1989, 1990; Morgan and Christy 1997). A combination of experiments, field surveys, and comparative data show that interspecific variation in larval morphology (spination), pigmentation, body size, and behavior are all consistent with predation as an important selective pressure molding these phenotypic traits. Crab species whose larvae remain in predator-rich estuarine habitats during development tend to be larger, more heavily spined, and less pigmented than species whose larvae are exported to the coastal ocean. Species who release larvae during daytime also have less pigmented larvae than those with the typical patterns of nighttime release. Similarly, among sessile benthic invertebrates such as sponges, gorgonians, and ascidians, larvae that are chemically defended from fishes tend to be more brightly colored, to stay close above the reef where predators are common, and to be released during the day when they can use photic cues to help choose appropriate microsites for settlement (Lindquist and Hay 1996). In contrast, larvae without chemical defenses tend to be less visually obvious, released at night, and to stay in the plankton for long enough to disperse into offshore waters, rather than staying on consumer-rich reefs. Among coastal plankton, Hobson and Chess (1976) found that large and pigmented taxa entered the water column primarily at night when least visible to fish predators. Similarly, Hays et al. (1994) found that large and pigmented species of oceanic zooplankton showed more pronounced vertical migration than small, less pigmented species, as expected if these migrations function primarily to avoid predation. Thus, it appears that predation has been a primary selective force driving one of the most conspicuous biological processes in the world ocean.

Evolution of Grazing Tolerance: A Cautionary Tale

There are few rigorous data bearing on the evolution of grazing tolerance in marine organisms. One of the initially most convincing examples of apparent coevolution between marine consumers and prey involved such a case—the interaction between the encrusting coralline alga *Clathromorphum circumscriptum* and its relatively specialized limpet grazer *Tectura testudinalis* (previously *Acmaea testudinalis*). Initial studies found a number of apparently coevolved adaptations that were of mutual benefit to both organisms (Steneck 1982). Evidence of this coevolved relationship included: (a) positive correlation between abundances of the alga and limpet, (b) production of a unique protective covering of tissue over the alga's regions of active growth, (c) apparent adaptation of the limpet's radula to eat this thickened tissue in a way that minimally damages the host alga or its sunken reproductive structures, (d) prevention by limpet grazing of the algal host's being overgrown by potentially lethal epiphytic algae, (e) reduced susceptibility of the limpet to its predators when clamped down on the hard smooth surface of the alga (Steneck 1990), and (f) a balance, over a wide range of depths, between the rate of cell removal by limpets and algal production.

Fortunately, in addition to this very suggestive ecological information, Steneck (1992) was also able to evaluate the paleontological record involving coralline algae and herbivores. Because coralline algae are calcified, they have left an excellent fossil record that includes a history of their anatomical characteristics, which have been interpreted as evolutionary responses to herbivores, as well as grazing scars on their surfaces that can be identified as being produced by limpets, urchins, fishes, and so on (Steneck 1983, 1986). Thus, the fossil record for coralline algae and their associated herbivores is apparently the most complete record for any plant–herbivore association, either terrestrial or marine (Steneck 1992). This record shows that virtually all of the coralline's major morphological characteristics that had been interpreted as adaptations to herbivores were present at least 100 million years before the evolution of marine herbivores that could feed on corallines (Steneck 1992). Recent analysis of 12 specialist molluscs and their temperate seaweed hosts similarly suggests that these associations are more opportunistic than coevolved (Vermeij 1992). In 50% of the cases studied, Vermeij found that the associations were geologically recent (no earlier than the Pliocene) and resulted following invasion of the plant or the herbivore from geographical regions other than the one in which the association was forged. In contrast to the commonly held view that associations between specialized herbivores and host plants evolve by reciprocal adaptation over a long period of time, Vermeij's study suggests that many such relationships originate opportunistically and rapidly with little, if any, reciprocal evolution. Of course it is quite possible that, once the plant and grazer have come into contact, their physiology, behavior, and/or life history, which are not generally detectable in the fossil record, are molded by reciprocal adaptation. Nevertheless, these examples emphasize the difficulty of extrapolating evolutionary from ecological interactions.

Evolution of Consumer Deterrence

MORPHOLOGICAL DEFENSES. There is abundant evidence that consumer pressure selects for the evolution of deterrent traits in prey. The next best thing to an experimental demonstration of evolution would be convincing historical evidence of a change in phenotype coincident with increases in predation pressure. Several such cases have been described. Perhaps the best documented involves the rapid change in shell thickness and strength of the intertidal snail *Littorina obtusata* following introduction of the predatory European green crab (*Carcinus maenas*) into northern New England around 1900. This example is important both because of the fine time resolution of the process and as an additional cautionary tale for interpreting historical evidence. Seeley (1986) showed that shells collected from northern New England prior to 1900 were relatively thin and had high spires, whereas shells collected in the 1980s (and in 1915 at one site), after crabs were established in the region, were significantly thicker and lower-spired. Laboratory and field experiments confirmed that the thicker, lower-spired morphs were substantially less vulnerable to crab predation than thinner, high-spired morphs (Seeley 1986). Although these data strongly indicate that crab predation caused phenotypic change in the snail populations, it is less clear whether or how much of this change was genetically based, and thus whether natural selection or only phenotypic plasticity was involved. Trussell and Smith (2000) have shown experimentally that shell thickness and shape in *L. obtusata* are phenotypically plastic, with exposure to crabs inducing changes similar to those seen after the invasion of green crabs in the field (Seeley 1986; see also the section above on inducible defenses). Such experiments are of course not possible with fossils and suggest caution in interpretation of similar patterns in the fossil record, at least on relatively short time scales.

Large-scale trends in the fossil record provide numerous similar examples of the strengthening and diversification of morphological defenses and the adoption of cryptic and burrowing habits, coincident with evolution of increasingly effective consumers (Vermeij 1977, 1987). As one of several possible examples, Palmer (1982) described parallel trends in morphological evolution within several barnacle lineages coincident with radiation of muricacean gastropods, which appear to be the primary predators of barnacles in most temperate areas. Observations of predation on extant barnacles in the field and lab showed that drilling predation by gastropods (*Thais* spp.) is 2 to 3 times more successful at sutures between the barnacle's skeletal plates than is drilling through the plate. Remarkably, the fossil data indicate ~18 independent reductions in plate number (and thus number of sutures) during the evolution of balanomorph barnacles, and they indicate a major increase in proportion of genera with reduced plate number, during or shortly after the period when muricacean predators radiated. Interestingly, the exception to this trend also supports the rule: The barnacle genus *Chelonibia* lives on the carapace of sea turtles where it rarely if ever encounters drilling gastropods; consistent with the predation hypothesis, this barnacle retains evidence of the ancestral condition of eight parietal plates. Similar trends toward stronger, more heavily sculptured exoskeletons occurred in many benthic invertebrate taxa during the late Mesozoic, coincident with the radiation of more powerful predators (the "Mesozoic marine revolution"; Vermeij 1977), and in benthic algae and their grazers during the same period (Steneck 1983). These trends suggest that consumers have had a profound and pervasive influence both on evolution of organismal phenotypes and on the organization of communities (Vermeij 1987; Vermeij, this volume).

In the absence of historical data, evidence for the evolution of defenses against consumers comes from arguments from design and from comparative data. In the first category, Morgan (1989) conducted critical tests of alternative hypotheses for the adaptive significance of the long spines common in zoea larvae of crabs. Experiments with larvae of the mud crab *Rhithropanopeus harrisii* rejected the hypothesis that spines functioned to retard sinking; settling velocity, swimming and sinking behavior of spined and unspined larvae were similar. Nor did spines deter invertebrate predators: only one of ten invertebrate predators ate more unspined than spined larvae. Instead, the primary function of spines appears to be reduction of predation by planktivorous fishes, whose feeding was deterred by spines. Moreover, spines enhanced survival of attacked larvae, regenerated quickly, and were effective when partially regenerated. Individual fish quickly learned to avoid spined prey. These results suggest that individual-level natural selection could have favored the evolution of spines, as has also been argued for the evolution of chemical defense in larvae (Lindquist and Hay 1996). Finally, comparative experiments with larvae of six decapod species (Morgan 1987) showed that small planktivorous fish preferred the two zoea species that are exported from the estuary over four species that are retained in the estuary. The exported species are smaller and have shorter spines than retained species. Two of the retained species combined morphological defenses (spines) with postcontact evasive and escape behavior that helped them escape predation. Taken together, the various lines of evidence are most consistently explained as reflecting adaptation to minimize predation by fishes.

CHEMICAL DEFENSES. Comparative approaches have been applied to explore the evolution of chemical defenses. For example, Estes and Steinberg (1988) noted that rocky shores in temperate Australasia support broadly similar communities as those of the northeast Pacific, dominated by large brown seaweeds and grazing gastropods and sea urchins. Australasian shores, however, have apparently never supported top predators ecologically equivalent to the sea otter that occupies a keystone predator role in the northeast Pacific (see above). These authors (see also Steinberg et al. 1995) reasoned that the historical absence of such top predators in Australasia (probably since at least the late Tertiary) should have resulted in higher densities and feeding intensity of grazers, and consequently in stronger selection pressure for defenses in seaweeds in that region compared with the northeast Pacific. These predictions were consistent with results of experiments (Steinberg et al. 1995); rates of algal tissue loss to herbivory were significantly greater in Australasia than in otter-dominated locations in the northeast Pacific, and concentrations of hypothesized chemical defenses (phlorotannins) in Australasian brown seaweeds were five to six times greater than in related algae from the northeast Pacific. Moreover, there is also evidence of escalation (sensu Vermeij 1987) between Australasian seaweeds and grazers; grazers in this region were generally tolerant of seaweed phlorotannins, whether derived from co-occurring seaweeds or from northeast Pacific algae. In contrast, grazers from the northeast Pacific were consistently deterred from feeding by phlorotannins from either region. It is unsettling, however, that the high levels of phenolics in Australasian algae are not deterrent to local herbivores (Steinberg and Van Altena 1992). It is thus unclear why these seaweeds would continue to allocate high levels of resources to the production of these compounds when they appear to have no current function against local consumers.

We discussed above the evidence that selection for prey defenses is strongest at low latitudes. If tropical seaweeds more commonly produce chemical defenses, then tropical herbivores should also be under greater selection than temperate herbivores to tolerate or circumvent these defenses. This notion has rarely been tested, but the one such study we know of does support the hypothesis that tropical herbivores are more tolerant of chemical defenses than are temperate herbivores. Cronin et al. (1997) tested a series of secondary metabolites from the brown alga *Dictyota acutiloba* against both temperate and tropical fishes and sea urchins. In general, feeding by the temperate herbivores was suppressed by lower concentrations of metabolites than were necessary to suppress feeding by the tropical herbivores. Although many more such studies are needed before one could confidently draw rigorous conclusions, the available data suggest that herbivore activity in the tropics has selected for greater levels of chemical defenses in seaweeds and that tropical herbivores have, in turn, been under greater selection to tolerate or circumvent these defenses.

Evolution of Associational Defenses

In the absence of historical data, perhaps the most compelling evidence for antipredator adaptation comes from demonstration that intraspecific variation in defensive traits is correlated with consumer pressure. Stachowicz and Hay (1999, 2000) used such a comparative approach to explore variance in camouflaging behavior of the decorator crab *Libinia dubia* along the Gulf and East Coasts of the United States. Juvenile *L. dubia* camouflage themselves from predators by attaching bits of algae and sessile invertebrates to their carapace. In North Carolina, the crabs decorate almost exclusively with the brown macroalga *Dictyota menstrualis*, despite its low relative abundance in the habitat. This alga is chemically defended from the omnivorous fishes that are the dominant predators of decorator crabs in this area, and field experiments showed that crabs decorated with *D. menstrualis* were only ~20% as likely to be consumed by fishes as crabs decorated with an alga palatable to the fishes. That the specialized decorating behavior is an evolved response to predation pressure is supported by geographic variation in the crab's decorating preferences (Figure 5.6). Whereas *D. menstrualis* extends northward only as far as southern Virginia, the crab ranges into New England. Field surveys showed that crabs in the northern range decorated with a variety of algae and sessile invertebrates in approximate proportion to their availability, whereas crabs from North Carolina specialized on *D. menstrualis*. Lab assays corroborated these patterns, showing that northern crabs decorated with a variety of algae and did not specialize on *Dictyota*, even when it was made available to them, whereas southern crabs from North Carolina and Alabama used *D. menstrualis* almost exclusively. These patterns are consistent with the hypothesis that southern crabs

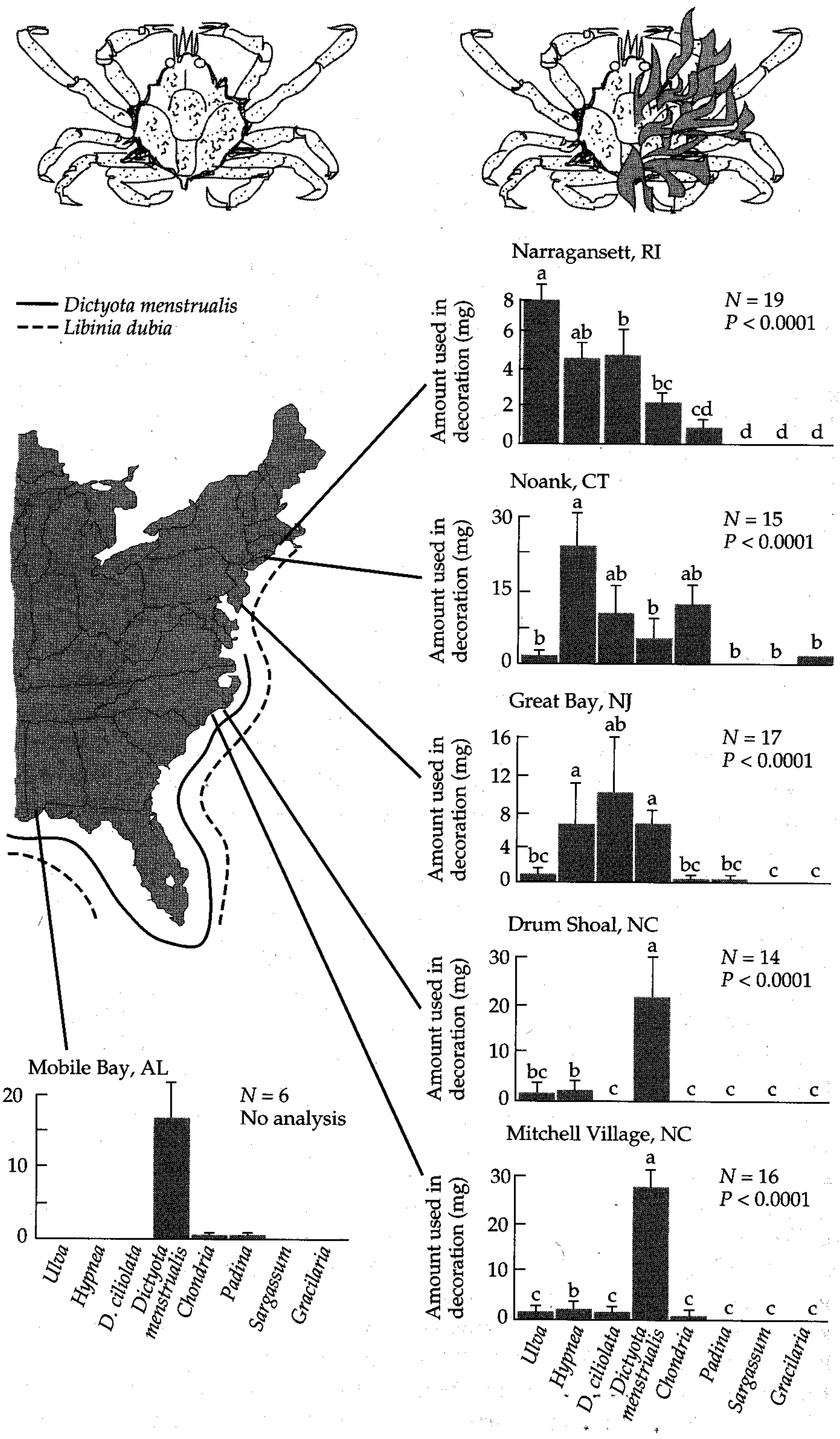

Figure 5.6 Apparently adaptive geographic variation in use of the chemically noxious seaweed *Dictyota menstrualis* by the decorator crab *Libinia dubia*. In laboratory choice assays, crabs collected within the range of this alga select it almost exclusively for decoration, thereby protecting themselves from omnivorous fish predators (Stachowicz and Hay 1999), whereas crabs collected from northern areas rely on camouflage, decorating themselves with various algae in proportion to their abundance in the environment. (From Stachowicz and Hay 2000.)

have been selected to recognize and preferentially decorate with a chemically defended seaweed that provides especially effective protection from omnivorous fish predators. Interestingly, although this alga produces multiple diterpene metabolites, the single compound that the crabs use as a cue for decorating is the compound that most strongly deters fish feeding. Northern crabs that do not normally have access to *Dictyota* decorate nonselectively and simply match their background. Given that these crabs will most commonly be attacked by carnivorous rather than omnivorous fishes, this behavior may be sufficient to avoid predation. Thus, *L. dubia* appears to have adapted to geographic variance in the protective value of potential algal associates as well as to varying consumer pressure.

Who Selects for Prey Defenses?

There are numerous patterns in prey defensive traits, suggesting that large mobile generalists like fishes and sea urchins have been the major consumers selecting for defense and that smaller mesograzers such as amphipods and polychaetes have played a secondary, but maybe not insignificant, role. A few examples that illustrate this include: (1) seaweeds on tropical reefs have more potent chemical defenses than seaweeds from temperate reefs. This increase in defense correlates with increased herbivory by fishes and urchins on tropical reefs, not with greater herbivory by mesograzers (Carpenter 1986; Hay 1991a); (2) in both the Caribbean and Pacific, seaweeds in the genus *Halimeda* produce their new and potentially more vulnerable growth at night during a short window of time when herbivorous fishes are inactive (Hay et al. 1988; Paul and Van Alstyne 1988); mesograzers are generally more, rather than less, active at night (Brawley 1992); and (3) experimental field studies have demonstrated that seaweeds that undergo large shifts in morphology in response to grazing pressure, generally do this in response to grazing by fishes and/or urchins rather than as a function of mesograzer densities (Steneck and Adey 1976; Hay 1981b; Lewis et al. 1987), although morphological responses of algae to mesograzers have not been explicitly tested. Finally, human harvesting has greatly reduced abundances of large marine consumers throughout the world, such that our perceptions of "pristine" environments probably greatly underestimate the former abundance of large animals (Safina 1995; Jackson 1997; Dayton et al. 1998), which must have had strong selective impacts on prey organisms.

General patterns in the effectiveness of prey chemical defenses also support the greater importance of larger generalist consumers in selecting for prey defenses. In both seaweeds and benthic invertebrates, many secondary metabolites strongly deter feeding by fishes and urchins, but often are relatively ineffective against a variety of mesograzers such as amphipods, small crabs, polychaetes, ascoglossan gastropods, nudibranchs, and flatworms (Hay and Fenical 1988, 1996; Hay 1991b, 1996; Paul 1992; Pawlik 1993). In many instances, the mesograzers are, in fact, stimulated to feed or choose hosts by the metabolites that most strongly deter the larger consumers. As discussed above, it appears that prey evolved defenses against the larger, generalist consumers, that these chemically defended prey then become microhabitats where small mesograzers can predictably escape their predators, and that the mesograzers then evolve a tolerance for these chemical defenses as a means of acquiring a safe microhabitat for both living and feeding (see reviews in Hay and Fenical 1988, 1996; Hay 1992, 1996).

PREY EFFECTS ON PREDATORS

A central point in understanding the evolutionary interaction between consumer and prey is that it is inherently asymmetrical. Whether or not a consumer is successful in a particular encounter with the victim is potentially a matter of life and death for the victim, but only one in a lifetime of meals for the consumer (the "life-dinner principle"; Dawkins and Krebs 1979). That is, a successful predator immediately reduces the prey's future fitness to zero, so we expect selection to be stronger for prey defenses than for consumer adaptations to catching particular prey, and we might guess that in an "arms race" between them, the prey will generally stay slightly ahead of the consumer (or it will go extinct). Nevertheless, prey defenses can have significant effects on consumer fitness and in some cases can select for evolutionary change in the consumer as well.

In marine systems, we know too little about the effects that prey defenses have on consumer fitness. That is, why do consumers evolve the ability to detect and avoid prey with certain traits? For morphological defenses, such as those common in shelled gastropods, the costs to a consumer of dealing with defended prey are often relatively straightforward to estimate in terms of increased handling time per unit food consumed (Palmer 1979; Bertness 1981) and potentially increased exposure of the consumer to its own predators. For example, Palmer (1979) showed experimentally that filing off the stout spines from the shells of tropical muricid gastropods decreased their effective diameter by 10–20%, rendering previously invulnerable shells crushable by pufferfish.

For chemical defenses, in contrast, there are many documented cases of prey defenses changing consumer feeding behavior, but very few where we can say what effect the avoided metabolite would have on the consumer if it ingested the compound. Such direct tests of the effects of defensive metabolites on consumer physiology or fitness are rare, in part because it is very difficult to get consumers to eat defended prey so that the effects of the compounds can be assessed. Hay et al. (1987b) demonstrated that a diterpene alcohol that deters fish from consuming the brown alga *Dictyota menstrualis* significantly slowed growth of the fish when the compound was consumed as 1% of the diet for a period of several days. Although this concentration can occur in some tropical species of the Dictyotales, the ecological relevance of this assay can be questioned because it is extremely unlikely that any fish would consume only this one genus of seaweed for an extended period. A different approach was taken by Targett and Targett (1990), who assayed the effect of crude extracts from a chemically deterrent green seaweed by coating this on a palatable seagrass and evaluating its effects on parrotfish assimilation efficiency. Although the extract had no effect on assimilation efficiency, this does not exclude the possibility of negative effects on growth, development, or fecundity. Irelan and Horn (1991) tested the physiological effects of *Fucus* extract (which the fish would not eat) by anesthetizing fish and force feeding them control diets versus diets treated with the *Fucus* extracts and then determining their digestive efficiency over the next several days. These treatments did not affect digestion of carbon, but *Fucus* polar extract did lower assimilation efficiency of nitrogen (often a limiting resource for herbivores) relative to the control. Boettcher and Targett (1993) used a similar approach to test the effects of different-sized algal phlorotannins on fish digestive efficiency and found that larger phlorotannins commonly suppressed digestive efficiency, whereas smaller ones did not. Such interference with consumer nutrition could translate to reduced fitness, a necessary requisite for natural selection to mold consumer-feeding biology.

If a newly arisen defensive trait is to increase to fixation in a prey population, it must confer a selective advantage when rare, as it will necessarily be immediately after its origin. Some experimental evidence points to significant negative consequences for the consumer's fitness because of limited feeding on chemically defended prey, such as might occur when a generalist consumer samples rare, defended prey in a diverse natural community (Figure 5.7). Lindquist and Hay (1995) fed anemones large meals of nutritious food followed several hours later by small meals of larval mimics containing either defensive compounds (treatment) or no defensive compounds (controls). This was meant to mimic anemones getting the majority of their food from appropriate sources but feeding at low levels (1.8% of the total daily diet) on defended foods (e.g., consuming a few chemically rich invertebrate larvae). Even this low-level consumption of defended prey strongly suppressed both growth and vegetative reproduction of treatment anemones. This demonstrates that, even at low frequency, chemical defenses can have negative effects on consumer fitness and thus select for recognition and avoidance of foods containing these compounds.

On a grander time scale, the number of families of marine animals specialized for shell-breaking predation increased dramatically in the late Cretaceous through early Tertiary, as did the frequency of fossils with drilling damage (Vermeij 1987) and the depth of penetration into the substratum of excavating herbivores (Steneck 1983). The timing and magnitude of these trends relative to the evolution of prey defenses argue that increasing effectiveness of consumers evolved at least partially in response to the increasing difficulty of obtaining their quarry (Vermeij 1987).

INDIRECT IMPACTS OF CONSUMERS ON COMMUNITIES AND ECOSYSTEMS

Trophic Cascades

In addition to their strong direct effects on prey documented above, consumers can have pervasive indirect impacts on community organization when the prey are themselves strong interactors with other species in the community. These indirect effects can extend well beyond the particular prey taxa consumed. The classic demonstration of this phenomenon was the fundamental change in community structure following removal of the predatory seastar *Pisaster ochraceous* from a northeast Pacific rocky intertidal habitat (Paine 1966, 1974). Despite its relatively low abundance at Paine's study site, removal of *Pisaster* resulted in a dramatic reduction in species diversity of primary space occupiers because its principal prey, the mussel *Mytilus edulis*, was competitively dominant and excluded other species when released from predation. Paine (1969) coined the term keystone for species that have strong community impacts that are dispoportionate to their abundance.

Such indirect interaction chains reach their most extreme development in "trophic cascades" (Carpenter et al. 1985), in which an apex predator's impact penetrates through the intervening trophic levels to influence plant abundance. A few experimental studies have shown that predation by marine birds and fish can cascade down to influence the standing stock and species composition of benthic algae (Wootton 1995; Duffy and Hay 2000). The most spectacular example of such far-reaching impacts is the case of the sea otter in the northeast Pacific (see Figure 5.3). Sea otters are voracious predators on herbivorous sea urchins and molluscs. Comparisons among islands with and without sea otter populations suggested that otter feeding drastically reduces herbivore abundance and grazing pressure on seaweeds to depths of tens of meters and that this grazing in turn releases the giant kelp *Macrocystis* and other seaweeds from grazer control (Estes and Palmisano 1974; Estes and Duggins 1995). Islands

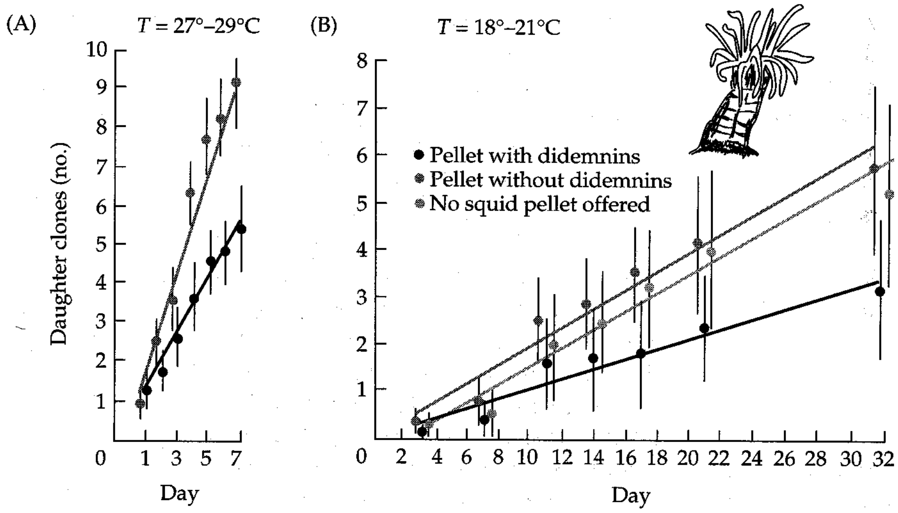

Figure 5.7 Consumption of even small quantities of chemically defended prey can significantly reduce predator fitness. In this case, food pellets laced with noxious compounds (didemnins) from the sea squirt *Trididemnum solidum* made up <2% of the daily food ration of the anemone *Aiptasia pallida*, yet the compounds reduced the rate of asexual reproduction (production of daughter clones) by ~40% relative to that of anemones fed with the same quantity of didemnin-free pellets. Such effectiveness enhances the probability that an initially rare defense mutation would confer sufficient advantage to spread through the population. (After Lindquist and Hay 1995.)

with otters thus have lush kelp forests, whereas islands without otters support mainly "urchin barrens," areas dominated by crustose coralline algae and sea urchins, but nearly devoid of fleshy algae. Since kelps dominate their physical and biological environment, their removal by grazers in otter-free areas has pervasive consequences not only for the benthos, but also for fishes and nearshore terrestrial wildlife that depend on the structure and production of kelp beds (Estes and Palmisano 1974; Duggins et al. 1989). Recently, Estes et al. (1998) demonstrated that the strong consumer–prey interactions driving this trophic cascade extend through four trophic levels: A sudden increase in killer whale predation on otters was correlated with dramatic decreases in otter densities, increases in urchin biomass and grazing intensity, and a drastic reduction in kelp abundance. This type of shifting trophic cascade may have been going on for thousands of years, with human hunters in the role played by killer whales in the above study. Analyses of Indian middens suggests that nearshore marine communities in Alaska shifted between urchin barrens and kelp communities as otters were overharvested by humans and then allowed to recover (Simenstad et al. 1978). Indeed, humans as apex predators increasingly provide the most dramatic and alarming examples of trophic cascades (Steneck 1998).

In the pelagic zone, there are several suggestive cases of trophic cascades, most involving zooplanktivorous ctenophores or medusae as top predators (Verity and Smetacek 1996). Among the more compelling cases is that involving the estuarine ctenophore *Mnemiopsis leidyi* in New England (Deason and Smayda 1982). Like many gelatinous zooplankters, this ctenophore periodically blooms to high densities and feeds heavily on crustacean zooplankton, most of which are herbivorous. A 6-year time series of plankton dynamics in Narragansett Bay revealed that the summer pulse in ctenophore abundance coincided with a rapid decline in zooplankton biomass and a concomitant phytoplankton bloom in four of the six years. When abundances of the ctenophore and the dominant phytoplankter (the diatom *Skeletonema costatum*) were integrated over the summer season for each year, there was a strong positive correlation across years between the predator and the phytoplankter ($r^2 = 0.77$). Anecdotal observations suggested that this trophic cascade could extend through a fourth level as well: In 1974 a large population of the predatory ctenophore *Beröe ovata* rapidly reduced *M. leidyi* populations. This was followed by a sharp increase in zooplankton and a crash of the diatom bloom (Deason and Smayda 1982).

Whereas the ctenophore example comes from a restricted estuary, recent data suggest that anthropogenic perturbations of upper trophic levels can cascade down to affect phytoplankton dynamics even in the open ocean. Shiomoto et al. (1997) presented time-series measurements of surface phytoplankton and zooplankton abundance in the subarctic Pacific from 1985 to 1994, along with abundance of juvenile pink salmon, which feed on zooplankton. Between 1990 and 1994, surface chlorophyll and salmon abundance alternated synchronously between high values in odd years and low values in even years, whereas zooplankton biomass was exactly opposite in phase, low in odd and high in even years. As temperature and nutrients (nitrate plus nitrite) were roughly constant throughout the time series, the variation in phytoplankton biomass is unlikely to be explained by bottom-up forcing. The most likely explanation for this curious interannual pattern involves the influence of hatchery-stocked salmon released in the northwestern United States. The importance of top-down control in these patterns is also supported by the finding that carnivorous zooplankton cycled with the same pattern as total zooplankton, suggesting that all zooplankton were similarly controlled by a higher trophic level (salmon). These examples support a growing recognition of the importance of top-down control of food-web structure in pelagic systems (Verity and Smetacek 1996).

Such examples of strong interactions cascading through the food web are spectacular, but how common are they? Micheli (1999) addressed this question for marine pelagic ecosystems by conducting a meta-analysis of published studies, including both mesocosm experiments and time series of trophic-level covariance in unmanipulated systems (Figure 5.8). The results suggest that trophic cascades are uncommon in marine pelagic ecosystems. In enclosed pelagic mesocosms, experimental additions of zooplanktivorous fishes or invertebrates consistently depressed zooplankton abundance, but their effects cascaded down to enhance phytoplankton abundance only in nitrogen (N)-enriched (eutrophic) conditions. Conversely, experimental enrichment with nitrogen (a limiting resource for plant production in many shallow marine systems) consistently increased phytoplankton abundance but had no significant effect on zooplankton abundance. Thus, bottom-up processes also do not penetrate far through the food chain. The latter result was corroborated by time-series analysis of unmanipulated pelagic ecosystems—estimates of nitrogen availability and plant production were consistently correlated with phytoplankton abundance but not with abundances at higher trophic levels (Figure 5.8). Micheli's (1999) meta-analysis of the results from marine pelagic systems differs from a similar meta-analysis of experiments in fresh water, which showed that cascading effects of predators are common therein (Brett and Goldman 1996). More such experimental tests of the influence of abiotic forcing and food-web structure (including diversity) on interaction strength will be necessary before we can make informed predictions about how global environmental perturbations will change ecosystems.

Patterns in Interaction Strengths within Communities

Examples of trophic cascades illustrate that individual consumers can have strong and far-reaching impacts throughout an entire ecosystem. In the few cases where interaction strength has been estimated for a large number of species in a benthic food web, it has generally been found that most interactions are weak, having negligible impacts on populations of the participants, whereas a few have strong impacts on other taxa (Paine 1992; Raffaelli and Hall 1995; Wootton

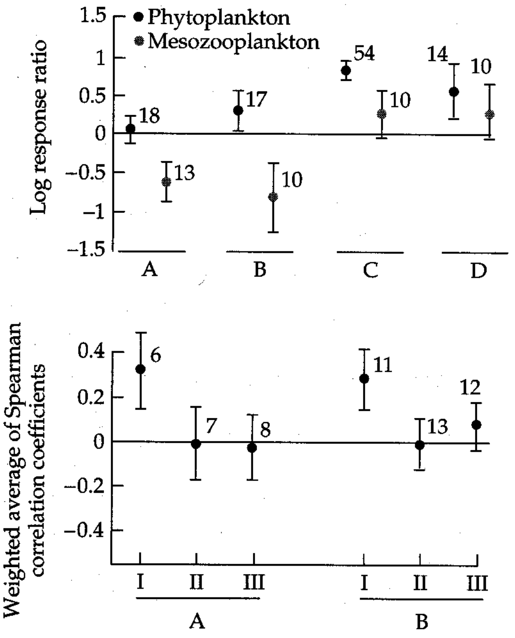

Figure 5.8 Trophic cascades are uncommon in marine pelagic ecosystems. Top: Log response (treatment biomass/control biomass) to addition of zooplanktivores (A and B) or inorganic nitrogen (C and D) in pelagic mesocosm experiments. In (A) both zooplanktivore and control treatments were conducted with unenriched water, whereas in (B) both treatments received nitrogen (N) enrichment. In (C) both unenriched (treatment) and N-enriched (control) treatments contained only phytoplankton and zooplankton, whereas in (D) both treatments also contained zooplanktivores. Plotted are the means + 95% CI from a meta-analysis (number of studies is shown above each mean). Note that zooplanktivore addition consistently depresses zooplankton biomass (A and B) but cascades down to increase phytoplankton only under N-enriched conditions (B). N addition consistently enhances phytoplankton, but not zooplankton, biomass 8, and D. Bottom: Correlations of winter nitrogen availability (left) and mean annual primary productivity (right) with biomass of (i) phytoplankton, (ii) mesozooplankton, and (iii) zooplanktivorous fishes in time series of unmanipulated pelagic systems. Consistent with the mesocosm results, N correlates only with phytoplankton and not with biomass of higher trophic levels. (After Micheli 1999.)

1997; Duffy and Hay 2000; Figure 5.9). Several plankton biologists also have recently emphasized that unique characteristics of particular species often have an overriding influence on energy and material fluxes in pelagic ecosystems; these investigators have called for a new focus on the biology of individual species in pelagic ecology (Lehman 1988, 1991; Banse 1994; Verity and Smetacek 1996). Thus, the degree of skew in interaction strengths within a community is of central importance to understanding the regulation of community structure and how structure will respond to perturbation.

Can we generalize about what characteristics of organism and environment result in keystone status, that is, which have disproportionately strong interaction strength? And how frequent is strong skew in interaction strength? Strong (1992) suggested that control by a few strong interactors, such as seen in the celebrated trophic cascades, is most likely in low-diversity systems where there is little functional re-

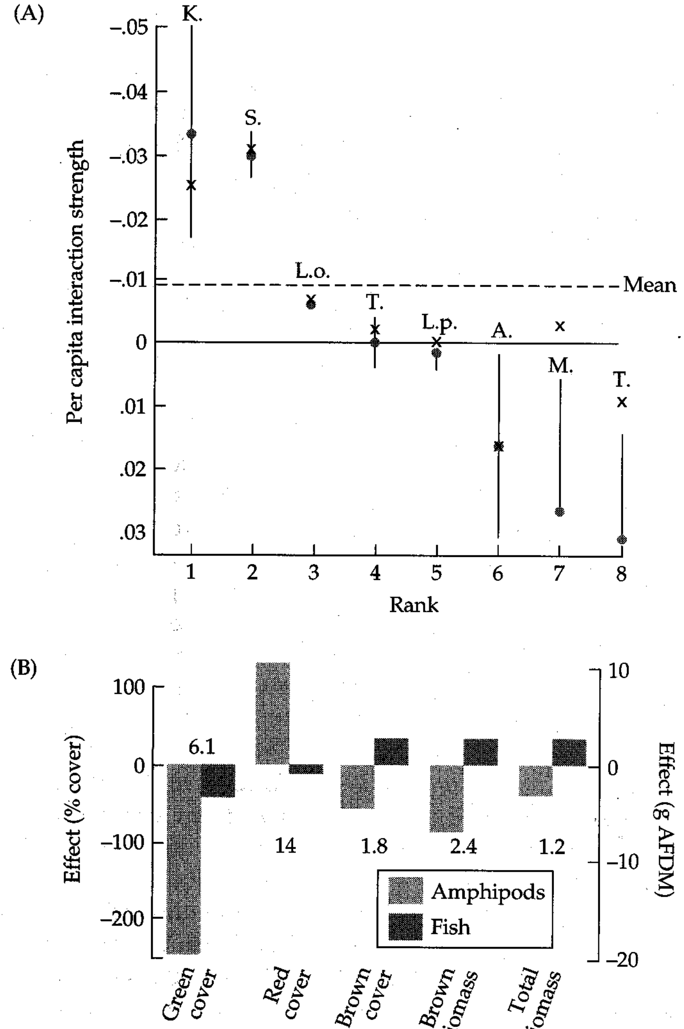

Figure 5.9 Two examples of variation in interaction strength among co-occurring consumers. (A) Variation in per capita interaction strength (impact on brown algae, the dominant space-occupiers in this system) among eight common invertebrate herbivores in a rocky intertidal community of Washington State. Per capita interaction strength = $(E - C)/Cd$, where E and C are brown algal sporeling densities in the herbivore removal and control treatments, respectively, and d is the number of individual herbivores in the C treatment. The chiton *Katharina tunicata* (K.) and the sea urchin *Strongylocentrotus purpuratus* (S.) strongly influence brown algal abundance, whereas effects of the other six species (all gastropods) are negligible. (After Paine 1992.) (B) Relative interaction strengths of omnivorous fish (*Diplodus holbrooki*) and herbivorous amphipods (mostly *Ampithoe longimana*) on major taxa of benthic space-occupiers, expressed per unit of herbivore biomass. Numbers show the ratio of amphipod to fish impacts for each algal taxon. Per-biomass impacts of the inconspicuous amphipods are up to an order of magnitude greater than those of the fish. AFDM = ash-free dry mass. (After Duffy and Hay 2000.)

dundancy among species and one or a few species dominate processes within each level. In more diverse systems, strong consumer impacts on one species are likely to be compensated by increased abundance in another species such that, for instance, aggregate biomass of that trophic level is little affected by the consumer. A key issue in evaluating this suggestion is the degree of functional redundancy among co-occurring species. Ecologists often have tended to approach functional diversity by lumping species with similar morphology and biology into guilds or functional groups (Littler and Littler 1980; Steneck and Watling 1982; Peters 1991) and such grouping has proven useful in many cases (e.g., Steneck and Dethier 1994). Yet even superficially similar consumer taxa can have substantially different impacts on community structure and function (Paine 1992; Wootton 1997; Duffy et al. 2001). For example, experimental comparisons of three similar-sized species of small crustacean grazers in an eelgrass bed showed that both grazer secondary production and per capita impacts on algal biomass varied by an order of magnitude among species and that their impacts on eelgrass differed in sign as well as magnitude (Duffy et al. 2001). Thus, effective generalization about how diversity and functional redundancy affect ecosystem structure and function will require more systematic empirical studies of how individual species traits translate to functional processes (see Lawton 1994).

Some Methodological Issues

Ecological research is necessarily constrained in spatial and temporal scale by a variety of social, economic, and other human factors. It is a well-known cliche, for example, that the duration of the average ecological study conforms closely to the duration of a dissertation project or funding cycle. What are we missing as a result?

The heightened awareness among both ecologists and the public of the importance of biodiversity has done little to change the fact that most ecologists focus on very small subsets of the communities they study. Kareiva (1994) observed that over 60% of the papers published in *Ecology* from 1981 to 1990 dealt with at most two species, and he emphasized the irony in our habit of using special jargon ("higher-order interactions," "indirect effects," and so on) to describe processes within more complete systems. This situation is worrisome: "[It is] clear that higher-order interactions and interaction modifications should be widespread in communities; but their presence is not what is at issue . . . . The question is whether a neglect of these higher-order effects causes us to get substantially wrong answers." In an exhaustive review of experimental studies in rocky intertidal habitats, Menge (1995) concluded that ~40% of the changes in community structure resulting from manipulation were indirect effects, and that each species was involved in more strong interactions and more indirect interactions as food-web diversity increased. The celebrated examples of trophic cascades, such as the sea otter–grazer–kelp interaction discussed above, surely have received widespread attention in part because they conform to simple, straightforward models of how we expect the world to function (e.g., Hairston et al. 1960). But the very fact that each new example of a trophic cascade generates attention suggests that such simple interaction chains are the exception in nature. Even these relatively simple examples illustrate dramatically a phenomenon with sobering implications for both basic and applied ecology, namely that perturbing an ecosystem may produce strong and unexpected effects on organisms that do not interact directly with the perturbed species. The apparent shift in feeding behavior of killer whales, and its pervasive consequences for coastal ecosystems in the northeast Pacific (see Figure 5.3), likely resulted from changes in abundance of the pinnipeds that formerly comprised the primary prey of killer whales; these changes in turn are probably related to human fishing pressure (Estes et al. 1998). Fishing pressure on top predators also appears to explain major shifts in marine community composition in several other putative cases of marine trophic cascades (Steneck 1998). And the changes in the north Pacific pelagic food web appear related to human stocking of predatory fish (Shiomoto et al. 1997). We need to know more about how such interactions ripple out across ecosystems if ecology is to be an effective tool for confronting environmental problems.

A related issue involves the extent to which we can extrapolate usually short-term manipulative experiments to longer-term field consequences. Most ecological manipulations are relatively short-term "press" experiments, adding or removing a component of the community and following the consequences. Such studies have shown repeatedly that consumers have major impacts on community composition, biomass, and so forth, in a variety of habitats and systems. Commonly, these results are extrapolated, usually implicitly, to conclusions about the likely states of the community in the presence and absence of the consumer. Leibold et al. (1997) noted that results of such manipulations are often at odds with correlational studies of unmanipulated ecosystems. They emphasized the potentially confounding, and underappreciated, role in such scenarios of species turnover—the change in prey-species composition that frequently accompanies large changes in consumer pressure in open systems over extended time periods. Changes in species composition—as from undefended to strongly defended prey in the presence of heavy consumer pressure—can largely compensate for the strong impacts of predators on, for example, prey trophic-level biomass, seen in short-term press experiments. Strong (1992) developed a similar argument to explain the relative rarity of well-defined trophic cascades in food webs with high species diversity. Understanding the role of species turnover will be important to predicting how open ecosystems will respond to accelerating global change.

ABIOTIC FORCING OF COMMUNITY STRUCTURE AND FUNCTION

The different traditions of benthic and pelagic marine ecology have resulted in distinctly different visions of what forces regulate biological structure and functional processes in the two realms (Lehman 1988; Verity and Smetacek 1996). Benthic ecologists have traditionally ascribed a primary role to the top-down processes of predation and grazing in regulating community structure, due in large part to the success and influence of the classic experimental studies of community structure on rocky intertidal shores, nearshore kelp beds, and coral reefs, where direct experimental manipulation of consumers produced dramatic changes in species distributions and community structure (Connell 1961; Randall 1961; Paine 1966, 1974; Dayton 1971; Ogden et al. 1973; Menge 1976; Lubchenco 1978; Carpenter 1986; Lewis 1986; Hay 1991a). In contrast, oceanographers working in the pelagic realm have emphasized bottom-up control of ecology through abiotic forcing of primary production and its transfer up the food chain (e.g., Parsons et al. 1984; Mann and Lazier 1991). This perspective is undoubtedly due in part to the microscopic sizes of the dominant pelagic organisms and the numerous difficulties of conducting controlled field experiments in the open ocean. Despite the history of different practical approaches in benthic and pelagic ecology, however, we see no clear a priori reason to believe that ecological processes governing community structure in the two realms are fundamentally different.

In recent years, these contrasting perspectives have begun to converge. Oceanographers increasingly emphasize the importance of top-down processes in the structure and function of pelagic communities (Hamner 1995; Verity and Smetacek 1996). And benthic ecologists increasingly recognize the pervasive influence on ecological structure and function of abiotic forcing, in the form of physical energy (Nixon 1988; Leigh et al. 1987), water flow (Leichter and Witman 1997; Leonard et al. 1998), factors affecting water-column productivity (Witman et al. 1993; Bustamante et al. 1995; Menge et al. 1997), and most particularly larval supply (Underwood and Denley 1984; Roughgarden et al. 1988; Grosberg and Levitan 1992). As is often the case with artificial dichotomies, it is increasingly clear that abiotic (bottom-up) forcing and consumer (top-down) regulation interact to mold ecological patterns and processes, rather than being alternative explanations (McQueen et al. 1986; Power 1992). A few examples from marine systems illustrate this interaction.

Menge et al. (1997) documented pervasive differences between two Oregon rocky intertidal communities that apparently reflect between-site differences in nearshore phytoplankton concentration, productivity, and suspended particulates. The site with higher phytoplankton production and biomass showed concomitantly higher recruitment, growth, and adult density of sessile (suspension-feeding) invertebrates, as well as higher density and feeding rates of both herbivores and predators. Ultimately the higher water-column productivity at this site appeared attributable to differences between the sites in the intensity of upwelling and circulation patterns that deliver phytoplankton and larvae to intertidal habitats.

Strikingly similar patterns were demonstrated in the intertidal community of a New England estuary as a function of water flow (Leonard et al. 1998). Comparison of three high-flow and three low-flow sites showed that flow resulted in a threefold higher flux of chlorophyll to the benthos at high-flow sites, with pervasive consequences for the intertidal community (Figure 5.10). As in the Oregon study, sites with higher phytoplankton flux supported higher cover of sessile organisms (mostly barnacles and mussels) and higher growth of passive suspension feeders, but also higher recruitment and adult abundances of both herbivores and predators. Growth of a carnivorous snail was also greater at high-flow sites. Thus, as in the Oregon study, enhanced recruitment and phytoplankton flux resulted in higher prey densities and growth rates, which "cascaded" up the food chain to predators. Flow simultaneously affected both production (larval supply) and predator effectiveness, so the strengths of bottom-up and top-down effects were correlated.

The patterns documented in these studies of intertidal communities thus suggest that bottom-up forcing resulted in higher abundances at all trophic levels, despite increasing the feeding rates of consumers. Although such "upward cascading" effects of resource supply have been shown or suggested in pelagic systems (e.g., Aebischer et al. 1990), they appear rare (see Figure 5.8; see discussion above). The marine data thus contrast with the simple model of Hairston et al. (1960; see also Oksanen et al. 1981), which predicts that resource subsidy affects alternate trophic levels most strongly, and with results of resource manipulation in some simple fresh-

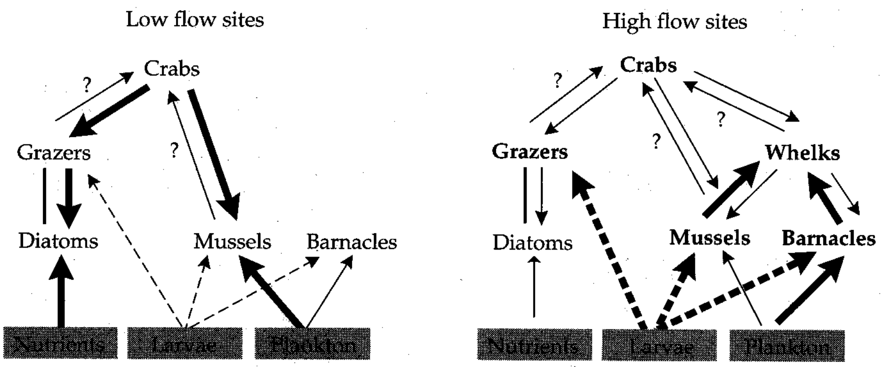

Figure 5.10 An example of abiotic forcing of community structure and function. The two food webs are schematic summaries derived from experimental studies of rocky intertidal communities at adjacent sites of low- and high-water flow in Rhode Island. Ascending and descending arrows indicate energy transfer and interaction effects, respectively. Biomass (font size) at all trophic levels, the relative strength of specific links in the food web (arrow width), and the presence of whelks differ among sites, responding to differences in the flux of planktonic larvae and resources (shown in boxes). (After Leonard et al. 1998.)

water food webs that support the model of Hairston et al. (Wootton and Power 1993). Meta-analyses of marine (Micheli 1999) and freshwater (Brett and Goldman 1997) results were in agreement, however, that resource subsidy generally has greatest impacts low in the food chain and diminishes upwards, rather than affecting alternate trophic levels.

These case studies indicate that, at least in some cases, productivity and the abiotic forces that regulate it can have pervasive effects on the organization of communities and the strength of consumer–prey interactions. Scaling up such processes to the broad sweep of evolutionary time, Vermeij (1987) has argued that consistently high energy availability (primary production and temperature) is the ultimate environmental factor limiting the "scope of adaptation," that is, the diversity and degree of expression of potential adaptations. The rationale is that where energy availability allows high metabolic rates, fitness differences among alternative phenotypes—whether genetic variants within a population, or co-occurring species—are greatest, and selection or interaction among them will be most intense. Moreover, high energy availability fosters larger population sizes, which are more likely to produce mutants, the raw material of adaptation. Although energy availability ultimately dictates the rate and scope of adaptation, Vermeij argues that competition and predation are the most important selective agents. As evidence, he offers the familiar patterns of increasing incidence of consumer pressure and defensive phenotypes with latitude, depth, and other ecological gradients that are correlated with energy availability.

SUMMARY

Consumer pressure is a pervasive influence on the evolution of populations and on the structure and function of nearly all marine communities and ecosystems. Studies conducted throughout temperate and tropical seas have shown that removal of herbivores or predators often produces profound changes in community organization, habitat structure, and ecosystem processes. The rise of humans as apex predators in an expanding range of marine (and terrestrial) habitats is similarly producing cascading impacts in both benthic and pelagic systems worldwide. Prey organisms may persist in the face of consumer pressure by escaping their consumers in time or space, by tolerating limited tissue loss to consumers, and/or by deterring consumers. Escape may be achieved through migration, rapid growth, other life history adaptations, or associations with defended neighbors. Tolerance often involves rapid growth or protection of reproductive structures in tissues inaccessible to consumers. Deterrence takes a wide array of forms, from deployment of diverse chemical compounds through various forms of structural armor. The generally positive association in time and space between intense consumer pressure and well-developed defenses implies that such defenses are costly to the prey and are selected against where consumer pressure is low. This cost hypothesis is supported by several experimental studies of phenotypically plastic or polymorphic species. In evolutionary time, consumers are important selective agents, molding the behavior, morphology, chemistry, and life history of prey organisms, particularly in the tropics where consumer pressure is especially intense. Many specific, and even obligate, associations between defended marine host species and undefended guest species appear to have evolved in response to intense predation pressure on the guest. Several unresolved issues deserve more attention in marine consumer–prey studies: What characteristics of organism and environment predispose a consumer to have strong (keystone) impacts on a community? Does the strength of consumer impacts in a system vary predictably as a function of community structure (species diversity, food chain length, and so on) or abiotic variables (physical energy, nutrient flux)? How do the results of typical experimental manipulations of marine communities scale up to broader scales in time and space, and how will evolutionary change and species turnover affect patterns seen in small-scale experiments? Answering such questions will be critical if we hope to predict, plan for, and mitigate the accelerating effects of global change on marine ecosystems.

ACKNOWLEDGMENTS

Our research during the preparation of this review has been supported by the National Science Foundation (OCE 95-21184 to JED and OCE-95-29784 to MEH), the Harry and Linda Teasley endowment to Georgia Tech, and the Virginia Institute of Marine Science. Discussions with Mark Bertness improved the manuscript. We are grateful to all. This is contribution # 2342 from the Virginia Institute of Marine Science.

LITERATURE CITED

Aebischer, N. J., J. C. Coulson and J. M. Colebrook. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347: 753–755.

Alder, R. A. and R. Karban. 1994. Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors. *Amer. Nat.* 144: 813–832.

Anderson, R. J. and B. Velimirov. 1982. An experimental investigation of the palatability of kelp bed algae to the sea urchin *Parechinus angulosus* Leske. *P.S.Z.N.I: Mar. Ecol.* 3: 357–73.

Appleton, R. D. and A. R. Palmer. 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. *Proc. Natl. Acad. Sci. USA* 85: 4387–4391.

Bakus, G. J. and G. Green. 1974. Toxicity in sponges and holothurians: A geographic pattern. *Science* 185: 951–953.

Baldwin, I. T. 1990. Herbivory simulation in ecological research. *Trends Ecol. Evol.* 5: 91–93.

Banse, K. 1994. Grazing and zooplankton production as key controls of phytoplankton production in the open ocean. *Oceanography* 7: 13–20.

Bell, S. S. 1991. Amphipods as insect equivalents? An alternative view. *Ecology* 72: 350–354.

Bertness, M. D. 1981. Crab shell-crushing predation and gastropod architectural defense. *J. Exp. Mar. Biol. Ecol.* 50: 213–230.

Bertness, M. D. and C. W. Cunningham. 1981. Crab shell-crushing predation and gastropod architectural defense. *J. Exp. Mar. Biol. Ecol.* 50: 213–230.

Bertness, M. D., S. D. Garrity and S. C. Levings. 1981. Predation pressure and gastropod foraging: A tropical–temperate comparison. *Evolution* 35: 995–1007.

Boettcher, A. A. and N. M. Targett. 1993. Role of polyphenolic molecular size in reduction of assimilation efficiency in *Xiphister mucosus*. *Ecology* 74: 891–903.

Bollens, S. M. and B. W. Frost. 1989a. Predator-induced diel vertical migration in a planktonic copepod. *J. Plankton Res.* 11: 1047–1065.

Bollens, S. M. and B. W. Frost. 1989b. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 34: 1072–1083.

Bolser, R. C. and M. E. Hay. 1996. Are tropical plants better defended? Palatability and defenses of temperate versus tropical seaweeds. *Ecology* 77: 2269–2286.

Brawley, S. H. 1992. Mesoherbivores. In D. M. John, S. J. Hawkins and J. H. Price (eds.), *Plant–Animal Interactions in the Marine Benthos*, pp. 235–263. Systematics Association Special Volume 46. Clarendon Press, Oxford.

Brawley, S. H. and W. H. Adey. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. *Mar. Biol.* 61: 167–177.

Brett, M. T. and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. *Proc. Nat. Acad. Sci. USA* 93: 7723–7726.

Brett, M. T. and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. *Science* 275: 384–386.

Brönmark, C. and J. G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science* 25: 1348–1350.

Buschmann, A. and B. Santelices. 1987. Micrograzers and spore release in *Iridaea laminarioides* (Rhodophyta: Gigartinales). *J. Exp. Biol. Ecol.* 108: 171–179.

Bustamante, R. H., G. M. Branch, S. Eekhout, B. Robertson, P. Zoutendyk, M. Schleyer, A. Dye, N. Hanekom, D. Keats, M. Jurd and C. McQuaid. 1995. Gradients of intertidal productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102: 189–201.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecol. Monogr.* 56: 345–363.

Carpenter, R. C. 1988. Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores. *Proc. Natl. Acad. Sci. USA* 85: 511–514.

Carpenter, S. R., J. F. Kitchell and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634–639.

Cetrulo, G. L. and M. E. Hay. 2000. Activated chemical defenses in tropical versus temperate seaweeds. *Mar. Ecol. Prog. Ser.* In press.

Chanas, B. and J. R. Pawlik. 1995. Defenses of Caribbean sponges against predatory reef fish. II. Spicules, tissue toughness, and nutritional quality. *Mar. Ecol. Prog. Ser.* 127: 195–211.

Chanas, B. and J. R. Pawlik. 1996. Does the skeleton of a sponge provide a defense against predatory reef fish? *Oecologia* 107: 225–231.

Clifton, K. E. 1997. Mass spawning by green algae on coral reefs. *Science* 275: 1116–1118.

Coen, L. D. 1988. Herbivory by crabs and the control of algal epibionts on Caribbean host corals. *Oecologia* 75: 198–203.

Coley, P. D. and T. M. Aide. 1990. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In P. W. Price, T. M. Lewinsotin, G. W. Fernandes and W. W. Besnon (eds.), *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, pp. 25–49. Wiley, New York.

Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacles *Balanus balanoides*. *Ecol. Monogr.* 31: 61–104.

Cronin, G. and M. E. Hay. 1996a. Within-plant variance in seaweed chemical defenses: Optimal defense theory versus the growth-differentiation balance hypothesis. *Oecologia* 105: 361–368.

Cronin, G. and M. E. Hay. 1996b. Susceptibility to herbivores depends on recent history of both the plant and animal. *Ecology* 77: 1531–1543

Cronin, G., V. J. Paul, M. E. Hay and W. Fenical. 1997. Are tropical herbivores more resistant than temperate herbivores to seaweed chemical defenses? Diterpenoid metabolites from *Dictyota acutiloba* as feeding deterrents for tropical versus temperate fishes and urchins. *J. Chem. Ecol.* 23: 289–302.

Dawkins, R. and J. R. Krebs. 1979. Arms races between and within species. *Proc. Royal Soc. London, Series B* 205: 489–511.

Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351–389.

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45: 137–159.

Dayton, P. K. 1985. The structure and regulation of some South American kelp communities. *Ecol. Monogr.* 55: 447–68.

Dayton, P. K., M. J. Tegner, P. B. Edwards and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* 8: 309–322.

Deason, E. E. and T. J. Smayda. 1982. Ctenophore–zooplankton–phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. *J. Plankton Res.* 4: 203–217.

Duffy, J. E. 1992. Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. *Mar. Ecol. Prog. Ser.* 90: 127–138.

Duffy, J. E. 1996. Resource partitioning, sibling species and the radiation of sponge-dwelling alpheid shrimp. *Biol. J. Linnean Soc.* 58: 307–324.

Duffy, J. E. and M. E. Hay. 1990. Seaweed adaptations to herbivory. *BioScience* 40: 368–376.

Duffy, J. E. and M. E. Hay. 1991a. Amphipods are not all created equal: A reply to Bell. *Ecology* 72: 354–358.

Duffy, J. E. and M. E. Hay. 1991b. Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* 72: 1286–1298.

Duffy, J. E. and M. E. Hay 1994. Herbivore resistance to seaweed chemical defense: The roles of mobility and predation risk. *Ecology* 75: 1304–1319.

Duffy, J. E. and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecol. Monogr.* 70: 237–263.

Duffy, J. E. and V. J. Paul. 1992. Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes. *Oecologia* 90: 333–339.

Duffy, J. E., K. S. Macdonald, J. M. Rhode and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: An experimental test. *Ecology*. In press.

Duggins, D. O., S. A. Simenstad and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245: 170–173.

Dunlap, M. and J. R. Pawlik. 1996. Video-monitored predation by Caribbean reef fishes on an array of reef and mangrove sponges. *Mar. Biol.* 126: 117–123.

Estes, J. A. and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecol. Monogr.* 65:75–100.

Estes, J. A. and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185: 1058–1060.

Estes, J. A. and P. D. Steinberg. 1988. Predation, herbivory, and kelp evolution. *Paleobiology* 14: 19–36.

Estes, J. A., M. T. Tinker, T. M. Williams and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473–476.

Faulkner, D. J. 1984. Marine natural products: Metabolites of marine algae and herbivorous marine molluscs. *Natural Prod. Rep.* 1: 251–280.

Faulkner, D. J. 1994. Marine natural products. *Natural Prod. Rep.* 11: 355–394.

Faulkner, D. J. 1999. Marine natural products. *Natural Prod. Rep.* 16: 155–198.

Fenical, W. 1980. Distributional and taxonomic features of toxin-producing marine algae. In I. A. Abbott, M. S. Foster and L. F. Eklund (eds.), *Pacific Seaweed Aquaculture*, pp. 144–151. California Sea Grant College Program, Institute of Marine Resources, University of California, La Jolla.

Fenical, W. 1993. Chemical studies of marine bacteria: Developing a new resource. *Chem. Rev.* 93: 1673–1683.

Gaines, S. D. and J. Lubchenco. 1982. A unified approach to marine plant–herbivore interactions. II. Biogeography. *Annu. Rev. Ecol. Syst.* 13: 111–138.

Gerhart, D. J., D. Rittschof and S. W. Mayo. 1988. Chemical ecology and the search for marine antifoulants. *J. Chem. Ecol.* 14: 1905–1917.

Glynn, P. W. 1980. Defense by symbiotic Crustacea of host corals elicited by chemical cues from predator. *Oecologia* 47: 287–290.

Glynn, P. W. 1981. Acanthaster population regulation by a shrimp and a worm. *Proc. Fourth Int. Coral Reef Symp.* 2: 607–612.

Glynn, P. W. 1983. Increased survivorship in corals harboring crustacean symbionts. *Mar. Biol. Lett.* 4: 105–111.

Grosberg, R. K. and D. R. Levitan. 1992. For adults only? Supply-side ecology and the history of larval biology. *Trends Ecol. Evol.* 7: 130–133.

Haahtela, I. 1984. A hypothesis of the decline of the bladder wrack (*Fucus vesiculosus* L.) in SW Finland in 1975–1981. *Limnologica* 15: 345–350.

Hairston, N. G., F. E. Smith and L. B. Slobodkin. 1960. Community structure, population control and competition. *Amer. Nat.* 94: 421–425.

Hamner, W. M. 1995. Predation, cover, and convergent evolution in epipelagic oceans. *Mar. Freshwat. Behav. Physiol.* 26: 71–89.

Harris, L. G., A. W. Ebeling, D. R. Laur and R. J. Rowley. 1984. Community recovery after storm damage: A case of facilitation in primary succession. *Science* 224: 1336–1338.

Harrison, P. L., R. C. Babcock, G. D. Bull, J. K. Oliver, C. C. Wallace and B. L. Willis. 1984. Mass spawning in tropical reef corals. *Science* 223: 1186–1189.

Harvell, C. D. 1984. Predator-induced defense in a marine bryozoan. *Science* 224: 1357–1359.

Harvell, C. D. 1986. The ecology and evolution of inducible defenses in a marine bryozoan: Cues, costs, and consequences. *Amer. Nat.* 128: 810–823.

Harvell, C. D. 1990. The ecology and evolution of inducible defenses. *Q. Rev. Biol.* 65: 323–340.

Harvell, C. D. 1992. Inducible defenses and allocation shifts in a marine bryozoan. *Ecology* 73: 1567–1576.

Harvell, C. D., W. Fenical and C. H. Greene. 1988. Chemical and structural defenses of Caribbean gorgonians (*Pseudopterogorgia* spp.). I. Development of an in situ feeding assay. *Mar. Ecol. Prog. Ser.* 49: 287–294.

Hay, M. E. 1981a. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Amer. Nat.* 118: 520–540.

Hay, M. E. 1981b. The functional morphology of turf-forming seaweeds: Persistence in stressful marine habitats. *Ecology* 62: 739–750.

Hay, M. E. 1984. Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* 64: 396–407.

Hay, M. E. 1985. Spatial patterns of herbivore impact and their importance in maintaining algal species richness. *Proc. Fifth Int. Coral Reef Congr.* 4: 29–34.

Hay, M. E. 1986. Associational plant defenses and the maintenance of species diversity: Turning competitors into accomplices. *Amer. Nat.* 128: 617–641.

Hay, M. E. 1991a. Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In P. F. Sale (ed.), *The Ecology of Fishes on Coral Reefs,* pp. 96–119. Academic Press, San Diego, CA.

Hay, M. E. 1991b. Marine-terrestrial contrasts in the ecology of plant chemical defenses against herbivores. *Trends Ecol. Evol.* 6: 362–365.

Hay, M. E. 1992. The role of seaweed chemical defenses in the evolution of feeding specialization and in the mediation of complex interactions. In V. J. Paul (ed.), *Ecological Roles for Marine Natural Products*, pp. 93–118. Comstock Press, Ithaca, NY.

Hay, M. E. 1996. Marine chemical ecology: What is known and what is next? *J. Exp. Mar. Biol. Ecol.* 200: 103–134.

Hay, M. E. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Coral Reefs* 16 (Suppl): S67–S76.

Hay, M. E. and W. Fenical. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. *Annu. Rev. Ecol. Syst.* 19: 111–145.

Hay, M. E. and W. Fenical. 1996. Chemical ecology and marine biodiversity: Insights and products from the sea. *Oceanography* 9: 10–20.

Hay, M. E. and P. D. Steinberg. 1992. The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In J. Rosenthal and M. Berenbaum (eds.), *Herbivores: Their Interaction with Secondary Metabolites, Evolutionary and Ecological Processes*, pp. 371–413. Academic Press, San Diego.

Hay, M. E., W. Fenical and K. Gustafson. 1987a. Chemical defense against diverse coral reef herbivores. *Ecology* 68: 1581–1591

Hay, M. E., J. E. Duffy, C. A. Pfister and W. Fenical. 1987b. Chemical defense against different marine herbivores: Are amphipods insect equivalents? *Ecology* 68: 1567–1580.

Hay, M. E., V. J. Paul, S. M. Lewis, K. Gustafson, J. Tucker and R. Trindell. 1988. Can tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth, nitrogen content, herbivory, and chemical versus morphological defenses. *Oecologia* 75: 233–245.

Hay, M. E., J. R. Pawlik, J. E. Duffy and W. Fenical. 1989. Seaweed–herbivore–predator interactions: Host-plant specialization reduces predation on small herbivores. *Oecologia* 81: 418–427.

Hay, M. E., J. E. Duffy, V. J. Paul, P. E. Renaud and W. Fenical. 1990a. Specialist herbivores reduce their susceptibility to predation by feeding on the chemically-defended seaweed *Avrainvillea longicaulis. Limnol. Oceanogr.* 35: 1734–1743.

Hay, M. E., J. E. Duffy and W. Fenical. 1990b. Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. *Ecology* 71: 733–743.

Hay, M. E., Q. E. Kappel and W. Fenical. 1994. Synergisms in plant defenses against herbivores: Interactions of chemistry, calcification, and plant quality. *Ecology* 75: 1714–1726.

Hay, M. E., J. J. Stachowicz, E. Cruz-Rivera, S. Bullard, M. S. Deal and N. Lindquist. 1998. Bioassays with marine and freshwater macroorganisms. In K. F. Haynes and J. G. Millar (eds.), *Methods in Chemical Ecology,* Volume 2, *Bioassay Methods*, pp. 39–141. Chapman and Hall, New York.

Hays, G. C. 1995. Zooplankton avoidance activity. *Nature* 376: 650.

Hays, G. C., C. A. Proctor, A. W. G. John and A. J. Warner. 1994. Interspecific differences in the diel vertical migration of marine copepods: The implications of size, color, and morphology. *Limnol. Oceanogr.* 39: 1621–1629.

Hays, G. C., R. P. Harris and R. N. Head. 1997. The vertical nitrogen flux caused by zooplankton diel vertical migration. *Mar. Ecol. Prog. Ser.* 160: 57–62.

Heck, K. L., Jr. and K. A. Wilson. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: A study of spatial and temporal variation using tethering techniques. *J. Exp. Mar. Biol. Ecol.* 107: 87–100.

Hixon, M. A. and W. N. Brostoff. 1983. Damselfish as keystone species in reverse: Intermediate disturbance and diversity of reef algae. *Science* 220: 511–513.

Hixon, M. A. and W. N. Brostoff. 1996. Succession and herbivory: Effects of differential fish grazing on Hawaiian coral reef algae. *Ecol. Monogr.* 66: 67–90.

Hobson, E. S. and J. R. Chess. 1976. Trophic interactions among fish and zooplankters near shore at Santa Catalina Island, California. *Fish. Bull.* 74: 567–598.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a coral reef. *Science* 256: 1547–1551.

Huntley, M., P. Sykes, S. Rohan and V. Martin. 1986. Chemically-mediated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*: Mechanism, occurrence and significance. *Mar. Ecol. Prog. Ser.* 28: 105–120.

Irelan, C. D. and M. H. Horn. 1991. Effects of macrophyte secondary chemicals on food choice and digestive efficiency of *Cebidichthys violaceus* (Girard), an herbivorous fish of temperate marine waters. *J. Exp. Mar. Biol. Ecol.* 153: 179–194.

Jackson, J. B. C. 1997. Reefs before Columbus. *Coral Reefs* 16 (Suppl.): S23–S32.

Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. *Ecology* 60: 1211–1224.

Kangas, P., H. Autio, G. Hällfors, H. Luther, Å. Niemi and H. Salemaa. 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–1981. *Acta Botanica Fennica* 118: 1–27.

Karban, R. and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago.

Kareiva, P. 1994. Higher order interactions as a foil to reductionist ecology. *Ecology* 75: 1527–1528.

King, G. M. 1986. Inhibition of microbial activity in marine sediments by a bromophenol from a hemichordate. *Nature* 323: 257–259.

Klumpp, D. W., A. D. McKinnon and C. N. Mundy. 1988. Motile cryptofauna of a coral reef: Abundance, distribution and trophic potential. *Mar. Ecol. Prog. Ser.* 45: 95–108.

Lawton, J. H. 1994. What do species do in ecosystems? *Oikos* 71: 367–374.

Lehman, J. T. 1988. Ecological principles affecting community structure and secondary production by zooplankton in marine and freshwater environments. *Limnol. Oceanogr.* 33 (part 2): 931–945.

Lehman, J. T. 1991. Interacting growth and loss rates: The balance of top-down and bottom-up controls in plankton communities. *Limnol. Oceanogr.* 36: 1546–1554.

Leibold, M. A., J. M. Chase, J. B. Shurin and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annu. Rev. Ecol. Syst.* 28: 467–494.

Leichter, J. J. and J. D. Witman. 1997. Water flow over subtidal rock walls: Relation to distributions and growth rates of sessile suspension feeders in the Gulf of Maine. *J. Exp. Mar. Biol. Ecol.* 209: 293–307.

Leigh, E. G., Jr., R. T. Paine, J. F. Quinn and T. H. Suchanek. 1987. Wave energy and intertidal productivity. *Proc. Natl. Acad. Sci. USA* 84: 1314–1318.

Leonard, G. H., J. M. Levine, P. R. Schmidt and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79: 1395–1411.

Leonard, G. H., M. D. Bertness and P. O. Yund. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology* 80: 1–14.

Levin, D. A. and B. M. York. 1978. The toxicity of plant alkaloids: An ecogeographic perspective. *Biochem. Syst. Ecol.* 6: 61–76.

Lewis, S. M. 1985. Herbivory on coral reefs: Algal susceptibility to herbivorous fishes. *Oecologia* 65: 370–375.

Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* 56: 183–200.

Lewis, S. M., J. N. Norris and R. B. Searles. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. *Ecology* 68: 636–641.

Lindquist, N. and M. E. Hay. 1995. Can small rare prey be chemically defended? the case for marine larvae. *Ecology* 76: 1347–1358.

Lindquist, N. and M. E. Hay. 1996. Palatability and chemical defenses of marine invertebrate larvae. *Ecol. Monogr.* 66: 431–450.

Lindquist, N., M. E. Hay and W. Fenical. 1992. Chemical defense of ascidians and their conspicuous larvae. *Ecol. Monogr.* 62: 547–568.

Littler, M. M. and D. S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: Field and laboratory tests of a functional form model. *Amer. Nat.* 116: 25–44.

Littler, M. M., D. S. Littler and P. R. Taylor. 1983a. Evolutionary strategies in a tropical barrier reef system: Functional-form groups of marine macroalgae. *J. Phycol.* 19: 229–237.

Littler, M. M., P. R. Taylor and D. S. Littler. 1983b. Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2: 111–118.

Littler, M. M., P. R. Taylor and D. S. Littler. 1986. Plant defense associations in the marine environment. *Coral Reefs* 5: 63–71.

Littler, M. M. , P. R. Taylor and D. S. Littler. 1989. Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80: 331–340.

Littler, M. M., D. S. Littler and P. R. Taylor. 1995. Selective herbivore increases biomass of its prey: A chiton–coralline reef-building association. *Ecology* 76: 1666–1681.

Lively, C. M. 1986a. Competition, comparative life histories and the maintenance of shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Ecology* 67: 858–864.

Lively, C. M. 1986b. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution* 40: 232–242.

Longhurst, A. R., A. Bedo, W. G. Harrison, E. J. H. Head, E. P. Horne, B. Irwin and C. Morales. 1989. NFLUX: A test of vertical nitrogen flux by diel migrant biota. *Deep-Sea Res.* 36: 1705–1719.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *Amer. Nat.* 112: 23–29.

Lubchenco, J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64: 1116–1123.

Lubchenco, J. and J. Cubit. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61: 676–687.

Mann, K. H. and J. R. N. Lazier. 1991. *Dynamics of Marine Ecosystems: Biological–Physical Interactions in the Oceans*. Blackwell Scientific, Oxford.

McClintock, J. B. 1994. An overview of the chemical ecology of Antarctic marine invertebrates. The Ireland Lecture 1993, University of Alabama at Birmingham.

McClintock, J. B. and Janssen. 1990. Pteropod abduction as a chemical defence in a pelagic Antarctic amphipod. *Nature* 346: 462–464.

McClintock, J. B., D. P. Swenson, D. K. Steinberg and A. A. Michaels. 1996. Feeding-deterrent properties of common oceanic holoplankton from Bermudian waters. *Limnol. Oceanogr.* 41: 798–801.

McCook, L. J. 1996. Effects of herbivores and water quality on *Sargassum* distribution on the Great Barrier Reef: Cross-shelf transplants. *Mar. Ecol. Prog. Ser.* 139: 179–192.

McCook, L. J. 1997. Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. *Mar. Biol.* 129: 713–722.

McCook, L. J., I. R. Price and D. W. Klumpp. 1997. Macroalgae on the Great Barrier Reef: Causes or consequences, indicators or models of reef degradation. *Proc. 8th Int. Coral Reef Symp.* 2: 1851–1856.

McQueen, D. J., J. R. Post and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. *Canad. J. Fish. Aquat. Sci.* 43: 1571–1581.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46: 355–393.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecol. Monogr.* 65: 21–74.

Menge, B. A. and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: Prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.* 51: 429–450.

Menge, B. A., J. Lubchenco and J. R. Ashkenas. 1985. Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. *Oecologia* 65: 394–405.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down controls? *Proc. Natl. Acad. Sci. USA* 94: 14530–14535.

Meyer, K. D. and V. J. Paul. 1995. Variation in secondary metabolite and aragonite concentrations in the tropical green seaweed *Neomeris annulata*: Effects on herbivory by fishes. *Mar. Biol.* 122:. 537–545.

Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* 285: 1396–1398.

Miller, M. W. 1998. Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanogr. Mar. Biol. Annu. Rev.* 36: 65–96.

Morgan, S. G. 1987. Morphological and behavioral antipredatory adaptations of decapod zoeae. *Oecologia* 73: 393–400.

Morgan, S. G. 1989. Adaptive significance of spination in estuarine crab zoeae. *Ecology* 70: 464–482.

Morgan, S. G. 1990. Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. *Ecology* 71:1639–1652.

Morgan, S. G. and J. H. Christy. 1997. Planktivorous fishes as selective agents for reproductive synchrony. *J. Exp. Mar. Biol. Ecol.* 209: 89–101.

Nixon, S. W. 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. *Limnol. Oceanogr.* 33:1005–1025.

Ogden, J. C., R. A. Brown and N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum*: Formation of halos around West Indian patch reefs. *Science* 182:715–717.

Oksanen, L., S. D. Fretwell, J. Arruda and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. *Amer. Nat.* 118: 240–261.

Padilla, D. K. 1985. Structural resistance of algae to herbivores: A biomechanical approach. *Mar. Biol.* 90: 103–109.

Paine, R. T. 1966. Food web complexity and species diversity. *Amer. Nat.* 100: 65–75.

Paine, R. T. 1969. A note on trophic complexity and community stability. *Amer. Nat.* 103: 91–93.

Paine, R. T. 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93–120.

Paine, R. T. 1992. Food-web analysis through field measurements of per capita interaction strength. *Nature* 355: 73–75.

Palmer, A. R. 1979. Fish predation and the evolution of gastropod shell sculpture: Experimental and geographic evidence. *Evolution* 33: 697–713.

Palmer, A. R. 1982. Predation and parallel evolution: Recurrent parietal plate reduction in balanomorph barnacles. *Paleobiology* 8: 31–44.

Parsons, T. R., M. Takahashi and B. Hargrave. 1984. *Biological Oceanographic Processes*, 3rd ed. Pergamon Press, Oxford.

Patton, W. K. 1976. Animal associates of living reef corals. In O. A. Jones and R. Endean (eds.), *Biology and Geology of Coral Reefs*, Vol. III, *Biology* 2, pp. 1–43. Academic Press, New York.

Paul, V. J. 1987. Feeding deterrent effects of algal natural products. *Bull. Mar. Sci.* 41: 514–522.

Paul, V. J. 1992. *Ecological Roles of Marine Natural Products*. Comstock Press, Ithaca, NY.

Paul, V.J. 1997. Secondary metabolites and calcium carbonate as defenses of calcareous algae on coral reefs. *Proc. 8th Int. Coral Reef Symp.* 1: 707–711.

Paul, V. J. and W. Fenical. 1986. Chemical defense in tropical green algae, order Caulerpales. *Mar. Ecol. Prog. Ser.* 33: 255–264.

Paul, V. J. and M. E. Hay. 1986. Seaweed susceptibility to herbivory: Chemical and morphological correlates. *Mar. Ecol. Prog. Ser* 33: 255–264.

Paul, V. J. and K. L. Van Alstyne. 1988. Chemical defense and chemical variation in some tropical Pacific species of *Halimeda* (Halimedaceae; Chlorophyta). *Coral Reefs* 6: 263–269.

Paul, J. and K. L. Van Alstyne. 1992. Activation of chemical defenses in the tropical green algae *Halimeda* spp. *J. Exp. Mar. Biol. Ecol.* 160: 191–203.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese and F. Torres, Jr. 1998. Fishing down marine food webs. *Science* 279: 860–863.

Pawlik, J. R. 1983. A sponge-eating worm from Bermuda: *Branchiosyllis oculata* (Polychaeta, Syllidae). *P. S. Z. N. I. Mar. Ecol.* 4: 65–79.

Pawlik, J. R. 1993. Marine invertebrate chemical defenses. *Chem. Rev.* 93: 1911–1922.

Pawlik, J. R., B. Chanas, R. J. Toonen and W. Fenical. 1995. Defenses of Caribbean sponges against predatory reef fish. I. Chemical deterrency. *Mar. Ecol. Prog. Ser.* 127: 183–194.

Paya, I. and B. Santelices. 1989. Macroalgae survive digestion by fishes. *J. Phycol.* 25: 186–188.

Pennings, S. C. and V. J. Paul. 1992. Effect of plant toughness, calcification andchemistry on herbivory by *Dolabella auricularia*. *Ecology* 73: 1606–1619.

Pennings, S. C., M. P. Puglisi, T. J. Pitlik, A. C. Himaya and V. J. Paul. 1996. Effects of secondary metabolites and $CaCO_3$ on feeding by surgeonfishes and parrotfishes: Within-plant comparisons. *Mar. Ecol. Prog. Ser.* 134: 49–58.

Pennings, S. C., E. L. Siska and M. D. Bertness. In press. Latitudinal differences in plant palatability in Atlantic coast salt marshes. *Ecology*.

Peters, R. H. 1991. *A Critique for Ecology*. Cambridge University Press, Cambridge.

Pfister, C. A. 1992. Costs of reproduction in an intertidal kelp: Patterns of allocation and life history consequences. *Ecology* 73: 1586–1596.

Pfister, C. A. and M. E. Hay. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia* 77: 118–129.

Pitlik, T. J. and V. J. Paul 1997. Effects of toughness, calcite level, and chemistry of crustose coralline algae (Rhodophyta: Corallinales) on grazing by the parrotfish *Chlorurus sordidus*. *Proc. 8th Int. Coral Reef Symp.* 2: 701–706.

Porter, K. G. 1976. Enhancement of algal growth and productivity by grazing zooplankton. *Science* 192: 1332–1334.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73: 733–746.

Raffa, K. F. and E. B. Smalley. 1995. Interaction of pre-attack and induced monoterpene concentrations in host conifer defense against bark beetle-fungal complexes. *Oecologia* 102: 285–295.

Raffaelli, D. G. and S. J. Hall. 1995. Assessing the relative importance of trophic links in food webs. In G. Polis and K. Winemiller (eds.), *Foodwebs: Integration of Patterns and Dynamics*, pp. 185–191. Chapman and Hall, New York.

Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. *Ecology* 42: 812.

Randall, J. E. 1965. Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. *Ecology* 46: 255–260.

Reimer, O. and M. Tedengren. 1996. Phenotypical improvement of morphological defences in the mussel *Mytilus edulis* induced by exposure to the predator *Asterias rubens*. *Oikos* 75: 383–390.

Renaud, P. E., M. E. Hay and T. M. Schmitt. 1990. Interactions of plant stress and herbivory: Interspecific variation in the susceptibility of a palatable versus an unpalatable seaweed to sea urchin grazing. *Oecologia* 82: 217–226.

Reznick, D. N. and H. A. Bryga. 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). V. Genetic basis of parallelism in life histories. *Amer. Nat.* 147: 339–359.

Reznick, D. N., F. H. Rodd and M. Cardenas. 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). IV. Parallelism in life-history phenotypes. *Amer. Nat.* 147: 319–338.

Reznick, D. N., F. H. Shaw, F. H. Rodd and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275: 1934–1937.

Roughgarden, J., S. Gaines and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466.

Safina, C. 1995. The world's imperiled fish. *Sci. Amer.* 273: 46–53.

Santelices, B. and R. Ugarte. 1987. Algal life-history strategies and resistance to digestion. *Mar. Ecol. Prog. Ser* 35: 267–275.

Schupp, P. J. and V. J. Paul. 1994. Calcification and secondary metabolites in tropical seaweeds: Variable effects on herbivorous fishes. *Ecology* 75: 1172–1185.

Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc. Natl. Acad. Sci. USA* 83: 6897–6901.

Shanks, A. L. and W. M. Graham. 1988. Chemical defense in a scyphomedusa. *Mar. Ecol. Prog. Ser* 45: 81–86.

Shaw, B. A., P. J. Harrison and R. J. Anderson. 1995. Feeding deterrent properties of apo-fucoxanthinoids from marine diatoms. II. Physiology of production of apo-fucoxanthinoids by the marine diatoms *Phaeodactylum tricornutum* and *Thalassiosira pseudonana*, and their feeding deterrent effects on the copepod *Tigriopus californicus*. *Mar. Biol.* 124: 473–481.

Shiomoto, A., K. Tadakoro, K. Nagasawa and Y. Ishida. 1997. Trophic relations in the subarctic North Pacific ecosystem: Possible feeding effect from pink salmon. *Mar. Ecol. Prog. Ser* 150: 75–85.

Simenstad, C. A., J. A. Estes and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable state communities. *Science* 200: 403–411.

Sotka, E. E., M. E. Hay and J. D. Thomas. 1999. Host-plant specialization by a non-herbivorous amphipod: Advantages for the amphipod and costs for the seaweed. *Oecologia* 118: 471–482.

Stachowicz, J. J. and M. E. Hay. 1996. Facultative mutualism between an herbivorous crab and its coralline algal host: Advantages of eating noxious seaweeds. *Oecologia* 105: 377–387.

Stachowicz, J. J. and M. E. Hay. 1999. Reducing predation through chemically-mediated camouflage: Indirect effects of plant defenses on herbivores. *Ecology* 80: 495–509.

Stachowicz, J. J. and M. E. Hay. 2000. Geographic variation in camouflaging behavior by a decorator crab: Southern populations specialize on chemically noxious decorations. *Amer. Nat.* 156. In press.

Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.

Steinberg, P. D. 1992. Geographical variation in the interaction between marine herbivores and brown algal secondary metabolites. In V. J. Paul (ed.), *Ecological Roles for Marine Secondary Metabolites*, pp. 51–92. Comstock Press, Ithaca, NY.

Steinberg, P. D. 1994. Lack of short-term induction of phlorotannins in the Australasian brown algae *Ecklonia radiata* and *Sargassum vestitum*. *Mar. Ecol. Prog. Ser* 112: 129–133.

Steinberg, P. D. 1995. Interaction between the canopy dwelling echinoid *Holopneustes purpurescens* and its host kelp *Ecklonia radiata*. *Mar. Ecol. Prog. Ser* 127: 169–181.

Steinberg, P. D. and I. A. Van Altena. 1992. Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. *Ecol. Monogr.* 62: 189–222.

Steinberg, P. D., J. A. Estes and F. C. Winter. 1995. Evolutionary consequences of food chain length in kelp forest communities. *Proc. Natl. Acad. Sci. USA* 92: 8145–8148.

Steneck, R. S. 1982. A limpet–coralline alga association: Adaptations and defenses between a selective herbivore and its prey. *Ecology* 63: 507–522.

Steneck, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9: 44–61.

Steneck, R. S. 1986. The ecology of coralline algal crusts: Convergent patterns and adaptive strategies. *Annu. Rev. Ecol. Syst.* 17: 273–303.

Steneck, R. S. 1988. Herbivory on coral reefs: A synthesis. *Proc. 6th Int. Coral Reef Symp.* 1: 37–49.

Steneck, R. S. 1990. Herbivory and the evolution of nongeniculate coralline algae (Rhodophyta, Corallinales) in the North Atlantic and North Pacific. Evolutionary biogeography of the marine algae of the North Atlantic. *NATO Advanced Science Institutes Series* G22: 107–129.

Steneck, R. S. 1992. Plant–herbivore coevolution: A reappraisal from the marine realm and its fossil record. In D. J. John, S. J. Hawkins and J. H. Price (eds.), *Plant–Animal Interactions in the Marine Benthos*, pp. 477–491. Systematics Association Special Volume 46. Clarendon Press, Oxford.

Steneck, R. S. 1998. Human influences on coastal ecosystems: Does overfishing create trophic cascades? *Trends Ecol. Evol.* 13: 429–430.

Steneck, R. S. and W. H. Adey. 1976. The role of environment in control of morphology in *Lithophyllum congestum*, a Caribbean algal ridge builder. *Botanica Marina* 19: 197–215.

Steneck, R. S. and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476–498.

Steneck, R. S. and L. Watling. 1982. Feeding capabilities and limitations of herbivorous molluscs: A functional group approach. *Mar. Biol.* 68: 299–319.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology* 73: 747–754.

Tallamy, D. W. and M. J. Raupp. 1991. *Phytochemical Induction by Herbivores.* John Wiley and Sons, New York.

Targett, T. E. and N. M. Targett. 1990. Energetics of food selection by the herbivorous parrotfish *Sparisoma radians*: Roles of assimilation efficiency, gut evacuation rate, and algal secondary metabolites. *Mar. Ecol. Prog. Ser.* 66: 13–21.

Tegner, M. J. and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. *Adv. Ecol. Res.* 17: 243–279.

Trussell, G. C. and L. D. Smith. 2000. Induced defenses in response to an invading crab predator: An explanation of historical and geographic phenotypic change. *Proc. Natl. Acad. Sci. USA* 97: 2123–2127.

Underwood, A. J. and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In D. R. Strong, Jr., D. Simberloff, L. G. Abele and A. B. Thistle (eds.), *Ecological Communities: Conceptual Issues and the Evidence*, pp. 151–180. Princeton University Press, Princeton, NJ.

Underwood, A. J. and P. Jernakoff. 1981. Interactions between algae and grazing gastropods in the structure of a low-shore intertidal algal community. *Oecologia* 4: 221–233.

Van Alstyne, K. L. 1988. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology* 69: 655–663.

Van Alstyne, K. L. and V. J. Paul. 1992. Chemical and structural defenses in the sea fan *Gorgonia ventalina*: Effects against generalist and specialist predators. *Coral Reefs* 11: 155–159.

Van Alstyne, K. L., C. R. Wylie, V. J. Paul and K. Meyer. 1992. Antipredator defenses in tropical Pacific soft corals (Coelenterata, Alcyonacea). *Biol. Bull.* 182: 231–240.

Van Alstyne, K. L., C. R. Wylie and V. J. Paul. 1994. Antipredator defenses in tropical Pacific soft corals (Coelenterata, Alcyonacea). II. The relative importance of chemical and structural defenses in three species of *Sinularia*. *J. Exp. Mar. Biol. Ecol.* 178: 17–34.

Verity, P. G. and V. Smetacek. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.* 130: 277–293.

Vermeij, G. J. 1976. Interoceanic differences in vulnerability of shelled prey to crab predation. *Nature* 260: 135–136.

Vermeij, G. J. 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology* 3: 245–258.

Vermeij, G. J. 1978. *Biogeography and Adaptation: Patterns of Marine Life.* Harvard University Press, Cambridge, MA.

Vermeij, G. J. 1983. Intimate associations and coevolution in the sea. In D. J. Futuyma and M. Slatkin (eds.), *Coevolution*, pp. 311–327. Sinauer Associates, Sunderland, MA.

Vermeij, G. J. 1987. *Evolution and Escalation: An Ecological History of Life.* Princeton University Press, Princeton, NJ.

Vermeij, G. J. 1992. Time of origin and biogeographical history of specialized relationships between northern marine plants and herbivorous molluscs. *Evolution* 46: 657–664.

Vermeij, G. J. and J. D. Currey. 1980. Geographical variation in the strength of thaidid snail shells. *Biol. Bull.* 158: 383–389.

Wallerstein, B. R. and R. C. Brusca. 1982. Fish predation: A preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). *J. Biogeogr.* 9: 135–150.

Wiebe, P. H., L. P. Madin, L. R. Haury, G. R. Harbison and L. M. Philbin. 1979. Diel vertical migration by *Salpa aspersa* and its potential for large-scale particulate organic matter transport to the deep-sea. *Mar. Biol.* 53: 249–255.

Witman, J. D., J. J. Leichter, S. J. Genovese and D. A. Brooks. 1993. Pulsed phytoplankton supply to the rocky subtidal zone: Influence of internal waves. *Proc. Natl. Acad. Sci. USA* 90: 1686–1690.

Wolfe, G. V., M. Steinke and G. O. Kirst. 1997. Grazing activated chemical defense in a unicellular marine alga. *Nature* 387: 894–897.

Woodin, S. A., R. L. Marinelli and D. E. Lincoln. 1993. Allelochemical inhibition of recruitment in a sedimentary assemblage. *J. Chem. Ecol.* 19: 517–530.

Wootton, J. T. 1995. Effects of birds on sea urchins and algae: A lower-intertidal trophic cascade. *Ecoscience* 2: 321–328.

Wootton, J. T. 1997. Estimates and tests of per capita interactions strength: Diet, abundance, and impact of intertidally foraging birds. *Ecol. Monogr.* 67: 45–64.

Wootton, J. T. and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. *Proc. Natl. Acad. Sci. USA* 90: 1384–1387.

Wylie, C. R. and V. J. Paul. 1989. Chemical defenses in three species of *Sinularia* (Coelenterata, Alcyonacea): Effects against generalist predators and the butterflyfish *Chaetodon unimaculatus* Bloch. *J. Exp. Mar. Biol. Ecol.* 129: 141–160.

Zipser, E. and G. J. Vermeij. 1978. Crushing behavior of tropical and temperate crabs. *J. Exp. Mar. Biol. Ecol.* 31: 155–172.