Mutualisms and Aquatic Community Structure: The Enemy of My Enemy Is My Friend

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■ **Abstract**   Mutualisms occur when interactions between species produce recipro-
cal benefits. However, the outcome of these interactions frequently shifts from positive,
to neutral, to negative, depending on the environmental and community context, and
indirect effects commonly produce unexpected mutualisms that have community-wide
consequences. The dynamic, and context dependent, nature of mutualisms can trans-
form consumers, competitors, and parasites into mutualists, even while they consume,
compete with, or parasitize their partner species. These dynamic, and often diffuse,
mutualisms strongly affect community organization and ecosystem processes, but the
historic focus on pairwise interactions decoupled from their more complex commu-
nity context has obscured their importance. In aquatic systems, mutualisms commonly
support ecosystem-defining foundation species, underlie energy and nutrient dynamics
within and between ecosystems, and provide mechanisms by which species can rapidly
adjust to ecological variance. Mutualism is as important as competition, predation, and
physical disturbance in determining community structure, and its impact needs to be
adequately incorporated into community theory.

INTRODUCTION

Ecologists have made significant advances in understanding community structure
and function by focusing on negative interactions such as predation, competi-
tion, and physical disturbance (Bertness et al. 2001). However, positive interac-
tions, such as facilitation and mutualism, also play pivotal roles in organizing
communities, and incorporating positive interactions into ecological theory can

fundamentally alter our understanding of the processes and mechanisms that shape communities (Stachowicz 2001, Bruno et al. 2003). In this review, we focus on mutualisms in aquatic communities and demonstrate that (*a*) mutualisms are surprisingly widespread, (*b*) mutualists in one ecological setting can be adversaries in another setting, (*c*) conversely, interactions traditionally viewed as antagonistic can be mutualistic, depending on environmental and community settings, (*d*) mutualists need not be coevolved or consistently coupled in space or time, and (*e*) mutualisms have large effects on community structure and function. Our treatment extends the traditional view of coevolved, obligate mutualisms between species pairs into a broader community context, where indirect interactions among many species are common and context dependent and can dampen or reverse direct effects as well as play significant roles in affecting community and ecosystem organization (Berlow 1999).

Mutualisms are frequently viewed as obligate, coevolved interactions uniformly benefiting both partners, such as the mutualism between yucca plants and their moth pollinators. This unconditional, pairwise focus is commonly presented in textbooks (e.g., Purves et al. 2001) and theoretical treatments of mutualism (Doebeli & Knowlton 1998, Holland et al. 2002; but see Bacher & Friedli 2002) and drives research focused on the evolution and stabilization of mutualisms (Bronstein 1994, Connor 1995, Knowlton & Rohwer 2003, Stanton 2003, Thomson 2003). However, recent experimental and theoretical investigations (e.g., Stanton 2003, Thomson 2003) have noted that well-studied mutualisms, such as those between plants and pollinators, are usually conditional and can vary tremendously, depending on which pollinators occur locally. A pollinator can switch from mutualist to parasite because of the addition of a single, more efficient pollinator to the community; this dramatic change can occur without alteration in the behavior of either initial partner (Thomson 2003). Thus, between-species associations that are mutually beneficial in one ecological setting may become neutral or harmful in another (Bronstein 1994, Connor 1995, van Baalen & Jansen 2001, Knowlton & Rohwer 2003). In this review, we argue that the consideration of mutualisms within a community context not only underscores the dynamic nature of mutualisms but also illuminates the pivotal role that mutualisms play in community-level and ecosystem-level processes (van Baalen & Jansen 2001, Gomulkiewicz et al. 2003, Stanton 2003, Thomson 2003).

Although some authors have argued that mutualists must exhibit coevolved traits, there is no compelling rationale for such a restriction, and we view mutualisms less restrictively. Like Bronstein (1994), we use mutualism to refer to interspecific interactions in which the benefits exceed the costs for both participants. We define mutualisms by the outcome of the interaction, rather than by assumptions about the coevolution of the interaction. Interactions that seem coevolved because of reciprocal traits of the participants can occur without a coevolutionary history (Steneck 1992, Vermeij 1992), thus casting doubt on our ability to distinguish interactions that are coevolved from those that are simply fortuitous. Therefore, in this review, we make no assumptions about evolutionary history, and we

recognize that ecologically important mutualisms can occur fortuitously when each partner receives "by-product" benefits from the other, as when a trait of species A incidentally benefits species B, and vice versa (Connor 1995). Damselfish, for example, escape predators by sheltering in branching corals; these corals grow faster because of the nutrients excreted by the sheltering damselfish (Liberman et al. 1995). The branching morphology of the coral is intended to meet the feeding and hydrodynamic needs of the coral, yet it provides the fish with shelter; damselfish excretion is a physiological necessity for the fish, yet it benefits the coral.

Here, we explore how mutualisms structure the communities in which they occur and how community context can alter the outcomes of interactions to the extent that apparent antagonists can function as mutualists. We focus on aquatic systems because fewer mutualisms are broadly known and well investigated in these communities and because aquatic patterns provide useful contrasts with terrestrial mutualisms.

MUTUALISMS THAT SUPPORT FOUNDATION SPECIES

Foundation species such as corals, kelps, seagrasses, and marsh plants provide structure and definition to entire ecosystems (Dayton 1975, Jones et al. 1997, Bruno et al. 2003). Interactions between foundation species and their residents are not unidirectional, as residents often benefit foundation species. When foundation species support organisms that reciprocate with critical benefits, these mutualisms can be pivotal to the persistence and function of entire ecosystems.

Deep-Sea Hydrothermal Vent and Hydrocarbon-Seep Communities

Hydrothermal vent communities represent oases of high production and physical structure in a featureless landscape with few energetic resources. Unknown until 1977, these systems are examples of extreme biotic adaptation, much of it based on mutualisms between foundation species and the endosymbiotic, chemosynthetic microbes that provide their nutrition. Physical rigors at vents are extreme; fluids exiting some vents may be 400°C, have a pH of 2.8, and contain high concentrations of toxic hydrogen sulfide and other unusual cations (Tunnicliffe 1992). These hot fluids enter water that is only 2°C, but chemoautotrophic bacteria from these systems can grow at temperatures of up to 110°C, which allows them to cope with these rigors and capture the energy that powers these communities.

Foundation species such as bivalves (*Bathymodiolus* spp.) and the giant (1 m long) tubeworm *Riftia pachyptila* have neither mouth nor gut; they acquire their nutrition from sulfur-oxidizing chemoautotrophic bacteria that live within their bodies (Fiala-Medioni & Felbeck 1990). The host delivers carbon dioxide, oxygen, and hydrogen sulfide to bacteria held in special body tissues, and the bacteria use hydrogen sulfide as an electron donor to synthesize organic compounds that are

utilized by the host. This mutualism enables the biomass at vent communities to become 500 to 1000 times greater than in the surrounding deep sea and forms the base of an extensive food web supported entirely by chemosynthesis (Tunnicliffe 1992, Micheli et al. 2002). Similar assemblages of hosts and endosymbiotic sulfide-oxidizing or methane-oxidizing bacteria are found at hydrocarbon seeps (Brooks et al. 1987). Stable-isotope studies indicate that some mobile predators acquire nearly 100% of their nutrition from seep production, and even vagrant predators can be substantially subsidized by this production (MacAvoy et al. 2002).

The host-microbe mutualisms of these deep-sea habitats allow a method of energy acquisition and produce a community of organisms that are among the most novel on Earth. This mutualism not only supports the foundation species of these communities but also captures biologically novel sources of nutrition in ecosystems where such high densities of macroorganisms would be impossible with only photosynthetic inputs. Of the 300 species that occur at vents, 97% were previously unknown; they represent 1 new class, 3 new orders, 22 new families, and 96 new genera (Tunnicliffe 1992).

Coral Reefs

Corals are foundation species that provide the ecological infrastructure for one of the most biologically diverse ecosystems on Earth. Perhaps the most widely studied marine mutualisms are those between corals and their photosynthetic dinoflagellate symbionts (*Symbiodinium* spp.), known as zooxanthellae (Muller-Parker & D'Elia 1997). Zooxanthellae donate carbohydrates derived from photosynthesis to the coral, while receiving nutrients in the form of nitrogenous wastes derived from the prey of the carnivorous corals. Photosynthesis by zooxanthellae provides up to 95% of the coral's carbon budget and enhances coral calcification and growth; this leads to carbonate accretion and massive amounts of reef framework in tropical seas. In the absence of zooxanthellae-assisted growth, corals could not grow fast enough to stay in well-lit surface waters during periods of rapid sea-level rise, and slow-growing reefs would drown (Neumann & MacIntyre 1985). Thus, without the coral-zooxanthellae mutualism, coral reef ecosystems would be unlikely to persist.

Corals were initially thought to coevolve pairwise mutualisms with a single species of zooxanthellae, but recent investigations suggest the existence of several distinct genetic clades and many species of zooxanthellae; these studies also show that some zooxanthellae can be rejected and new strains acquired when corals are exposed to changing environmental conditions (LaJeunesse 2002, Baker 2003). Zooxanthellae clades differ in their photosynthetic capacity, tolerance of light, and production of photoprotective compounds such as mycosporine-like amino acids (Banaszak et al. 2000, Savage et al. 2002), which makes them differentially useful to their hosts as light levels change. Baker (2001) demonstrated that several species of Caribbean corals replaced resident zooxanthellae clades with new zoo-xanthellae clades when moved from low-light to high-light environments but not

when moved from high-light to low-light environments. Corals that did not bleach or acquire new symbionts died more frequently than corals that bleached but then acquired new symbionts. This suggests that a failure of corals to change symbionts when encountering new environmental conditions can be fatal. Such alterations in the coral-zooxanthellae mutualism may allow corals greater flexibility in adapting to global climate change (Baker 2002, Hoegh-Guldberg et al. 2002). This observation illustrates the context dependence of the coral-zooxanthellae mutualism that ultimately contributes to the success of corals as ecosystem engineers.

Although the coral-zooxanthellae mutualism drives the growth of corals that create coral reefs, a different, more diffuse and indirect, mutualism between corals and herbivores may be critical for the development and maintenance of coral reefs on both ecological and evolutionary time scales. Strong interactions between herbivorous fishes and reef corals suggest that their relationship constitutes a by-product mutualism. By feeding on seaweeds that are competitively superior to corals, herbivorous fishes both clear the substrate for settling coral larvae and prevent seaweed overgrowth of established corals (Lewis 1986, Hughes 1994). In return, the biogenic structure and topographic complexity of reef corals indirectly benefit herbivorous reef fishes by providing both habitat and food. The porous hard substrate allows rapidly growing filamentous algae (the preferred food of many reef fishes) to persist and maintain rapid rates of production, despite the constant removal of greater than 90% of algal production by reef herbivores (Carpenter 1986). When reef fishes are removed experimentally (Lewis 1986, Carpenter 1986) or by overfishing (Hughes 1994, Jackson et al. 2001), seaweeds replace corals and the biogenic structure of the reef degrades. Both reductions in coral structure and increases in seaweeds are associated with losses of herbivorous reef fishes (Jones 1991, McClanahan et al. 2000).

In fact, the diffuse mutualisms between corals and herbivorous reef fishes may have allowed the evolution of massive coral reefs. Intense herbivory probably did not exist on coral reefs until after the diversification of herbivorous fishes roughly 40 to 50 million years ago (Mya) (Vermeij 1977, Streelman et al. 2002). The reductions in seaweed biomass that followed may have been the tipping point that allowed widespread formation of coral reefs. Large scleractinian-dominated reefs first appeared 25 to 35 Mya during the Oligocene epoch, roughly 15 to 20 million years after the diversification of herbivores but almost 200 million years after the zooxanthellate corals evolved (Veron 1995, Hallock 1997). The rise of modern coral reefs may be a direct result of the evolution of intense herbivory by fishes and invertebrates, which shifted tropical benthic communities from seaweed-dominated to coral-dominated ecosystems (Wood 1998). If this hypothesis is true, then the diffuse mutualism between herbivorous fishes and corals may have been critical in allowing the development of modern reef communities.

Fishes and corals participate in other mutualisms in which fishes benefit by refuging among coral branches and corals benefit from nutrient supplements provided by the fish. For example, carnivorous grunts (*Haemulidae*) forage in seagrass beds overnight but school around stands of coral such as *Acropora palmata* and

Porites furcata during the day as a refuge from predators (Ehrlich 1975, Ogden & Ehrlich 1977). Coral stands that harbor fish schools receive nutrient supplements from fish excretion (Meyer et al. 1983, Meyer & Schultz 1985a), grow up to 23% faster, and have more nitrogen and zooxanthellae per unit area than do corals without resident fishes (Meyer & Schultz 1985b). This process of nutrient concentration and transfer also occurs on smaller spatial scales when planktivorous fishes shelter among the branches of individual corals and increase coral growth rates by as much as 40% (Shpigel & Fishelson 1986, Liberman et al. 1995). Thus, fishes that have no direct trophic link with corals collect nutrients from other communities (seagrass beds or the plankton) and concentrate these nutrients near their host coral. This nutrient subsidy facilitates coral growth and enhances the coral's value as a refuge for these fishes and for other reef organisms.

Mangroves

Mangroves dominate shallow coastlines throughout the tropics and are important habitats for a host of marine and terrestrial species. Their submerged prop roots serve as necessary hard substrate for a variety of seaweeds and invertebrates, with sponges being especially common on mangrove roots. Challenges to mangrove growth include low-nutrient soils and failure of prop roots during storms. Both challenges are lessened through mutualistic interactions with sponges such as *Tedania ignis* and *Haliclonia implexiformis*. When sponges are transplanted onto clean prop roots, fine rootlets proliferate, and nitrogen moves from the sponge to the tree while carbon moves from the tree to the sponge (Ellison et al. 1996). This exchange increases sponge growth by 40% to 100% and root growth by 100% to 300%, which is predictive of increased leaf production and net aboveground primary productivity (Farnsworth & Ellison 1996). Roots covered by sponges are also less frequently attacked by the boring isopod *Sphaeroma terebrans*, and if sponge-covered roots are attacked, they suffer less decline in growth than do attacked roots without a sponge cover (Ellison et al. 1996). Isopod attack reduces root growth by more than 50% (Perry 1988, Ellison & Farnsworth 1990) and can lead to mangroves toppling in storms and the shrinkage of mangrove islands (Rehm & Humm 1973, Svavarsson et al. 2002). Thus, protection by mutualist sponges has significant value. Furthermore, fragmentation of mangrove habitats can cause local extinctions of resident species (Grant & Grant 1997), decrease nutrient exports to other coastal ecosystems (Marshall 1994, Robertson & Alongi 1995), and reduce ecological resources such as fish and timber that are economically important to local human populations (Alongi 2002).

Seagrass and Saltmarsh Communities

Seagrasses support diverse communities of benthic invertebrates and fishes by providing biogenic structure and high productivity to otherwise featureless sand and mud flats. Seagrass blades are rapidly fouled by attached algae, sessile invertebrates, and detritus that decrease seagrass growth through shading and can

cause whole plants to be ripped from the substratum through increased leaf drag (Jernakoff et al. 1996). Nutrient eutrophication generally favors epibionts over sea-grasses (Jernakoff et al. 1996), and regional declines in seagrass abundance—and the fisheries they sustain—are correlated with increased nutrient supply and the deleterious impacts of fouling epibiota (Orth & Moore 1983).

Small consumers (mesograzers), such as amphipods, isopods, snails, shrimps, and crabs live on seagrass, consume fouling epibiota from its surfaces (Orth & van Montfrans 1984) and, by doing so, increase seagrass growth up to 200% (Duffy et al. 2001). The seagrass provides mesograzers with substrate for food and with a structural refuge that decreases susceptibility to predation (Leber 1985). Meadows of seagrasses support dense assemblages of mesograzers that are the primary trophic link fueling production of fishes, shrimps, crabs, and other larger animals in seagrass beds (Edgar & Shaw 1995). Therefore, the health and per-sistence of seagrass beds, which are critical nursery grounds for many coastal fishes, may depend on the mutualistic interactions between seagrasses and their surface-associated mesograzers.

The strong interaction between seagrasses and mesograzers is conditional and can change from mutual, to neutral, to antagonistic, depending on the environ-mental setting. When high water temperatures and nutrient loads favor epibiota, seagrass growth is enhanced by the addition of a mixed-species assemblage of mesograzers, but when cool water temperatures and low nutrient loads favor seagrasses over epibiota, mesograzer feeding does not enhance seagrass growth (Neckles et al. 1993). When epibiota become scarce, mesograzers may ingest liv-ing seagrass tissues and sometimes consume entire plants (Duffy et al. 2001, Duffy et al. 2003). The mutualist thus becomes a parasite under these altered environ-mental conditions.

Like seagrasses, saltmarsh vegetation provides biogenic structure, high produc-tion, and substrate stability on intertidal muds and sands. Saltmarsh production fuels coastal food webs, sustains fisheries, and provides nursery areas for juve-niles of many coastal species. Both seagrasses and saltmarsh plants form facultative mutualisms with suspension-feeding bivalves (Peterson & Heck 2001b, Bertness 1984). Bivalves benefit rooted macrophytes by (*a*) harvesting plankton from the water column and enriching the substrate via feces and pseudofeces (Bertness 1984; Peterson & Heck 2001a,b), (*b*) stabilizing the substrate (Bertness 1984), (*c*) decreasing light limitation of macrophytes by filtering phytoplankton and in-creasing water clarity (Jackson 2001), and (*d*) indirectly reducing epiphytic loads on macrophytes by harboring epiphyte grazers (Peterson & Heck 2001a). In re-turn, macrophytes provide bivalves with increased food supplies and a refuge from predators (Irlandi & Peterson 1991, Peterson & Heck 2001a).

Kelp Forests

Temperate rocky reefs with kelp forests have greater primary production, species diversity, and food-web complexity, and they export more energy to adjacent

communities than do nearby reefs without kelps (Duggins et al. 1989, Estes & Duggins 1995). In Alaska, indirect interactions between sea otters and kelps form a by-product mutualism that causes dramatic shifts from rocky reefs dominated by sea urchins to high-diversity kelp forests that can support higher densities of otters (Estes 1990, Estes & Duggins 1995). By consuming large quantities of herbivorous sea urchins, sea otters diminish herbivory, allowing kelps to flourish. Productive kelps increase habitat complexity and fuel local food webs, thus increasing the abundance of nutritious prey (especially the fish, *Hexagrammos lagocephalus*) upon which Alaskan sea otters feed. High kelp production and diverse, persistent prey associated with kelp beds are positive feedbacks that increase local carrying capacity and stability of sea otter populations (Estes 1990). The excess production from kelps is exported to nearby ecosystems, where it enhances growth of other organisms, thus producing not only local but also regional effects on marine food webs (Duggins et al. 1989).

OTHER MUTUALISMS WITH COMMUNITY CONSEQUENCES

Community Impacts of Nitrogen Fixation by Symbionts

Mutualisms between nitrogen-fixing microbes and pelagic hosts can be critical to the functioning of many pelagic ecosystems. Nearly all nitrogen is energetically inaccessible to most organisms; only nitrogen-fixing microorganisms can break the triple bond of N_2 molecules and convert this nitrogen into a biologically available form. Thus, open-ocean ecosystems are commonly nitrogen limited, and nitrogen additions from nitrogen-fixing microorganisms (i.e., bacteria, cyanobacteria, and Archaea) can profoundly influence large-scale patterns of productivity by providing from less than 1% to as much as 82% of the biologically available nitrogen in pelagic ecosystems (Howarth et al. 1988, Zehr et al. 2000).

Nitrogen-fixing plankton have broad distributions and influence oceanic food-web structure and function, community composition, fisheries yield, biogeochemical cycles, and even global carbon budgets (Karl et al. 1999). When bioavailable nitrogen is limiting, planktonic diatoms and dinoflagellates adopt nitrogen fixers as symbionts to provide organic nitrogen, vitamins, growth factors, and nitrogen-rich defensive chemistry. In return, the nitrogen-fixing symbiont gains a reliable carbon source to drive nitrogen-fixation. For example, blooms of the diatom, *Hemiaulus haukii*, and its nitrogen-fixing endosymbiont, *Richelia intracelluaris*, can (*a*) be 2500 km across, (*b*) account for 25% of the total nitrogen demand of this system, (*c*) increase primary production 270% compared with areas dominated by nonmutualistic phytoplankters and cyanobacteria, and (*d*) contribute about 0.5 Tg of new nitrogen to the euphotic zone (Carpenter et al. 1999). To visualize the magnitude of this nitrogen addition, think of it as the mass of 1.5 million Harley-Davidson Road King motorcycles, 7.3 million undergraduate students, or 157 million laptop computers. When nitrogen is abundant, phytoplankton abandon their

nitrogen-fixing symbionts (Gordon et al. 1994), which shows the conditional nature of these mutualisms and suggests a cost to such relationships.

Cleaner-Client Mutualisms

Cleaner fishes on tropical reefs remove parasites, mucus, and dead or infected tissue from cooperative fishes (i.e., clients) (Cote 2000). Reef-based cleaner fish are found at specific cleaning stations, usually situated on prominent portions of the reef. On the Great Barrier Reef, individual clients can visit the cleaner fish *Labroides dimidiatus* up to 144 times a day (Grutter 1995), and *L. dimidiatus* may clean up to 2300 individuals (Grutter 1996) and 132 different species (Grutter & Poulin 1998) a day. The cleaner benefits by food delivery to its territory (Grutter 1996, Grutter 1997), while the client reduces its ectoparasite load. When *L. dimidiatus* are experimentally removed from patches of reef, reef-fish diversity declines (Bshary 2003, Grutter et al. 2003), with the decline being more pronounced for highly mobile clients that visit several reef patches than for less mobile clients that stay on a single reef patch. Cleaner fishes can, thus, have a strong effect on parasite loads in their client fish and on fish usage patterns across patchy reef environments. A similar cleaner-client relationship occurs between an oligochaete worm that cleans the branchial chamber of freshwater crayfish, thereby enhancing crayfish growth and survivorship (Brown et al. 2000).

Host-Microbe Mutualisms

Mutualistic microbes can defend their host by producing chemicals that deter enemies of the host. Healthy embryos of the shrimp *Palaemon macrodactylus* are completely covered by the bacteria *Alteromonas* sp., which produce 2,3-indolinedione as a defense against the fungus *Lagenidium callinectes*, which is pathogenic to the shrimp embryos (Gil-Turnes et al. 1989). If the mutualistic bacteria are removed from the embryos with antibiotics, the embryos are killed by the fungus. If the symbiotic bacteria or the compound 2,3-indolinedione are added back to the embryos following antibiotic treatment, the embryos are protected from fungal attack. In this mutualism, the embryos provide a preferred surface for bacterial growth, and the bacteria chemically defends this resource, enhancing the survivorship of its host.

Microbial gut endosymbionts can also enhance host fitness by facilitating digestion and providing important growth factors for their hosts. In return, hosts provide their microbes with food and a predictable environment (Hungate 1975). Much like terrestrial ruminants, marine herbivorous fishes use gut microflora to help digest algal material (Choat & Clements 1998). Fishes in the genus *Kyphosus* house gut symbionts in a hindgut cecum that acts as a digestive chamber. The cecum keeps microbes under anaerobic conditions and allows fermentation of carbohydrates from the seaweed diet (Rimmer & Wiebe 1987, Seeto et al. 1996). Rates of digestive fermentation in these herbivorous fishes are comparable to those of many terrestrial vertebrate herbivores, which suggests that microbial

symbionts play an important role in the digestive process (Mountfort et al. 2002) and that endosymbionts may facilitate the large impacts that herbivores have on marine communities. In addition to aiding digestion directly, microbes are known for their ability to detoxify bioactive chemicals (Iranzo et al. 2001), such as those that seaweeds produce as chemical defenses against herbivores (Hay & Fenical 1988). Therefore, herbivore gut symbionts could act as bioremediators to detoxify seaweed chemical defenses. However, this hypothesis has yet to be investigated.

Sea urchins, such as *Strongylocentrotus droebachiensis*, benefit from endosymbiotic bacteria that fix nitrogen in the digestive tract (Guerinot & Patriquin 1981). When food quality is poor, microbial nitrogen-fixation rates increase, which suggests that bacteria subsidize the nitrogen requirements of sea urchins (Guerinot & Patriquin 1981). This nutritional subsidy could provide urchins with a competitive advantage over other grazers during periods when foods are scarce, and it helps urchins avoid mortality and maintain large populations despite limited food availability (Levitan 1988). This mutualism may facilitate the dramatic impacts urchins have on benthic community structure and their ability to sustain urchin barrens (Estes & Duggins 1995).

Bodyguards

Because sessile invertebrates have a limited behavioral capacity to fend off enemies, they often recruit mutualist bodyguards to ward off attackers. Along the coast of Pacific Panama, branching pocilloporid corals are abundant and commonly harbor the crab *Trapezia ferruginea* and the shrimp *Alpheus lottini*. These crustacean mutualists shelter in corals, where they feed on energy-rich coral mucus and are only 5% as likely to be consumed by predators as are crabs that are not sheltered in a coral host; in return, the crustaceans protect corals from attack by the crown-of-thorns starfish *Acanthaster planci* (Glynn 1976). As starfish mount the coral to feed, the symbionts drive them off by nipping at their tube feet. These crustaceans significantly alter *Acanthaster* feeding preference among coral species and thus alter the impact of coral predation on reef community structure (Glynn 1976). If massive corals are surrounded by barriers of branching pocilloporid corals, crown-of-thorns starfish are prevented from attacking the palatable, massive species by the crustacean symbionts in the encircling pocilloporids (Glynn 1985). When elevated temperatures kill large areas of pocilloporids, and crustacean symbionts abandon their hosts, *Acanthaster* crosses these former barriers and almost completely consumes massive corals that had been a successful part of the coral community for 190 years (Glynn 1985). Although pocilloporids and massive corals regularly compete for space, these pocilloporids and their bodyguards protect massive corals from *Acanthaster* predation, demonstrating the dynamic and context-dependent nature of mutualisms and showing how indirect effects of mutualisms can cascade to impact other community members.

Temperate corals are especially at risk for algal overgrowth because temperate reefs lack herbivorous fishes that prevent seaweeds from overgrowing corals

(Miller 1998). Some temperate corals solve this problem by recruiting herbivorous crabs to shelter among their branches and remove competing seaweeds (Stachowicz & Hay 1999). The branching coral *Oculina arbuscula* harbors the crab *Mithrax forceps* that feeds on all encroaching seaweeds, even those that are chemically defended from other herbivores. Corals with resident crabs grow and survive in well-lit habitats, whereas those without crabs die because of overgrowth (Stachowicz & Hay 1999). Crabs in live coral have significantly enhanced growth and survivorship compared with crabs in dead coral or crabs with access to no coral. This structurally complex but competitively inferior coral provides a biogenic habitat that is used by as many as 309 other local species, and as many as 161 species occur on a single *Oculina* head (McCloskey 1970). Thus, this mutualism not only allows both the coral and the crab to persist in areas where neither could survive alone, but it also produces a biogenic habitat used by many other species.

DANGEROUS LIAISONS (NEGATIVE PAIRWISE INTERACTIONS THAT BECOME POSITIVE IN A COMMUNITY CONTEXT)

Previous authors have noted that antagonistic interactions can evolve into mutualisms (Thompson 1982, van Baalen & Jansen 2001). This finding may be expected, given the close ecological and evolutionary connections between interacting consumers and prey, or parasites and hosts. Because traits for tolerating enemies are more likely to spread through prey populations than are traits for resisting enemies (Roy & Kirchner 2000), enemy-host interactions may commonly evolve toward more benign relationships. In the following sections, we do not discuss antagonistic interactions that have evolved into mutualisms, but rather we discuss antagonistic interactions that are still antagonistic from a pairwise perspective but become mutualistic when imbedded within the nexus of community interactions.

Consumer-Prey Mutualisms

SEAWEED-HERBIVORE MUTUALISMS   Encrusting coralline algae are heavily calcified seaweeds that resemble paint on a rock. Although their hardness and morphology make them resistant to attack by many herbivores (Steneck 1986), they are often fed on by gastropods that have hardened radulae that can scrape into the alga. Littler et al. (1995) demonstrated that about 50% of the diet of the herbivorous chiton *Choneplax lata* consisted of its preferred host coralline, *Porolithon pachydermum*. This alga covers a substantial portion of reef crest habitats along the Belizian Barrier Reef, and feeding by the chiton produces excavations and burrows in the alga. When this herbivore was experimentally removed from its coralline prey, the prey became fouled by epiphytic algae that attracted powerful-jawed, deep-biting parrotfishes. These parrotfishes consumed not only the palatable epiphytes, but also the coralline host. The deep bites of the parrotfish caused much

more damage to the coralline host than had been done by the chiton. With the chiton present, the coralline built up carbonate framework at a rate of 1 to 2 mm/y. When the chiton was removed, reef crest areas dominated by the coralline experienced net erosion because of heavy fish grazing. Thus, removal of the herbivorous chiton increased, rather than decreased, grazing damage to the coralline. Additionally, removal of the coralline caused a steep decline in the chiton population. In this mutualism, the grazer keeps its host free of fouling seaweeds, thus reducing attacks by damaging fishes. In return, the plant provides its consumer with a predictable food resource and a complex habitat in which to escape its own consumers. Neither the coralline nor the chiton are obligate mutualists. Each can be found without the other, but each is generally much more abundant and persistent when found together. This mutualism produces an important structural habitat that caps and protects many Caribbean reef crests and serves as a habitat for a diverse assemblage of other invertebrates (Littler et al. 1995). Steneck (1982, 1992) described a similar mutualism between the temperate coralline *Clathromorphum circumscriptum* and its major grazer, the limpet *Acamea testudinalis*. In these mutualisms, herbivore removal of some host mass in return for preventing greater loss is not fundamentally different from conventional mutualisms such as ant-plant, plant-pollinator, or seed-disperser interactions in which plants lose energy to their mutualists in the form of nectar, food bodies, or appreciable portions of their pollen or seeds in return for some offsetting benefit.

Herbivorous damselfishes form similar mutualisms with some seaweeds on tropical reefs. Through aggressive defense of the algal mats on which they feed, territorial damselfish create patches of intermediate grazing intensity where algal species richness, evenness, and diversity are increased relative to areas that are available to all grazers and relative to caged areas where all larger herbivores are excluded (Hixon & Brostoff 1983, 1996). Several algae are locally distributed only within damselfish territories. Although the rapidly growing filamentous algae in the fish's territory are its prey, they are also dependent on the territorial behavior of the fish to protect them from being grazed to local extinction by other groups of reef herbivores. If the territorial fish is removed, its algal lawn is completely consumed within hours (Hixon & Brostoff 1996, Ceccarelli et al. 2001). The presence of the territorial fish also increases algal productivity (both per unit area and per unit algal biomass), but the mechanisms that produce this effect are uncertain (Ceccarelli et al. 2001). Because of the density and ecological importance of damselfish territories to coral reefs, this consumer-prey mutualism can substantially augment reefwide production, algal biomass, and species richness (Hixon & Brostoff 1996, Ceccarelli et al. 2001).

PHYTOPLANKTON-ZOOPLANKTON MUTUALISMS   Some phytoplankton, such as *Sphaerocystis schroeteri*, pass through zooplankton guts (*Daphnia*) with minimal digestion, and their growth after gut passage is dramatically elevated compared with uneaten cells (Porter 1976). Although initially described as a mutualism (Porter 1976) in which the phytoplankton received nutrients to enhance growth

and the zooplankton received some gelatinous sheath material from the alga, the advantage to the grazer became less certain when it was realized that some phytoplankton species that withstood gut passage did not have gelatinous coverings and thus no covering to sacrifice (Epp & Lewis 1981). However, phytoplankton may continue appreciable photosynthesis while in zooplankton guts. The resistant algae are possibly trading photosynthate to zooplankton in return for viable gut passage (Epp & Lewis 1981), which would make this relationship a mutualism. Effects at the community level could be considerable; in grazing experiments, densities of species resistant to gut passage increase as more consumers are added (Porter 1976).

FUNGAL FARMERS   Just as leaf-cutter ants harvest tree leaves on which to culture their fungal gardens and damselfish kill corals as sites on which to culture their algal gardens, the salt marsh periwinkle, *Littoraria irrorata*, damages fresh blades of the marsh grass, *Spartina alterniflora*, as a substrate on which to culture its fungal food. The periwinkle commonly consumes ascomycete fungi in the genera *Phaeosphaeria* and *Mycosphaerella* that grow on blades of *S. alterniflora*. Although senescent blades of *S. alterniflora* are often colonized by fungi, younger blades are relatively resistant to fungal attack when undamaged. However, the periwinkle thwarts this defense by scraping surficial cells from *Spartina* and depositing fungal-rich and nutrient-rich feces onto the wounds (Silliman & Newell 2003). This process enhances fungal growth on *Spartina* by as much as 170%. Thus, the fungus is continually introduced to new resource patches that are less available without the scraping activity of the snails, and the snails harvest fungi from their expanded fungal farm (Silliman & Newell 2003). Although the snails directly damage only modest amounts of *Spartina*, their mutualism with fungi produces a large top-down effect on *Spartina* abundance. Areas of marsh where periwinkle densities are high can be nearly denuded of *Spartina* (Silliman & Zieman 2001, Silliman & Bertness 2002).

CONSUMERS AS DISPERSAL AGENTS   Consumers such as waterfowl and fishes have long been known to disperse aquatic propagules, just as terrestrial frugivores disperse seeds (Darwin 1859). In both cases, the prey lose some reproductive effort to consumers but gain the movement of their offspring over a greater area than would otherwise be possible. In ephemeral freshwater habitats, this consumer-mediated dispersal may critically affect both community dynamics (Shurin 2000) and the genetic structure of populations (De Meester et al. 2002).

Laboratory and field observations show that (*a*) 7% of seeds consumed by mallard ducks are viable after gut passage, (*b*) gut passage can increase germination success, (*c*) individual ducks may transport 5,000 to 10,000 intact seeds among wetlands during annual migration, and (*d*) many seeds are transported 13 to 75 km during short-range dispersal and up to 300 to 1400 km during "grand-passage" migrations (Figuerola & Green 2002, Holt Mueller & van der Valk 2002). Additional benefits to waterfowl could accrue because they deposit seeds of forage

species in newly available or newly disturbed sites that they visit repeatedly during migrations, thus eventually reaping what they sow.

Aquatic vertebrates such as fishes also can play a strong role in flood-plain forest dynamics by eating fruits, dispersing seeds, and thereby affecting tree recruitment and nutrient cycling (Goulding 1980). Goulding (1983, in Horn 1997) argued that a greater mass of fruits and seeds were consumed by fishes than by monkeys and birds in many flood-plain forests. Horn (1997) demonstrated that germination of fig seeds (*Ficus glabrata*) was unaffected after gut passage through the characid fish *Brycon guatemalensis*; he estimated that 500 million fig seeds were consumed and dispersed by *B. guatemalensis* annually along a 6-km river segment in Costa Rica.

For some marine macroalgae, spore dispersal increases when invertebrate herbivores consume nutritious reproductive fronds. This activity is analogous to Janzen's (1984) "foliage is the fruit" hypothesis for terrestrial herbivores, where large herbivores consume and disperse seeds inadvertently while foraging on foliage. The amphipod *Hyale media* preferentially grazes reproductive versus nonreproductive fronds of the red alga *Iridaea laminarioides* and, while feeding, releases up to nine times more algal spores than are released from ungrazed individuals (Buschmann & Santelices 1987). Few of the eaten spores survive gut passage, but those that do survive grow faster than uneaten spores, possibly because of nutrient absorption during gut passage or being deposited within nutrient-rich feces. Preferential feeding on reproductive fronds, along with the presence of viable algal spores and vegetative fragments in herbivore fecal pellets (Paya & Santelices 1989, Santelices & Paya 1989), can result in greater algal recruitment and persistence at sites with high herbivore damage to reproductive blades (Gaines 1985, Buschmann & Vergara 1993). The positive correlation between levels of herbivory and algal success in some species suggests that grazers could have a net positive impact via dispersal despite the negative impacts of grazing on adult tissues. Additionally, seaweeds adapted to rapid colonization and growth are the species whose spores are most likely to survive gut passage (Santelices & Ugarte 1987), which suggests that these species may profit from being deposited in areas where herbivores have removed other competitors.

Competitors as Mutualists

Interspecific competition is traditionally regarded as a negative interaction (−,−) for both participants. This assessment is true when only the two competing species are considered, but in a community context, the effects that a nearby competitor may have in lessening physical stresses or preventing successful attacks by enemies can counteract the negative effects of competition (Hay 1986, Stachowicz 2001, Bruno et al. 2003). Among coral reef sponges, it is more common to find morphologically similar species growing intermingled in multispecific groups of up to 12 individuals than it is to find a sponge colony growing alone (Wulff 1997). In field experiments, growth rates of the sponges *Iotrochota birotulata* and *Aplysina fulva*

and survivorship of *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva* were higher when the sponges were grown with heterospecifics than when they were grown alone or with conspecifics (Wulff 1997). Although the mechanisms conferring advantages to heterospecific groups are uncertain, these sponge species differ idiosyncratically in their susceptibility to predation, pathogens, and physical disturbance. The summed traits of the sponge consortia may enable participants to survive environmental challenges that would be insurmountable for any of them growing alone.

As a second example, congeneric species of scale-eating cichlids may benefit each other even though they share the same prey. These predatory fishes consume the scales of other living fish using a species-specific approach and attack sequence. In two congeneric species, attack success was greater when in the presence of the congeneric, but not conspecific, scale eaters (Hori 1987). Presumably, prey fish were unable to be as vigilant against multiple attack strategies. Thus, two species using a similar resource (scales on a given fish) facilitated, rather than interfered with, each other's success. Mutualism also may occur among individuals within a species, as exemplified by frequency-dependent selection in the scale eater *Perissodus microlepis*. Individual *P. microlepis* have asymmetrical mouthparts and corresponding attack strategies: "right-handed" individuals have mouthparts oriented to the right and attack the left side of their prey; "left-handed" individuals have mouthparts oriented to the left and attack the right side of their prey. Deviations from an even ratio of morphs within a population resulted in lower attack success in the dominant morph (Hori 1993). These observations suggest that these two morphs act mutually to increase attack success by decreasing prey-fish alertness for attacks from one side or the other.

Parasite-Host Mutualisms

Parasites, by definition, have direct negative effects on their hosts. Being parasitized could, however, be advantageous if the parasite also infects and has even stronger negative impacts on the host's competitors or predators (Thomas et al. 2000). The potential for parasites to influence community structure via such interactions is particularly relevant to species invasions, as introduced species can harbor pathogens that are much more virulent to native species that have never encountered the parasite. *Myxobolus cerebralis*, for example, is a protozoan parasite of salmonids that causes whirling disease in rainbow trout, cutthroat trout, brook trout, and several species of salmon, yet brown trout—thought to be the ancestral hosts of the parasite—are rarely symptomatic (Bartholomew & Reno 2002, Gilbert & Granath 2003). Where exotic brown trout co-occur with other salmonids in the western United States, the disease has been blamed for catastrophic declines of other trout populations and resulting increases in brown trout (Nehring & Walker 1996). Thus, the high virulence of *M. cerebralis* in North American salmonids may provide a net benefit to brown trout by excluding or reducing populations of competing salmonids. Furthermore, *M. cerebralis* may have benefited brown trout

within its native European range by preventing the widespread establishment of
rainbow trout, despite many attempted introductions (Lever 1996).

Parasites also might benefit their final host by manipulating the behavior of their
intermediate host to make it more susceptible to predation by the final host (Lafferty
1992, Lafferty & Morris 1996). By definition, parasites have direct negative effects
on their final host; however, if the value of the greater ease with which the final host
can feed on the intermediate host outweighs the costs of parasitism for the final host,
then the result can be a net mutualism. The host gets more food, and the parasite is
able to complete its life cycle. For example, killifish infected with larval trematodes
are 25 times more likely to be eaten by seabirds than are uninfected killifish,
probably because parasitized fish frequently expose themselves to predators via
conspicuous behaviors at the water's surface (Lafferty & Morris 1996). Larval
trematodes are hypothesized to have negligible effect on bird fitness (Martin 1950),
so the net gain associated with eating infected killifish could be substantially greater
than the negative impacts of trematode infection. Although we know of no data that
indicate trematode parasites and seabirds together can affect community structure,
both seabirds (Micheli 1997) and killifish (Vince et al. 1976) have strong impacts
on marine communities.

DIFFUSE MUTUALISMS

Although mutualisms generally are between species coupled in space and time,
reciprocally beneficial interactions can also arise between individuals and species
that interact only from afar or through multiple trophic links. Because diffuse
mutualisms can occur across ecosystem boundaries or have significant time lags,
they are rarely noticed. However, recent studies suggest that strong reciprocal
interactions can occur between species that appear to interact weakly (Berlow
1999), if at all, because of their spatial separation. Here, we discuss a mutualism
between marine fishes and the terrestrial trees that line the rivers and streams in
which these fish spawn and die—in some cases, more than 1000 km inland.

Juvenile salmonids spend up to two years feeding in freshwater streams and
rivers before migrating to marine waters, where they mature and gain nearly all
of their biomass, after which they return to their natal habitats to spawn and
die. Trees subsidize production in these streams with the input of nutrients, leaf
litter, and woody debris that supports higher populations of aquatic invertebrates,
the main food source for juvenile salmon (Everett & Ruiz 1993, Wallace et al.
1999, Helfield & Naiman 2002). At the landscape scale, forested streams typically
support up to three times more salmon than unforested streams (Pess et al. 2002).
Salmon, thus, benefit from living in streams surrounded by trees, but the benefit is
not unidirectional.

Spawning salmon migrations inject huge amounts of marine-derived nitrogen,
carbon, and phosphorous into relatively nutrient-starved systems. These massive
inputs of marine-derived nutrients can be detected in the surrounding watershed,
and streamside trees derive up to 26% of their nitrogen directly from spawning

salmon (Helfield & Naiman 2001). As a result, annual forest growth per unit area can be up to three times higher in forests adjacent to salmon spawning sites (Helfield & Naiman 2001). Furthermore, this subsidy of nutrients may alter the competitive balance among tree species. Whereas Sitka spruce dominate nitrogen-rich stream flood plains around salmon spawning sites, western hemlock dominate similar nitrogen-poor areas upstream of spawning sites (Helfield & Naiman 2001, 2003).

Salmon often return to the same stream in which they were spawned, and salmon from particular reaches of streams are more likely to be related to one another than they are to salmon from other reaches, which suggests a heritable basis for spawning site selection (Bentzen et al. 2001). Thus, when adult salmon return to a stream and die, their carcasses effectively fertilize not only their own offspring but potentially the offspring of relatives as well. In essence, adult salmon leave a bodily inheritance, the biomass accrued during a lifetime at sea, which fertilizes the resource base that feeds their offspring.

SUMMARY

Mutualisms are more than biological oddities that enhance our understanding of evolution. They are pivotal in affecting the organization, structure, and function of communities, yet this broader-scale importance of mutualisms is rarely appreciated. Many ecologically important mutualisms are not coevolved or obligate; they are instead conditional and provide partner species with novel options for adjusting to changing physical and biotic environments. Mutualisms commonly support the foundation species that define entire ecosystems, and they can play critical roles in moving energy and nutrients across ecosystem borders—as when mutualistic nitrogen fixers convert atmospheric N_2 into bioavailable nitrogen in oceanic gyres, when bivalves or fishes move planktonic nutrients to benthic communities, and when marine fishes and riparian forests produce reciprocal benefits. Through indirect interactions within a community setting, benefits gained can offset the negative effects of competition, predation, parasitism, and physical stresses to the extent that potential enemies interact as mutualists. These interactions may allow persistence within communities or the invasion of new ones. Historically, ecology has been dominated by the study of negative interactions (e.g., competition, predation, or parasitism). However, when mutualisms are investigated within their community matrix, positive interactions become as important as negative interactions in affecting community organization and thus deserve full incorporation into basic community theory.

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