

# Fine-Scale Interspecific Interactions on Coral Reefs: Functional Roles of Small and Cryptic Metazoans

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**ABSTRACT.** Direct underwater observations and experiments aided by scuba technology have greatly advanced the science of coral reef ecology. Coral community species interactions of small (macrofauna) and cryptic metazoans can exercise pivotal roles in the vitality, protection, and perpetuation of reef-building corals. Advances in the understanding of mechanisms underlying coral–metazoan symbiotic and facilitative interactions are examined in six invertebrate phyla (Porifera, Cnidaria, Acoelomorpha, Annelida, Mollusca, and Arthropoda) and in fishes, the latter with emphasis on cryptic coral reef fishes in the eastern Pacific. Crustacean associates of zooxanthellate corals, especially those inhabiting corals with branching morphologies, are notably diverse and can exhibit complex behaviors that greatly benefit their hosts. Several recently proposed positive effects of coral associates are reviewed, including evidence for increased colony stabilization, asexual fragmentation, interbranch circulation, cleansing of coral surfaces, mineral nutrient regeneration, reduction in the settlement of fouling organisms, and the removal of algal overgrowth. In several instances, the shared positive effects resulting from symbiotic interactions suggest that formerly regarded relationships of commensalism and parasitism are best viewed as mutualisms. The presence of a diverse and abundant cryptic fauna in coral communities suggests important roles in predation, selective recruitment effects, scavenging, and nutrient regeneration processes.

## INTRODUCTION

Fine-scale studies of interspecific interactions on coral reefs have demonstrated important roles of small and often inconspicuous invertebrate and fish metazoans. Notable advances have been made recently in our understanding of various trophic relationships in this often-neglected area. This paper offers a brief overview of biotic interactions of selected coral reef metazoans with emphasis on trophic relationships involving small, generally unseen or cryptic fauna. Coral symbioses (beyond the well-known microscopic, symbiotic zooxanthellae), reef scavengers, and cryptic fish carnivores are the chief areas addressed because of my personal involvement with research on these topics. Consequently, other groups of organisms such as herbivores, suspension feeders, deposit feeders, and parasites, while of paramount importance to the trophodynamics of reef ecosystems, are considered here only peripherally. This treatment considers mainly field-based observations via scuba diving, a principal method for observation, collection, and experimentation; however,

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Manuscript received 25 January 2012; accepted 5 March 2013.

relevant laboratory studies are referenced where they shed light on particular processes and relationships.

Coral-metazoan symbioses were generally considered to be interesting and novel when first reported, but with little if any ecological importance. Field studies conducted during the past few decades, however, have revealed several pivotal roles of coral-metazoan associations that can affect the survivorship of both symbionts and hosts and even influence coral community structure, reef growth, and recovery from disturbances.

Several excellent reviews are available on the animal associates of living corals (e.g., Garth, 1964; Patton, 1974, 1976, 1994; Bruce, 1976, 1998; Castro, 1976, 1988), however many new symbiotic relationships and functions have been described over the past two decades. This is due in large measure to a renewed interest in biodiversity and the development of new methodologies. To illustrate the breadth and depth of coral-metazoan interactions, examples are selected from documented studies in six invertebrate phyla (Porifera, Cnidaria, Acoelomorpha, Annelida, Mollusca, and Arthropoda) as well as fishes. Due to the great variety of coral-crustacean symbioses, relationships among the Cnidaria and Arthropoda are highlighted.

In addition to the many invertebrates associated with living corals, an abundant and diverse community of sessile and vagile metazoans is known to take refuge in dead coral crypts, including suspension feeders, necrophagous or scavenging species, carnivorous predators, and grazers (e.g., Jackson and Winston, 1982; Choi and Ginsburg, 1983; Gischler and Ginsburg, 1996; Wunsch et al., 2000). In most studies there has been a bias toward describing sessile taxa due in large measure to their ease of collection and quantification. Here I consider predominantly ecological interactions of motile cryptic fauna. Assemblages of cryptic scavengers from the eastern Pacific are compared with those reported from Lizard Island, Great Barrier Reef, Australia. Finally, the diets of cryptic reef fishes from 20 families in Colombia and Panama are considered. The data collectively indicate the prevalence of predation in cryptic coral reef habitats.

## TERMINOLOGY AND PERSPECTIVE

Emphasis in this essay is on the macrofauna (i.e., small invertebrates and fishes in the size range of 1–40 mm body length). This group also includes mesograzers and mesoherbivores, herbivorous taxa that are not microscopic but not easily seen when undisturbed (Hay et al., 1987; Carpenter, 1997). Occasionally reference is made to some taxa (e.g., ostracods, mysids, and isopods) that belong to the microfauna, with body length <1 mm. Moreover, some species examined exceed the size limits of the macrofauna (e.g., cryptic sponges, bryozoans, and tunicates in large cavities that can attain maximum body length in excess of 10–20 cm). Also, small postsettlement and juvenile stages of species that shelter in reefs are only temporary members of the macrofauna, attaining larger size as they grow, mature, and leave the confines of reef frameworks.

Most members of the macrofauna occupy cryptic habitats and remain hidden in reef structures that range from intra- to interskeletal cavities, borings, and interparticle spaces. The complexity of cryptic habitats in terms of physical conditions and biotic composition is highlighted in Ginsburg (1983) and Kobluk (1988). While many coelobites (i.e., cryptofauna or cryptic biota) remain permanently hidden (e.g., various intraskeletal and benthic species), large numbers also are transient and emerge from reefs daily (reef plankton), seasonally, or during development as they mature (e.g., mollusks, crustaceans, and fishes).

Some cautionary remarks are necessary regarding the classification of feeding modes. Clear distinctions between predators, scavengers, and parasites are often difficult to determine. Many consumer species are opportunists, assuming the role of predators or scavengers depending on the availability, variety, and condition of prey. For example, some omnivorous polychaete worms will pursue, attack, and consume preferred live prey when abundant, but will also resort to feeding on moribund and dead animals if their usual prey is in short supply. These feeding modes can also change depending on the developmental stage of the consumer. Other groups of metazoans exhibit feeding behaviors that may be considered to belong to two or more different feeding modes. For example, mesopredators that live in intimate association with coral colonies (e.g., flatworms, prosobranch and nudibranch gastropods, copepods, barnacles, crabs, shrimps, and gobies) typically consume small amounts of tissue and/or secretory products, causing only partial mortality, and therefore they may also be classified as parasites (Castro, 1988; Glynn, 1988). They also may be considered omnivores or even deposit feeders if they feed primarily on mucus or other byproducts of their coral hosts. Additionally, scavengers and detritivores that feed on dead and decaying plant and animal remains differ primarily in the relative size and state of degradation (microbial decay) of the organic matter ingested, which can vary widely depending on the size of the consumers.

Much debate surrounds the definition of symbiosis. Some researchers restrict the term to mutualisms (i.e., mutually beneficial relationships resulting from intimate heterospecific associations). Others have applied more restrictive criteria (e.g., requiring the demonstration of some degree of metabolic dependency [see Castro, 1988] or dismissing relationships in which a host responds to an organism's presence by forming a kind of physical barrier [Pantos and Bythell, 2010]). In this essay Anton de Bary's (1879) broad definition of symbiosis is employed, slightly modified as follows: an intimate and prolonged association between two or more organisms in which at least one partner obtains some benefit from the relationship. This definition avoids the categorization of relationships and preconceptions about outcomes (Saffo, 1993).

Not all cryptic metazoans are engaged in symbiotic interactions, but they may still benefit from the presence of associated species. Positive or facilitative interactions involve encounters that are beneficial to at least one of the participants and harmful to neither (Bruno et al., 2003). Facilitation is best regarded

as all encompassing; it can bring about positive effects under many guises. Various types of symbioses can have positive effects, and even predation and parasitism can result in indirect positive effects. For example, several metazoan symbionts of corals that were formerly regarded as harmful or neutral to their hosts are now known to provide various benefits (e.g., defense against predators, tissue irrigation, protection from fouling organisms, and nutrient enrichment). Many of the coral–metazoan associations considered below that are beneficial to at least one member can best be considered under the rubric of facilitation. The challenge is to rigorously quantify such positive interactions so that they can be related to individual fitness, species population dynamics, and community-scale composition and diversity.

## REEF MACROFAUNA: CASE STUDIES AND INTERACTIONS

### PORIFERA

Coral–sponge interactions are often perceived to be detrimental to corals because of the destructive effects of bioerosion as well as the competitive dominance and overgrowth of corals by sponges. At least two mutually beneficial interactions have been reported, however. These were observed by Goreau and Hartman (1966), who showed that the demosponge *Mycale laevis*, which is often present on the undersurfaces of plat-ing *Montastraea annularis* corals, may provide a benefit to the partnership. Sponge and coral growth are in balance, with neither overgrowing the other. The peripheral skeletal folds of the coral grow around the oscules of the expanding sponge. Potential competitors of sponges (i.e., fouling organisms) and boring organisms capable of penetrating coral skeletons are absent from those parts of the colony overgrown by the sponge. Additionally, the coral may benefit nutritionally from an enhanced feeding efficiency caused by the sponge's effluent currents. The sponge in turn occupies increasing substrate space as the coral grows.

Even excavating sponges, despite their bioerosive effects, may not have a negative influence in all situations. Highsmith (1982) noted several studies in which boring sponges were shown to promote asexual fragmentation in corals. The carbonate skeletons of most coral species are susceptible to erosion by clionaid sponges; both branching and massive coral colonies have been shown to shed live fragments that contribute to lateral reef expansion. This has been reported in the Caribbean for *Acropora* spp. and *Porites furcata* (branching taxa) and *Montastraea annularis* (a massive taxon), and in the eastern Pacific for *Pocillopora damicornis* (branching) and *Pavona clavus* (massive). The shedding, survival, and dispersal of fragments following disturbance events can aid in the rapid recovery of coral cover.

Several sponge species contribute to the stabilization of reef framework structures (Wulff and Buss, 1979; Rützler, 2004; Wulff, 2006). Both epibenthic and cryptic sponges temporarily stabilize coral rubble as they attach to and bind loose coral

fragments. Field experiments have demonstrated that sponge fragments can consolidate coral rubble quickly, within a 10-month period (Wulff, 1984). Small corals that had originated from asexual fragmentation (or sexual recruitment) were dependent on sponge binding. Sponge-mediated substrate stabilization provides an opportunity for the successful settlement and survival of corals, bryozoans, vermetid mollusks, and serpulid worms. Another result of the sponge-mediated stabilization was an increase in topographic relief, which was twice that of experimental rubble piles without sponges. Encrusting coralline algae contributed importantly in later stages of the consolidation cycle.

Some quantitative measures of the contribution of cryptic sponge filter feeders to ecosystem-scale trophodynamics have been reported for a fringing Red Sea reef by Richter et al. (2001). By means of endoscopic exploration, these researchers determined that the surface area of reef cavities greatly exceeded that of reef surfaces by factors of 2.5–7.4 m<sup>2</sup>. Sponge cover predominated in cavities, amounting to 60% of all coelobites, and exceeded surface filter feeder biomass by twofold. This study concluded that the consumption and mineralization of allochthonous organic matter by cryptic sponges is a principal source of nutrients that support endosymbiotic algal and coral growth. The magnitude of this cycling could help explain how high coral reef productivity occurs in often nutrient-deficient waters.

### CNIDARIA

Cnidarians offer numerous resources to reef organisms, and this is reflected in the great variety of taxa associated with zooxanthellate corals, from bacteria and fungi (Rohwer et al., 2002; Knowlton and Rohwer, 2003) to invertebrates and fishes (e.g., Patton, 1976; Castro, 1988; Cole et al., 2008; Glynn and Enochs, 2011). Reef-building or zooxanthellate corals (i.e., those harboring endosymbiotic photobionts [*Symbiodinium*]) provide shelter and protection (cnidocytes) from predators, and trophic resources (mucus, tissues, lipids, zooxanthellae) for their metazoan residents.

Perhaps the most celebrated corals offering shelter and trophic resources to diverse metazoan symbionts are several species in the scleractinian families Acroporidae and Pocilloporidae. Their tissues, secretory products, and endosymbiotic algae provide a rich source of nutrition for numerous crustacean associates, many of which are obligate symbionts of specific coral host taxa. No fewer than four trophic pathways were identified by Rinkevich et al. (1991) for a pocilloporid species (*Stylophora pistillata*) in the Red Sea (Figure 1). At the base of this food web are the microbial community and particulate organic detritus plus minute plankton organisms embedded in the coral host's mucus. This organic matrix is consumed by obligate *Trapezia* crabs and other coral symbionts, as well as various facultative and free-living grazing metazoans. Metabolic byproducts (nutrients) of the coral host are utilized by zooxanthellae, which in turn supply corals with photosynthates. Although early investigators surmised that crustacean symbionts fed primarily on coral mucus,

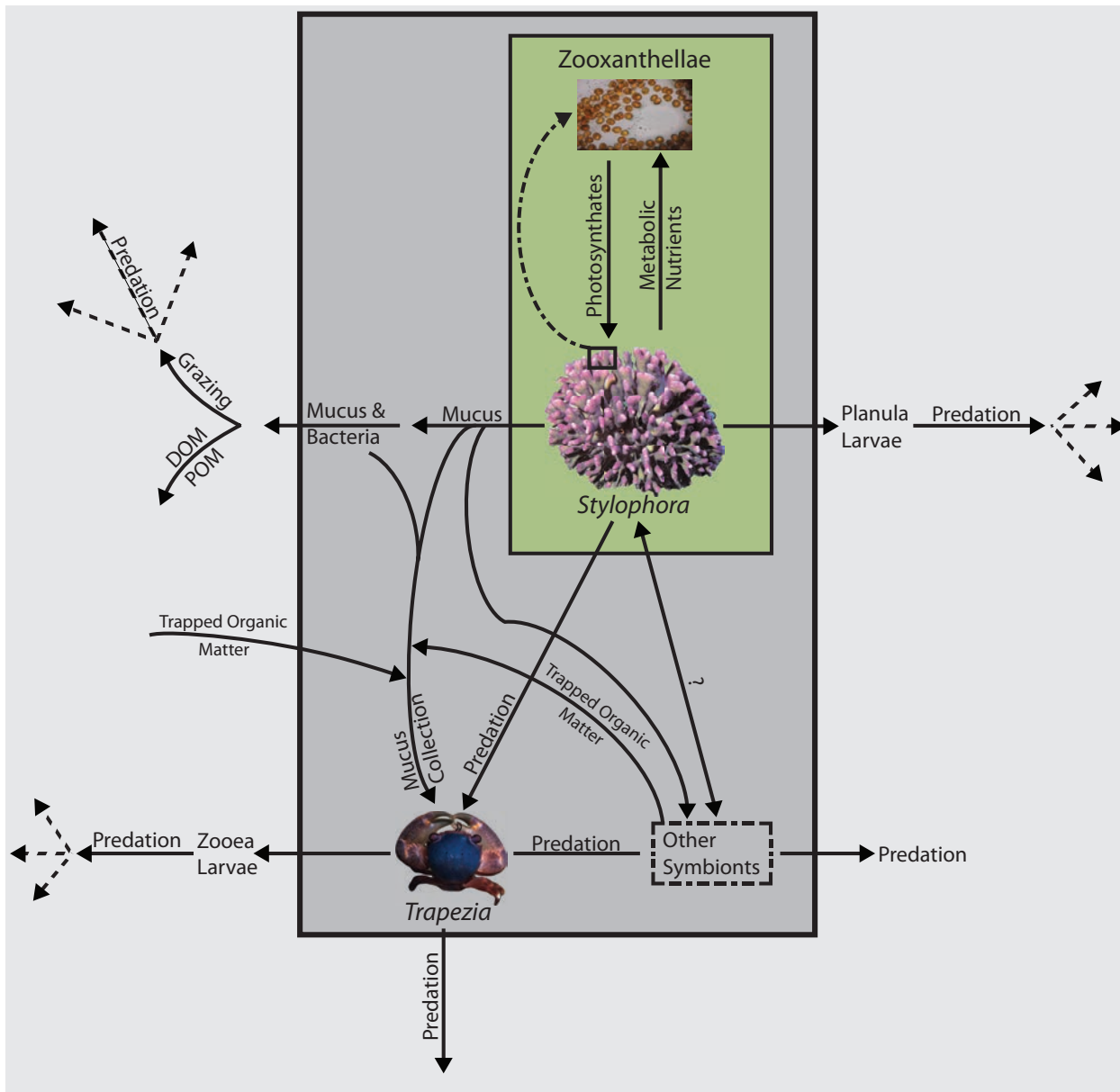


FIGURE 1. Multiple trophic pathways in a coral/microbial/zooxanthella/crab symbiosis (modified from Rinkevich et al., 1991).

Rinkevich et al. (1991) demonstrated conclusively—by employing C-14 isotopic labeling—that *Trapezia* grazes directly on coral host tissues. An additional trophic pathway involves predation of crustacean and other symbiont associates by free-living invertebrates and fishes. Finally, the larvae released by host corals and metazoan symbionts into the water column are consumed by planktivores.

Not only are zooxanthellate corals essential for building reef frameworks, but they also provide a limestone substrate that is actively eroded and occupied by numerous excavating taxa such as fungi, microfilamentous algae, sponges, annelid worms, bivalve mollusks, crustaceans, and fishes (Hutchings, 1986; Glynn,

1996; Perry and Hepburn, 2008; Tribollet and Golubic, 2011). Early studies have described the symbiotic relationship between endolithic bivalve mollusks and fungiid corals, and how embedded mytilid bivalves engulf various items (e.g., phytoplankton, mucus, and extruded zooxanthellae) from the coral host's coelenteron (Goreau et al., 1970). In a classic study, Goreau and Yonge (1968) described the unique relationship between a free-living dendrophyliid coral (*Heteropsammia*) and a sipunculid worm (*Aspidosiphon*). The coral host provides a refuge for the sipunculid, which pulls the coral along the muddy-sandy bottom. This enhanced mobility increases the feeding efficiency of the coral,

which sweeps its tentacles across the mud surface. The sipunculid in turn probes subsurface sediments while feeding—neither partner in competition with the other.

A diverse suite of nonexcavating organisms also finds refuge in available cavities. This community of hidden organisms, including those that occupy interskeletal spaces, is referred to as the opportunistic cryptobiota or nestling fauna. Several researchers maintain that the cryptobiota may exceed in diversity and biomass the visible surface biota (Ginsburg, 1983; Reaka-Kudla, 1997; Richter et al., 2001).

#### ACOELOMORPHA

Another complex symbiotic association, involving corals, epizoid acoel worms, and algal symbionts, is being actively investigated in the northern Red Sea (Barneah et al., 2007). *Waminoa brickneri*, possibly one of a multispecies complex, has been found on the surface tissues of 13 zooxanthellate scleractinian coral species at Eilat. The acoel worms generally demonstrate a low infestation rate (<5%); however, notably high abundances have been observed on some coral hosts. Both *Waminoa* and the coral hosts contain endosymbiotic dinoflagellates. *Symbiodinium* sp. and ?*Amphidinium* sp. were present in the worm, as was *Symbiodinium* sp. in the corals. Molecular genetic evidence and histological examination indicated that the two genera of dinoflagellates in the acoel worm are unique and therefore not present in the coral host. The symbionts are independently and vertically transmitted by the worm via oocytes during gametogenesis. This is the first evidence of maternal transmission of dinoflagellates in a triploblastic organism. These worms probably consume coral mucus and may have a negative impact on their host coral's photophysiology when present in large numbers.

#### ANNELIDA

To date, the amphinomid polychaete *Hermodice carunculata* is the only annelid species known to prey consistently on coral tissues (Fauchald and Jumars, 1979). This worm is widely distributed on western Atlantic reefs, where it typically preys on branching corals within the genera *Acropora* and *Porites*. Its preference for these corals is of increasing concern due to population declines of acroporids following hurricane disturbances (Knowlton et al., 1990) and disease outbreaks (Williams and Miller, 2005). In the eastern Mediterranean Sea, *H. carunculata* preys on *Oculina patagonica* and in the process inadvertently infects its prey with *Vibrio shiloi*, a causative agent of coral bleaching (Sussman et al., 2003). It is not presently known if *H. carunculata* can infect acroporid prey in the tropical western Atlantic.

*Pherecardia striata*, an eastern Pacific amphinomid, is an aggressive reef predator/scavenger and vigorously attacks wounded or moribund *Acanthaster planci* sea stars (Glynn, 1982). *Acanthaster* that are wounded by harlequin shrimp (see below) or fish predators attract the worms, which enter the sea star's body cavity and consume soft organs such as hepatic caeca and gonads.

*Pherecardia* are cryptic and patchily distributed within pocilloporid reef frameworks; where present, they can attain median population densities of 90–380 individuals m<sup>-2</sup> (Glynn, 1984).

A sessile polychaete worm that constructs and occupies calcareous tubes embedded in massive corals has been shown to promote polyp survival following damage from corallivores and bleaching. The polychaete in question has been tentatively identified as *Spirobranchus giganteus*, a member of a possibly 10–12 species complex (Fiege and ten Hove, 1999). Many but not all individuals were observed to defend their coral hosts (*Porites* spp.) on the central Great Barrier Reef by thrusting their hook-adorned operculum at the tube feet and arms of attacking *Acanthaster*. This reaction interrupted the sea star's feeding response, resulting in localized polyp survivorship. Surviving polyps contributed to the regeneration of large, old colonies that experienced tissue mortality on surfaces lacking defending worm symbionts (DeVantier et al., 1986).

Ben-Tzvi et al. (2006) have suggested that *Spirobranchus giganteus* worms living embedded in corals may also benefit their hosts during bleaching events. They found that coral tissues immediately surrounding the serpulids showed no damage and quickly recovered after bleaching events. This led these researchers to hypothesize that sessile tube worms positively influence their immediate surroundings by causing (1) improved water circulation, (2) more efficient dispersal of waste products, and (3) increased availability of nutrients. Additional evidence that nutrients from spionid polychaete worms may be involved in coral tissue regeneration was offered by Wielgus and Levy (2006) in a study at Eilat in the northern Red Sea. Via the application of an active fluorescence technique over infested and noninfested coral colony surfaces, these researchers observed marked differences in holobiont primary production. Photosynthetic activity and coral tissue proliferation were greatest at worm-infested sites, leading to the conclusion that spionid waste products contribute to localized eutrophication. Also, the experimental coral, *Astreopora myriophthalma*, showed knobby growth aberrations at the sites of infestation. They concluded that this was due to an increased nitrogen/carbon ratio near the worms that resulted in greater tissue proliferation compared with calcification.

#### MOLLUSCA

Most studies examining the effects of mollusks on zooxanthellate corals highlight their negative influences. Noteworthy are the several species of gastropods that graze on coral tissues (Robertson, 1970; Hadfield, 1976; Schuhmacher, 1992; Rotjan and Lewis, 2008) and bivalves that bore into coral skeletons (Kleemann, 1980; Valentich-Scott and Tongkerd, 2008). Obligate gastropod corallivores—for example *Drupella* spp. in the western Pacific and Indian Oceans, *Jenneria pustulata* in the eastern Pacific, and *Coralliophila* spp. in the Caribbean—have caused significant mortality on some reefs. Additionally, *Phesittia lugubris* (= *sibogae*), an aeolid nudibranch, lives its entire life and feeds extensively on *Porites compressa* colonies in Hawaii



(Hadfield, 1976). It is highly secretive, which helps it to avoid potentially intense fish predation. Remarkably, Haramaty (1991) presented indirect evidence that *P. lugubris* may utilize the photosynthetic products of endosymbiotic zooxanthellae that are ingested (and remain viable) along with coral tissues.

Like the corallivorous polychaete noted above (*Hermodice carunculata*), *Coralliophila abbreviata* was observed to concentrate on remnant corals (*Acropora* spp.) that survived a severe hurricane disturbance (Knowlton et al., 1981, 1990). Field experiments in the Florida Keys have demonstrated that *C. abbreviata* can transmit a coral disease (tentatively termed “rapid tissue loss”) to acroporid corals (Williams and Miller, 2005). Thus, acroporid corals that have experienced recent population declines due to stress and disturbance events may be subject to additional mortality from increased predation and disease outbreaks.

Epizoic vermetid gastropods have been shown generally to reduce coral growth and survival (Colgan, 1985; Shima et al., 2010). *Porites lobata* colonies at Moorea, French Polynesia, suffered both reduced growth (up to 82%) and survival (up to 52%) from the smothering effect of the mucus feeding net of *Dendropoma maxima*. This vermetid also has a marked effect on the morphology of massive and branching corals, transforming both growth forms to flat-surfaced colonies (Zvuloni et al., 2008). *Trapezia* crab symbionts, however, have been observed to mitigate the negative effects of vermetids on coral growth (Figure 2; Stier et al., 2010). This is accomplished by *Trapezia*'s

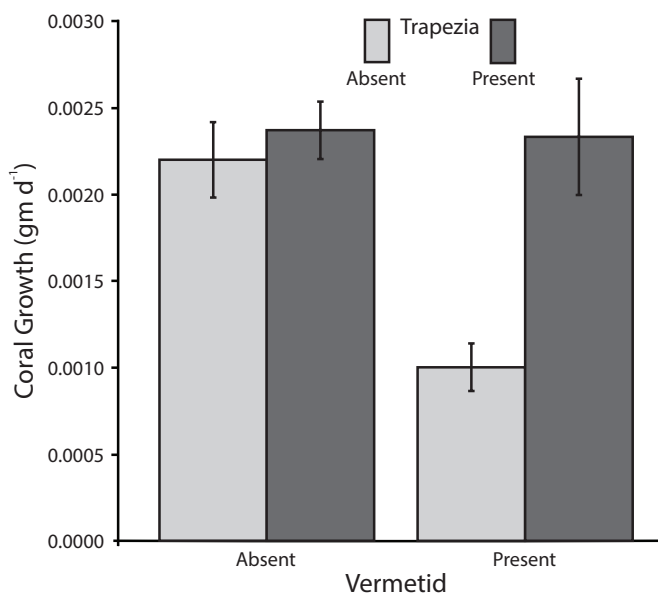


FIGURE 2. Mean ( $\pm 1$  SE) effects of *Dendropoma maximum*, a vermetid gastropod, and *Trapezia serenei* on the growth of *Pocillopora* cf. *verrucosa*. In the presence of vermetids, *Trapezia* can prevent the negative influence of the gastropod's mucus feeding net on its coral host's growth (modified from Stier et al., 2010).

consumption of vermetid mucus, as well as by its both inadvertent and directed dislodging of mucus.

Positive effects of bivalve mollusks on corals range from increased asexual reproduction to coral host defense and nutrient enrichment. Bivalve borers promote skeletal breakage and disintegration, which can enhance the asexual propagation of corals and also provide microhabitats for cryptic metazoans. Similar to *Spirobranchus giganteus*, the polychaete worm noted earlier, the scallop *Pedum spondyloideum* was observed to defend *Porites* spp. colonies on the Great Barrier Reef (DeVantier and Endean, 1988). This scallop lives embedded in the skeletons of *Porites* spp. and often prevents *Acanthaster* from feeding on nearby polyps by repeatedly expelling jets of water. Surviving polyps may then reproduce asexually and assist in colony recovery. Mokady et al. (1998) have questioned the parasitic role of boring bivalves in association with coral hosts. From field and laboratory studies in the northern Red Sea, they found that ammonium nitrogen recycled by *Lithophaga simplex* supplied a significant amount of this nutrient to zooxanthella symbionts in a massive coral (*As-treopora*). They concluded that this tripartite symbiosis may be best regarded as a mutualism.

#### ARTHROPODA

Crustaceans are the principal invertebrates present on living corals, with numerous species of copepods, barnacles, shrimps, and crabs represented. In terms of species richness and abundance, copepod associates of reef-building corals are noteworthy (Humes, 1985; Stock, 1988). Also, sessile pyrgomatine barnacles are common on eight major scleractinian and hydrocoral higher taxa (updated from Ross and Newman, 1973; Glynn and Enochs, 2011). At least 48 species of pontonine shrimps in 16 genera are obligate symbionts in several coral genera, especially in branching species of *Acropora* and pocilloporid species of *Pocillopora*, *Stylophora*, and *Seriatopora* (Bruce, 1998). These same branching coral taxa are also known to host numerous species of obligate trapeziid crab symbionts (Patton, 1966, 1974, 1976; Castro, 1988; Castro et al., 2004).

Copepods that belong to the species-rich Xarifiidae inhabit the gastrovascular cavity of corals and have been assumed to be obligate endoparasites. Up to nine copepod species have been found on individual colonies of *Acropora*, and a single colony of *Pocillopora* was found to host 668 individuals belonging to a single copepod species (Humes, 1994). A recent study by Cheng and Dai (2010) presented evidence suggesting that *Xarifia fissilis* associated with *Pocillopora damicornis* consumes zooxanthellae from its coral host. Furthermore, their study indicated that ingested algal cells remained photosynthetically active, and in an experimental starvation treatment copepod hosts supplied with light suffered significantly lower mortality than copepods maintained in the dark. This result suggests that photosynthetically active algae in the gut may provide photosynthate to the copepod, at least over the short term. If zooxanthellae are still viable when voided, it is possible they could disperse to other corals,

serve as an inoculum source for planular larvae, or assist in the repopulation of zooxanthellae in bleached corals.

With respect to feeding interactions, barnacles interact in various ways with their coral hosts. While most are suspension feeders, a few barnacles consume coral tissues directly (Ross and Newman, 1995, 2000). For example, *Pyrgoma monticulariae* stimulates coral tissue growth into its aperture to facilitate feeding (Ross and Newman, 1969). Species of *Lithotrya* bore into dead coral skeletons and extend their cirri into the surrounding water when feeding. They probably play a more important role in bioerosion than in any nutritional exchange. Several researchers, however, have hypothesized a mutualistic relationship between barnacles and their scleractinian and hydrocoral hosts. From a study utilizing stable carbon isotopes, Achituv et al. (1997) found that several species of coral-inhabiting barnacles assimilate carbon from their coral hosts via coral tissues (presumably abraded) and zooxanthellae. Barnacle symbionts can also have a positive effect on coral holobionts. The phosphorus and nitrogen excreted by barnacles can be absorbed by endosymbiotic zooxanthellae (Cook et al., 1991; Achituv and Mizrahi, 1996). Finally, a provocative experiment testing the effects of filter-feeding pyrgomatine barnacles on their hydrocoral host suggested an antifouling role (Pasternak et al., 2001). *Millepora* hydrocorals without their barnacle symbionts (experimentally stripped) were subject to higher rates of fouling by algae and fungi compared to corals with their usual complement of barnacles. These results suggest that the filtering capacity of barnacles can offer corals protection from fouling by water-borne organisms.

Some hermit crabs—members of the crustacean order Anomura—are also known to live symbiotically with corals. Species of *Paguritta* live in polychaete tubes present on corals (Schuhmacher, 1977) or in self-constructed boreholes in living coral (Lewinsohn, 1978). Juveniles of *Paguritta harmsi* were reported to live within the tissue-containing corallites of the massive coral *Astreopora* (Patton and Robertson, 1980). Since the corallites of the host coral lack columellae, the hermit crab is able to extend its soft abdomen into the corallite for protection. The crab's right cheliped is flat and covered with spines, thus serving as an operculum when the crab is disturbed and withdraws within the corallite. It was hypothesized that small hermit crab recruits likely remain in the corallites while the coral grows, keeping pace with the growth and thus producing an elongated pit. *Paguritta* spp. possess feathered antennae and depend entirely on a filtering mode of feeding. Species recognition is often difficult; at least six species are known in this genus (McLaughlin and Lemaitre, 1993).

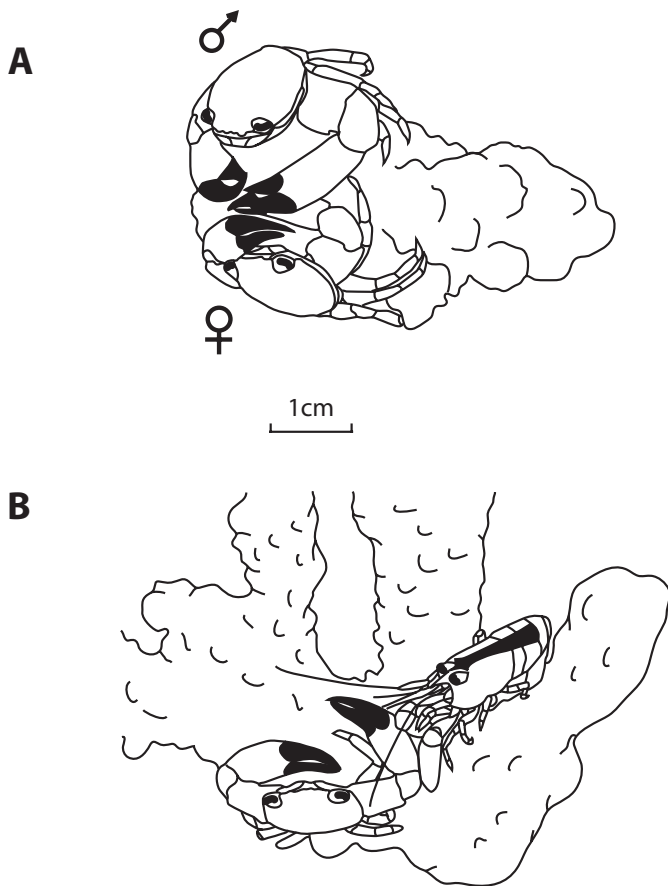
Gall crabs, members of the order Brachyura, are also sedentary obligate crustacean symbionts of reef-building corals. These crabs were long thought to be suspension feeders until Kropp (1986) found that they feed on coral mucus and tissues. Evidence from a chlorophyll spectral analysis indicates that excreta from a gall crab species of *Cryptochirus* fertilizes the immediate surroundings and thus enhances endosymbiotic zooxanthella production (Simon-Blecher et al., 1996).

A rich fauna of mobile trapeziid crabs and pontoniine shrimps occur as obligate associates on pocilloporid and acroporid corals. Branching coral hosts typically provide quality shelter and trophic resources for these crustacean taxa. Early studies suggested that crustaceans were the sole beneficiaries of this partnership, feeding on coral mucus plus entrapped particulate organic matter. Accordingly, these crab and shrimp crustaceans were classified as ectoparasites (Knudsen, 1967) or commensals (Patton, 1974). More recent studies have demonstrated that *Trapezia* spp. crabs actually consume coral tissues directly (Rinkevich et al., 1991) as well as "fat bodies" or lipid globules produced by the coral hosts (Stimpson, 1990). The crabs harvest this food source by inserting their pereopods into polyps. Movements of the pereopods stimulate fat body production, which occurs only when crab symbionts are present.

There are now several lines of evidence showing that mobile crustaceans provide various levels of facilitation to their hosts. Demonstrated positive effects include protection from corallivores (e.g., Glynn, 1983a; Pratchett, 2001); improved water flow within interbranch spaces and the removal of foreign organisms and contaminants (Glynn, 1983b); and reduced sediment deposition and increased coral growth and survivorship (Stewart et al., 2006). Crab and shrimp agonistic behaviors also help regulate the abundances of potential competitors by preventing the over-exploitation of host resources. It is likely that strong and persistent selective forces have resulted in the evolution of aggressive behaviors that both reduce competition and limit mortality by corallivores.

In the remainder of this section, a few noteworthy obligate crab and shrimp interaction effects are considered first, followed by selected examples of free-living species that can directly or indirectly affect coral survival. Trapeziid crabs typically form heterosexual pairs and aggressively defend their coral hosts from conspecific individuals (Preston, 1973; Patton, 1974). This aggressive behavior is also directed toward other species that could potentially compete for resources or harm the coral host. *Trapezia* crabs and *Alpheus* shrimp, however, coexist in stable populations on *Pocillopora* corals, with both the crabs and shrimp defending their coral hosts against intruders of both species.

Movement between colonies, usually at night, commonly occurs in *Trapezia* crabs (Castro, 1978). At such times, the migrating crabs are vulnerable to fish invertivores and quickly associate with a coral host. Vannini (1985) observed that a *Trapezia* crab attempting to enter a coral colony must perform cheliped rubbing and body contact with a conspecific resident crab before being accepted (Figure 3A). These appeasement behaviors usually allow an alien crab to successfully establish residency in the colony. *Alpheus* shrimp must also perform similar behaviors with crabs (i.e., cheliped rubbing and body contact to gain access to a defended colony; Figure 3B). While other behaviors occur between resident and intruding (alien) shrimp, cheliped rubbing and body contact are performed almost exclusively between shrimps and crabs and seldom between alpheid shrimps themselves. Vannini (1985) speculated that shrimp, the weaker



**FIGURE 3.** Crustacean appeasement interactions preceding acceptance of a nonresident associate into a *Pocillopora* sp. colony. (A) Intruder female *Trapezia ferruginea* rubbing her right cheliped against left cheliped of resident male crab. (B) Intruder *Alpheus lottini* shrimp rubbing both chelipeds against resident *T. ferruginea* (modified from Vannini, 1985).

of the two combatants, needed to adopt the “language” of the stronger crab aggressor. Since crabs tolerate shrimp more than their own conspecifics, Vannini further suggested that snapping shrimp could be exploited by resident crabs as a clarion warning of approaching intruders and predators (see below).

Behavioral interactions among obligate crab, shrimp, and gobiid fish symbionts of *Pocillopora damicornis* colonies have been shown to facilitate the coexistence and stability of symbiont assemblages (Lassig, 1977). Resident crab–fish interactions were generally nonagonistic. Gobies made contact with crabs in various positions and performed shivering movements (rapid flexion of the entire body and median fins, particularly the caudal fin) similar to those employed in courtship behavior (Figure 4A–C). However, nest sites on coral branches were vigorously defended by *Paragobiodon* spp. during the breeding season. There are two species of gobiid fishes present in *Pocillopora*; *Paragobiodon*

*lacunicola* mostly occurs near the base of corals, where it overlaps spatially with *Alpheus* more than with the other gobiid species, *P. echinocephalus*. The appeasement signal system—shivering and antennal contact—exists between the shrimp and *P. lacunicola*, but not between the shrimp and *P. echinocephalus* (Figure 4D–E).

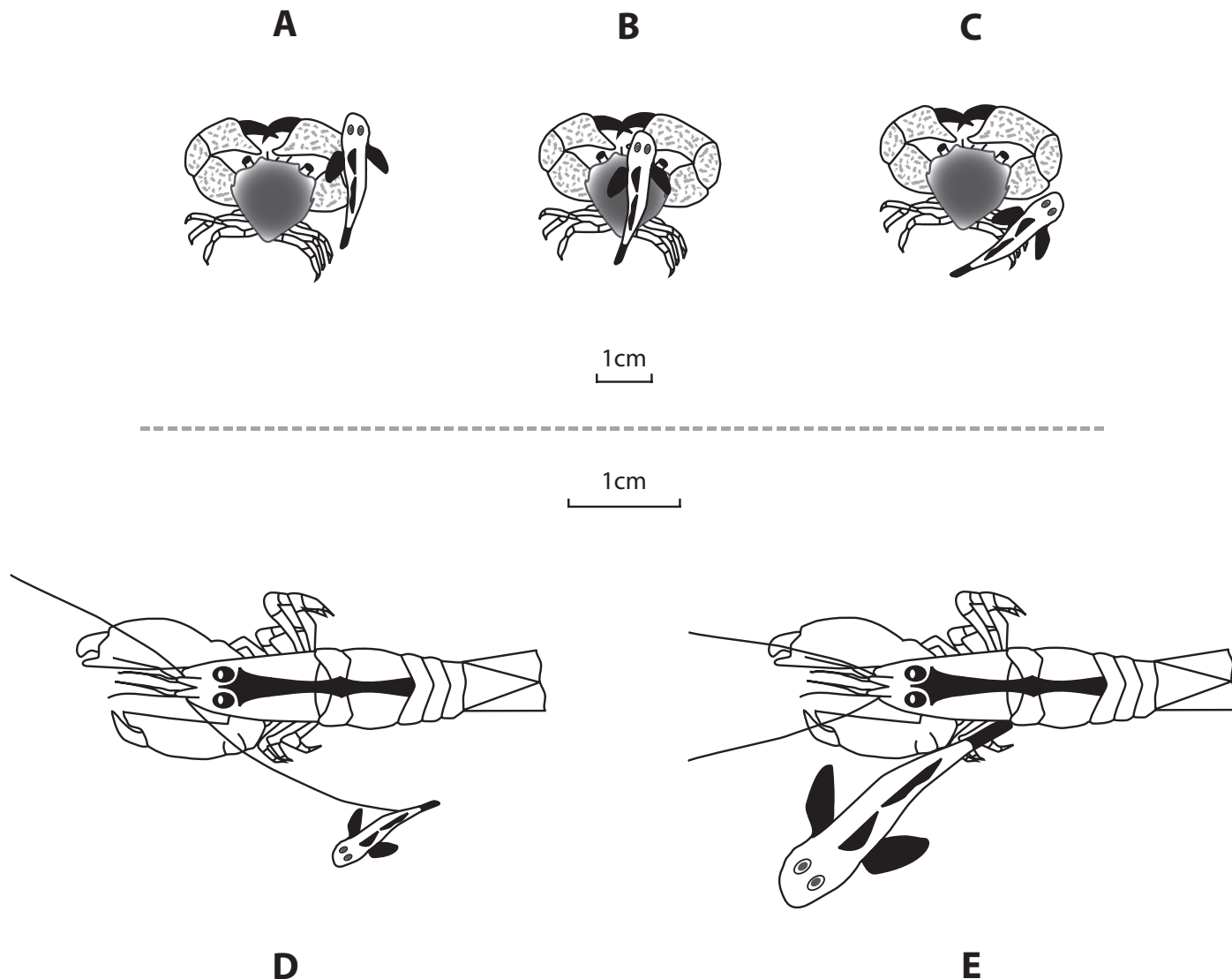
The first reported observations of trapeziid crabs defending their coral hosts from predator attack were by Pearson and Endean (1969) and Weber and Woodhead (1970). These researchers noted how the obligate crab associates of pocilloporid corals could repel attacking sea stars (*Acanthaster planci*) on southern Pacific reefs. Although I refer to the single taxon *A. planci*, four distinct species of *Acanthaster*, each with well-defined geographic distributions, are now recognized (Vogler et al., 2008). It is possible that these species have different feeding preferences and elicit different defensive responses. However, observations in the eastern Pacific have demonstrated a repertoire of relatively consistent crustacean defensive behaviors when compared with coral guards from other Indo-Pacific regions.

Five defensive activities of *Trapezia ferruginea* on eastern Pacific reefs in Panama have also been observed in Guam, American Samoa, and Oman (Glynn, 1976, 1980, 1983a, 1987). An approaching *Acanthaster* typically elicits a startle or meral display in which an alerted crab will move to the coral’s peripheral branches and flex its chelipeds widely (Figure 5A). If *Acanthaster* attempts to mount the colony, *Trapezia* may then begin to push the sea star away, executing several thrusts per minute (Figure 5B). If the pushing response is unsuccessful, the defensive behaviors often escalate to the following three patterns: (1) up–down jerking, (2) pinching and clipping of spines and tube feet, and (3) resisting retreat of *Acanthaster* (Figure 5C–E). In the last response, a defending crab will grip a pair of spines near the arm tip and temporarily prevent the sea star from fleeing. When the crab is maximally stretched it will suddenly release its grip, causing the sea star to lurch forward and then quickly retreat from the guarded coral.

If attacking sea stars are approaching corals from an up-current direction, chemical cues or danger signals (kairomones) move down-current and alert the crustacean guards, which quickly move to peripheral branches where they assume defensive postures. The first agonistic responses toward attacking *Acanthaster* are pronounced snapping by *Alpheus* and meral displays by *Trapezia*, both of which are directed toward the predator from the coral’s peripheral branches (Figure 6). Glynn (1980) demonstrated experimentally that some unknown factor diffuses from the sea star and arouses the crustaceans. It is possible that the high concentrations of saponins in *Acanthaster*, which function as surfactant repellents to predators, alert the crustacean guards, but experimental testing of this hypothesis is necessary (Birkeland and Lucas, 1990).

The most common agonistic response of *Alpheus lottini* was a loud snapping sound that culminated in a directed shock wave. This snapping increased in frequency as an *Acanthaster* attack escalated from approaching a coral to contact and finally





**FIGURE 4.** Behavioral interactions among crab (*Trapezia cymodoce*), shrimp (*Alpheus lottini*), and gobiid fish (*Paragobiodon echinocephalus*) associates of the coral *Pocillopora damicornis*. (A–C) Various contact positions assumed by crab and fish (modified from Lassig, 1977). (D) Antennal and (E) body contact between shrimp and fish.

mounting. The most extreme response involved the shrimp in rapid succession pinching spines and tube feet, grasping the terminal arm spines of *Acanthaster*, and snapping at the sea star while it was in contact with the coral (Figure 5F).

Field observations in Panama indicated that the defensive responses of crustacean guards were overwhelmingly directed toward *Acanthaster* and not at other corallivores such as sea urchins, hermit crabs, snails, and fishes (Glynn, 1983a). This specific, high level of defense against *Acanthaster* corresponds with the level of harm this corallivore could cause to the coral host (i.e., death of the entire colony). *Culcita* spp., sea star corallivores in the Indo-Pacific, commonly feed on small acroporid

and pocilloporid branching corals. In Hawaii, only about 50% of small *Pocillopora* colonies harbored crustacean guards (*Trapezia* and *Alpheus*) compared with 100% of large colonies (Glynn and Krupp, 1986). When present in small colonies, the crustacean guards would engage in defensive behaviors when attacked by *Culcita*, but these were generally weak responses that seldom curtailed a sea star attack. Thus, unguarded juvenile corals were particularly vulnerable to predation by *Culcita*.

Scuba-supported field and laboratory studies conducted throughout the Indo-Pacific region have demonstrated that metazoan symbionts significantly affect the feeding preferences of *Acanthaster*. Field observations in the Gulf of Oman revealed

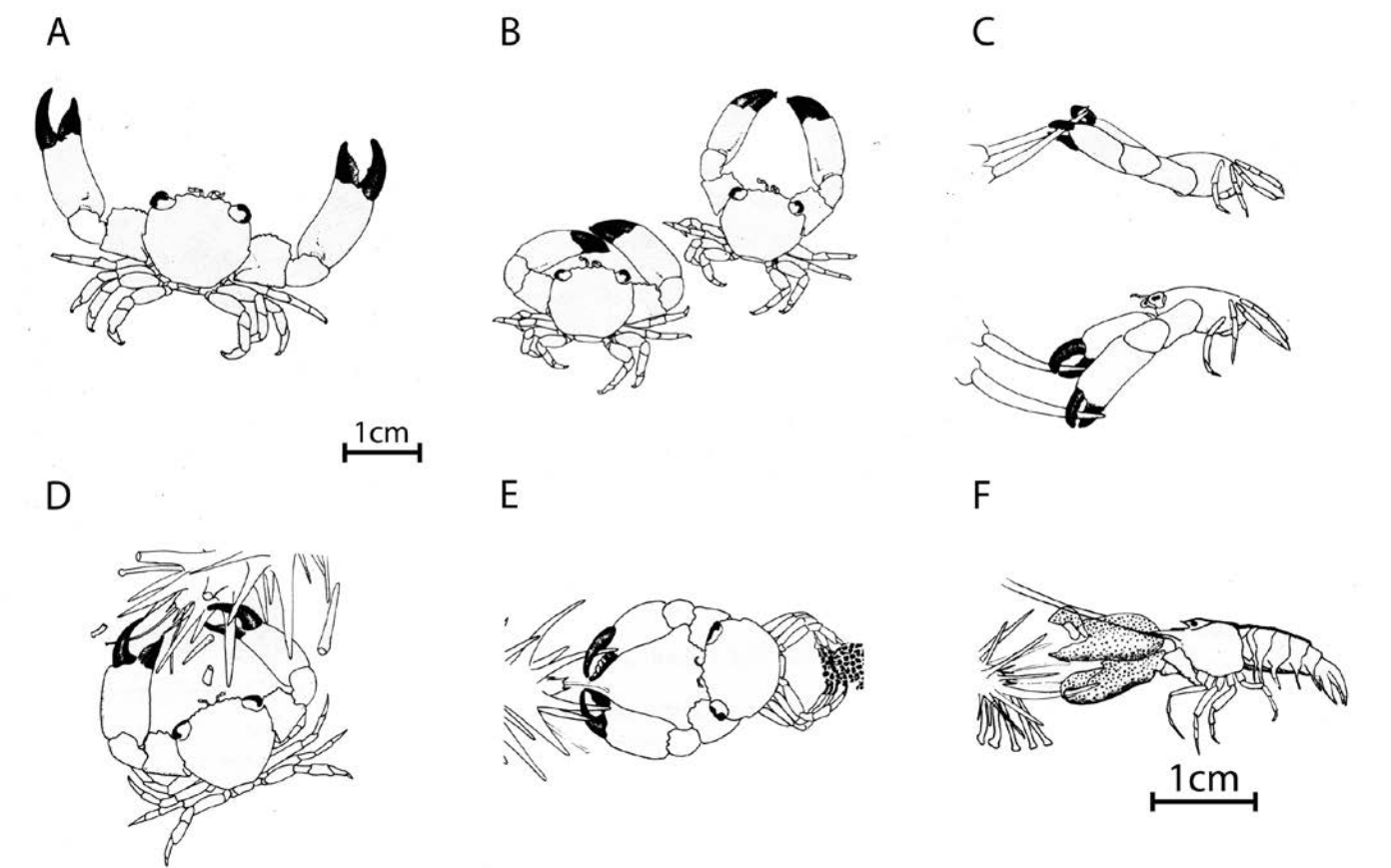


FIGURE 5. Commonly observed defensive responses of crab and shrimp guards toward *Acanthaster* threatening to mount and feed on their coral host. *Trapezia ferruginea*: (A) startle display, (B) pushing sea star, (C) grasping spines with up-down jerking, (D) clipping spines and tube feet, (E) resisting sea star's retreat. *Alpheus lottini*: (F) snapping in contact and pinching sea star's arm tip (from Glynn, 1983a).

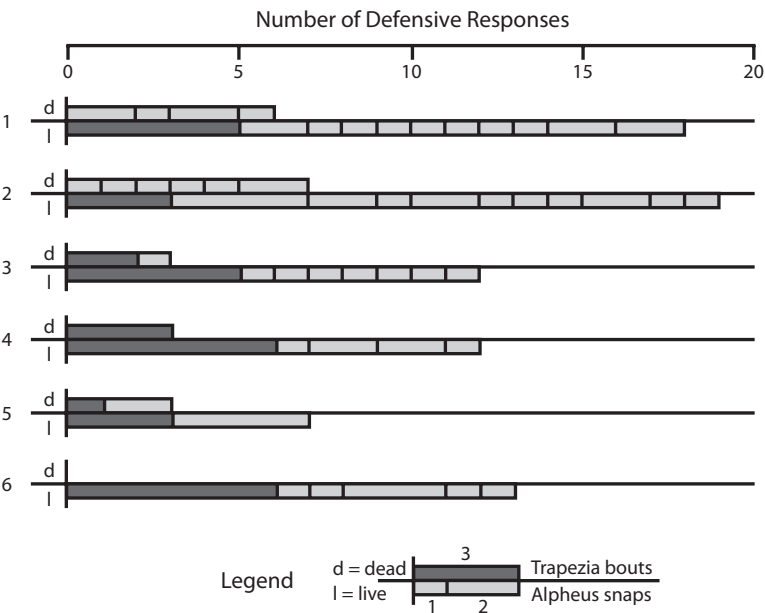


FIGURE 6. Defensive responses of *Trapezia* and *Alpheus* toward simulated attacks of dead (boiled) and live *Acanthaster*. The frequency of *Alpheus* snaps per bout is indicated by the length of each open horizontal bar; the total frequency of *Trapezia* bouts is indicated by the length of each occluded bar (see legend; from Glynn, 1980).

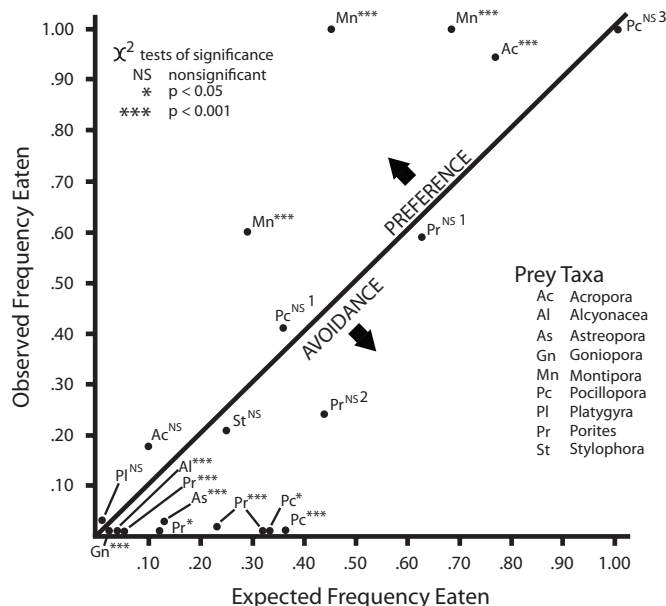


FIGURE 7. Field-sampled coral prey preferred and avoided by *Acanthaster* in the Gulf of Oman. Chi-square significance values are noted beside prey genera eaten and compared to their relative abundances (from Glynn, 1987).

distinct feeding preferences and avoidances of several coral genera (Figure 7). Coral genera in the family Acroporidae (*Acropora*, *Montipora*) were significantly preferred over several genera in other families (e.g., *Astreopora*, *Goniopora*, *Porites*, and *Pocillopora*). There was a close relationship between branching coral taxa and (1) the colonies avoided, (2) the species and numbers of crustacean guards per colony, and (3) the intensity of colony defense. For example, pocilloporid colonies hosting large and aggressive *Trapezia cymodoce* and *Trapezia tigrina* crab guards were seldom attacked by *Acanthaster*, but acroporid colonies with small and less aggressive *Tetralia cavimana* guards were frequently eaten by the sea star. *Montipora* spp. without crustacean guards were preferentially fed upon by *Acanthaster*.

In order to quantify the efficacy of defense by symbiotic crabs, shrimps, gobies, and the entire symbiont assemblage, Pratchett (2001) related coral avoidance interactions of *Acanthaster* to combinations of symbiotic taxa in controlled feeding trials. Two coral species were tested: *Acropora nasuta* with *Tetralia* and *Coralliocaris* guards, and *Pocillopora damicornis* with *Trapezia* and *Alpheus* guards. Crab guards elicited the strongest *Acanthaster* avoidance interactions but were not significantly different from the avoidance of all symbionts present in the two coral species tested (Figure 8). The most pronounced avoidance response was to *P. damicornis* with the aggressive crab guard *Trapezia cymodoce*. The small and weak acroporid crab guard *Tetralia fulva* also performed defensive behaviors, but these were less effective compared with *Trapezia*. *Acanthaster* avoided

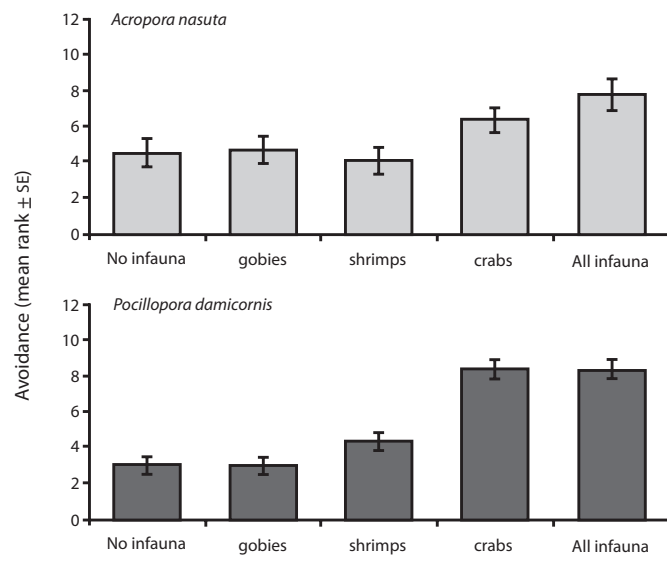


FIGURE 8. Avoidance interactions of *Acanthaster* experimentally presented with different metazoan symbiont assemblages apportioned between two potential coral species prey (modified from Pratchett, 2001). *Acropora nasuta*: crabs (*Tetralia*), shrimps (*Coralliocaris*, *Periclimenes*), and gobies (*Gobiodon*). *Pocillopora damicornis*: crabs (*Trapezia*), shrimps (*Alpheus*), and gobies (*Paragobiodon*).

*Pocillopora* colonies with the *Alpheus* guard alone, but not *Acropora* colonies with *Coralliocaris* shrimp symbionts. Goby symbionts alone in both corals were not effective in thwarting *Acanthaster* attacks.

The effects of *Acanthaster* predation on coral community structure is complex and depends on several factors, such as population size of attacking sea stars, absolute and relative abundances of preferred and nonpreferred coral prey, colony morphology, coral availability, past experience in prey choice, and symbiont defenses. In-depth reviews on this subject are offered by Moran (1986) and Birkeland and Lucas (1990). Observed effects have involved changes in species richness, diversity (both increases and decreases), coral cover (slight to near-total elimination), colony sizes, age distributions, and spatial patterns. Two examples of the last have involved symbiont-defended corals in Panama and Guam. Symbiont-defended corals in Panama were observed to form a protective barrier around preferred, nondefended corals (Glynn, 1985). In this situation, *Acanthaster* was prevented from crossing the barrier and thus denied access to a coral (*Gardineroseris planulata*) ranking high in preference. In Guam, Colgan (1987) observed a halo of uneaten corals surrounding a colony defended by crustacean guards.

In addition to defending corals from corallivores, trapeziid crabs promote the growth and survival of their host corals by increasing interbranch circulation and removing organisms and contaminants from coral surfaces (Glynn, 1983b). A recent study at Moorea quantified the positive effects of crab symbionts in

clearing sediments from branching pocilloporid and acroporid corals (Stewart et al., 2006). In a 24-day field experiment, corals without *Tetralia* (*Acropora hyacinthus*) or *Trapezia* (*Pocillopora verrucosa*) experienced ~50% and ~80% mortality, respectively. The crab symbionts were experimentally removed from test colonies. Crabs were observed to predominantly remove sediments of large particle size (0.5–4.0 mm), which were the most damaging to coral tissues. They responded quickly to increased sediment loads by removing sediments with their rear pereopods and chelae. The corals that survived without crabs showed significantly lower colony growth, increased tissue bleaching, and higher sediment loading.

Facultative majid crabs living cryptically with branching *Porites* on a Caribbean reef have been shown experimentally to benefit their coral host indirectly (Coen, 1988). In treatments where *Mithrax* had access to coral colonies (i.e., crab enclosures and natural controls), foliose algae were significantly reduced compared to crab exclosure treatments (Figure 9) after about one month. The feeding activities of the herbivorous crabs were found to prevent algae from overgrowing and killing the corals. This study and others suggest that mesograzers, such as amphipods, isopods, and polychaete worms, may exercise strong control over algal abundance and community structure in some reef habitats (Brawley, 1992; Carpenter, 1997).

Field observations on a coral reef in the Gulf of Chiriquí, Panama, have revealed an abundance of the painted shrimp, *Hymenocera picta* (Glynn, 1977, 1982). This shrimp lives cryptically in reef framework cavities and among the branches of both live scleractinians and hydrocorals (Figure 10), but is visible



FIGURE 10. Harlequin shrimp, *Hymenocera picta*, perched on a branch of the hydrocoral *Millepora intricata*, at Uva Island, Gulf of Chiriquí, Panama, 20 m depth. A second member of the pair is only partly visible. Photo courtesy of B. Harris.

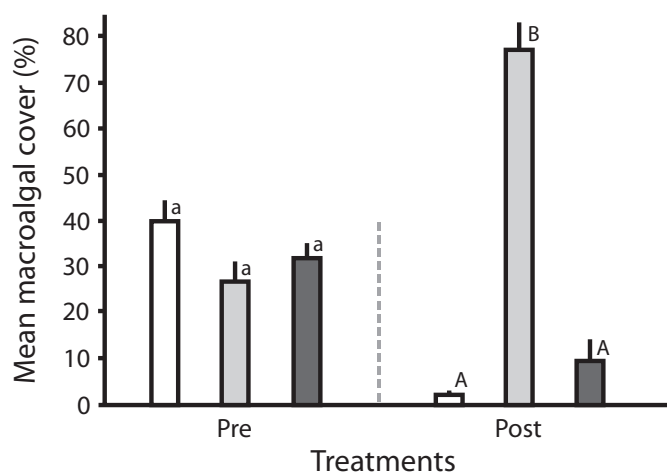


FIGURE 9. Mean ( $\pm 1$  SE) cover of algae on *Porites porites* colonies in relation to the presence of *Mithrax sculptus*, a facultative majid crab associate. Pre- and posttreatment effects: clear bars indicate crab enclosures; light gray bars indicate crab exclosures; dark gray bars indicate natural controls. The same letter is shared among treatments not significantly different ( $p > 0.05$ ).

when attacking and feeding on adult *Acanthaster* and other sea stars. Population abundances, which were determined in part by sea star baiting, reached maximum density estimates of 54–118 shrimp  $\text{ha}^{-1}$ . These shrimp attack asteroid echinoderms only, cutting through the body wall and amputating arm tips with their sharp chelae; exposed internal organs such as gonads and hepatic caeca are then consumed (Wickler, 1973). While feeding on *Acanthaster*, the shrimp (often a pair) are carried on the sea star's aboral surface for up to several days as it moves about. *Pherecardia striata*, a cryptic polychaete worm, was often observed entering the wounded sea star's coelom, where it also fed on soft tissues. From *Acanthaster* immigration and mortality rates, Glynn (1982) concluded that the shrimp and polychaete worm could control the population size of adult *Acanthaster* on the eastern Pacific study reef. Fiedler (2002) found that the post-larvae of *Hymenocera* begin eating sea stars only five days after metamorphosis. Therefore it is possible that postsettlement and juvenile *Acanthaster* are consumed in cryptic reef habitats before they mature and emerge onto exposed reef surfaces.

Early observations with scuba prompted the pioneer marine ethologist Eibl-Eibesfeldt (1955) to propose that cleaner shrimps could benefit reef fishes by removing parasites. Whether or not cleaner shrimp can effectively remove ectoparasites from coral reef fishes has been vigorously debated (Spotte, 1998). Although this type of interaction is not considered here, convincing evidence that cleaner shrimp do remove crustacean (copepod, isopod) and monogenean flatworm parasites is presented in Bunkley-Williams and Williams (1998) and Becker and Grutter (2004). These new findings, aided by controlled laboratory procedures, support a mutualistic relationship between some shrimps and fishes.

It is apparent that trapeziid crab symbionts have received considerable attention from researchers, due mainly to their



relatively large size, complex behaviors, and extraordinary capacity to defend their coral hosts against predators. The ecological roles of smaller taxa (e.g., copepods and smaller shrimps) are still largely unknown with regard to host effects (e.g., tissue consumption or protection from micropredators). Similarly, the potential importance of crustacean symbionts vis-à-vis predation on settling metazoan larvae, recruits, and residents, as well as transmission of zooxanthellae and coral diseases, are also research areas in need of further study. These are all vital ecological functions that can determine the persistence or demise of particular coral populations.

#### CHORDATA

Relatively few fishes form close or obligate relationships with living corals. To illustrate fish–coral symbioses, examples are briefly noted from three families, namely Gobiidae (gobies), Cirrhitidae (hawkfishes), and Pomacentridae (damselfishes). These examples range from obligate to facultative associations with branching corals where shelter and food are assumed to be the chief resources sought. For additional information on the range of fish corallivore diets, see Cole et al. (2008). Since the majority of the 128 coral reef fishes (in 11 families) they list are relatively large and conspicuous, they fall outside the scope of this paper.

Several species in four gobiid genera are closely associated with live corals (Munday et al., 1997; Herler, 2007). Among obligate goby symbionts, *Gobiodon* spp. inhabit acroporid corals and *Paragobiodon* spp. reside in pocilloporid corals. Both coral families exhibit branching colony morphologies. Gut content analysis on the Great Barrier Reef has established that three species of *Gobiodon* consume the tissues of their acroporid hosts (Brooker et al., 2010). In addition, relatively large amounts of algae are consumed, which may benefit the host by preventing algal overgrowth and the fish symbionts by maintaining open living spaces.

Even though gobies alone are not effective in repelling *Acanthaster* (Pratchett, 2001), Lassig (1981) found that *Gobiodon quinquestrigatus* could effectively reduce predation by butterflyfishes. In field experiments with *Acropora* colonies with and without *Gobiodon*, Lassig found that the number of bites and time spent at colonies by feeding *Chaetodon* were significantly reduced when the goby was present. *Gobiodon* spp. produce an epidermal secretion that is ichthyotoxic and likely plays an important role in reducing the grazing of butterflyfishes. Due to the mobility of butterflyfishes feeding around a colony and likely rapid dilution of the toxic agent, the efficacy of such a deterrent might be questioned. An ichthyotoxin would be effective, however, if accurate delivery were possible. Lassig speculated that *Gobiodon* could be attracted to areas threatened by butterflyfishes and may abrade their epidermis against the coral in order to release the repellent at targeted feeding sites. This hypothesized defensive behavior is in need of further study.

Donaldson (1990) lists two species of hawkfishes that are obligate coral dwellers, and eight species that occupy either coral

or other noncoral microhabitats. *Paracirrhites arcatus* is a facultative associate of *Pocillopora meandrina* in Hawaii, where it finds shelter among this coral's branches and uses the coral as a foraging base (DeMartini, 1996). In Panama, *Cirrhitichthys oxycephalus* is a facultative associate of pocilloporid corals. It typically perches on coral branches, from which it locates and presumably preys on symbiotic and pelagic crustaceans as well as small fishes (Dominici-Arosemena and Wolff, 2006; Robertson and Allen, 2008).

Cole et al. (2008) listed eight species of pomacentrid corallivores; two of these feed exclusively on zooxanthellate corals. Some species of zooplanktivorous damselfishes (*Dascyllus*) seek refuge from piscivores in branching corals. The experimental removal of *Dascyllus* from *Stylophora* in the Red Sea resulted in significantly lowered coral growth compared to colonies hosting fish (Lieberman et al., 1995). Similar results were obtained by Holbrook et al. (2008) for *Dascyllus* that shelter in *Pocillopora* colonies at Moorea; sheltering damselfish enhanced coral growth by about 50% and up to nearly 100% when large groups of fish were present. Elevated coral growth was dependent on nutrients (ammonium) excreted by the fish. The magnitude of this effect was positively related to the biomass of fish resident on each coral. Another factor that could indirectly affect coral growth is the presence of predatory hawkfish, which can co-occur with and prey on *Dascyllus* in *Pocillopora* colonies. Hawkfish predation would result in a reduction of the number and biomass of *Dascyllus*, thus resulting in reduced coral growth. A final beneficial effect of note is the sleep-swimming behavior of pomacentrids (*Dascyllus*, *Chromis*) that are closely associated with pocilloporid and acroporid corals (Goldshmid et al., 2004). These fishes enhance water replenishment, and hence oxygen availability, in the inner branch zones of corals at night (Goldshmid et al., 2004). This sleeping behavior, which involves high-frequency fin motion even when the fish are at rest, is unique; non-coral-associated pomacentrids are motionless during their quiescent period.

When a disturbance disrupts a symbiosis, the proximate cause of the breakdown is not always obvious. In a few cases, however, the reason(s) for the disappearance of coral symbionts has been revealed. For example, during coral bleaching on Panamanian reefs, obligate crustacean symbionts starved and died due to the loss of their coral host and nutritional resources (Glynn et al., 1985). Coral bleaching in Australia has resulted in marked declines of damselfishes that inhabit *Pocillopora* corals. It has been shown experimentally that the predation rate of coral-dwelling damselfishes increased in degraded host colonies (Coker et al., 2009). Predation was highest on bleached and algal-covered corals. In bleached corals, this was likely a result of increased prey visibility against a bleached coral background; in algal-covered corals, it was possibly a result of changes in the behavior of prey fishes that would increase their susceptibility to predation, such as increased movement in search of live corals.

The contribution of small cryptic fishes to reef assemblages and processes is largely unknown (Ackerman and Bellwood, 2000). Although cryptic reef habitats are often noted to be



important as refuges for postsettlement and juvenile life history stages of invertebrates and fishes, the presence of diverse cryptic predators is usually not acknowledged. A study focused on the trophic roles of a cryptobenthic fish community on the Great Barrier Reef revealed an abundant carnivore presence (Depczynski and Bellwood, 2003). Five of 16 of the most abundant species examined, representing 40.5% of all individuals, were carnivores. Detritivores made up a large portion of this cryptic assemblage as well (see below). In two eastern Pacific studies conducted on reefs in Colombia (Mora and Zapata, 2000) and Panama (Glynn, 2006), 37 fish species in 20 families were found inhabiting experimentally constructed dead coral rubble structures (Table 1). Thirty-three (~89%) of these cryptic species belong to carnivore or other consumer guilds (planktivores, parasites). The most common dietary items were crustaceans and fishes. The fishes sampled in Colombia recruited to cryptic substrates during a maximum time of just two months. This short period indicates the rapidity with which cryptic predators can invade and become established in newly formed shelters. Thus, cryptic fish predators are likely early colonizers in disturbed reef communities and effective in modulating recruitment dynamics (e.g., species composition and abundances). The presence of particular macropredators could limit the recruitment of species that would positively or negatively affect coral growth.

### MESOSCAVENGERS

The first quantitative study of small scavengers on a coral reef, carried out at Lizard Island on the Great Barrier Reef, revealed high abundances of crustacean and mollusk species (Keeble, 1995). Traps baited with dead fish were deployed overnight for 18 hours in three reef zones and surrounding sedimentary substrata. From 410 baited traps, 108 crustacean, mollusk, and polychaete species were collected, yielding a total of 112,690 individuals. Amphipod, isopod, and ostracod crustaceans were the most abundant taxa, with maximum capture numbers per trap reaching hundreds to thousands of individuals. The overall mean capture rate was 275 individuals per trap. The dominance of crustacean scavengers was evident in traps sampled in leeward reef slope and reef flat habitats (Figure 11).

Scavenger trap baiting on Panamanian coral reefs in the eastern Pacific revealed a diverse scavenger guild, but with lower abundances than those reported at Lizard Island. Since the trapping methodology in Panama was similar to that employed in Australia—small entrance aperture, fish baits, and overnight, 18-hour deployment—a region-wide comparison is justified (Figure 12). Of the 55 traps set on a Panamanian coral reef, a total of 1,219 individuals were captured, with a mean capture rate of 22 individuals per trap. In addition to the shrimp and crab crustaceans, gastropods, and polychaete scavengers that were likewise captured in Australia, a few other invertebrate taxa were present in Panama, including holothurians, hermit crabs, and one

individual each of a polyclad flatworm, bivalve mollusk, and muraenid eel (Figure 13). One small moray eel (*Gymnothorax panamensis*) also was observed to enter a trap and consume part of the bait. At both Australian and Panamanian study reefs, cirrolanid isopods were in high abundance and often numerically dominant. Ostracod abundances and diversity were higher in Australia than in Panama. In traps with scavengers, commonly one-half to all of the ~8 cm<sup>3</sup>–baits were consumed during the 18-hour period. The rapidity of this consumption suggests a critical role of cryptic reef scavengers in nutrient regeneration processes, and possibly a paucity of food resources.

In the Depczynski and Bellwood (2003) study noted above, detritivores were also well represented, especially small gobiid fishes. Ten of 16 species and 39.3% of individuals examined were assigned to the detritivore guild. Like cryptic invertebrate scavengers, cryptic fishes may also contribute importantly to the recycling of primary production through detrital pathways.

### CONCLUSIONS

This overview has shown that several coral–metazoan interactions that were formerly regarded as neutral or harmful to corals are in many instances beneficial. With greater awareness of the critical roles played by small, cryptic reef metazoans, new insights and research directions have emerged.

Sponges offer several key ecosystem services, including water column filtering, nutrient regeneration, binding and stabilization of reef substrates, and facilitation of coral community regeneration and recovery processes. Since sponges represent a vital component of coral communities, their abundances and diversity should be protected. Polychaete worm and gastropod mollusk corallivores can serve as vectors and promote the spread of coral diseases. It is also possible that copepod parasites of corals may assist in the transmission of distinct *Symbiodinium* types among potential coral hosts. This may increase the survival of certain coral species during bleaching stress events. Crustaceans have been highly successful in establishing a variety of facultative and obligate symbiotic associations with live corals. Of note are copepods, barnacles, shrimps, hermit crabs, gall crabs, and trapeziid crabs. In measures of species richness, abundances, and variety of interactions, crustaceans exceed all other metazoans.

Diverse epizoic taxa and endolithic borers (e.g., sponges, polychaete annelids, bivalve mollusks, gall crabs, and barnacles) enhance nitrogen sources for use by coral holobionts. This can lead to localized eutrophication, increased primary production, and elevated coral growth. The activities of epizoic symbionts in thinning boundary layers and creating microturbulence can have several beneficial effects on massive and branching coral hosts. This function has been observed in suspension-feeding sponges, polychaete worms, bivalve mollusks, and barnacles. Mobile crustaceans (e.g., trapeziid crabs and alpheid shrimps) and symbiotic fishes such as gobies and certain pomacentrids also increase

**TABLE 1.** Juvenile and adult fishes occupying cryptic habitats on eastern Pacific coral reefs. Habitats: G, 0.5 m aggregate of dead pocilloporid rubble secured in netting and resting on bottom; M&Z, 0.4 m aggregate of dead pocilloporid rubble secured with line and positioned 0.2 m above sand bottom. Trophic roles: CAR, carnivore; PLK, planktivore; PAR, parasite; OMN, omnivore; CLN cleaner; HRB, herbivore.

Family	Species	Trophic role	Diet <sup>a</sup>	Habitat <sup>b</sup>
Muraenidae	<i>Anarchias galapagensis</i> <sup>c</sup>	CAR	Crustacea <sup>d</sup> , worms, gastropods/bivalves	G
	<i>Gymnothorax panamensis</i>	CAR	Crustacea, bony fishes	G
	<i>Gymnothorax undulata</i>	CAR	Crustacea, cephalopods, bony fishes	G
	<i>Gymnothorax dovii</i> <sup>e</sup>	CAR	Crustacea, cephalopods, bony fishes	G
	<i>Muraena lentiginosa</i>	CAR	Crustacea, bony fishes	G
Carapidae	<i>Carapus mourlani</i>	CAR/PLK	Benthic/planktonic crustacea <sup>f</sup>	G
	<i>Encheliophis vermicularis</i> <sup>e</sup>	PLK/PAR	Plankton, echinoderms	G
Bythitidae	<i>Ogilbia</i> sp. <sup>c</sup>	CAR	Crustacea, bony fishes	G
	<i>Grammonus</i> sp. <sup>c</sup>	CAR	Crustacea, bony fishes	G
Antennariidae	<i>Antennarius sanguineus</i>	CAR	Crustacea, bony fishes	G, M&Z
	<i>Antennarius coccineus</i>	CAR	Crustacea, bony fishes	G, M&Z
	<i>Antennatus strigatus</i>	CAR	Crustacea, bony fishes	G, M&Z
Scorpaenidae	<i>Scorpaena mystes</i>	CAR	Crustacea, cephalopods, bony fishes	G
	<i>Scorpaenodes xyris</i> <sup>e</sup>	CAR	Crustacea, cephalopods, bony fishes	G, M&Z
	<i>Scorpaenid</i> sp. <sup>c</sup>	CAR	Crustacea, cephalopods, bony fishes	G
Serranidae	<i>Serranus psittacinus</i> <sup>e</sup>	CAR	Crustacea, cephalopods, bony fishes	G, M&Z
	<i>Paranthias colonus</i>	CAR/PLK	Pelagic crustacea, zooplankton, bony fishes	M&Z
	<i>Alphestes immaculatus</i>	CAR	Crustacea, bony fishes	M&Z
	<i>Cephalopholis panamensis</i>	CAR	Crustacea, cephalopods, bony fishes	M&Z
Grammistidae	<i>Pseudogramma thaumasium</i>	CAR	Crustacea, bony fishes	G
Apogonidae	<i>Apogon dovii</i> <sup>e</sup>	PLK	Zooplankton, pelagic fish eggs/larvae	G, M&Z
Labrisomidae	<i>Starksia fulva</i> <sup>c</sup>	CAR	Crustacea, worms	G
Gobiidae	<i>Gobulus hancocki</i> <sup>c</sup>	CAR	Benthic worms, crustacea, gastropods/bivalves	G
Tetraodontidae	<i>Canthigaster punctatissima</i> <sup>e</sup>	OMN	Benthic microalgae, sessile invertebrates	G, M&Z
Gerreidae	<i>Eucinostomus gracilis</i> <sup>e</sup>	CAR	Benthic worms, crustacea, gastropods/bivalves	M&Z
Blenniidae	<i>Plagiotremus azaleus</i> <sup>e</sup>	CAR/PAR	Crustacea, bony fishes	M&Z
Lutjanidae	<i>Lutjanus guttatus</i>	CAR	Crustacea, bony fishes	M&Z
	<i>Lutjanus viridis</i>	CAR	Crustacea, cephalopods, bony fishes	M&Z
Pomacanthidae	<i>Pomacanthus zonipectus</i>	CLN/OMN	Microalgae, sessile invertebrates	M&Z
Pomacentridae	<i>Stegastes flavilatus</i>	OMN	Microalgae, crustacea, sessile worms/crustacea	M&Z
	<i>Chromis atrilobata</i>	PLK	Zooplankton, pelagic fish eggs	M&Z
Cirrhitidae	<i>Cirrhitichthys oxycephalus</i>	CAR/PLK	Benthic/pelagic crustacea, bony fishes	M&Z
Labridae	<i>Halichoeres dispilus</i> <sup>c</sup>	CAR/PLK	Crustacea, worms, gastropods/bivalves	M&Z
	<i>Halichoeres nicholsi</i>	CAR/PLK	Crustacea, worms, gastropods/bivalves, echinoderms	M&Z
	<i>Thalassoma lucasanum</i>	CAR/PLK	Crustacea, worms, gastropods/bivalves, echinoderms	M&Z
Acanthuridae	<i>Acanthurus xanthopterus</i>	HRB	Microalgae, detritus, soft corals/hydroids	M&Z
Balistidae	<i>Sufflamen verres</i>	CAR	Crustacea, worms, gastropods/bivalves, echinoderms	M&Z

<sup>a</sup> After Robertson and Allen (2008) unless otherwise noted. The majority of the dietary items listed are probably mostly for adult fishes. Even though some juvenile carnivores emigrated to reef surface locations as they matured (e.g., serranids, lutjanids, and labrids), their membership in the feeding guilds noted probably remained the same.

<sup>b</sup> G, Glynn (2006); M&Z, Mora and Zapata (2000).

<sup>c</sup> Diet and trophic assignment inferred from family-level feeding habits.

<sup>d</sup> Crustacea noted under carnivore trophic guild are primarily benthic, and those under the planktivore guild are present in the water column.

<sup>e</sup> Diet and trophic assignment inferred from genus-level feeding habits.

<sup>f</sup> Glynn et al. (2008).

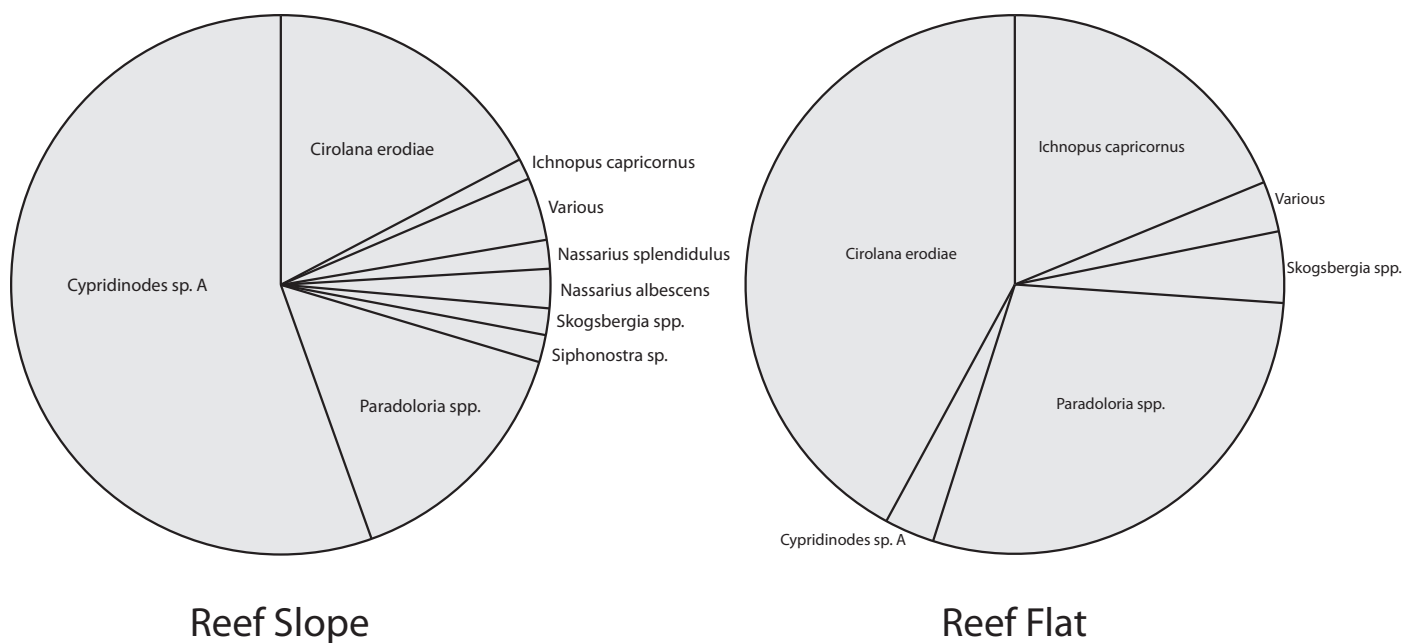


FIGURE 11. Small invertebrate taxa and relative abundances captured in baited scavenger traps, Lizard Island, Australia (1989–1990). Right: Leeward reef flat; Left: Leeward reef slope (modified from Keable, 1995).

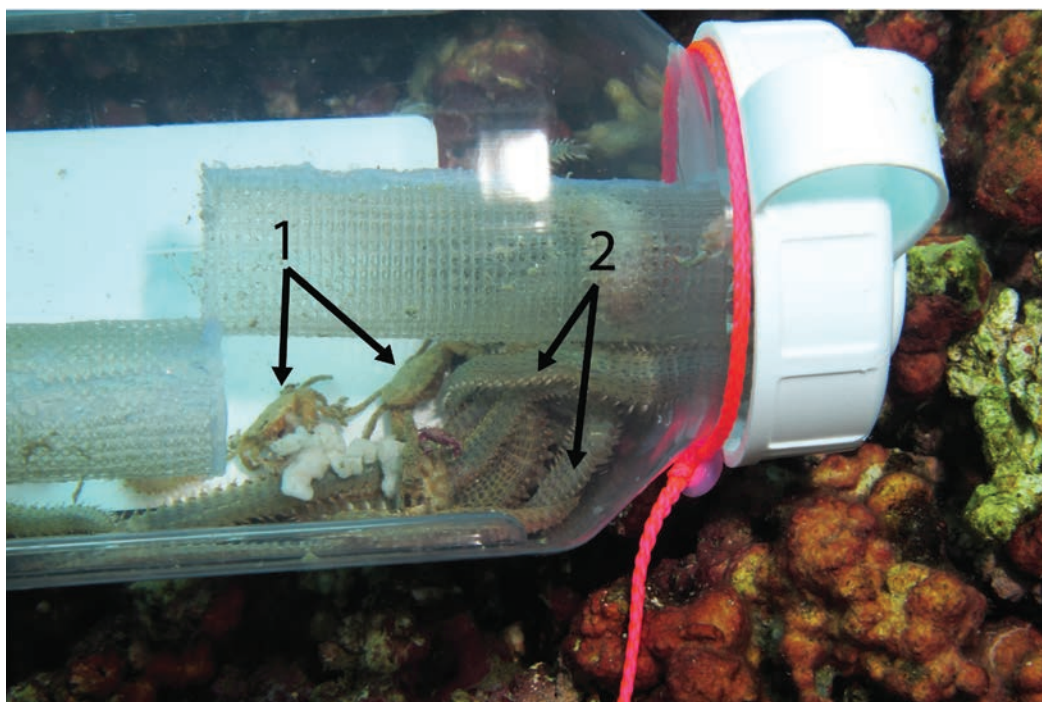
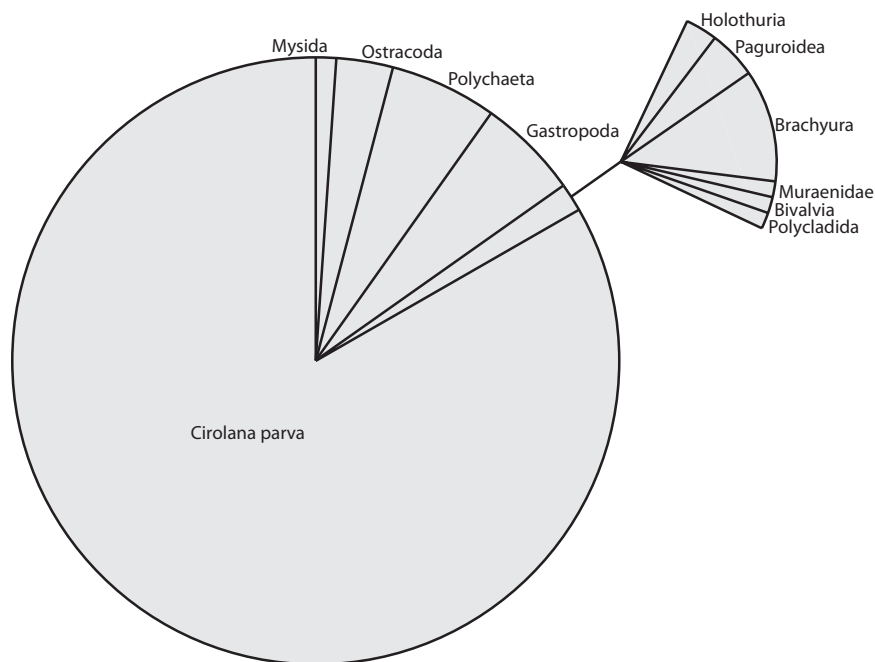


FIGURE 12. Invertebrate scavengers inside a trap being retrieved after overnight exposure on the Uva Island coral reef, Gulf of Chiriquí, Panama, 3 m depth. Arrows 1 and 2 respectively denote captured brachyuran crabs and amphinomid worms *Pherecardia striata*. The polychaete worms are ~1 cm wide. Photo courtesy of V. W. Brandtneris.



**FIGURE 13.** Small scavenger taxa and relative abundances captured in 55 baited traps set in pocilloporid framework on the Uva Island coral reef, Gulf of Chiriquí, Panama, 2–4 m depth.

circulation in the interbranch spaces of corals. Positive effects include increased availability of nutrients, dissolved oxygen, and food and dispersal of waste products, including reactive oxygen species generated during stress events. Overgrowth by fouling organisms can also be restricted by filter-feeding barnacles and shrimps and crabs that scrape coral surfaces.

Metazoan symbionts of corals employ diverse mechanisms to defend their host colony from corallivores. A serpulid polychaete worm thrusts an armed operculum and a scallop directs jets of water at attacking *Acanthaster*. Xanthid crabs employ a variety of agonistic responses toward sea stars, including pinching, clipping spines and tube feet, and body thrusts and dislodgment of large corallivores. Alpheid pistol shrimps direct aggressive snapping and water jets toward attacking corallivores. Gobies limit the grazing of chaetodontids probably by releasing an ichthyotoxic repellent.

Care should be exercised in establishing the identity of coral reef organisms in light of widespread species-specific interdependencies. For example, molecular genetic studies of the morphospecies of *Pocillopora damicornis* in the western Indian Ocean has shown the existence of two distinct species (Souter, 2010), and eight morphospecies of *Pocillopora* in the far eastern Pacific may in fact represent only three species (Pinzón and LaJeunesse, 2010). Other noted sibling species complexes are *Acanthaster planci* and *Spirobranchus giganteus*, representing four and 10–12 species respectively.

Sampling of cryptic reef scavengers in Australia and Panama suggests that this is a taxonomically diverse feeding group dominated by various crustacean orders, especially isopods. Mesosavengers affect the rapid breakdown of reef carrion and particulate organic matter, driving nutrient recycling and coral reef primary production. Small, cryptic fish carnivores on eastern Pacific reefs (Panama and Colombia) were represented by 37 species in 20 families, and consisted of adult resident and immature transient members. Crustaceans ranked high in the diets of these fishes, as did other invertebrate taxa (e.g., polychaete worms, gastropod and bivalve mollusks, and cephalopods) and fishes. This cryptic carnivore guild likely exerts heavy consumer pressure on other cryptic metazoans, including biota recruiting to reefs via planktonic larval stages. Coral reef frameworks and associated habitats providing shelter can no longer be perceived as predator-free refuges.

From the variety of newly described coral–metazoan symbioses and a clearer understanding of functional interrelationships, it is apparent that small cryptic animals play numerous and essential ecological roles in many host corals. Their effects, both positive and negative, need to be understood with regard to the nature of key ecosystem processes and their influence on the dynamics of populations in reef systems and the diversity and structure of coral reef communities overall. The importance of understanding the various interactions and nuances involved in cryptic reef communities is critical in light of projected and



unknown responses that are sure to accompany climate change impacts on coral reefs.

## ACKNOWLEDGMENTS

I especially thank Michael A. Lang for the invitation to participate in this symposium highlighting research through the aid of scuba. Diane S. and Mark M. Littler are acknowledged for their help in editing this section on ecological interactions. Helpful suggestions for improving this paper were offered by V. W. Brandtneris, I. C. Enochs, T. C. LaJeunesse, and J. Serafy. Symposium attendance was supported by the Smithsonian Institution, National Research Council, and the National Science Foundation. Research support was provided by the U.S. National Science Foundation Biological Oceanography Program grant OCE-0526361 and earlier awards. I am also grateful for support provided by the Ministry of Agriculture and Fisheries, Sultanate of Oman, Omani–American Joint Commission for Economic and Technical Cooperation; the Department of Marine and Wildlife Resources, American Samoa; the Smithsonian Tropical Research Institute and Scholarly Studies Program, Smithsonian Institution; and the Marine Laboratory, University of Guam, facilitated by C. Birkeland.

## REFERENCES

- Achituv, Y., I. Brickner, and J. Erez. 1997. Stable carbon isotope ratios in Red Sea barnacles (Cirripedia) as an indicator of their food source. *Marine Biology*, 130:243–247. <http://dx.doi.org/10.1007/s002270050244>.
- Achituv, Y., and L. Mizrahi. 1996. Recycling of ammonium within a hydrocoral (*Millepora dichotoma*): Zooxanthellae–cirripede (*Savignium milleporum*) symbiotic association. *Bulletin of Marine Science*, 58:856–861.
- Ackerman, J. L., and D. R. Bellwood. 2000. Reef fish assemblages: A re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series*, 206:227–237. <http://dx.doi.org/10.3354/meps206227>.
- Barneah, O., I. Brickner, M. Hooge, V. M. Weis, and T. C. LaJeunesse. 2007. Three party symbiosis: Acoelomorph worms, corals and unicellular algal symbionts in Eilat (Red Sea). *Marine Biology*, 151:1215–1223. <http://dx.doi.org/10.1007/s00227-006-0563-2>.
- Becker, J. H., and A. S. Grutter. 2004. Cleaner shrimp do clean. *Coral Reefs*, 23: 515–520.
- Ben-Tzvi, O., S. Einbinder, and E. Brokovich. 2006. A beneficial association between a polychaete worm and a scleractinian coral? *Coral Reefs*, 25:98. <http://dx.doi.org/10.1007/s00338-005-0084-3>.
- Birkeland, C., and J. S. Lucas. 1990. *Acanthaster planci*: Major management problem of coral reefs. Boca Raton, Fla.: CRC Press.
- Brawley, S. H. 1992. Mesoherbivores. In *Plant–animal interactions in the marine benthos*, ed. D. M. John, S. J. Hawkins, and J. H. Price, pp. 235–263. Systematics Association Special Volume 46. Oxford, U. K.: Clarendon Press.
- Brooker, R. M., P. L. Munday, and T. D. Ainsworth. 2010. Diets of coral-dwelling fishes of the genus *Gobiodon* with evidence of corallivory. *Journal of Fish Biology*, 76:2578–2583. <http://dx.doi.org/10.1111/j.1095-8649.2010.02644.x>.
- Bruce, A. J. 1976. Shrimps and prawns of coral reefs, with special reference to commensalism. In *Biology and geology of coral reefs, Volume 3: Biology 2*, ed. O. Jones and R. Endean, pp. 37–94. New York: Academic Press.
- . 1998. New keys for the identification of Indo-West Pacific coral associated pontonine shrimps, with observations on their ecology. *Ophelia*, 49:29–46. <http://dx.doi.org/10.1080/00785326.1998.10409371>.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18:119–125. [http://dx.doi.org/10.1016/S0169-5347\(02\)00045-9](http://dx.doi.org/10.1016/S0169-5347(02)00045-9).
- Bunkley-Williams, L., and E. H. Williams, Jr. 1998. Ability of Pederson cleaner shrimp to remove juveniles of the parasitic cymothoid isopod, *Anilocra haemuli*, from the host. *Crustaceana*, 71:862–869. <http://dx.doi.org/10.1163/156854098X00888>.
- Carpenter, R. C. 1997. Invertebrate predators and grazers. In *Life and death of coral reefs*, ed. C. Birkeland, pp. 198–229. New York: Chapman & Hall. [http://dx.doi.org/10.1007/978-1-4615-5995-5\\_9](http://dx.doi.org/10.1007/978-1-4615-5995-5_9).
- Castro, P. 1976. Brachyuran crabs symbiotic with scleractinian corals: A review of their biology. *Micronesica*, 12:99–110.
- . 1978. Movements between coral colonies in *Trapezia ferruginea* (Crustacea: Brachyura), an obligate symbiont of scleractinian corals. *Marine Biology*, 46:237–245. <http://dx.doi.org/10.1007/BF00390685>.
- . 1988. Animal symbioses in coral reef communities: A review. *Symbiosis*, 5:161–184.
- Castro, P., P. K. L. Ng, and S. T. Ah Yong. 2004. Phylogeny and systematics of the Trapeziidae Miers, 1886 (Crustacea, Brachyura), with the description of a new family. *Zootaxa*, 643:1–70.
- Cheng, Y.-R., and C.-F. Dai. 2010. Endosymbiotic copepods may feed on zooxanthellae from their coral host, *Pocillopora damicornis*. *Coral Reefs*, 29:13–18. <http://dx.doi.org/10.1007/s00338-009-0559-8>.
- Choi, D. R., and R. N. Ginsburg. 1983. Distribution of coelobites (cavity dwellers) in coral rubble across the Florida reef tract. *Coral Reefs*, 2:165–172. <http://dx.doi.org/10.1007/BF00336723>.
- Coen, L. D. 1988. Herbivory by crabs and the control of algal epibionts on Caribbean host corals. *Oecologia*, 75:198–203. <http://dx.doi.org/10.1007/BF00378597>.
- Coker, D. J., M. S. Pratchett, and P. L. Munday. 2009. Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology*, 20:1204–1210. <http://dx.doi.org/10.1093/beheco/arp113>.
- Cole, A. J., M. S. Pratchett, and G. P. Jones. 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries*, 9:286–307. <http://dx.doi.org/10.1111/j.1467-2979.2008.00290.x>.
- Colgan, M. W. 1985. Growth rate reduction and modification of a coral colony by a vermetid mollusc *Dendropoma maxima*. *Proceedings of the fifth International Coral Reef Symposium*, 6:205–210.
- . 1987. Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology*, 68:1592–1605. <http://dx.doi.org/10.2307/1939851>.
- Cook, P. A., B. A. Steward, and Y. Achituv. 1991. The symbiotic relationship between the fire coral *Millepora dichotoma* and the barnacle *Savignium milleporum*. *Hydrobiologia*, 216/217:285–290. <http://dx.doi.org/10.1007/BF00026476>.
- De Bary, H. A. 1879. *Die Erscheinung der Symbiose*. Strasburg: Author.
- DeMartini, E. E. 1996. Sheltering and foraging substrate uses of the arc-eye hawkfish *Paracirrhites arcatus* (Pisces: Cirrhitidae). *Bulletin of Marine Science*, 58:826–837.
- Depczynski, M., and D. R. Bellwood. 2003. The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series*, 256:183–191. <http://dx.doi.org/10.3354/meps256183>.
- DeVantier, L. M., and R. Endean. 1988. The scallop *Pecten spondyloideum* mitigates the effects of *Acanthaster planci* predation of the host coral *Porites*: Host defence facilitation by exaptation. *Marine Ecology Progress Series*, 47: 293–301. <http://dx.doi.org/10.3354/meps047293>.
- DeVantier, L. M., R. E. Reichelt, and R. H. Bradbury. 1986. Does *Spirobranchus giganteus* protect *Porites* from predation by *Acanthaster planci*: Predator pressure as a mechanism of coevolution? *Marine Ecology Progress Series*, 32: 307–310. <http://dx.doi.org/10.3354/meps032307>.
- Dominici-Arosemena, A., and M. Wolff. 2006. Reef fish community structure in the tropical eastern Pacific (Panamá): Living on a relatively stable rocky reef environment. *Helgolander Marine Research*, 60:287–305. <http://dx.doi.org/10.1007/s10152-006-0045-4>.
- Donaldson, T. J. 1990. Reproductive behavior and social organization of some Pacific hawkfishes (Cirrhitidae). *Japanese Journal of Ichthyology*, 36:439–458.
- Eibl-Eibesfeldt, I. 1955. Über Symbiosen, Parasitismus und andere besondere zwischenartliche Beziehungen tropischer Meerestische. *Zeitschrift für Tierpsychologie*, 12:203–219. <http://dx.doi.org/10.1111/j.1439-0310.1955.tb01523.x>.
- Fauchald, K., and P. A. Jumars. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology, an Annual Review*, 17: 193–284.
- Fiedler, G. C. 2002. The influence of social environment on sex determination in harlequin shrimp (*Hymenocera picta*: Decapoda, Gnathophyllidae). *Journal*



- of *Crustacean Biology*, 22:750–761. [http://dx.doi.org/10.1651/0278-0372\(2002\)022\[0750:TIOSES\]2.0.CO;2](http://dx.doi.org/10.1651/0278-0372(2002)022[0750:TIOSES]2.0.CO;2).
- Fiege, D., and H. A. ten Hove. 1999. Redescription of *Spirobranchus gaymerdi* (Quatrefages, 1866) (Polychaeta: Serpulidae) from the Indo-Pacific with remarks on the *Spirobranchus giganteus* complex. *Zoological Journal of the Linnean Society*, 126:355–364.
- Garth, J. S. 1964. The crustacean Decapoda (Brachyura and Anomura) of Eniwetok Atoll, Marshall Islands, with special reference to the obligate commensals of branching corals. *Micronesica*, 1:137–144.
- Ginsburg, R. N. 1983. Geological and biological roles of cavities in coral reefs. In *Perspectives on coral reefs*, ed. D. J. Barnes, pp. 148–153. Manuka, Australia: Brian Clouston Publisher.
- Gischler, E., and R. N. Ginsburg. 1996. Cavity dwellers (coelobites) under coral rubble in Southern Belize barrier and atoll reefs. *Bulletin of Marine Science*, 58:570–589.
- Glynn, P. W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs*, 46:431–456. <http://dx.doi.org/10.2307/1942565>.
- . 1977. Interactions between *Acanthaster* and *Hymenocera* in the field and laboratory. *Proceedings of the third International Coral Reef Symposium*, 1:210–215.
- . 1980. Defense by symbiotic crustacea of host corals elicited by chemical cues from predator. *Oecologia*, 47:287–290. <http://dx.doi.org/10.1007/BF00398518>.
- . 1982. *Acanthaster* population regulation by a shrimp and a worm. *Proceedings of the fourth International Coral Reef Symposium*, 2:607–612.
- . 1983a. Crustacean symbionts and the defense of corals: Coevolution on the reef? In *Coevolution*, ed. M. H. Nitecki, pp. 111–178. Chicago: University of Chicago Press.
- . 1983b. Increased survivorship in corals harboring crustacean symbionts. *Marine Biology Letters*, 4:105–111.
- . 1984. An amphinomid worm predator of the crown-of-thorns sea star and general predation on asteroids in eastern and western Pacific coral reefs. *Bulletin of Marine Science*, 35:54–71.
- . 1985. El Niño-associated disturbance to coral reefs and post disturbance mortality by *Acanthaster planci*. *Marine Ecology Progress Series*, 26:295–300. <http://dx.doi.org/10.3354/meps026295>.
- . 1987. Some ecological consequences of coral-crustacean guard mutualisms in the Indian and Pacific oceans. *Symbiosis*, 4:301–324.
- . 1988. Predation on coral reefs: Some key processes, concepts and research directions. *Proceedings of the sixth International Coral Reef Symposium*, 1:51–62.
- . 1996. Bioerosion and coral growth: A dynamic balance. In *Life and death of coral reefs*, ed. C. Birkeland, pp. 68–94. New York: Chapman & Hall.
- . 2006. Fish utilization of simulated coral reef frameworks versus eroded rubble substrates off Panamá, eastern Pacific. *Proceedings of the tenth International Coral Reef Symposium*, 1:250–256.
- Glynn, P. W., and I. C. Enochs. 2011. Invertebrates and their roles in coral reef ecosystems. In *Coral reefs: An ecosystem in transition*, ed. Z. Dubinsky and N. Stambler, pp. 273–326. Berlin: Springer. [http://dx.doi.org/10.1007/978-94-007-0114-4\\_18](http://dx.doi.org/10.1007/978-94-007-0114-4_18).
- Glynn, P. W., I. C. Enochs, J. E. McCosker, and A. N. Graefe. 2008. First record of a pearlfish, *Carapus mourlani*, inhabiting the aplysiid opisthobranch mollusk *Dolabella auricularia*. *Pacific Science*, 62:593–601. [http://dx.doi.org/10.2984/1534-6188\(2008\)62\[593:FROAPC\]2.0.CO;2](http://dx.doi.org/10.2984/1534-6188(2008)62[593:FROAPC]2.0.CO;2).
- Glynn, P. W., and D. A. Krupp. 1986. Feeding biology of a Hawaiian sea star corallivore, *Culcita novaeguineae* Muller and Troschel. *Journal of Experimental Marine Biology and Ecology*, 96:75–96. [http://dx.doi.org/10.1016/0022-0981\(86\)90014-6](http://dx.doi.org/10.1016/0022-0981(86)90014-6).
- Glynn, P. W., M. Perez, and S. L. Gilchrist. 1985. Lipid decline in stressed corals and their crustacean symbionts. *Biological Bulletin*, 168:276–284. <http://dx.doi.org/10.2307/1541240>.
- Goldshmid, R., R. Holzman, D. Weihs, and A. Genin. 2004. Aeration of corals by sleep-swimming fish. *Limnology and Oceanography*, 49:1832–1839. <http://dx.doi.org/10.4319/lo.2004.49.5.1832>.
- Goreau, T. F., N. I. Goreau, and Y. Neumann. 1970. On feeding and nutrition in *Fungiacava eilatensis* (Bivalvia, Mytilidae), a commensal living in fungiid corals. *Journal of Zoology, London*, 160:159–172. <http://dx.doi.org/10.1111/j.1469-7998.1970.tb02901.x>.
- Goreau, T. F., and W. D. Hartman. 1966. Sponge: Effect on the form of reef corals. *Science*, 151:343–344. <http://dx.doi.org/10.1126/science.151.3708.343>.
- Goreau, T. F., and C. M. Yonge. 1968. Coral community on muddy sand. *Nature* (London), 217:421–423. <http://dx.doi.org/10.1038/217421a0>.
- Hadfield, M. G. 1976. Molluscs associated with living tropical corals. *Micronesica*, 12:133–148.
- Haramaty, L. 1991. Reproduction effort in the nudibranch *Phestilla sibogae*: Calorimetric analysis of food and eggs. *Pacific Science*, 45:257–262.
- Hay, M. E., J. E. Duffy, and C. A. Pfister. 1987. Chemical defense against different marine herbivores: Are amphipods insect equivalents? *Ecology*, 68:1567–1580. <http://dx.doi.org/10.2307/1939849>.
- Herler, J. 2007. Microhabitats and ecomorphology of coral- and coral-rock associated gobiid fish (Teleostei: Gobiidae) in the northern Red Sea. *Marine Ecology, An Evolutionary Perspective*, 28(Suppl. s1):82–94.
- Highsmith, R. C. 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series*, 7:207–226. <http://dx.doi.org/10.3354/meps007207>.
- Holbrook, S. J., A. J. Brooks, R. J. Schmitt, and H. L. Stewart. 2008. Effects of sheltering fish on growth of their host corals. *Marine Biology*, 155:521–530. <http://dx.doi.org/10.1007/s00227-008-1051-7>.
- Humes, A. G. 1985. Cnidarians and copepods: A success story. *Transactions of the American Microscopical Society*, 104:313–320. <http://dx.doi.org/10.2307/3226484>.
- . 1994. How many copepods? *Hydrobiologia*, 292/293:1–7. <http://dx.doi.org/10.1007/BF00229916>.
- Hutchings, P. A. 1986. Biological destruction of coral reefs. *Coral Reefs*, 4:239–252. <http://dx.doi.org/10.1007/BF00298083>.
- Jackson, J. B. C., and J. E. Winston. 1982. Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. *Journal of Experimental Marine Biology and Ecology*, 57:135–147. [http://dx.doi.org/10.1016/0022-0981\(82\)90188-5](http://dx.doi.org/10.1016/0022-0981(82)90188-5).
- Keable, S. J. 1995. Structure of the marine invertebrate scavenging guild of a tropical reef ecosystem: Field studies at Lizard Island, Queensland, Australia. *Journal of Natural History*, 29:27–46. <http://dx.doi.org/10.1080/00222939500770021>.
- Kleemann, K. H. 1980. Boring bivalves and their host corals from the Great Barrier Reef. *Journal of Molluscan Studies*, 46:13–54.
- Knowlton, N., J. C. Lang, and B. D. Keller. 1990. *Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals*. Smithsonian Contributions to the Marine Sciences, No. 31. Washington, D.C.: Smithsonian Institution Press.
- Knowlton, N., J. C. Lang, M. C. Rooney, and P. Clifford. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. *Nature*, 294:251–252. <http://dx.doi.org/10.1038/294251a0>.
- Knowlton, N., and E. Rohwer. 2003. Multispecies microbial mutualisms on coral reefs: The host as a habitat. *American Naturalist*, 162:551–562. <http://dx.doi.org/10.1086/378684>.
- Knudsen, J. W. 1967. *Trapezia* and *Tetralia* (Decapoda, Brachyura, Xanthidae) as obligate ectoparasites of pocilloporid and acroporid corals. *Pacific Science*, 21:51–57.
- Kobluk, D. R. 1988. Cryptic faunas in reefs: Ecology and geologic importance. *Palaos*, 3:379–390. <http://dx.doi.org/10.2307/3514784>.
- Kropp, R. K. 1986. Feeding biology and mouthpart morphology of three species of coral gall crabs (Decapoda: Cryptochiridae). *Journal of Crustacean Biology*, 6:377–384. <http://dx.doi.org/10.2307/1548178>.
- Lassig, B. R. 1977. Communication and coexistence in a coral community. *Marine Biology*, 42:85–92. <http://dx.doi.org/10.1007/BF00392016>.
- . 1981. Significance of the epidermal ichthyotoxic secretion of coral-dwelling gobies. *Toxicon*, 19:729–735. [http://dx.doi.org/10.1016/0041-0101\(81\)90068-4](http://dx.doi.org/10.1016/0041-0101(81)90068-4).
- Lewinsohn, C. 1978. Bemerkungen zur Taxonomie von *Paguritta harmsi* (Gordon) (Crustacea Decapoda, Anomura) und Beschreibung einer neuen Art der gleichen Gattung aus Australien. *Zoologische Mededelingen*, 53:243–252.
- Liberman, T., A. Genin, and Y. Loya. 1995. Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*. *Marine Biology*, 121:741–746. <http://dx.doi.org/10.1007/BF00349310>.
- McLaughlin, P., and R. Lemaitre. 1993. A review of the hermit crab genus *Paguritta* (Decapoda: Anomura: Paguridae) with descriptions of three new species. *Raffles Bulletin of Zoology*, 41:1–29.
- Mokady, O., Y. Loya, and B. Lazar. 1998. Ammonium contribution from boring bivalves to their coral host—A mutualistic symbiosis? *Marine Ecology Progress Series*, 169:295–301. <http://dx.doi.org/10.3354/meps169295>.
- Mora, C., and F. A. Zapata. 2000. Effects of a predatory site-attached fish on abundance and body size of early post-settled reef fishes from Gorgona Island, Colombia. *Proceedings of the ninth International Coral Reef Symposium*, 1:475–480.
- Moran, P. J. 1986. The *Acanthaster* phenomenon. *Oceanography and Marine Biology, An Annual Review*, 24:379–480.

- Munday, P. L., G. P. Jones, and M. Julian Caley. 1997. Habitat specialization and the distribution and abundance of coral-dwelling gobies. *Marine Ecology Progress Series*, 152:227–239. <http://dx.doi.org/10.3354/meps152227>.
- Pantos, O., and J. C. Bythell. 2010. A novel reef coral symbiosis. *Coral Reefs*, 29:761–770. <http://dx.doi.org/10.1007/s00338-010-0622-5>.
- Pasternak, Z., A. Rix, and A. Abelson. 2001. Episymbionts as possible anti-fouling agents on reef-building hydrozoans. *Coral Reefs*, 20:318–319. <http://dx.doi.org/10.1007/s003380100177>.
- Patton, W. K. 1966. Decapod crustacea commensal with Queensland branching corals. *Crustaceana*, 10:271–295. <http://dx.doi.org/10.1163/156854066X00180>.
- . 1974. Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. In *Symbiosis in the sea*, ed. W. B. Vernberg, pp. 219–243. Columbia, S.C.: University of South Carolina Press.
- . 1976. Animal associates of living reef corals. In *Biology and geology of coral reefs, Volume 3: Biology 2*, ed. O. A. Jones and R. Endean, pp. 1–36. New York: Academic Press.
- . 1994. Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great Barrier Reef, Australia. *Bulletin of Marine Science*, 55:193–211.
- Patton, W. K., and D. R. Robertson. 1980. Pair formation in a coral inhabiting hermit crab. *Oecologia*, 47:267–269. <http://dx.doi.org/10.1007/BF00346831>.
- Pearson, R. G., and R. Endean. 1969. A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef. *Fisheries Notes, Department of Harbours and Marine, Queensland*, 3:27–68.
- Perry, C. T., and L. J. Hepburn. 2008. Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: Taphonomic signatures of reef accretion and reef depositional events. *Earth-Science Reviews*, 86:106–144. <http://dx.doi.org/10.1016/j.earscirev.2007.08.006>.
- Pinzón, J. H., and T. C. LaJeunesse. 2010. Species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis ecology. *Molecular Ecology*, 20:311–325. <http://dx.doi.org/10.1111/j.1365-294X.2010.04939.x>.
- Pratchett, M. S. 2001. Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the western Pacific. *Marine Ecology Progress Series*, 214:111–119. <http://dx.doi.org/10.3354/meps214111>.
- Preston, E. M. 1973. A computer simulation of competition among five sympatric congeneric species of xanthid crabs. *Ecology*, 54:469–483. <http://dx.doi.org/10.2307/1935333>.
- Reaka-Kudla, M. L. 1997. The global biodiversity of coral reefs: a comparison with rain forests. In *Biodiversity II: Understanding and protecting our biological resources*, ed. M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, pp. 83–108. Washington, D.C.: Joseph Henry Press.
- Richter, C., M. Wunsch, M. Rasheed, I. Kötter, and M. I. Badran. 2001. Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature*, 413:726–730. <http://dx.doi.org/10.1038/35099547>.
- Rinkevich, B., Z. Wolodarsky, and Y. Loya. 1991. Coral-crab Association: A compact domain of a multilevel trophic system. *Hydrobiologia*, 216/217:279–284. <http://dx.doi.org/10.1007/BF00026475>.
- Robertson, D. R., and G. R. Allen. 2008. Shorefishes of the tropical eastern Pacific online information system. Version 1.0. Balboa, Panama: Smithsonian Tropical Research Institute. [www.neotropicalfishes.org/sfstep](http://www.neotropicalfishes.org/sfstep).
- Robertson, R. 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. *Pacific Science*, 24:43–54.
- Rohwer, F., V. Seguritan, F. Azam, and N. Knowlton. 2002. Diversity and distribution of coral-associated bacteria. *Marine Ecology Progress Series*, 243:1–10. <http://dx.doi.org/10.3354/meps243001>.
- Ross, A., and W. A. Newman. 1969. A coral eating barnacle. *Pacific Science*, 23: 252–256.
- . 1973. Revision of the coral-inhabiting barnacles (Cirripedia: Balanidae). *Transactions of the San Diego Society of Natural History*, 17:137–174.
- . 1995. A coral-eating barnacle, revisited (Cirripedia, Pyrgomatidae). *Contributions to Zoology*, 65:129–175.
- . 2000. A new coral-eating barnacle: The first record from the Great Barrier Reef, Australia. *Memoirs of the Queensland Museum*, 45:585–591.
- Rotjan, R. D., and S. M. Lewis. 2008. Impact of coral predators on tropical reefs. *Marine Ecology Progress Series*, 367:73–91. <http://dx.doi.org/10.3354/meps07531>.
- Rützler, K. 2004. Sponges on coral reefs: A community shaped by competitive co-operation. *Bollettino dei Musei e degli Istituti Biologici dell Università di Genova*, 68:85–148.
- Saffo, M. B. 1993. Coming to terms with a field: Words and concepts in symbiosis. *Symbiosis*, 14:17–31.
- Schuhmacher, H. 1977. A hermit crab, sessile on corals, exclusively feeds by feathered antennae. *Oecologia*, 27:371–374. <http://dx.doi.org/10.1007/BF00345570>.
- . 1992. Impact of some corallivorous snails on stony corals in the Red Sea. *Proceedings of the seventh International Coral Reef Symposium*, 2:840–846.
- Shima, J. S., C. W. Osenberg, and A. C. Stier. 2010. The vermetid gastropod *Dendropoma maximum* reduces coral growth and survival. *Biological Letters*, doi:10.1098/rsbl.2010.0291. <http://dx.doi.org/10.1098/rsbl.2010.0291>.
- Simon-Blecher, N., Y. Aчитuv, and Z. Malik. 1996. Effect of epibionts on the microdistribution of chlorophyll in corals and its detection by fluorescence spectral imaging. *Marine Biology*, 126:757–763. <http://dx.doi.org/10.1007/BF00351342>.
- Souter, P. 2010. Hidden genetic diversity in a key model species of coral. *Marine Biology*, 157:875–885. <http://dx.doi.org/10.1007/s00227-009-1370-3>.
- Spotte, S. 1998. “Cleaner” shrimps? *Helgolander Meeresuntersuchungen*, 52:59–64. <http://dx.doi.org/10.1007/BF02908736>.
- Stewart, H. L., S. J. Holbrook, R. J. Schmitt, and A. J. Brooks. 2006. Symbiotic crabs maintain coral health by clearing sediments. *Coral Reefs*, 25:609–615. <http://dx.doi.org/10.1007/s00338-006-0132-7>.
- Stier, A. C., C. S. McKean, C. W. Osenberg, and J. S. Shima. 2010. Guard crabs alleviate deleterious effects of vermetid snails on a branching coral. *Coral Reefs*, 29:1019. <http://dx.doi.org/10.1007/s00338-010-0663-9>.
- Stimpson, J. 1990. Stimulation of fat-body production in the polyps of the coral *Pocillopora damicornis* by the presence of mutualistic crabs of the genus *Trapezia*. *Marine Biology*, 106:211–218. <http://dx.doi.org/10.1007/BF01314802>.
- Stock, J. H. 1988. Copepods associated with reef corals: A comparison between the Atlantic and the Pacific. *Hydrobiologia*, 167/168:545–547. <http://dx.doi.org/10.1007/BF00026350>.
- Sussman, M., Y. Loya, M. Fine, and E. Rosenberg. 2003. The marine fireworm *Hermodice carunculata* is a winter reservoir and spring–summer vector for the coral-bleaching pathogen *Vibrio shiloi*. *Environmental Microbiology*, 5:250–255. <http://dx.doi.org/10.1046/j.1462-2920.2003.00424.x>.
- Tribollet, A., and S. Golubic. 2011. Reef bioerosion: Agents and processes. In *Coral reefs: An ecosystem in transition*, ed. Z. Dubinsky and N. Stambler, pp. 435–449. Berlin: Springer.
- Valentich-Scott, P., and P. Tongkerd. 2008. Coral-boring bivalve mollusks of south-eastern Thailand with the description of a new species. *The Raffles Bulletin of Zoology*, 18(Suppl.):191–216.
- Vannini, M. 1985. A Shrimp that speaks crab-ese. *Journal of Crustacean Biology*, 5:160–167. <http://dx.doi.org/10.2307/1548228>.
- Vogler, C., J. Benzie, H. Lessios, P. Barber, and G. Worheide. 2008. A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. *Biological Letters*, 4:696–699. <http://dx.doi.org/10.1098/rsbl.2008.0454>.
- Weber, J. N., and P. M. J. Woodhead. 1970. Ecological studies of the coral predator *Acanthaster planci* in the South Pacific. *Marine Biology*, 6:12–17. <http://dx.doi.org/10.1007/BF00352602>.
- Wickler, W. 1973. Biology of *Hymenocera picta* Dana. *Micronesica*, 9:225–230.
- Wielgus, J., and O. Levy. 2006. Differences in photosynthetic activity between coral sections infested and not infested by boring spionid polychaetes. *Journal of the Marine Biological Association of the United Kingdom*, 86:727–728. <http://dx.doi.org/10.1017/S0025315406013622>.
- Williams, D. E., and M. W. Miller. 2005. Coral disease outbreak: Pattern, prevalence and transmission in *Acropora cervicornis*. *Marine Ecology Progress Series*, 301:119–128. <http://dx.doi.org/10.3354/meps301119>.
- Wulff, J. L. 1984. Sponge-mediated coral reef growth and rejuvenation. *Coral Reefs*, 3:157–163. <http://dx.doi.org/10.1007/BF00301960>.
- . 2006. Rapid diversity and abundance decline in a Caribbean coral reef sponge community. *Biological Conservation*, 127:167–176. <http://dx.doi.org/10.1016/j.biocon.2005.08.007>.
- Wulff, J. L., and L. W. Buss. 1979. Do sponges help hold reefs together? *Nature*, 281:374–375. <http://dx.doi.org/10.1038/281474a0>.
- Wunsch, M., S. M. Al-Moghrabi, and I. Kötter. 2000. Communities of coral reef cavities in Jordan, Gulf of Aqaba (Red Sea). *Proceedings of the ninth International Coral Reef Symposium*, 1:595–600.
- Zvuloni, A., R. Armoza-Zvuloni, and Y. Loya. 2008. Structural deformation of branching corals associated with the vermetid gastropod *Dendropoma maxima*. *Marine Ecology Progress Series*, 363:103–108. <http://dx.doi.org/10.3354/meps07473>.