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UNIVERSITY OF MIAMI

MOTILE CRYPTOFAUNA OF AN EASTERN PACIFIC CORAL REEF: BIODIVERSITY AND TROPHIC CONTRIBUTION

By

Ian C. Enochs

A DISSERTATION

Submitted to the Faculty
of the University of Miami
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MOTILE CRYPTOFAUNA OF AN EASTERN PACIFIC CORAL REEF: BIODIVERSITY AND TROPHIC CONTRIBUTION

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Motile Cryptofauna of an Eastern Pacific Coral Reef: Biodiversity and Trophic Contribution (December 2010)

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Coral reef cryptofauna (coelobites) are metazoans that occupy the hidden recesses formed by structural taxa such as corals. While cryptic communities are thought to account for the majority of reef biodiversity and play important roles in reef trophodynamics, little empirical evidence exists supporting these claims. Quantitative sampling of coelobites has been thus far limited due to highly heterogeneous reef topographies as well as difficulties associated with identification of large numbers of species. In the eastern Pacific, monogeneric stands of *Pocillopora* form reef structures that are homogeneous across a horizontal plane and support a relatively depauperate fauna, thereby permitting detailed multispecies analysis. Sampling of motile cryptofauna associated with live coral and dead coral frameworks typifying four levels of degradation, was conducted at Playa Larga Reef on Contadora Island in the eastern Pacific, Gulf of Panamá. Communities associated with live coral colonies were less diverse than those associated with dead corals and the species richness of cryptofauna living on dead coral substrates was higher in more degraded habitats. Living coral colonies, however, support significantly greater densities of cryptofauna and more biomass per volume substrate than their dead coral counterparts. On dead coral frameworks, numbers of individuals and biomass were significantly greater per volume in areas of intermediate degradation. A

field experiment was conducted to test the effects of flow, porosity and coral cover on cryptic communities associated with artificial reef frameworks (ARFs). Coral cover (live vs. dead) was not observed to affect the structure of communities occupying underlying frameworks, however, lower porosity substrates sheltered greater abundances of individuals per volume substrate and low flow environments supported elevated biomass. Additionally, porosity and flow were both found to significantly affect relative species abundances as well as overall community diversity. Data from quantitative sampling of natural reef environments and experimental manipulation of cryptic reef habitats suggest novel and unexplored responses to mass coral mortality and reef habitat degradation. Coral death is considered to be vital to the maintenance of reef ecosystem habitat and biotic diversity. Contrary to the popular paradigm that a healthy reef ecosystem has high coral cover, the most diverse reef ecosystems are those which have experienced intermediate levels of degradation. Furthermore, while living corals support elevated cryptofauna abundances and biomass, the magnitude of communities associated with dead framework materials suggest that abundant cryptofauna populations persist in highly degraded reef environments.

To my grandfather who showed me the water,
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Introduction

Coral reefs are among the most species rich ecosystems on the planet. Seemingly endless varieties of fishes swim through every shape, size, and color of hard and soft coral. Yet even if you were to count all of the species inhabiting exposed reef habitats, you would literally not scratch the surface of the biodiversity and complexity that is a coral reef ecosystem. Hidden within reef frameworks, under rubble and between coral branches are thousands of animals, aptly named cryptofauna for their cryptic and secretive nature. If reefs are the rainforests of the sea, then cryptofauna are the marine equivalent of insects whose overwhelming biodiversity and countless numbers have long been recognized by terrestrial ecologists. This so called “inner life of coral reefs” is an integral component of a multitude of ecosystem processes ranging from growth and reproduction to death and destruction (Ginsburg 1983). Yet despite their diversity, abundance, and close association with reef dynamics, these organisms remain true to their name, hidden and understudied.

Those studies that do exist boldly highlight the magnitude of the cryptofauna within reef ecosystems (Table 1.1). Grassle (1973) found over 2,000 individuals living cryptically within a single 4.7 kg colony of *Pocillopora damicornis*. Of these, 1,441 were polychaetes comprising 103 species. Also present were a variety of arthropod taxa including specimens belonging to the Amphipoda, Decapoda, Isopoda, and Tanaidacea, as well as echinoderms belonging to Ophiuroidea, annelids of the Oligochaeta, and species of Sipuncula. Considering just sessile taxa living under rubble surrounding reefs in Bonaire and Curaçao, Meesters et al. (1991) found 367 species belonging to Porifera, Chordata, and Bryozoa. Nearly all marine metazoan phyla can be found within reef ecosystems and all major groups within these phyla, with the sole exception of Mammalia, are known to occupy or forage within crypts (Kobluk 1988; Paulay 1997). Several studies have carefully documented the abundances of various cryptic taxa associated with specific substrates and determined that abundances are orders of magnitude higher than those found in exposed coral and reef environments (Table 1.1). McCloskey (1970) recorded 56,616 individuals associated with eight colonies of the coral *Oculina arbuscula*. Kohn and White (1977) estimated that densities of polychaetes living within reef carbonates in Guam reached 43,500 m^{-2}. In coral rock collected from Kaneohe Bay, Hawaii, Brock and Brock (1977) observed densities of cryptic polychaetes up to 127,900 m^{-2}, comprising 16 families and accounting for roughly 12% of 796 $g\ m^{-2}$ (dry weight) total infaunal biomass. Ginsburg (1983) hypothesized that the biomass of cryptic organisms is greater than that of reef surface biota. Indeed, Enochs and Hockensmith (2008) found that after a single year, motile cryptic metazoans colonized living *P. damicornis* at mean biomass densities of 4.2 grams per liter of coral skeleton.

Considering their great biodiversity, abundance, and biomass, it is not surprising that cryptofauna play an integral role in reef ecosystem function. At fine scales, cryptic sponges (Goreau and Hartman 1966), copepods (Dojiri 1988), crabs (Simon-Blecher 1997), barnacles (Vago et al. 1998), polychaetes (Liu and Hsieh 2000), and shrimp (Bruce & Trautwein 2007) modify the form of the structural species that construct reef habitat (reviewed in Glynn & Enochs, in press). Still other species of cryptic sponges (Tunnicliffe 1979) and lithophage bivalves (Guzmán 1988) may weaken coral skeletons, thereby facilitating their asexual reproduction. Many species of cryptofauna are corallivores (e.g., acoelomorph worms, asteroids, echinoids, hermit crabs, polychaetes, prosobranch and nudibranch gastropods) and in high densities may have devastating effects on corals and reef ecosystems alike (reviewed in Rotjan & Lewis 2008). Bioeroding taxa such as barnacles, lithophage bivalves, polychaetes, sipunculans, and sponges may bore into dead skeletons and degrade reef carbonate materials (Glynn 1997). Still other species of cryptic sponges and bryozoans may bind to and consolidate the resulting coral fragments, thereby stabilizing the substrate long enough for further coral recruitment and reef growth (Wulff 1984). Brachyuran crabs and caridean shrimps that live hidden within the branches of pocilloporid corals have been shown to clean (Glynn 1983) and defend their hosts from predation (Glynn 1980).

Cryptic fauna are prominent members of all metazoan trophic guilds and as such, are vital to ecosystem function. As detritivores (e.g., Crustacea, Echinodermata, Pisces), they ingest organic deposits (Depczynski & Bellwood 2003) and feces (Rothans & Miller 1991), transforming this material into more bioavailable forms. As suspension feeders (e.g., Bivalvia, Bryozoa, Ophiuroidea, Porifera) cryptic metazoans capture planktonic nutriment from the water column and convert it into benthic biomass (Richter & Wunsch 1999). Cryptic herbivorous gastropods (Taylor 1968) and crustaceans (Klumpp et al. 1988) graze on reef algae and may be especially prominent where they are sufficiently sheltered from predation, such as in damselfish territories. Macro- (e.g., Stomatopoda; Reaka 1987) and micro-predators (e.g., Isopoda, Jones & Grutter 2008) that shelter within reef crypts have been shown to significantly affect the distribution and health of their prey, respectively.

Cryptic organisms are by no means a closed sub-web within reef ecosystems and there are a variety of trophic linkages connecting cryptic biomass to the epibenthos and nekton. Plankton (Alldredge & King 1977) and benthic cryptofauna (Reichelt 1982), that shelter within reef frameworks during the day, emerge at night where they are consumed by nocturnal fishes. Some species such as muraenid eels are intermittently cryptic and may forage within reef recesses (Glynn 2006). Large nektonic taxa such as triggerfishes (Guzmán 1988), sharks (Jiménez 1997-1998), and turtles (Glynn 2004) are known to break apart frameworks and destroy endolithic shelters in order to consume the fauna within.

Cryptic biota and cryptic habitats have been a ubiquitous feature of reefs long before the evolution of modern scleractinian corals. Though often difficult to differentiate from surface taxa in the geological record, there is evidence that ancient cryptofauna existed within the archaeocyathid reefs of the Lower Cambrian (Figure 1.1; Kobluk & James 1979; Kobluk 1988). Examples of cryptic Cambrian taxa include several genera of algae, metazoan bioeroders, brachiopod-like organisms, sponges, foraminiferans, trilobites, archaeocyathids and fungi (reviewed in Kobluk 1988). It is unknown what happened to cryptic reef communities in light of the disappearance of archaeocyathid structures in the lower Cambrian. However, the evolution of more complex skeletal taxa in the early Ordovician and their great prevalence among reef ecosystems in the middle Ordovician gave rise to abundant cryptic habitats suitable for a diverse assemblage of associated fauna (Kobluk 1988). For reviews of the evolution of reef structures, cavities, and the associated cryptic biota see Kobluk (1988) and Wood (1999).

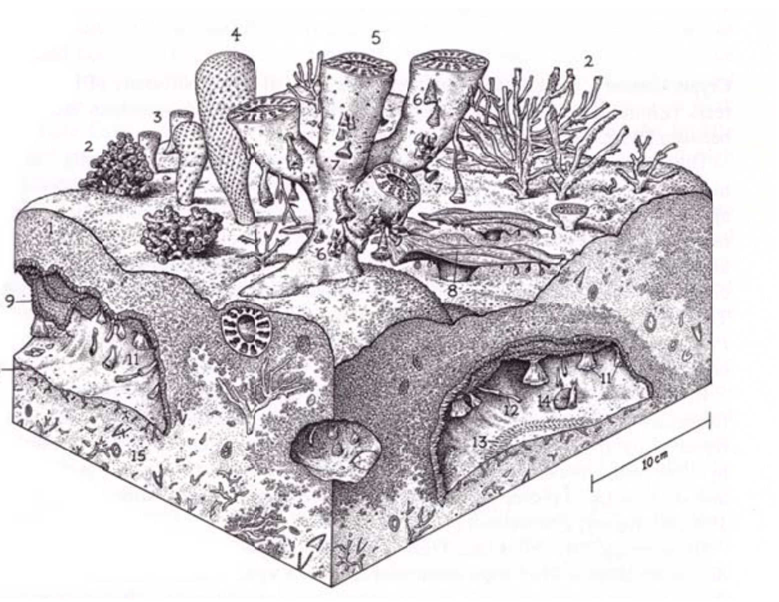

Figure 1.1. Radiocyath-archaeocyath-cribricyanth reef community. Cryptic biota: 10, deposit-feeder micro-burrows; 11, cryptic archaeocyaths and coralomorphs; 12, Cribricyath; 13, trilobite trackway (Wood 1999).

Several workers have developed classification schemes for the great variety of cryptic reef metazoans. Kobluk (1988) recognized “sessile” and “vagrant cryptos” based on motility as well as “endolithic cryptos,” which refers to organisms that create their own cavities within reef carbonates. Hutchings (1983) divided cryptofauna into two categories: the “true borers” and “opportunistic” species. These categories are consistent with the “borers” and the “nestlers” or “crevice-dwellers” recognized by McCloskey (1970). To these groups, which he termed “destroyers” and “dwellers” respectively, Fagerstrom (1987) used “binders” to describe organisms that consolidate and stabilize carbonates (e.g., Porifera, Bryozoa). Additionally Fagerstrom (1987) recognized that the cryptic habitat is primarily occupied by “colonial encrusting invertebrates” and to a lesser extent by “accessory species” which include brachiopods, bivalve and vermetid mollusks, serpulid annelids, barnacles, crinoids, and ascidians. Moreno-Forero et al. (1998) divided cryptic organisms into three categories based on their body size and microhabitat use:

"mobile epibenthos," including crustaceans and gastropod mollusks that live on the surface of carbonates but remain sheltered in cavities; "boring microcryptobiota," referring to the algae, bacteria, fungi, and sponges that bore into the surface of coral skeletons and live primarily between epilithic biota and reef carbonates; and finally "perforating macrocryptobiota," including crustaceans, mollusks, polychaetes, and sipunculans that penetrate deep into coral skeletons. Perhaps the most thorough division of coelobites is that of Ginsburg (1983). He identified six categories based on the organism's motility and relationship to their substrate.

1. "Encrusting" – organisms that form surfaces over reef substrates (e.g., Bryozoa, Foraminifera, some forms of Porifera, Tunicata).
2. "Attached" – taxa which remain sessile on reef carbonates but are not laminar in form (e.g., Bivalvia, Brachiopoda, Crinoidea, Porifera, Urochordata).
3. "Boring" – species which form tunnels and cavities within reef carbonates (e.g., Bivalvia, Cirripedia, Polychaeta, Porifera, Sipuncula)
4. "Burrowing" – organisms forming shelters between sediment particles (e.g., Annelida, Crustacea, Mollusca).
5. "Vagile" – motile taxa living on hidden carbonate surfaces (e.g., Annelida, Crustacea, Echinodermata, Echiura, Gastropoda, Nemertea, Opisthobranchia, Sipuncula).
6. "Nektonic/planktonic" – organisms which may swim or float within the water column but are also known to utilize cryptic reef habitats (e.g., Actinopterygii, Annelida, Cephalopoda, Chondrichthyes, Crustacea, Reptilia).

When considering the aforementioned classification schemes, it is important to remember their anthropogenic nature and not rely too heavily upon their admittedly artificial distinctions. It is recognized that there are examples of organisms which may be classified differently during different life stages or times of the day, and that there are animals whose behavior may be considered to fall into more than one of the above categories.

Adding to the difficulty of studying cryptic taxa are the variety of terminologies used throughout the literature to describe them. Perhaps one of the first names used to describe hidden reef animals was sciaphiles, proposed by the French worker Laborel (1960), from the Greek words “skia” and “philia,” meaning shadow lover. Bakus (1966) later adopted the word “cryptofauna” because he considered it to be more descriptive of the animal’s hidden nature. The term coelobites was first used by Ginsburg and Schroeder (1973) to describe the organisms that they found living within the cavities of cup-shaped algal reefs off Bermuda. Ginsburg was dissatisfied with the ambiguity of the word “cryptic” and the limited root of the word “sciaphiles,” which only describes one of the many environmental characteristics (darkness) of the cryptic habitat (Ginsburg, pers. comm.). In his words:

> When we excavated reefs in Bermuda and found their cavities lined with living organisms, I decided to give their habitat a more appropriate name than hidden. I tried cavity-dwelling organisms but found it too long, then somehow by someone I chanced on coelom for cavity or hollow and I added bios for life. That combination was my one word substitute for ‘cavity-dwelling organisms’. Moreover, a reader with only a slight familiarity with Latin might understand it.

Ginsburg's discontent with the vagueness of the word "cryptic" was especially prescient considering modern uses of the word to describe sibling species uneasily distinguished on the basis of morphological differences (Knowlton 1986). In addition to the aforementioned names, Kobluk (1988) lists various other terms that have been used to refer to coelobites including coelobiont, troglodite, chasmolith, chasmoendolith, cryptoendolith, cryptone, cavernicole, skiophile, shade-dweller, cavity-dweller, cave-dweller, hidden encruster, photophobe, and cryptobiont. Hiatt and Strasburg (1960) use the word "fossorial," which is more often seen in the terrestrial literature to describe hidden and burrowing organisms. Still other terms synonymous with cryptofauna may be found listed in Hutchings (1983) including names describing organisms living within carbonates (infauna, endo-cryptolithic fauna, endolithic species, marine bioeroders, lithophagic species) and those living cryptically on the surface of skeletal materials (opportunistic or nestling species).

Examples exist where these names are used inconsistently to refer to organisms from different taxonomic groups, that occupy different substrates, or that have different life history strategies. Throughout this manuscript, the terms "cryptofauna" and "coelobites" are used literally, to describe metazoans occupying reef cavities either intermittently or throughout the entirety of their life. These terms may be further modified with: sessile or motile, to describe their motility; nektonic, planktonic, or benthic, to describe their principal habitat; endolithic or epilithic, to describe their occurrence within or on the surface of carbonate substrates, respectively; intermittent or permanent, to describe the amount of time spent in the cryptos; and constructive, erosive, burrowing (between already separate framework pieces), binding, or nestling, to describe their potential relationship to reef carbonate substrates. Symbionts of live coral may be termed cryptofauna if their relationship to their substrate includes, but is not limited to shelter. Similarly, when considering taxa classically labeled "bioeroders" it is important to take into account their relationship to the eroded substrate. Endolithic lithophage bivalves and clionaid sponges utilize carbonate frameworks as protection from potential predators (e.g. balistid fishes and turtles respectively) and are therefore cryptofauna. Adult parrotfishes (Scaridae), which are nektonic and may scrape off surface carbonates while foraging, are not considered cryptic. However, post-settlement juveniles may find shelter within dead coral substrates and are therefore cryptic. Erosive diadematid echinoids may be considered cryptic in some environments where both substrate rugosity and predation pressure is high (e.g. eastern Pacific pocilloporid reefs). In other environments (e.g., sand planes or urchin barrens), they may adopt lifestyles not considered cryptic.

The last review of reef cryptofauna was written over two decades ago. This manuscript will synthesize, expand upon and update the detailed geologically focused reviews of Ginsburg (1983), Fagerstrom (1987), and Kobluk (1988) as well as Hutchings' (1983) expert review of modern cryptofauna. The unique conditions of the cryptic reef habitat will be discussed with attention to the different environmental (flow, light, structure, disturbance, nutrients, seasons), biological (food availability, succession, benthic cover, predation, competition), and anthropogenic (over fishing, nutrification, offshore drilling, climate change, acidification) factors that influence the distribution of cryptic organisms. There is a growing appreciation of the trophic role that cryptofauna play within reef ecosystems. I will detail their importance as suspension feeders, deposit feeders, herbivores, predators, and corallivores, as well as highlight the myriad trophic linkages between cryptic communities and reef surface biota. Finally, I will discuss the magnitude and importance of coral reef biodiversity, of which cryptofauna composes a substantial proportion.

Cryptic habitat and factors affecting distribution

The size and shape of cryptic reef habitats are highly dependent on the structure of the skeletal taxa composing them as well as the degree of taphonomic alteration that they have undergone. Consider two Pacific reefs, one formed primarily from the branching coral *Pocillopora damicornis* and the other from the massive coral *Pavona clavus*. In the *Pocillopora* reef environment, motile organisms can find shelter among bifurcating branch structures. Water moving unimpeded through the porous open channels of the cryptic habitat provides nutriment to abundant sessile suspension feeders. Because branch diameter is narrow, there is relatively little habitat for cryptic endoliths. Those bioeroders that do exist (mostly in thick basal branches) weaken the corals, creating large quantities of rubble and eventually sand, both of which provide shelter to cryptofauna. On *Pavona* reefs, the abutment of massive colonies gives rise to cracks and crevices, occupied by nestling cryptic taxa. Reef carbonates are riddled with voids formed by bioeroding bivalves, polychaetes, and sponges. These cavities are, in turn, utilized by a suite of opportunistic fauna. The flat undersides of unattached colonies and fissures underneath semi-attached corals are colonized by sessile sponges, bryozoans, and foraminifers as well as a diverse array of motile annelids, crustaceans, echinoderms, mollusks, and fishes. Rubble in these environments is often larger than that of branching reef environments and consequently may be more stable, allowing the colonization and growth of sessile colonial biota. The vast majority of reefs are not monotypic stands. In heterogeneous reef environments with high coral diversity, a great variety of cryptic microhabitats may be present within a few square meters (Figure 1.2).

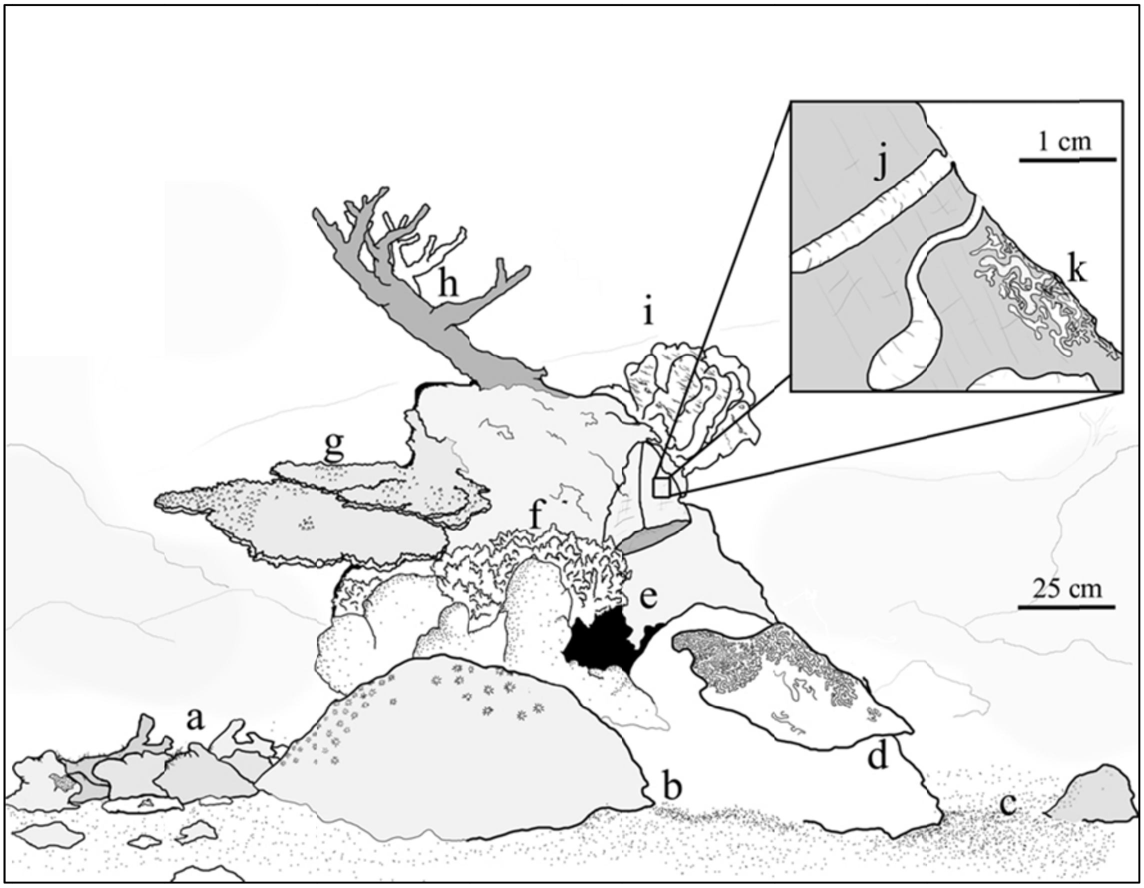

Figure 1.2. Selected examples of cryptic reef habitats. a, spaces between rubble fragments; b, crevices below massive corals; c, burrows and interparticle cavities within sand beds; d, planar voids beneath encrusting corals; e, cavities within framework structures; f, shelters within arborescent coral colonies; g, laminar voids between plating corals; h, crevices formed by the abutment of large colony branches; i, voids formed by the closely-spaced plates of foliose corals; j, intraskeletal bore tubes; k, irregular networks formed by erosive sponges.

Several workers have developed classification schemes in order to maintain consistency when referring to specific cryptic microhabitats. Garrett et al. (1969) identified three types of cavities from Bermudian reefs: cavities below and between coral colonies; cavities beneath large framework “knobs”; cavities present on reef faces or fronts. Garrett et al. (1971) subsequently named these categories “knob cavities”, “basal knob cavities”, and “reef face cavities” respectively. Scoffin and Garrett (1974) identified cryptic habitats based on the morphology of the coral species in which they are located. Fagerstrom (1987) adopted a more simplified system, distinguishing between large and small cavities formed by corals in growth position as well as voids between dead coral rubble. Kobluk (1988) adopted a classification scheme that combines Garrett’s structural approach towards framework crypts with Fagerstrom’s recognition of motile rubble as a separate habitat. Kobluk uses the term “cavity crypts” to refer to habitats enclosed by upper, lower and at least one side surface; “crevice crypts” to refer to narrow crack-like crypts with an open upper surface; “intraskeletal crypt” to refer to voids within a single or skeletal organism or colony and “shelter crypt” for the sheltered voids underneath and between mobile rubble.

Ginsburg (1983) provided the most detailed classification scheme to date. He broadly divided reef crypts into four groups based on their origin and subdivided each according to specific morphological criteria. His scheme follows with descriptions and examples.

1. <u>Intraskeletal</u> – Cavities that exist as a product of the natural shape of biogenic structures.
    - *a. Cellular* – Voids with coral coenosteum as the result of septal, costal, and columellar intersections.
    - *b. Tubular* – Gastropod mollusk shells, serpulid and sabellid worm tubes.

   c. *Chambers* – Bivalve and gastropod mollusk shells, coral gall formation.

2. <u>Growth, framework and shelter cavities</u> – Crypts formed as a result of the close proximity of two or more skeletal structures (e.g., living coral colonies and branches, coralline algae, dead coral frameworks).
   a. *Planar, lens, and wedge-shaped cavities* – Thin spaces between taxa with laminar morphologies (e.g., crustose coralline algae, plating, and encrusting corals).
   b. *Shelter cavities* – Sheltered spaces underneath flat structures (e.g., bivalve shells, plating coral fragments).
   c. *Caves and networks of irregular cavities* – Caves formed from the successive colonization and growth of diverse and irregular shaped skeletal taxa.
3. <u>Interparticle cavities</u> – Voids between sediment grains (fine sand to large rubble), occupied by meiofauna or larger nestling taxa.
4. <u>Borings</u> – Cryptic spaces formed as a result of the destructive behaviors of various bioeroding taxa.
   a. *Cellular* – Small anastomosing networks formed from the erosive activities of clionid sponges.
   b. *Tubules* – Small straight borings (~2 – 10 μm) created by endolithic cyanobacteria and fungi.
   c. *Tubular and vase-shaped* – Larger straight borings (mm to cm) formed by boring bivalves, polychaetes, sipunculans, and cirripedes.

d. *Equant and irregular chambers* – Voids (~2 – 10 cm) created by animals such as the poriferan *Siphonodictyon* spp.

Because of the diversity of habitat structures and the stigma associated with destructive sampling regimes, it is often difficult to obtain reliable estimates of the depth of the cryptic habitat. It is probable that in some reef ecosystems, cryptofauna may penetrate meters into reef frameworks. However, in environments with more sedimentation, they may be restricted to depths less than one centimeter below the reef surface (Ginsburg 1983). Similarly, the diameter of reef cavities can range from millimeters to meters, depending on how they were created and what taxa they are formed from (Zankl & Schroeder 1972). The volume of reef cavities is especially difficult to measure as samples must be taken which are large enough to encompass meter-long cavities and of high enough resolution to detect voids millimeters in diameter (Ginsburg 1983). Garrett et al. (1971) used dynamite to blast apart framework structures composed primarily of massive corals (e.g., *Diploria* spp., *Montastraea* spp., *Porites astreoides*, *Siderastrea* spp.) on patch reefs in Bermuda. From visual analysis of framework cross-sections, they estimated that reef cavities (both open and sediment-filled) accounted for 30-50% of the reef volume. Working in the same area Meischner and Meischner (1977) approximated the volume of cryptic recesses to be 50% of the reef. Kobluk and van Soest (1989), studying cryptic sponges from cavities with solid reef frameworks in Bonaire, estimated that cavities accounted for greater than 50% of the reef volume in some areas. General estimates by Ginsburg (1983) place the volume at between 75 and 90% of the reef.

The surface area of cryptic reef environments is considered to be larger than that of the epibenthos, thereby providing extensive substrate for sessile encrusting taxa (Jackson et al. 1971; Buss & Jackson 1979; Logan et al. 1984). In their investigation of suspension feeding within the cavities of fringing coral reef frameworks in the Red Sea, Richter and Wunsch (1999) conservatively estimated that there was twice as much cryptic surface area as planar reef surface. Working on the same reefs, Richter et al. (2001) three-dimensionally reconstructed photographs taken with an underwater endoscope and calculated that the actual cryptic surface area ranged from 3.5-7.4 m^2 per planar square meter of reef. These values are remarkably similar to those obtained by Scheffers et al. (2004; 1.5–8 times surface), using a similar apparatus within reef framework cavities off Curaçao in the Netherlands Antilles.

Despite their great structural variability, it is necessary to consider coral reef crypts as a distinct habitat due to the unique combination of environmental conditions that they share. They receive less light than the surface, a phenomenon that simultaneously restricts the distribution of phototrophic biota and encourages the proliferation of organisms not physiologically adapted to deal with harsh solar radiation. Framework structures and cavity walls act to baffle wave action and reduce flow through cryptic habitats. Consequently, coelobites may receive less suspended nutriment and experience higher rates of sediment deposition. Shelter from wave stress may facilitate the growth of more fragile morphologies and can lessen the impact of adverse environmental perturbations such as hurricanes. Shelter may also provide protection from abundant nektonic and epibenthic reef predators. However, those species that are adapted to penetrate the cryptic habitat may encounter abundant prey with restricted motility.

Considering the aforementioned properties, it is clear that the cryptic habitat experiences a level of stability unparalleled within the coral reef environment. Organisms are not subjected to the full range of light intensities experienced by surface biota across diel and annual time scales. They do not experience the full spectrum of flow velocities that vary across tidal and seasonal cycles. Stochastic environmental perturbations as well as chance encounters by roving predators have a reduced effect on coelobites that remain sheltered within reef crypts. Yet despite this increased consistency, many environmental and biological conditions do vary across both spatial and temporal scales within cryptic reef habitats. Differences in the magnitude and fluctuation of these conditions are often strongly correlated with patterns in coelobite community composition. Several of these relationships are discussed below, though it should be noted that many environmental factors (e.g., light vs. depth, flow vs. sedimentation) and biological processes (e.g., competition for space vs. availability of food) known to influence cryptofaunal communities co-vary and it is often difficult or impossible to isolate causal mechanisms.

Factors influencing community composition – Physical and temporal

Water movement

The flow dynamics of cryptic reef habitats are dependent on the magnitude and direction of the surface flow as well as the structure of the crypts through which they pass (reviewed in Wolanski 1994). In most situations, carbonate structures baffle surface flows, leading to increased particle deposition. Richter and Wunsch (1999) observed the velocity of pore waters within framework cavities in the Gulf of Aqaba to be roughly 22% of that of surface waters two meters above the reef. In the less-porous, lower-energy reef environment of Checker’s reef, Hawaii, the residence time of pore water 1 m deep within the reef is roughly two days (Tribble et al. 1992). The limited exchange of reef interstitial waters may lead to reduced dissolved oxygen concentrations, limit the supply of planktonic food sources, or even inhibit the availability/settlement of pelagic larval recruits (Sansone et al. 1988; Richter & Wunsch 1999; Falter & Sansone 2000).

Water moving over a depression (or cavity) encounters an environment of greater cross-sectional area and therefore slows down. This reduces shear stress and results in greater sedimentation (Nowell & Jumars 1984). Additionally, slow moving pore waters adjacent to faster moving surface waters may create a pressure gradient accompanied by the vertical transport of suspended matter, a phenomenon that occurs in some sponges and with winds in terrestrial termite mounds (Richter & Wunsch 1999).

Many researchers have drawn attention to the fact that cryptic reef communities are composed primarily of suspension feeders (Vasseur 1977; Andrews & Muller 1983; Richter & Wunsch 1999; Wunsch et al. 2000; Richter et al. 2001; Scheffers et al. 2004). Significant depletion of diatoms (Glynn 1973) and other plankton (Ayuki 1995) have been observed in waters over reef flats and similar processes occur within cryptic environments. Gischler and Ginsburg (1996) observed that total colonized area and abundance of sessile coelobites under reef rubble off Belize was greatest in areas of high flushing. They attributed this correlation to the dependence of the primarily suspension and deposit-feeding community on water-born nutriment. Choi and Ginsburg (1983) also found flushing to be beneficial to sub-rubble communities along the Florida Reef Tract. Buss and Jackson (1981) observed that the restriction of flow velocity through artificial cryptic environments resulted in reduced colonization by sessile cryptic organisms, presumably due to food limitation. Working with endolithic bioeroders on pocilloporid reefs on the Pacific coast of Colombia, Londoño-Cruz et al. (2003) found that the primarily suspension feeding fauna (e.g., lithophage bivalves and cirripedes) more rapidly eroded high wave-energy environments, evidently aided a greater availability of planktonic food sources.

The positive correlation between flow and cryptofauna abundance may not hold true for all taxa in all reef environments. Different environmental and biological conditions (e.g., substrate structures, recruitment events, food requirements) may supersede, complicate or obscure this relationship. In some environments, cryptic biota may even be negatively influenced by flow (Cinelli et al. 1977). Hutchings and Weate (1977) observed that cryptofauna distributions were affected by a variety of factors. However, between reefs, sheltered environments corresponded to greater biomass accumulation. Depczynski and Bellwood (2005) recorded greater numbers of species and higher abundances of small cryptic fishes within sheltered reef environments. Preston and Doherty's (1990) observations on cryptic coral-dwelling shrimps on the Great Barrier Reef suggest that within reefs, exposure is not an important determinant of community composition or abundance. However across separate reefs, mid-shelf environments had higher abundances than outer or inner-shelf environments.

Before considering the effects of light and depth on cryptofauna communities, it is important to recognize their close correlation with water movement/turbulence as shown by Martindale (1992) for reefs off Barbados (Figure 1.3). Shallow environments often experience more flushing as they are in closer proximity to surface waves (Wunsch et al. 2000). In addition to increasing food availability, decreasing sedimentation, and providing greater supplies of larval recruits, wave- and storm-induced turbulence may lead to the increased instability of mobile substrates and thereby limit the proliferation of slow-growing and sessile taxa (Gischler & Ginsburg 1996). Deeper reef habitats are not as affected by these types of flow-induced disturbances and consequently cryptic communities living with these environments are structured by a variety of other factors (Moran & Reaka 1988).

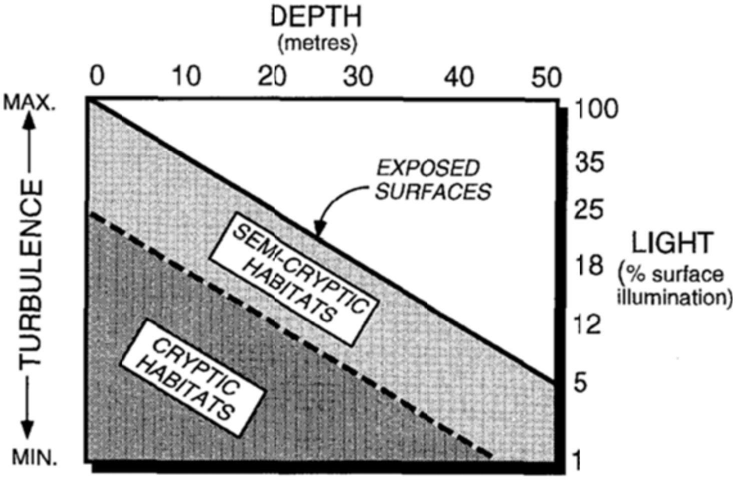

Figure 1.3. The relationship between depth, light, and water turbulence within cryptic, semi-cryptic, and exposed reef environments at Bellairs, Barbados (Martindale 1992).

Light and depth

Light is one of the most important physical conditions influencing the location and zonation of coral reef ecosystems (e.g., Done 1983). Its rapid attenuation with depth limits the vertical distribution of photosynthetic corals and algae. Cryptic environments that are shaded provide conditions similar to those found at much greater depths (Figure 1.4). Kobluk (1988) reviewed two studies describing shallow-water cryptic (Logan 1981) and deep-water epibenthic communities (up to 300 m; James & Ginsburg 1979) associated with reefs off Grand Cayman and Belize, respectively. In cavities that experience community zonation due to light attenuation, community gradation was mirrored by that of epibenthic communities with depth. As the abundance of photosynthetic organisms decreased, heterotrophic bryozoans and sponges began to proliferate, ultimately giving rise to a deep-water or deep-crypt community, composed of sclerosponges and brachiopods (Kobluk 1988).

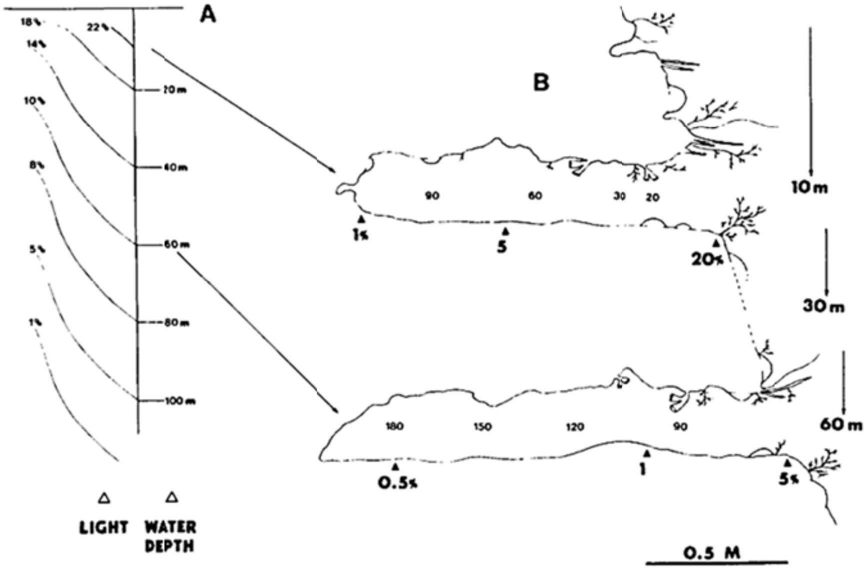

Figure 1.4. A. the relationship between light (% surface) and water depth. B. The equivalent depth-related light levels experienced with increasing distance into submerged reef cavities (Kobluk 1988).

Many workers have reviewed (Ginsburg 1983; Fagerstrom 1987; Kobluk 1988) and documented (Garrett 1969; Garrett et al. 1971; Logan 1981; Logan et al. 1984) reduced light intensities within reef cavities. Garrett (1969) and Garrett et al. (1971) identified three sequential photic zones within reef cavities including "open" (50% – 6% surface illumination), "gloomy" (observers' eyes must adjust to low light levels), and "dark" (no light present). Both papers recorded a reduction in photosynthetic organisms with increasing distance from the cavity opening, ultimately leading to completely heterotrophic species assemblages occupied by bryozoans, sponges, foraminiferans, polychaetes, and bivalves. Logan (1981) found light levels to be a strong determinant of community composition within reef cavities at Grand Cayman and identified three distinct biotic assemblages structured accordingly. Logan et al. (1984) recognized similar irradiance dependent zonation in Bermuda and identified two distinct community assemblages using cluster analysis.

Spectral filtering of incident light may occur within reef cavities and at depth (Kobluk 1988). This follows in an ordered manner, with longer wavelengths extinguished first (Figure 1.5). Short wavelength ultraviolet light is therefore poorly absorbed by water. However, filtering may occur due to dissolved organics and suspended particulates (Jokiel 1980). In coral reef environments, where waters are often clear and devoid of high concentrations of organic matter, ultraviolet light may reach and, if unmitigated, adversely affect surface biota (Jokiel 1980). It is no surprise then that many surface taxa, that are limited to the photic zone due to phototrophic dependency, produce a variety of chemicals that absorb radiation and counteract its potentially harmful effects (reviewed in Dunlap & Shick 1998). Alternatively, many taxa are known to limit their exposure by sheltering within reef crypts. Jokiel (1980) transferred rubble from reef environments into aquaria and overturned them in order to expose them to levels of UV radiation comparable to that experienced on reef surfaces. Within three days, UV-exposed communities of cryptic sponge, bryozoans, and tunicates experienced approximately 80% mortality. Communities that were exposed to identical intensities of solar radiation, but with UV spectra experimentally filtered out, experienced little to no mortality, suggesting that UV radiation was responsible for the death of exposed coelobites.

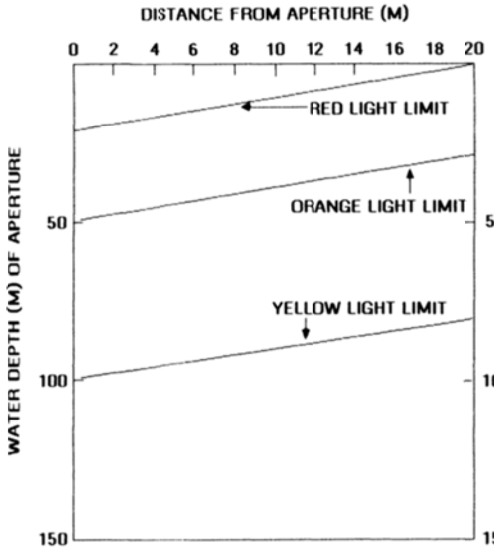

Figure 1.5. The attenuation of light wavelengths with vertical water depth (m) and distance into a cave (distance from aperture m; Kobluk 1988).

The relationship between light availability and coelobite community structure is not immediately clear in all habitats (e.g., Dinesen 1983). Wunsch et al. (2000) corroborated that increasing depth within a cavity corresponds to shifts in coelobite community assemblages, however they pointed out that predation and algae co-vary with light and may therefore be responsible for zonation. Cinelli et al. (1977) argued that metazoan coelobite responses to light are indirect, mediated by that of benthic flora. In the presence of light, photosynthetic organisms may outcompete and overgrow other sessile heterotrophic biota, thereby reducing overall biodiversity (Navas et al. 1998). Furthermore, cryptic herbivores such as brachyuran crabs, which rely on light-limited algae for sustenance, may have distributions mirroring that of their food source (Peyrot-Clausade 1989). The importance of algae may be further confounded by latitudinal trends in their competitive ability within cryptic environments. At higher latitudes on the Great Barrier Reef, algae have been shown to be more successful in outcompeting cryptic scleractinian corals (Dinesen 1982).

In some localities, higher densities of cryptic macroborers may be found at depth (e.g., Kobluk & Kozelj 1985). However, like epilithic cryptofauna, this relationship may be due in part to a variety of correlated factors. For example, crustose coralline algae, which may tolerate lower light levels than fleshy varieties (Littler & Littler 1994), have been shown to provide a substrate more favorable to the settlement and infestation of endolithic coelobites (Cinelli et al. 1977). Furthermore, the bore holes and cavities created by these erosive taxa may in turn provide habitat for epilithic fauna, thereby perpetuating and extending the indirectly-related correlation with depth.

Conversely, several workers have noted a negative correlation between depth and the abundance of cryptofauna associated with living *Acropora* (Patton 1994), *Oculina* (Reed et al. 1982), *Pocillopora* (Gotelli & Abele 1983; Chang et al. 1987), and *Stylophora* colonies (Edwards & Emberton 1980). Gotelli and Abele (1983) discuss co-varying factors including coral density and tidal exposure that are possibly responsible for this trend. To these, Edwards and Emberton (1980) add branch density. Deeper water colonies of the arborescent coral *Stylophora pistillata* exhibited wider spaced branches, presumably for more efficient capture of less-available light. Crustaceans that hide between these corals' branches were less abundant within deeper water colonies, likely due to reduced shelter from predators.

Substrate structure

The morphology of reef substrates is of paramount importance to the organisms that intimately associate with them. For example, the surface area and porosity of coral rubble is a key factor in predicting infaunal density, with endolithic polychaetes preferring high surface area and highly porous framework pieces (Hutchings 1974a). Shirayama and Horikoshi (1982) developed a “growth-form index” for living reef corals by dividing the surface area of a colony by its weight raised to the two thirds power. Based on this equation, they collected and separated corals into four growth forms: massive, irregular shaped, branching, and highly branching. Associated fauna were removed from each colony and classified according to their “mode of living,” including motile and sessile epilithic biota, boring cryptofauna, and finally “secondary cryptobionts”, which occupy the internal burrows and cavities created by bioeroders but do not themselves actively erode. Massive coral morphologies were observed to support abundant communities of dominantly endolithic fauna, including both boring and secondary varieties. Branching and highly-branching forms were more often colonized by epilithic associates and both motile and sessile taxa were present.

As previously noted, variation in branch density has been investigated as a causative agent behind decreasing cryptofauna abundance at depth (Edwards & Emberton 1980). It has also been considered irrespective of depth. Vytopil and Willis (2001) collected four species of *Acropora*, each typifying a different branch density (Figure 1.6). The richness and abundance of cryptic associates were found to be highest on closely branching species and depauperate or absent on more open corals. The same cryptic community parameters were found to be unrelated to surface area and colony volume.

The authors concluded that closely spaced branches provide greater protection from predators, which were unable to locate, reach, and remove taxa hidden therein. This hypothesis was further supported by the observation that defenseless juvenile crabs were found to recruit only to the most sheltered coral species, *Acropora hyacinthus*. A similar analysis was conducted by Kirsteuer (1969) for nemertean worms associated with six species of branching coral (in order of increasing branch openness: *Seriatopora angulata*, *Porites iwayameaensis*, *Acropora corymbosa*, *Millepora tenella*, *Acropora pharaonis*, *Porites nigrescens*). Coral species with closely spaced branches were found to support more abundant nemertean populations. Again, colonies which afforded their occupants greater protection from predators hosted greater abundances of associates.

Similar to the branch density of living corals, the structural complexity of reef frameworks and their heterogeneity, or number and variety of microhabitats, is closely correlated to the number and diversity of associated cryptofauna. Diaz et al. (1990), working with coral reef associated Mollusca on the Atlantic coast of Colombia, collected 201 living and another 61 species of dead mollusks (shells). Comparison of the substrate structure between sampling sites led them to conclude that areas with more structural complexity and higher numbers of crypts had greater species richness. (Note: this pattern may also reflect abundance though it is unclear whether the “abundance of molluscan species” that the authors refer to actually indicates abundance, as they paraphrase its meaning as “species-richer” communities. It appears that neither sampling effort nor abundances were standardized and therefore these observations must be treated as quasi-quantitative). The diversity of reef-associated gastropods in the genus *Conus*, which may be as high as 27 congeners on one reef, is positively correlated with the structural heterogeneity (Kohn & Nybakken 1975) and microhabitat diversity of their substrates (Leviten & Kohn 1980). Additionally, the abundance of demersal plankton sheltering within reef carbonates (Porter & Porter 1977), benthic stomatopods occupying rubble crypts (Moran & Reaka 1988), and decapods occupying reef frameworks (Peyrot-Clausade 1981) have been related to the number of available shelters as well as the protective potential of their cryptic habitats. Idjadi and Edmunds (2006) recorded a strong positive relationship between topographic complexity and the generic richness of coral-associated macro invertebrates, but unlike the aforementioned references, they observed little correlation with abundance.

The abundances and species richness of many coral associates are positively correlated with the size of their host colony, though some exceptions are known where coelobite species exhibit distributions that are independent or negatively correlated with colony size (Abele & Patton 1976). Several cryptic symbionts of *Pocillopora* are known to only occupy colonies greater than a certain size (Caley et al. 2001). However at large sizes, the density of commensal decapod crustaceans declines (Abele and Patton 1976). Caley et al. (2001) have shown that fragmentation of *Stylophora pistillata* can increase the abundance of associated *Trapezia cymodoce*, presumably because this territorial species may exclude conspecifics in uninterrupted habitats. Lewis and Snelgrove (1990) have shown that isolated hemispherical colonies of *Madracis mirabilis* host a higher diversity of decapod and amphipod associates than continuous stands of living coral, a finding that the authors attributed in part to branch spacing.

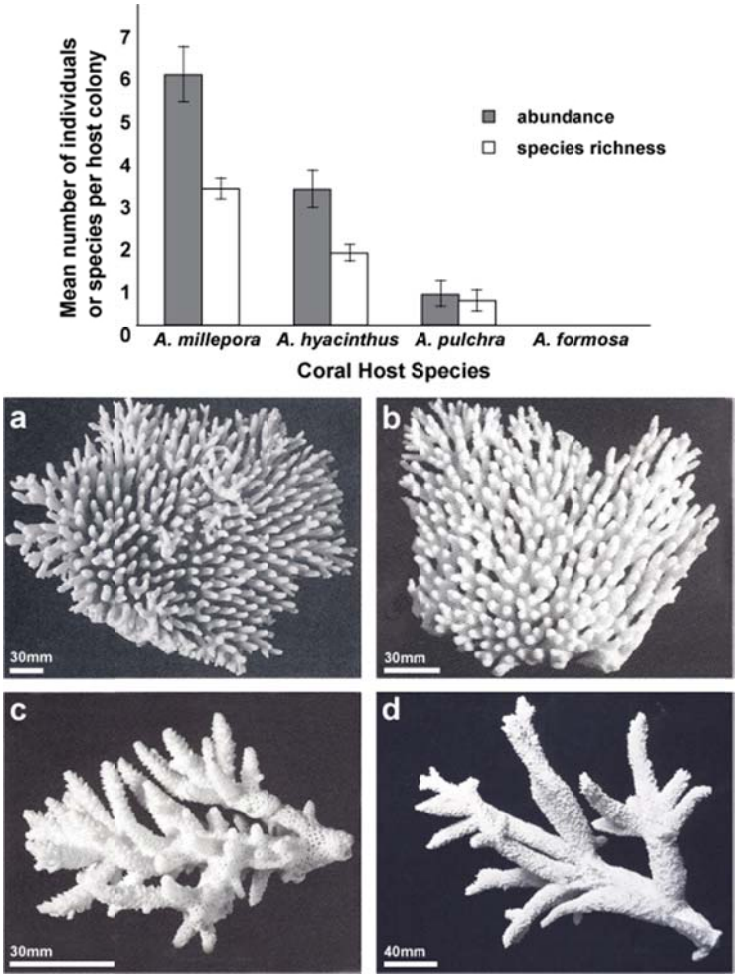

Figure 1.6. The abundance and richness of cryptofauna associated with a. *Acropora millepora*, b. *Acropora hyacinthus*, c. *Acropora pulchra*, d. *Acropora formosa.* (Glynn & Enochs in press, modified after Vytopil & Willis 2001).

Bioerosion and taphonomy of reef framework materials result in structural alteration of coelobite shelters. Several researchers have shown that various cryptic bioeroders create crevices necessary for the colonization of opportunistic nestling species (McCloskey 1970; Hutchings & Weate 1977; Moran & Reaka 1988). Alternatively, bioeroded but well-cemented substrates may have reduced abundances of cryptic associates (Rice & Macintyre 1982; Preston & Doherty 1994). At extreme levels, bioerosion may simply lead to habitat loss and therefore depress community abundances (Enochs & Hockensmith 2008). Glynn (2006) has hypothesized that coral death and subsequent framework erosion after El Niño-related thermal anomalies may lead to depauperate cryptofaunal communities. In support of this, he used simulated reef frameworks to show that cryptic fish populations are more rich and abundant in areas of greater structural complexity. Certainly, where reef frameworks and rubble are compared to extremely eroded substrates such as fine sands, diversity (Bailey-Brock et al. 2007), biomass (Brock & Smith 1983) and abundances (Brander et al. 1971) are higher in the former, less degraded habitats.

The relationship between the position of reef substrates (e.g., growth position, toppled, etc.) and their associated communities is poorly known. Moreno-Forero et al. (1998) found no difference between community composition of cryptofauna living with fallen and standing *Acropora palmata* branches. However, Navas et al. (1998) suggested that the angle of the same dead *A. palmata* substrate could have an effect on associated coelobites as horizontal coral fragments would presumably collect more sediment than vertical branches. Additionally, substrate position can affect the local hydrology, light availability, and shelter potential, all of which may in turn alter coelobite community composition.

Environmental perturbation

While coelobites are sheltered and often considered to be removed from major environmental perturbations, this is not always the case. Disturbances, especially those of a physical nature (storms, waves, human trampling), are known to alter substrate structure and may therefore have widespread effects on cryptofauna communities. The shape or size of rubble may affect its stability during storm-associated wave assault, thereby affecting the composition and abundance of its associates (Gischler & Ginsburg 1996). Alternatively, storms may fragment large corals. This can create rubble suitable for coelobite colonization and, given the right periodicity, increase community abundances over large time scales (Moran & Reaka-Kudla 1991; Rasser & Riegl 2002).

At extreme magnitudes, high periodicities, localized scales, or for sensitive species, environmental perturbations may have devastating consequences. Sheltered environments may quickly become prisons if cavity openings are obscured by sand and debris; even partial blockage can lead to reduced food or light availability (Kobluk & James 1979). Choi (1982) observed that mud and iron, a byproduct of the installation of an off-shore drilling well, accumulated in cavities and adversely affected the coelobitic biota.

Several types of disturbances, other than the physical accumulation of sediments, are known to adversely affect cryptic reef communities. Low tide conditions coupled with rainstorms can kill gastropods in the genus *Conus* and potentially affect their distribution across intertidal reef rock benches (Leviten & Kohn 1980). Trampling of reef sediments by waders in Oahu, Hawaii has been linked to reductions in cryptofauna biodiversity (Bailey-Brock et al. 2007). Finally, the wreck of a large container ship on the outer Great Barrier Reef induced a phase shift that encouraged macroalgae growth, ultimately resulting in the proliferation of cryptic micrograzers (Hatcher 1984).

In some cases perturbation of a more environmentally sensitive epibenthic species may have cascading affects reaching, among others, cryptic populations. Coral bleaching, due to thermal anomalies too small to directly influence other taxa, causes discoloration and whitening of coral tissues. Cryptically colored animals, that otherwise hide among a host coral’s branches, suddenly stand out following coral bleaching and effectively become “bullseyes” for predators. In aquarium manipulations, Coker et al. (2009) observed predation rates rise from 25% on fishes associated with healthy colonies to 33% on those associated with bleached and to 37% on those associated with recently killed colonies. Dead colonies overgrown by algae, representing coral habitats long after disturbance-induced mortality, hosted fishes with the highest incidences of mortality caused by predators (42%). The authors attributed this to a decrease in the habitat’s sheltering ability due to space utilization by algae and sessile invertebrate taxa. Presumably, decreasing structural complexity due to the ubiquitous process of bioerosion would further increase a predators access to what was once a functional shelter.

Recovery of coelobite communities following disturbance events is likely variable and is dependent on, among other things, the magnitude of the disturbance as well as the reproductive capacity and growth capability of the fauna in question. In some cases cryptofauna communities are known to be highly resilient. Choi (1984) observed that cryptic climax communities had established themselves only three years after their substrate was created/denuded by a shipwreck. Moran and Reaka-Kudla (1991) found that less than two years after a hurricane damaged reefs on St. Croix, cryptofauna densities had exceeded pre-disturbance levels and were likely still rising.

Disturbances may interrupt normal ecological processes leading towards low diversity climax communities and at intermediate levels may increase biodiversity (Connell 1978). Abele (1976) collected decapod crustaceans associated with *Pocillopora damicornis* in two Pacific Panamanian Gulfs. Despite close geographic proximity and similar reef environments, the Gulf of Panamá is unlike the Gulf of Chiriquí in that it experiences seasonal upwelling of cold nutrient-rich waters. *Pocillopora* colonies from the more environmentally stable Gulf of Chiriquí were found to contain 55 species of decapod, compared with 37 from the fluctuating Gulf of Panamá. In a similar study, Kropp and Birkeland (1981) examined *Pocillopora* associates on a “high island” and an offshore atoll. They postulated that higher numbers of non-obligate associates at the high island site may be due to greater fluctuations in temperature and salinity relative to the offshore atoll.

While environmental perturbations of a significant magnitude have been seen to alter cryptic community assemblages, reef cavity shelters undoubtedly provide a degree of protection from environmental disturbances. It is therefore likely that cosmopolitan species residing both in crypts and on reef surfaces may find refuge in the former habitat during adverse surface conditions. As such, Kobluk and Lysenko (1987) found cryptic reef environments in Fiji to be refuges for corals during hurricanes and postulated that these sheltered populations may help to reseed exposed areas that are more affected by disturbance. Meesters et al. (1991) found abundances of cryptic coral in the Netherlands Antilles to be of insufficient size to reseed disturbed surface environments; however, they postulated that other taxa (sponges, tunicates, bryozoans) may benefit from cryptic refuges.

Finally it should be noted that not all environmental perturbations are of sufficient frequency or magnitude to affect reef coelobite communities. Kohn and White (1977) found that thermal pollution from a power plant had no adverse effect on cryptic polychaete populations. Austin et al. (1980) found no significant difference between cryptic symbiont communities of pocilloporid corals from sites subject to different amounts of physical disturbance. They did, however, find that disturbed sites had on average, smaller coral colonies which may have implications for cryptic community populations at reef-wide scales.

Nutrification and sedimentation

It is often difficult to separate the effects of nutrification and sedimentation as these parameters often parallel each other along both natural and artificial gradients. Their collective effects on cryptic community composition are complex and may differ among reef communities. Nutrients and nutrient-rich sediments provide food to suspension feeding symbionts (Brock & Smith 1983) and deposit feeding cryptic biota (Preston & Doherty 1994). Yet high sediment deposition may impede the growth of sessile cryptic biota (Choi & Ginsburg 1983).

Takada et al. (2008) examined cryptic communities inhabiting coral rubble across a terrestrial-sourced sediment gradient. They observed distinct community assemblages across this gradient and identified indicator species exhibiting above-average sensitivity. Similarly Kropp and Birkeland (1981) examined cryptic crustacean associates of *Pocillopora verrucosa* from two sites in French Polynesia, one in close proximity to an island (Moorea) and the other from an off-shore atoll (Takapoto). Among other things, they point to higher productivity around island habitats as an explanation for higher species richness and increased numbers of non-obligate symbiont species. Peyrot-Clausade and other's (1989) examination of crab cryptofauna inhabiting dead coral rubble at Tikehau Atoll yielded similar results, as communities were found to be depauperate compared with those near Polynesian high islands and Malagasian reefs.

Again, the authors attributed this trend in part to lower terrigenous nutrient inputs in the offshore habitats. In apparent contrast to these findings, Snelgrove and Lewis (1989) observed little difference between the species composition and species richness of crustacean associates of *Madracis mirabilis* under different nutrient regimes in Barbados. They did, however, observe lower densities of coral associates in eutrophic environments.

The effects of nutrients on bioeroding cryptofauna are not entirely clear and most likely are dependent on the location, concentration of nutrients, type of nutrients, and type of bioeroders. Endolithic coelobites are often suspension feeders (e.g. clionaid sponges, lithophage bivalves), suggesting that productive waters would be favorable to their proliferation. Highsmith (1980) found a positive correlation between boring bivalve abundances and the phytoplankton productivity of the region from which their host corals were collected. Reviewing all coral reef bioeroders (both cryptic and exposed) Hallock (1988) qualitatively observed higher abundances in nutrient rich waters.

Studies in Kaneohe Bay suggest a positive relationship between nutrients and erosive activity of internal bioeroders. Brock and Brock (1977) used nitric acid to dissolve sections of dead coral frameworks and observed higher concentrations of endolithic coelobites, primarily polychaetes, at sampling stations subject to higher nutrient concentrations. In the same bay, using the same acid-dissolution methodology, Brock and Smith (1983) measured cryptofauna biomass (both epi- and endolithic) before and after the termination of a large nutrient outflow. Once the effluent was halted, the biomass of cryptic communities near the source dropped 60-75%, suggesting that the outflow was providing nutriment to food-limited cryptic populations. Nutrients were likely incorporated into the coelobite community through plankton and suspended organic matter as most of the collected cryptofauna were observed to be suspension feeders.

The pattern of more abundant endolithic and bioerosive coelobite communities in eutrophic environments is by no means applicable to all reef communities. Tribollet et al. (2002) examined rates of bioerosion by external grazers and both micro- and macro-endolithic bioeroders along a cross-shelf transect on the Great Barrier Reef. They noted that it is often difficult to distinguish between sedimentation and but nevertheless made some qualified observations. Rates of internal bioerosion by endolithic microborers were negatively correlated with the presence of nutrients and sediments. They proposed that sediment reduced light penetration into coral skeletons and subsequently restricted the depth to which photosynthetic microbioeroders could bore. Chazottes et al. (2002) observed that high nutrients were correlated with higher rates of microboring as well as an increased growth of crustose coralline algae, which may have inhibited the erosion rates of macroborers. Though this last relationship is in apparent contradiction with Cinelli et al. (1977), who hypothesized that crustose corallines may facilitate the settlement of endolithic bioeroders by providing a soft substrate suitable for settling larvae.

Temporal variability

The abundance and distribution of cryptofauna populations vary across both daily and seasonal time periods. Diel patterns are primarily accounted for by the migration of taxa into and out of reef frameworks. Over seasonal time scales, patterns in animal abundance are dependent on reproductive periodicity and food availability.

Both nocturnal and diurnal fishes utilize reef crypts for shelter during their quiescent periods. Many triggerfishes, that prey upon reef invertebrates during the day, wedge themselves into framework crevices at night and erect their dorsal spines to lock themselves into place. Conversely, muraenid eels often hide within reef cavities during the day and emerge at dusk to forage on the reef surface. Luckhurst and Luckhurst (1978) have observed that some nocturnal fish species, such as squirrelfishes and cardinalfishes, consistently return to the same shelter after their foraging excursions. Benthic invertebrates exhibit the same nocturnal foraging patterns, leaving their shelters only at night when predation pressure on the reef surface is lowest. Caribbean spiny lobsters display size-dependent nocturnal foraging duration with larger individuals spending more time unsheltered; suggesting that crypts are necessary for avoiding predation and of paramount importance during vulnerable juvenile stages (Weiss et al. 2008). Reichelt (1982) observed that worm-eating gastropods (*Conus* spp., *Nassarius gaudiosus*, *Vasum turbinellus*) occupy structurally complex reef topographies during the day, venturing into smooth habitats to feed during the night. Vivien and Peyrot-Clausade (1974) analyzed the gut contents of holocentrid fishes and attributed greater abundances of polychaete worms during the night to the nocturnal activity of the worms themselves. Furthermore, the authors were able to deduce from the fragmentation of some families (Glyceridae) and the intact nature of others (Eunicidae) that the worms were exhibiting different behaviors, half and full emergence from reef burrows respectively.

Many of the nocturnal fishes that emerge from reef crypts to feed at night are planktivores and are influenced by the circadian rhythms of demersal zooplankton (Hobson & Chess 1979). These “resident” reef plankton, including members of the

Amphipoda, Foraminifera, Caridea, Copepoda, Cumacea, Isopoda, Mysidacea, Ostracoda, Polychaeta, andTanaidacea, emerge from shelters at night and migrate into the water column (Alldredge & King 1977; Hobson and Chess 1986). Unlike more transient plankton, they actively avoid currents and remain in reach of their day-time shelters (Hobson & Chess 1986). Nightly emigration has been observed to be greatest over living coral and may involve more than 13,000 individuals m^{-2} (Alldredge & King 1977).

Demersal reef plankton densities are also subject to seasonal fluctuations. Densities are usually lowest in the winter months and highest in the summer when many benthic species rise into the water column to reproduce (McWilliam et al. 1981). Seasonal patterns are evident in non-planktonic cryptic populations as well. Takada et al. (2007) have observed species-specific seasonal patterns in colonization of motile cryptofauna to dead coral rubble in Japan. In the eastern Pacific, abundances of decapod associates of *Pocillopora* are highest in April and June (Gotelli & Abele 1983), corresponding to the recruitment of trapezid crabs (Gotelli et al. 1985). In a two year study of 144 polychaete species living on and within dead coral blocks on the Great Barrier Reef, Hutchings (1981) observed that recruitment was highest in the spring and summer. She hypothesized that the time of year that a substrate becomes available is an important determinant of community composition as seasonal recruitment pulses may lead to the establishment of different faunal assemblages. Windward areas, possibly subject to greater numbers of pelagic larvae, may experience more pronounced seasonal differences (Hutchings 1985).

Factors influencing community composition - Biological

Living vs. dead coral habitats

Living and dead corals provide very different conditions for the fauna associated with them. Comparisons between the two habitats and the composition of their respective communities are discussed in Coles (1980), Enochs and Hockensmith (2008), Peyrot-Clausade (1980), and Preston and Doherty (1990, 1994). A variety of live coral associates, many of them obligate, are known and reviewed in Patton (1976) and Glynn and Enochs (in press).

Live corals provide a variety of potential food sources for fauna associated with them including tissues (Rotjan & Lewis 2008), mucus (Knudsen 1967), fat-bodies (Stimson 1990), and gametes (Guest 2008). This may be responsible for the larger size (Coles 1980) and elevated biomass of cryptofauna populations associated with live corals (Alldredge & King 1977; Enochs & Hockensmith 2008). It should be noted, however, that dead coral substrates may provide a greater diversity of food resources than their living counterparts. Sessile flora (e.g., crustose coralline and filamentous algae, seagrasses) and fauna (e.g., bryozoans, sponges, and foraminiferans) which do not grow on live tissues may proliferate on dead carbonate surfaces, thus providing food sources for a diverse array of feeding guilds.

In many respects, corals are inherently inhospitable, adapted to survive within reef ecosystems despite high levels of competition and predation. They contain potent nematocysts within their tissues and have evolved a variety of competitive/deterrence mechanisms including sweeper tentacles, sweeper polyps, mucus secretion, mesenterial filaments, and allelopathic chemicals (Lang and Chornesky 1990). For these reasons, taxa that are not adapted to cope with a coral's defenses are found in reduced densities among live tissues (e.g., nemerteans; Kirsteuer 1969). Those species that are adapted to avoid or endure a living coral's defenses may incur benefit in the form of protection from predation. This may occur through the direct physical protection of coral branches and nematocysts or through camouflage and cryptic coloration (Coker et al. 2009).

In addition to the aforementioned food and deterrence qualities, coral mucous may also act as an efficient cleaning mechanism. Preston and Doherty (1994) observed that dead corals retain more sediment than live and hypothesized that this may be responsible for elevated abundances of deposit feeding cryptofauna on dead substrates. However, as previously noted, in other environments sediments are known to be detrimental to coelobite abundances (Choi & Ginsburg 1983).

Many workers have observed that endolithic bioeroders are more abundant within dead substrates than in living corals (Hutchings 1974a, 1983, 1985; Fagerstrom 1987; Fonseca et al. 2006). Live coral tissues may act as a barrier, inhibiting the settlement of boring taxa. Furtheremore, it is probable that coral polyps directly consume coelobite larvae, thereby reducing successful settlement. Despite these impediments, many species of endolithic cirripedes, polychaetes and other taxa have been found to attain great densities within live coral colonies. Additionally, it should be noted that while many individuals may be unable to penetrate the live coral face, some erosive taxa may enter living coral colonies through dead bases, undersurfaces, and localized necrotic patches. The unique conditions associated with live and dead coral substrates have important ramifications for the biodiversity of organisms that live cryptically within their recesses. The defensive nature of live coral tissues restricts the number of species that may intimately associate with them. Those species that do often exhibit uniquely adapted morphologygies (Patton 1974, 1994). Given the inhospitable nature of live corals, and the relatively depauperate quality of their obligate symbionts (Coles 1980; Black & Prince 1983), it is not surprising that community composition is highly similar among live coral associates, much more so than those associated with dead corals (Enochs & Hockensmith 2008).

Following coral mortality, coelobite community composition changes. Initially, species richness and abundances may decline as symbionts are deprived of nutriment and preyed upon (Caley et al. 2001; Coker et al. 2009). Biomass decreases, likely due to the cessation of nutriment normally provided by the coral to its associates (Enochs & Hockensmith 2008). As sessile biota colonize the dead substrate, microhabitat diversity increases; coelobite richness may rise and the species composition of different colonies may become more dissimilar. As erosive taxa take their toll on the skeleton, habitat degradation will lead to reduced abundances and ultimately to community loss.

Colonization and succession

Recruitment of organisms to a reef crypt may occur through pelagic larvae or through the immigration of motile adult cryptofauna from surrounding substrates. In rubble communities the latter may occur very quickly, with motile organisms arriving to newly available substrate within one week (Peyrot-Clausade 1977; Takada et al. 2007). Many motile organisms found within cryptic recesses are juveniles (Peyrot-Clausade 1977), which suggests high recruitment from pelagic larvae. Some cryptofaunal species are highly fecund and reach sexual maturity at early ages (e.g. sipunculans and terebellids reach sexual maturity within three months; Hutchings 1983). It is therefore not surprising that some workers have hypothesized that most coelobite recruitment occurs from pelagic larvae (McCloskey 1970; Hutchings 1983). It is not entirely clear whether these workers also consider lateral movement of adult individuals as recruitment per se; however, certainly among boring endoliths and non-colonial sessile fauna, larval recruitment cannot be discounted.

Peyrot-Clausade (1980) used bags of *Acropora* rubble to trace the colonization and evolution of cryptic communities at Tuléar, Madagascar. Three distinct phases were identified: initial settlement by small motile crustaceans (Day 1-14), an influx of larger, primarily anomuran fauna (Day 16-35), colonization by sessile taxa and stabilization of community composition (Day 35-Month 7). Succession in motile epilithic cryptofauna may occur as a substrate evolves. Peyrot-Clausade (1977) observed that the polychaete *Nereis caudata* is attracted to the mucus production of dying corals. As mucus production and coral tissues decreased, so did the associated species. The colonization of *Ceratonereis mirabilis* and *Platynereis calodonta* parallel the successive establishment of algal communities, and finally eunicid polychaetes predominate.

Succession of cryptic communities may proceed through facilitation (see Bruno et al. 2003). McCloskey (1970) discussed facilitative succession within cryptic communities, not as a replacement of faunal assemblages but as the addition of new species and the evolution of the community towards greater diversity. In his example, this was accomplished by the boring-mediated alteration of coral skeletons which resulted in niche creation (Figure 1.7). Endolithic algae created bore-tubes immediately under the surface of coral skeletons. These were subsequently colonized and enlarged by clionaid sponges, which in turn provided a habitat suitable for boring polychaetes in the genera *Polydora* and *Dodecaceria*. In areas where coral skeletons were abraded by sand, the subsurface cavities created by *Cliona* were opened, creating pockmarks on the outer face of the coral. These depressions were suitable for the settlement of endolithic bivalves in the genera *Gastrochaena* and *Lithophaga* which were accompanied by their symbionts (*Odostomia seminuda*) and predators (*Stylochus ellipticus*). The bivalves created larger borings in the coral rock that were ultimately colonized by a suite of nestling or opportunistic fauna. Similar instances of structural facilitation have been subsequently observed in other coelobite communities. For example, following hurricane disturbances, the new availability of uncolonized substrate allowed the elevated recruitment of erosive cryptofauna. These species increased the structural complexity of the framework fragments and created microhabitats necessary for the colonization of nestling taxa (Moran & Reaka-Kudla 1991).

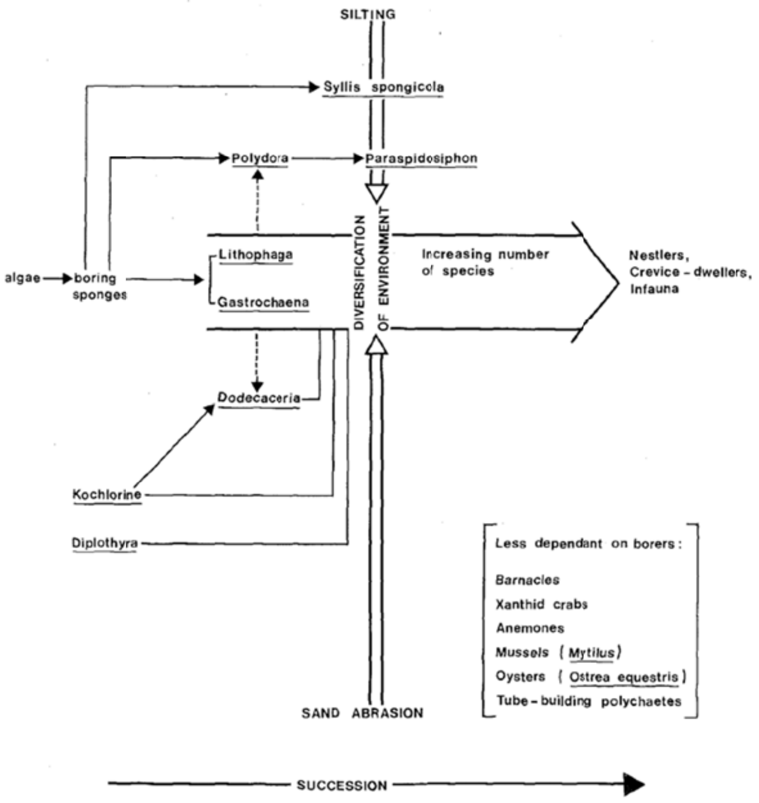

Figure 1.7. The bioeroder- (sponges, *Gastrochaena*, *Lithophaga*) and environment-mediated (sand abrasion) succession of cryptic communities associated with *Oculina arbuscula* (McCloskey 1970).

In addition to facilitation, succession among cryptic reef communities is known to occur through competitive processes. Jackson and Winston (1982) observed that newly available substrates are initially colonized by poor competitors with relatively high recruitment rates and are later outcompeted by sponges. In Belize, Gischler and Ginsburg (1996) traced the successional stages of sub-rubble coelobite communities and found that colonial forms overgrew and outcompeted early-colonizing solitary forms. Disturbances associated with wave action and rubble movement allowed the co-occurrence of different successional stages as habitats were opened up when competitively dominant organisms were eliminated. Choi (1984) observed that the colonization and maturation of cryptic rubble communities in Florida were also mediated by competition. As time progressed, undisturbed communities consisted of increasingly competitively superior taxa, and in several cases, ultimately culminated in the complete overgrowth by the tunicate *Didemnum candidum*. It should be noted that in the absence of disturbance these competitive processes may not always lead to climax communities of competitively dominant taxa. For instance, several studies have suggested that competitive networks rather than hierarchies may play a role in the maintenance of biodiversity within cryptic reef habitats (Jackson & Buss 1975; Buss & Jackson 1979)

Benthic cover

The distribution of cryptofauna within reef ecosystems is closely related to the biotic composition of the substrates with which they are associated. This relationship, coupled with highly heterogeneous reef environments, has made it nearly impossible to characterize cryptic reef fauna on a reef-wide scale (Brander et al. 1971). Instead, research has progressed exploring the responses of community abundance and composition with specific substrates such as living coral and algae. It is expected that trophic requirements are responsible for many of the close relationships between cryptofauna and their substrates. Certainly this is more apparent for less motile species that must maintain close proximity to their food sources.

Cryptic corallivores (e.g., *Jenneria pustulata*, *Quoyula madreporarum*, *Coralliophila abbreviata*) and symbionts (e.g., *Trapezia* spp., *Alpheus lottini*) display distributions highly dependent on coral cover and as previously mentioned, several studies have underscored the importance of coral mucus in providing nutriment to coral reef communities. However on small spatial scales, Idjadi and Edmunds (2006) found that percent living coral cover was not significantly correlated with invertebrate richness or abundance. They did find that topographic complexity (as a result of coral architecture) and coral diversity positively influenced the generic richness of invertebrate associates. As previously mentioned, on even smaller scales (single colonies) Enochs and Hockensmith (2008) observed associate biomass to be higher on live substrates. The relationships and mechanisms between live corals and cryptic reef fauna are as yet unclear. It is possible that there are spatial scales where patterns are discernable or even thresholds, above or below which the benefits of live coral cover break down. In support of this, Kohn (1983) has observed that *Conus* spp. in the tropical west Pacific preferred substrates of less than 20% coral and greater than 20% algae cover. Within algae microhabitats, the gastropods found abundant prey and were able to shelter among rubble that had previously been formed by living coral. Conversely, living coral habitats supplied little food and gastropods were found to avoid contact with live coral tissues. Further evidence for the negative nature of living corals comes from the observation that some coral species may consume the settling larvae of cryptic organisms and even feed directly upon adult polychaetes (Porter 1974; Hutchings & Weate 1977). It should be emphasized that, aside from these relatively few negative characterisitics, corals themselves are not inherently detrimental to reef cryptofauna. In fact, they are necessary habitat providers, creating the carbonate substrate in which cryptofauna shelter. Instead, it is suggested that continuous stands of live coral may, in some situations, inhibit the settlement or growth of certain coelobite fauna.

Algae can have a positive effect on cryptic communities in large part due to the herbivorous diets of many cryptic species. The abundance of cryptic herbivorous decapods (Brachyura and Anomura) is correlated with algae abundance at Tikehau Atoll (Peyrot-Clausade 1989). At Eniwetok Atoll, polychaete abundances were roughly eight times higher in habitats that contained algal mats compared with those that did not (Bailey-Brock et al. 1980). Risk and Sammarco (1982) observed higher abundances of cryptic bioeroders inside algae-covered damselfish lawns on the Great Barrier Reef. Similarly, Klumpp et al. (1988) recorded elevated abundances (roughly 3.6 times higher) of small (<1 cm) motile cryptic metazoans such as copepods within damselfish territories. It is possible that these effects are due to the exclusion of invertivore fishes which may exert a top-down control on cryptic invertebrate community abundances. However, Valles et al. (2006) found that algal cover is likely more important than protection from predation. The authors observed that predator exclusion from experimental units used to monitor the settlement of fishes to cryptic recesses had little effect on species abundances. However, algae that grew on the net surfaces resulted in higher abundances of *Sparisoma* spp. and decreased abundances of *Stegastes partitus*. In addition to the obvious trophic benefits, macroalgae may directly provide shelter (e.g., microcrustaceans; Hatcher 1984) or make available material for camouflage (e.g., decorating majid crabs; Kilar & Lou 1986) and thereby reduce the predation pressure on its cryptic inhabitants.

Predation pressure

The effects of predation on the inhabitants of reef crypts has been explored and in some areas has been determined to control the abundance and distribution of various cryptic species (e.g., sponges; Richter et al. 2001). It is cautioned that the relationship between predators and their cryptic prey is complex, dependent on the species involved, the structure of the cryptic habitat, and the local environmental conditions. For example, porous reef frameworks may be relatively inaccessible to predatory epibenthic reef fishes. However, muraenid eels and cryptic stomatopods may easily forage within them, possibly influencing the abundances of their cryptic prey. Similarly, coral rubble shields the fauna below and provides protection from all but the largest reef fishes, which may easily overturn and break apart cryptic shelters. Several studies have observed that predation pressure is of differential importance at various depths due to the distribution of predators. For example bonefish predation in Belize limits the distribution of its xanthid crab prey to shallow environments (Engstrom 1984). Similarly, decapod associates of *Pocillopora* are more abundant in shallower reef habitats, where the influence of fish predators is reduced (Gotelli et al. 1985). Alternatively, *Diadema antillarum*, which feeds on sessile organisms and algae within reef recesses, has been observed to be four times more abundant at 10 m than 20 m depth and may consequently influence the abundances of cryptic sessile prey (Jackson & Winston 1982). These contrasting patterns illustrate the importance of closely examining both the species and habitat in question before extending generalizations to other predatory interactions.

Regardless, the sheltering capacity of cryptic habitats is undeniable (e.g., Jackson & Buss 1975). Bakus (1966) hypothesized that cryptic reef communities have become distinctly speciose because they have been able to escape the high predation pressure experienced on reef surfaces. Additionally, lower rates of predation within cryptic habitats help explain why the antipredatory behaviors and morphologies, that are otherwise common among exposed reef taxa, are conspicuously absent among the cryptofauna. This is evident when examining the relative palatability of cryptic and exposed reef sponges. Wulff (1997) observed that of the 18 species of cryptic sponge offered to parrotfish only six were rejected, compared with 11 of 12 epibenthic sponge species. Further evidence for the protective nature of reef cavities is provided by Peyrot-Clausade (1977) who observed high concentrations of relatively defenseless juvenile fauna recruiting to her artificial cryptic habitats. Vytopil and Willis (2001) have related the protective ability of coral colonies to the abundance and richness of their associates. Castro (1978) found that the *Pocillopora* associate *Trapezia* had restricted inter-colony movement under elevated predation pressure, suggesting that fish predators reduce the degree to which coelobites may venture from their shelters.

Many species that shelter within reef crypts, such as fishes (Glynn 2006), gastropods (Taylor 1984), octopuses (Forsythe & Hanlon 1997), polychaetes (Glynn 1984), and stomatopods (Steger 1987), are themselves predators. These taxa are often present in great abundances and likely influence the behavior and distribution of their prey (Reaka 1987). Nektonic species, not normally occurring in reef crypts, are also known to alter coelobite abundances (Wolf et al. 1983). Indeed, despite their sheltered nature, coelobites are commonly consumed by reef fishes (Randall 1967; Peyrot-Clausade 1980). Many species of reef nekton (e.g., turtles, sharks, triggerfishes) are known to break apart corals and frameworks in order to expose cavities and gain access to cryptofauna (Guzmán 1988; Jiménez 1996-1997; Glynn 2004). Other species of fishes (e.g., squirrelfishes, soldierfishes) are known to prey on coelobites which either partially or fully reveal themselves from their framework shelters (Vivien & Peyrot-Clausade 1974). Finally, it should be noted that the effects of predation by fishes on cryptic reef communities are not intrinsically negative. For instance, Day (1977) hypothesized that predation could serve to increase the biodiversity of faunal communities colonizing a reef cavity.

Territoriality and competition

Competition is omnipresent within reef ecosystems. Like their epibenthic counterparts, cryptofauna must constantly compete for food and space. While competition has already been treated as a mechanism of succession, here it is considered in its most basic sense, as the interaction between two or more organisms, both seeking to utilize some limiting resource.

Competition for food is often difficult to demonstrate within reef ecosystems as complex food webs and brief feeding interactions are difficult to accurately and comprehensively quantify. For sessile suspension feeding and photosynthetic organisms, competition for food is intimately associated with the amount of space occupied and it is therefore difficult to distinguish between the two. Perhaps the most conclusive experimental demonstration of competition for food between sessile organisms within reef crypts is that of Buss and Jackson (1981). The authors used open and partially-obstructed settlement boxes to manipulate the amount of planktonic food (naked and bacterial cells) available to sessile coelobite communities. Experimental units with reduced flow experienced significantly more food depletion, resulting in the stunted growth of associated coelobite communities. This suggests that when food sources are limiting, competition for food may result in restricted growth and abundance. Sponges, which are efficient suspension feeders and have more diverse diets than cheilostome bryozoans, were able to outcompete the latter over the duration of the experiment. Jackson and Winston (1982) observed natural species distributions which corroborate these findings. Within cavities underneath large coral colonies, sponges were able to occupy more recessed spaces, competitively excluding the cheilostomes through efficient filtration of their naked flagellate food source.

Evidence of competition for food among motile cryptic fauna is evident in crustacean communities associated with *Madracis mirabilis* (Lewis & Snelgrove 1990). Colonies with morphologies providing greater food to their epizoic inhabitants contained richer faunal assemblages, suggesting that when food was limiting only a few competitively dominant species were able to proliferate; when food was present in excess, more competitively inferior taxa were able to coexist with their otherwise dominant neighbors. Whether this is the mechanism behind their observations, has not been conclusively tested and it would be interesting to identify competitive hierarchies for the fauna in question.

It has been hypothesized that there are more heterotrophic suspension feeders (e.g., brachiopods and coralline sponges) in reef crypts due to intense competition for space by corals and other phototrophic organisms on reef surfaces (Jackson et al. 1971; Wood 1999). While this is likely true, it is important to note that complex competitive networks and chemical defense mechanisms are also known from cryptic reef habitats and likely act to maintain diversity in the absence of intense predation or disturbance (Jackson & Buss 1975; Buss & Jackson 1979).

Territoriality is common among cryptofauna and is especially prevalent in those associated with living coral. For example, adult *Trapezia ferruginea* and *Alpheus lottini* exist in male-female pairs within colonies of *Pocillopora damicornis* and territorially exclude conspecifics, congenerics, as well as other invading species (Abele & Patton 1976; Glynn 1980). Heterosexual pairing and space competition have also been observed in associates of acroporid corals (Patton 1994). Many of these coral symbionts feed on organic deposits, tissues, and various metabolic products of their host corals. However, among trapezid crabs, there is evidence that the size of an animal's territory is often larger than that needed to meet its metabolic requirements (Huber & Coles 1986). The degree of interspecific territoriality and competitive ability of species within this genus varies. In Hawaii, *Trapezia intermedia* is found on *Pocillopora* hosts of all sizes and it appears to restrict congenerics to hosts larger than 2-4 l, where up to 5 species may co-occur (Huber & Coles 1986). It is likely that these types of territorial interactions are in large part responsible for the structure of *Trapezia* communities associated with pocilloporid corals (Preston 1973).

Factors influencing community composition – Anthropogenic

Deleterious anthropogenic impacts on coral reefs and their cryptic fauna are numerous and diverse, operating via different mechanisms at widely varying spatial scales. Widespread mass-bleaching events and worldwide declines in corals and coral reef frameworks due to global warming will probably lead to reduced cryptofauna abundances, biomass, and biodiversity. Similarly, ocean acidification is expected to result in reductions in the ability of structural taxa to calcify, offsetting the delicate balance between reef accretion and erosion, and ultimately leading to habitat loss. At regional scales, overfishing may either directly or indirectly influence coelobite assemblages. At more localized reef-wide or site-specific scales, ship groundings, nutrient outflows, drilling rigs, as well as physical trampling have all been implicated as harmful anthropogenic influences significantly impacting cryptic communities.

It is accepted that the anthropogenic release and subsequent accumulation of greenhouse gasses within the earth's atmosphere have led to global warming, which is expected to continue for many years (IPCC 2007). It is likely that this human-induced climate change will have myriad effects on cryptic reef biodiversity. Hermatypic corals, which naturally occur in waters near their thermal maximum, are expected to be increasingly subjected to temperatures coincident with mass-bleaching and mortality (Baker et al. 2008). As discussed earlier, bleaching of a host colony may lead to increased predation on its cryptic occupants (Coker et al. 2009), reductions in symbiont biodiversity and abundance (Caley et al. 2001), as well as community shifts and decreases in coelobite biomass (Enochs & Hockensmith 2008). Global warming and coral mortality have been linked to long-term worldwide declines in coral cover, reef ecosystem health, as well as framework structural complexity (Gardner et al. 2003; Hughes et al. 2003; Bruno & Selig 2007; Alvarez-Filip et al. 2009). Cryptic reef organisms are invariably affected by the degradation, erosion, and loss of their habitats (Coles 1980; Glynn 2006; Idjadi & Edmunds 2006; Enochs & Hockensmith 2008). Coral mortality does, however, create newly available substrate that temporarily increases the abundance of endolithic coelobites (Scott et al. 1988). However, in the absence of rapid coral growth, the erosive activities of many endoliths will invariably lead to the elimination of habitat for successive generations. It is likely that warming-related trends in cryptofauna abundance and diversity will be further compounded by a variety of climate change related environmental impacts. As examples, altered weather patterns and increased storm activity could lead to physical disturbance of coelobite habitats (Moran & Reaka-Kudla 1991), death of cryptic biota through osmotic shock (Leviten & Kohn 1980), or increased runoff and sedimentation (Takada et al. 2008).

Elevated atmospheric CO_2 from the burning of fossil fuels has been linked to a decrease in seawater pH and a reduction in the concentration of carbonate ions necessary for biogenic calcification (Kleypas et al. 1999). This phenomenon, known as ocean acidification, will likely have complex consequences for cryptic reef biota. Directly, those cryptofauna known to calcify (e.g., cnidarians, echinoderms, foraminiferans, mollusks) may exhibit stunted growth rates or weakened skeletons while other non-calcifying cryptic biota may experience disruptions in a variety of physiological processes (e.g., fertilization, larval development, reduced metabolism) and even mortality (Fabry et al. 2008). Acidification-related reduction in the calcification and growth of reef building corals may lead to erosional reef systems and the steady loss of cryptic habitat (Manzello 2010).

The impacts of fishing on cryptic reef communities are complex, dependent on the species harvested and their trophic connections to other organisms within the ecosystem. In areas where the predators of cryptofauna are removed, increased abundances of prey species have been observed. For example, McClanahan and Muthiga (1988) monitored cryptic urchin densities on reefs under varying fishing pressures off the coast of Kenya. In highly fished areas, reductions in urchin predators led to the proliferation of *Echinometra mathaei*, which exhibited elevated biomass to a point (up to five times) where it was observed to occupy exposed surfaces. In overfished reefs, *E.*

mathaei was the dominant urchin species, likely excluding competitively inferior diadematid species. In waters off Egypt, no-take-zones (NTZs) for both fish and invertebrate (many cryptic) populations have complex responses based on whether the species in question is normally exploited (Ashworth et al. 2004). Species that are normally fished (e.g., *Tridacna* and *Tectus dentatus*) often have higher abundances within NTZs. Conversely, yet similar to the Kenyan example, holothurians, echinoids and non-commercially exploited gastropods exhibited higher abundances in fished areas, presumable due to reductions in fish predator abundances. McClanahan (1989) recorded higher diversity of gastropods within marine protected areas, but the densities of commercially exploited species were not significantly different. In Fiji, Dulvy et al. (2002) observed a negative correlation between fishing pressure and the richness of motile invertebrate taxa (most display cryptic tendencies despite being termed epifauna).

The impacts of more destructive fishing practices are more obvious. For example, dynamite fishing on coral reefs in the Philippines leads to the fragmentation of high-complexity reef structures and the elimination of framework shelters. The resulting rubble substrates support significantly lower abundances of demersal plankton relative to intact undisturbed counterparts (Porter & Porter 1977).

A variety of other human activities have been investigated with respect to their effects on cryptofauna communities. While not all are of a magnitude sufficient to harm coelobites (e.g., power plant thermal pollution; Kohn & White 1977), it is apparent that the mechanisms by which humans adversely affect reef coelobites are diverse. As mentioned earlier, nutrient outflows, specifically in Kaneohe Bay, Hawaii have been linked to shifts in cryptofauna biomass (Brock & Smith 1983). In waters off the

Philippines, the installation of oil wells was found to produce large quantities of mud and small iron fragments which accumulated in cryptic recesses (Choi 1982). Coelobite communities living within 100 m of the well site and drill ship were found to be adversely affected and those within 40 m were severely damaged. Relatively brief anthropogenic disturbances have been observed to have long-term consequences for cryptic reef communities. In 1976, the M.V. Florida, carrying 700 tons of Pozzalin, was wrecked at a site on the outer margin of the Great Barrier Reef (Hatcher 1984). Within three months, all traces of the insoluble Pozzalin were observed to have been washed away. Regardless, by some unknown mechanism, a state shift occurred and a stable macroalgal community was present at the wreck site four years later. Cryptofauna were observed to shelter and feed within the algal structures that had previously not been present. Though much less conspicuous than oil well drilling and ship wrecks, trampling of reef sediments by bathers at public beaches has also been linked to adverse effects on the reef fauna that shelter within its interstices. Bailey-Brock et al. (2007) observed reef sands below wading depths (>3 m) hosted more diverse cryptofauna communities than those at 0.6 m. Large rubble, which likely afforded greater protection and was avoided by waders, was found to shelter communities of even greater diversity.

It is apparent that human activities are harming reef habitats and their coelobite occupants. Given their great biodiversity, abundance, and their importance in ecosystem function, it is imperative that attempts to limit or mitigate anthropogenic stressors and restore reef habitats consider the cryptofauna. Environmental and biological factors influencing cryptic communities are both numerous and complex and should not be ignored if we hope to preserve coral reef ecosystems as presently known.

Trophic role of reef cryptofauna

Cryptofauna are integral to the myriad of trophic pathways that compose a coral reef ecosystem, a fact often overlooked. Their collective biomass, though hidden, is immense and likely to be much greater than that of the surface fauna (Ginsburg 1983). This biomass is far from static, experiencing high rates of turnover and constant incorporation into nearly all heterotrophic trophic levels (Hutchings 1985; Opitz 1996). Coelobites graze directly on benthic algae (Figure 1.8.12). They recycle organic byproducts and moribund tissues (Figure 1.8.5) and consume organic deposits trapped in sediments (Figure 1.8.7). They capture transient organic matter passing through the water column and transform it into forms which remain within the ecosystem for long periods of time (Figure 1.8.6). They are corallivores (Figure 1.8.13) and invertivores (Figure 1.8.14), zooplankton (Figure 1.8.9) and zooplanktivores (Figure 1.8.10). They are important reef predators (Figure 1.8.15), which are in turn fed upon by higher trophic-level organisms living on reef surfaces and in the water column (Figure 1.8.16). As such, coelobites are some of the most important sources of secondary and tertiary production with coral reef ecosystems.

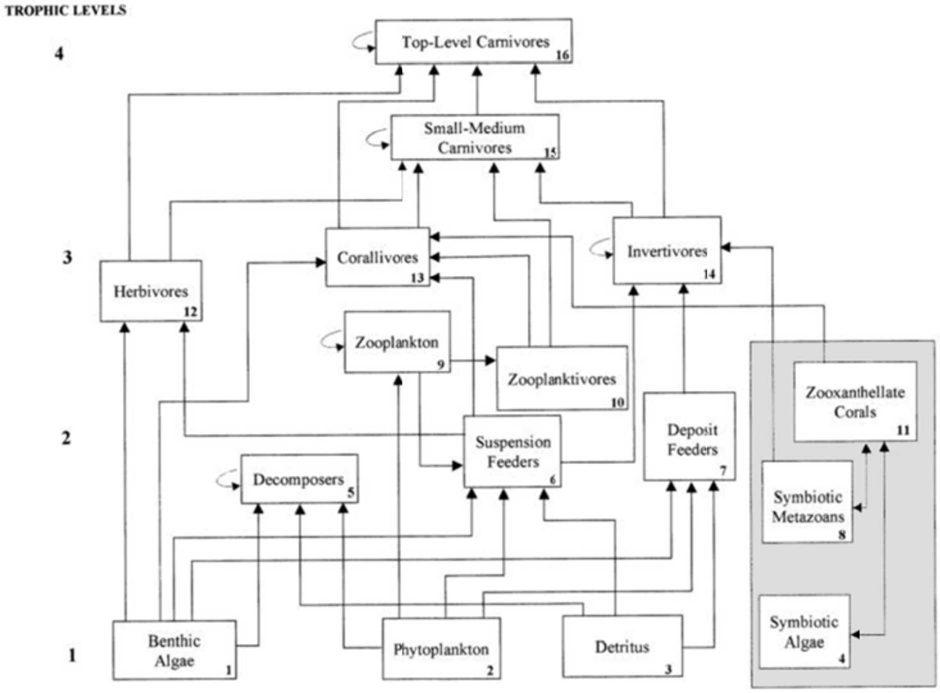

Figure 1.8. Generalized food web diagram of a coral reef ecosystem arranged according to vertically increasing trophic levels (1-4). Boxes denote trophic groups. Arrows denote the direction of energy flow. Shaded rectangle represents organisms in the coral-algal-metazoan symbiont consortium (Glynn 2004).

In order to examine the various roles that cryptofauna play in reef trophodynamics, it is important to first group the taxa comprising this community into categories based on presumed function. These divisions are necessarily artificial and not without limitation. The guild concept, often used in ecological literature, defines groups of organisms based upon their common use of a resource and a shared method by which they acquire it (Simberloff & Dayan 1991). The term “functional group” is often used synonymously with “guild.” However, it should be considered to be a broader category as its original use did not strongly consider the method of acquisition (Cummins 1974; Simberloff & Dayan 1991). Strict adherence to either of these schemas reveals inherent problems when considering reef cryptofauna. For example, the functional group “carnivores” necessarily includes at least three disparate mechanisms: suspension feeding, predation, and grazing. The suspension feeding methodology is easily recognizable among marine taxa, however it is often difficult to determine the specific food items consumed, i.e. whether it be of plant, animal, decomposed organic matter origin, or all of the above. Furthermore, animals exist which either utilize multiple feeding methodologies or employ mechanisms not easily classified into a single category.

One could treat every possible combination of resource and acquisition method, though categories would likely be so numerous as to obscure the simplification that is the rationale for their division. Clearly therefore, this is a problem of scale and it is an author's responsibility to define which characters of the biota are of sufficient importance to merit separation. Herein, four broad categories are considered. "Suspension feeders" are defined loosely as those organisms which capture materials suspended in the water column for sustenance. The unique nature of their food source, difficulty of determining its origin (e.g., animal, bacteria, plant, protist), and ecological importance of their water-cleansing activity is sufficient to merit the categorization of "suspension feeders." While the term "filter feeders" is often used synonymously, it is noted that the filtering behavior is only one of the many strategies that organisms utilize to capture suspended matter and therefore is not inclusive of all "suspension feeders" (Jørgensen 1966). "Deposit feeders" are here defined as organisms which sustain themselves on organic deposits, whether as mucus on a coral's surface or decomposed organic matter within interstitial spaces between sediments. Organisms normally termed detritivores are considered within this category as they consume dead organic matter from the benthos. "Herbivorous grazers" encompass taxa which consume benthic algae and plant materials. Finally, "predatory and grazing carnivores" include grazers of both sessile and motile animals as well as predators of benthic, nektonic, and planktonic fauna.

Suspension feeders

In many reef ecosystems and among many cryptic communities, capture of suspended matter from the water column is one of the predominant feeding strategies (Logan 1981; Jackson & Winston 1982; Logan et al. 1984; Gischler & Ginsburg 1996). Cryptic reef suspension feeders include the sessile Bivalvia, Bryozoa, Cnidaria, Crinoidea, Foraminifera, Gastropoda, Porifera, and Tunicata as well as motile species of Bivalvia, Crustacea, Ophiuroidea, and Polychaeta. Given the diversity of taxa, it is not surprising that the methods by which organisms capture suspended material differ widely (reviewed in Jørgensen 1966). In the Porifera, specialized flagellated cells known as choanocytes draw water in through ostia. Food particles are consumed by a variety of cells (choanocytes, archaeocytes, pinacocytes) and filtered water is expelled through oscula. Porcelain crabs (Porcellanidae) employ a very different filtering technique whereby fine setae on their third maxillipeds strain particulate matter out of the water column. Food particles are subsequently scraped off the setae, sorted by inner mouth parts and then ingested.

The diets of cryptic reef suspension feeders are as diverse as the taxa employing this mechanism. They are known to consume phytoplankton, zooplankton, bacterioplankton, protozoans, and suspended organic matter (Richter & Wunsch 1999). Many cryptic suspension feeding species are selective. Within reef cavities in the Gulf of Aqaba, Richter and Wunsch (1999) observed the depletion of chlorophyll a and relatively constant pheopigment concentrations, prompting the researchers to conclude that cryptic reef taxa were preferentially removing picoplankton-sized suspended materials. As previously mentioned, Jackson and Winston (1982) implicated differences in food selectivity between cryptic cheilostomes (<50 µm, primarily naked flagellates, not bacteria or POM) and coelobitic sponges (diverse particles <50 µm, mostly bacteria and POM) in the competitive exclusion of the former by the latter.

The biomass of cryptic suspension feeders is known to be great within reef ecosystems. Cryptic sponges alone, comprising only 60% of cavity cover, can account for more than two orders of magnitude greater biomass than all surface suspension feeding taxa combined (Richter et al. 2001). In her 50-box Ecopath model of a Caribbean coral reef, Opitz (1996) found the biomass of suspension feeding groups (e.g., sponges, 800 g m^{-2}; ascidians, barnacles, bryozoans, 137 g m^{-2}; bivalves, 109 g m^{-2}; wet weight, numbers include epibenthic fauna) to be much larger than other heterotrophic functional groups. In areas of elevated nutrients, cryptic biomass composed primarily of suspension feeders has been known to reach 300 g m^{-2} (dry weight; Brock & Smith 1983).

Rates of suspended matter capture within reef crypts are known to be high. Richter and Wunsch (1999) estimated that suspension feeding rates in reef framework cavities may be one order of magnitude higher than that of coral-dominated surface communities. Within cavities lined with suspension feeders in the Red Sea, Richter et al. (2001) recorded a 60% reduction in phytoplankton from waters entrapped for only five minutes. Averaged over an entire day, this translated into approximately 0.9 g carbon per m^2. Furthermore, they calculated that this level of ingestion could account for roughly 22% of the gross metabolism of the entire reef ecosystem. Also in the Red Sea, Yahel et al. (2006) calculated that cryptofauna within the outer centimeters of exposed reef rocks were able to filter seawater at mean rates of 2.1 ± 0.9 m^3 m^{-2} d^{-1}. This corresponded to capture of 1.5 ng chlorophyll a cm^{-2} h^{-1} in the nutrient-poor summer and 6 ng chlorophyll a cm^{-2} h^{-1} during spring plankton blooms. Within reef cavities off Curaçao, van Duyl et al. (2006) recorded bacterioplankton removal rates of 50-100 mg C m^{-2} d^{-1} (cavity surface area, CSA). Scheffers et al. (2004), working in the same region, sealed reef framework cavities and measured internal bacterial concentrations over time. After 30 min, they observed that suspension feeders had reduced bacterioplankton concentrations by 50-60%, equal to rates of 30.1 mg C m^{-2} d^{-1} CSA.

Coral reefs exist as seemingly paradoxical concentrations of biomass and biodiversity within largely oligotrophic waters. Richter et al. (2001) have astutely recognized that knowledge of cryptic suspension feeders may help us rectify this apparent dilemma. Their efficient capture of otherwise transient organic matter is instrumental in the accumulation of their biomass and through various trophic interactions, the biomass of the reef ecosystem. Nutrient capture through their means has been found to account for 22.3 and 1.4 mmol m^{-2} d^{-1} nitrogen and phosphorus respectively, far greater than other recorded rates of nutrient capture including cross-shore advection (1.9 N and 0.3 mmol P m^{-2} d^{-1}), nitrogen fixation (0.6-1.0 mmol N m^{-2} d^{-1}) and migrating fish (2.4-7.2 mmol N m^{-2} d^{-1}; Richter et al. 2001 and references therein).

Deposit feeders

Nutrient capture aided by cryptic suspension feeders is insufficient to completely rectify the coral reef paradox. In order to accumulate biomass in nutrient poor waters, it is necessary to have mechanisms of efficient recycling. Otherwise, organic matter would quickly leak out of the system in the form of metabolic byproducts and dead tissues. Feces and detritus are prevalent within coral reef cavities and their recycling, largely through the action of deposit feeding cryptofauna, is an important component of reef trophic pathways and ecosystem function (Szmant-Froelich 1983).

Deposit feeding and detritivory are utilized by diverse reef cryptofauna, employing different methodologies of ingestion and food particle selection (reviewed in Lopez & Levinton 1987; Levinton 1989). Crustaceans such as brachyurans, carideans, and tanaids use their periopods and mouthparts to grasp or scrape organic deposits off substrates. Numerous additional feeding methodologies/behaviors are known from deposit feeding taxa found within reef ecosystems. Species belonging to Bivalvia, Echiura, Holothuroidea, and Polychaeta are known to use tentacles to feed both on top of reef substrates and within reef sediments. Behaviors and mechanisms of tentacular feeding are numerous even when considering the single echinoderm class Holothuroidea (see Roberts 1979; Massin 1982). Information on the deposit feeding methodologies employed by the other echinoderm classes prevalent within reef crypts (Echinoidea, Ophiuroidea, and Asteroidea) may be found among the detailed chapters of Jangoux and Lawrence's (1982) volume. Family-specific information on polychaete feeding behaviors can be found in Fauchald & Jumars (1979).

Many deposit feeding organisms may also exhibit suspension feeding behaviors and in some taxa, mechanisms are employed that are difficult to assign to one category or the other. For example, the amphipod *Corophium volutator* (known from British mud flats rather than coral reefs) is known to re-suspend and subsequently capture fine particles/organic deposits within its burrow, employing a combination of respiratory currents and filter-like setae (Meadows & Reid 1966).

Deposit feeding taxa are known to consume bacteria, protozoa, fungi, meiofauna, microalgae, as well as organic detritus and there is substantial evidence that varying degrees of food-source/particle-size selectivity occur (Lopez & Levinton 1987). Many species of deposit feeders obtain much of their nutriment from the microorganisms (bacteria and fungi) living on the surface of dead organic matter rather than the detritus itself (Yingst 1976). The rapid consumption of organic detritus by microorganisms and their subsequent ingestion by deposit feeders are of special importance to coral reef ecosystems, which may experience dramatic pulses of organic matter in the form of mass spawning events. Decaying, unfertilized and unsuccessfully settled spawn accumulates in crypts where it is consumed by heterotrophic protozoans (Guest 2008). Their elevated biomass is consumed in turn by deposit feeding fauna and is thereby reincorporated into reef food webs.

Reviews by Ginsburg (1983), Hutchings (1983), and Fagerstrom (1987) have highlighted deposit feeding as one of the most widely used methods of food capture within reef crypts. It is likely the dominant feeding methodology utilized by reef polychaetes in terms of the number of individuals, number of species employing it, and proportion of biomass (Vittor & Johnson 1977). A high percentage (39.3%) of the cryptic fish species sampled by Depczynski and Bellwood (2003) were detritivores and 34 of the 55 dominant taxa (65.49% of total individuals) collected by McCloskey (1970) from living *Oculina* colonies can be classified as deposit feeders.

Mucus, produced by living coral tissues, is used as a means of protection and for cleaning colony surfaces. It may be released at rates of 1.7 to 4.8 liters per m^2 (*Acropora*) of reef per day by submerged and tidally exposed colonies, respectively (Wild et al. 2004). While some debate the trophic importance of coral mucus (e.g., Coffroth 1990), others argue that mucus production accounts for 40% of net carbon fixation by the coral-algal symbiosis (Crossland et al. 1980) and may therefore be an important source of energy for a variety of coral reef taxa (Wild et al. 2004). In addition to its intrinsic nutritional value, coral mucus accumulates bacteria, plankton, and organic detritus, which may increase its nutrient content (C and N) by three orders of magnitude within two hours of its production (Wild et al. 2004). Mucus may be consumed directly by fishes and symbiotic crustacean associates of live corals (Richman et al. 1975; Patton 1994) as well as zooplankton (e.g., copepods, mysids; Gottfried & Roman 1983). Alternatively, it may accumulate at the base of a colony or around its perimeter, where it may in turn be consumed by a suite of different metazoan taxa (McCloskey 1970) or by sediment-associated bacteria which are in turn consumed by both cryptic and non-cryptic deposit feeders. Thus corals and coral mucus are both sources and concentrators of organic matter utilized by cryptic deposit feeding fauna.

Fecal matter is another source of food utilized by deposit feeding cryptofauna. While coprophagy is doubtlessly important in recycling of excretory products, it may also act as a novel source of nutrients incorporated into the reef ecosystem. Some fishes, such as those in the family Haemulidae, feed in surrounding seagrass beds at night and return to the reef where they excrete feces during their quiescence (Meyer & Schultz 1985).

Cryptic reef detritivores (mainly crustaceans) are attracted to and consume feces and are in turn preyed upon by higher trophic level reef fauna (Rothans & Miller 1991).

Herbivorous grazers

Reef crypts are important shelters for a variety of herbivorous reef organisms. Intermittently cryptic urchins have strong influences on algal dynamics. Smaller mesograzers including amphipods, copepods, crabs, shrimps, chitons, gastropods, and polychaetes are known to alter algal community composition in certain reef environments. Herbivorous fish species, which are nektonic in their adult life (e.g., parrotfishes), are known to recruit to reef crypts as juveniles. A review of the herbivorous behavior of many of these metazoans can be found in Steneck (1988), Carpenter (1997), and Hay (1997).

Herbivorous urchins have received considerable attention for their potential to efficiently graze algae from reef substrates (Birkeland 1989; Carpenter 1997). Of the echinoids, the genera *Diadema*, *Echinometra*, and *Eucidaris* have perhaps received the most attention for their grazing activities. *Diadema* spp. are nocturnally active herbivores that feed on hard reef surfaces, removing algae with a calcified tooth-lined mouth called an Aristotle’s lantern. During the day *Diadema* are known to shelter within reef crypts and therefore display distributions strongly affected by the presence of topographically complex substrates (Lewis & Wainwright 1985). In herbivory experiments designed to evaluate the relative efficacy of three groups of grazers (small invertebrates, urchins, fishes), Carpenter (1986) observed that *Diadema antillarum* was able to remove the greatest amount of algal biomass.

Dynamic fluctuations in herbivorous and semi-cryptic echinoids play an important role in reef community structure. A Caribbean-wide die-off of *Diadema antillarum* highlighted the importance of this keystone grazer in the maintenance reef-algae standing stocks (Lessios 1988). In St. Croix, five days after the mass *D. antillarum* mortality, algal biomass increased by 20%, however productivity dropped by 37% per unit area (Carpenter 1988). *Diadema mexicanum*, which has a cryptic lifestyle on eastern Pacific pocilloporid reefs (Glynn 2008), is known to experience rapid population increases due to abnormally high recruitment. Under these conditions grazing intensity may be elevated to levels whereby the rasping activity of the urchins contributes significantly to reef bioerosion (Glynn 1988). It should be noted however, that not all herbivorous echinoid cryptofauna are conspicuous players in reef algal dynamics. For example, *Echinostrephus* spp. is largely sedentary within reef cavities, feeding on drift algal fragments transported by currents.

Micrograzers, microherbivores, or mesograzers are small herbivorous invertebrates which live cryptically among the stipes, fronds, and holdfasts of their algal food sources. They feed on a variety of photosynthetic food sources including macro and micro-filamentous algae, diatoms, and even cyanobacteria, which may be chemically protected from large herbivorous fishes and urchins (Cruz-Rivera & Paul 2000). While the importance of their effects on reef algae biomass is debatable (see Brawley & Adey 1981 vs. Carpenter 1986), micrograzers are known to alter the structure of algal assemblages and reduce epiphyte growth (Brostoff 1988). Known micrograzing species belong to Crustacea, Mollusca, and Polychaeta. Relative to other herbivorous reef taxa, they have small ranges (1-100 cm^2) and high grazing rates (Carpenter 1986). Amphipods are known to remove 1-2 cm^2 d^{-1} microalgae (Carpenter 1986) and limpets may completely graze their foraging territory within 2-3 days (Steneck pers. obs. in Carpenter 1986). Because of their dependence on their food source for shelter from predation, the presence of faster grazing macroherbivores (fishes and urchins) may reduce algae and algal complexity to levels not suitable to micrograzers (Bailey-Brock et al. 1980). For this reason, micrograzers may be found in greater abundances among algae that are less accessible to macroherbivores, such as that within cryptic reef recesses or on wave-swept algal ridges (Carpenter 1986).

Damselfishes are known to aggressively ward off other fish species, leading to elevated algal biomass and cryptofauna abundances within their territories (Lobel 1980). Klumpp et al. (1988) observed that damselfish territories provided shelter such that cryptofauna densities could reach 58,300 individuals m^{-2}, 3.6 times higher than areas directly outside of the damselfishes' influence. Copepods were numerically dominant and polychaetes comprised most of the biomass. It is likely that many of these species were herbivorous. Despite the protection conferred by their damselfish guards, it is probable that some degree of predation does occur within these territories. Accordingly, Zeller (1988) observed that caging of the algal substrates led to an elevation of cryptic micrograzer abundances and a reduction in algal standing stock. This last point is especially interesting because it underscores the potential of micrograzers to consume algae at rates high enough to depress algal biomass. However, this example may be extreme as some studies have shown that cryptofauna within damselfish territories only consume 1% of total algal biomass per day (Klumpp et al. 1988; Klumpp & Polunin

1989). Though apparently low, this consumption should not be overlooked as it can account for up to 31% of algal production or 2.145 g C m^{-2} d^{-1}.

Of the small cryptic herbivores, the Crustacea have received the most attention. In mesocosm experiments mimicking natural coral reef conditions, Brawley and Adey (1981) demonstrated that amphipod populations have the ability to depress microalgae biomass. At densities greater than one amphipod individual per cm^2, many microalgae species were completely eliminated and replaced by the larger macroalgae *Hypnea spinella*. Algal communities observed under intense amphipod grazing were similar to those present on algal ridges, which have fewer fish herbivores and are likely structured by the herbivorous action of cryptic micrograzers.

Majid crabs belonging to the genera *Mithrax* and *Microphrys* are relatively larger cryptic herbivores that consume diverse types of reef algae (Kilar & Lou 1986; Coen 1988). In Belize, *Mithrax sculptus* is known to associate with the finger coral *Porites porites*. Corals containing *M. sculptus* were observed to have algal coverage of only 10% of the colony. When the crabs were experimentally removed algal coverage rose to 75%, indicating that these crabs may be important herbivores on localized scales (Coen 1988).

Little is known concerning the feeding rates and ecological impact of cryptic herbivorous mollusks within coral reef ecosystems. Opisthobranchs are known to consume large amounts of algae in other marine ecosystems (*Aplysia* consume up to 1/3 of body weight daily; Carefoot 1987) and it is likely that they do the same on some reefs. Similarly, other gastropods (snails, limpets) and chitons are known to be abundant herbivores in intertidal as well as rocky and sandy subtidal habitats, but their impacts on reef ecosystems are poorly studied.

Herbivorous mollusks use an abrasive radula to rasp off and ingest plant matter. They prefer either small (filamentous) or very solid and large (crustose coralline) varieties of algae, avoiding species of intermediate size which are likely difficult to remove (Steneck & Watling 1982). Taylor and Reid (1984) described the trophic structure of reef associated mollusks in the Red Sea and found the dominant herbivorous families to be Trochidae, Turbinidae, Strombidae, Lambidae, and Columbellidae. Of the 263 species of mollusk (many cryptic in behavior) collected by Diaz et al. (1990) from Caribbean coral reefs off the coast of Colombia, roughly 10% were herbivores and they were most abundant in shallow reef zones with dead coral cover and high quantities of algae.

Even less is known concerning the role of cryptic herbivorous polychaetes in algae regulation and coral reef trophodynamics. Steneck (1988) cites Kohn and White (1977) when reporting potential densities of 40,000 herbivorous polychaetes m^{-2}. However, close examination of the polychaete families collected in their study reveals that other trophic strategies were employed. Regardless, the numerically dominant Syllidae (between 75% and 93% of individuals) is known to contains many herbivorous species and *Palola siciliensis,* the species which accounted for the most biomass in Kohn and White's (1977) study, is known to feed on algae (Fauchald & Jumars 1979). At Eniwetok Atoll, Bailey-Brock et al. (1980) reported polychaete densities up to eight times higher in areas with algal mats. While the authors document the presence of diverse feeding groups (carnivores, omnivores, detritivores) and describe the shelter potential of the algae substrate, it is likely that many of the collected polychaetes directly consumed algal biomass.

Predators and grazing carnivores

Though reef cavities are considered to shelter their occupants from the high predation pressure experienced on reef surfaces, many cryptofauna themselves are carnivorous predators and grazers. Examples of carnivorous cryptofauna are listed in the predation section above. Here I will discuss the relative abundances and trophic contribution of each of the major taxonomic groups as well as detail the important role that reef cryptofauna play in the parasitism of fishes and in corallivory. Reviews of reef predators including cryptic taxa can be found in Carpenter (1997) and in Glynn and Enochs (in press).

Piscivorous and invertivore fishes are often abundant within reef crypts. Families include the Antennariidae, Apogonidae, Holocentridae, Labrisomidae, Muraenidae, Ophichtidae, Ophidiidae, Scorpaenidae, and Serranidae as well as juvenile Lutjanidae (Glynn 2008). Nearly all of the fish species collected from artificial reef frameworks by Glynn (2006) were carnivorous. Five of the 16 species of cryptobenthic reef fishes collected by Depczynski and Bellwood (2003) were carnivores, second only to detritivorous taxa (7 species). Carnivorous fishes were, however, the most abundant, accounting for 45% of the total number of individuals collected. Cryptic predatory fishes display widely different feeding behaviors. Muraenid eels are known to forage within reef recesses and consume species that are otherwise sheltered from surface predators (Hobson 1974). Some predatory reef fishes are known to shelter within arborescent corals (e.g., *Paracirrhites arcatus* in *Pocillopora meandrina*), briefly leaving their protective confines only to feed on cryptic, epibenthic, and planktonic prey (DeMartini 1996). Other fish species, such as holocentrids, utilize crypts for shelter during the day and venture out at night to forage (Vivien & Peyrot-Clausade 1974).

Carnivorous and predatory cryptofauna belonging to the Crustacea are abundant within reef ecosystems. Nocturnally-active lobsters leave their daytime shelters to forage for their primarily molluscan and crustacean prey (Cox et al. 1997). Predatory swimming crabs (Portunidae) are known to associate with reef frameworks in the eastern Pacific (Glynn pers. comm.) and Ng and Takeda (2003) have described a genus (*Atoportunus*) specifically adapted to live within caves and coral rubble. Parasitic or micropredatory crustaceans (e.g., gnathiid and cirolanid isopods) shelter within reef substrates and attack juvenile fishes during crepuscular hours, ingesting tissue and detrimentally effecting the growth of their prey (Sikkel et al. 2006; Grutter et al. 2008; Jones & Grutter 2008). Other species of cryptic carnivorous crustaceans include cryptic brachyuran families, shrimps, and stomatopods (Reaka 1987). Of these, the stomatopods have received the most attention for their complex behavior (Dingle & Caldwell 1969) and evolutionarily advanced morphologies (Kunze 1981; Marshall et al. 2007) that allow them to aggressively and efficiently capture prey.

While octopods are likely the most conspicuous, many other groups of cryptic molluscan carnivores are known to inhabit coral reefs. Representatives may be found within Opisthobranchia, Caenogastropoda, and possibly within Polyplacophora. Of the mollusks collected by Taylor and Reid (1984) from reef habitats in the Sudanese Red Sea, predatory species were the most diverse. Families included the Buccinidae, Conidae, Fasciolariidae, Terebridae, Tonnidae, Marginellidae, Melongenidae, Mitridae, Muricidae, Nassariidae, Vasidae, and Vexillidae. Many, if not all of these families, are known to occupy reef crypts and their abundances have been shown to be closely correlated to topographic complexity and shelter availability (Kohn & Leviten 1976). Predatory reef gastropods have diverse food sources including bivalves, crustaceans, fishes, gastropods, ophiuroids, polychaetes, and sipunculans (Taylor 1968). Food webs (Figure 1.9) and trophic interactions involving predatory reef gastropods have been proposed by Kohn and Leviten (1976) and Kohn (1987). Detailed studies on species in the genus *Conus* (e.g., Kohn & Nybakken 1975; Leviten & Kohn 1980) have contributed significantly to an understanding of gastropod predators within reef ecosystems.

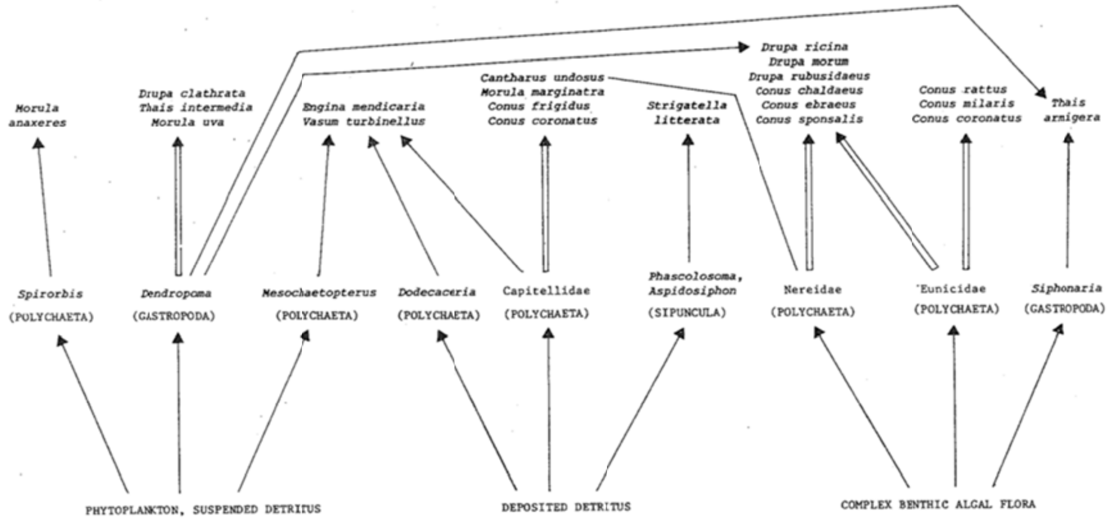

Figure 1.9. Trophic pathways involving predatory gastropods, polychaetes, sipunculans and detritus and algae on an intertidal reef platform at Eniwetok Atoll (Kohn 1987). Arrows point toward direction of food consumption. Double arrows indicate pathways involving the specialization of a predator on an indicated prey species.

Other cryptic predatory reef species belong to the phyla Annelida, Acoelomorpha, Echinodermata, Nemata, Nemertea, Platyhelminthes, Priapula, Pycnogonida and Rotifera (reviewed in Glynn & Enochs, in press). Carnivorous polychaete annelids are either jawed or unjawed and important cryptic reef families include the Amphinomidae and

Polynoidae (Fauchald & Jumars 1979). Carnivorous nemerteans have been observed to inject toxins in order to immobilize their prey and both suctorial and macrophagous feeding behaviors are known (McDermott & Roe 1985). Asteroid echinoderms primarily practice extraoral feeding through stomach eversion. They may capture faster moving prey (e.g., fishes, crustaceans) with their tube feet or may simply graze upon slow moving and sessile taxa (e.g., corals).

Cryptic corallivores deserve special attention due to their potential to significantly impact reef ecosystem dynamics. Corallivores exhibiting cryptic behaviors belong to the phyla Annelida, Arthropoda, Chordata, Echinodermata, Mollusca and likely Acoelomorpha and Platyhelminthes (Jokiel & Townsley 1974; Carpenter 1997; Rotjan & Lewis 2008; Glynn & Enochs in press). Many of these species (e.g., *Hermodice carunculata*) display cryptic tendencies throughout their entire lifecycle. Others such as *Acanthaster planci* and *Eucidaris galapagensis* recruit to reef crypts and adopt more exposed lifestyles as adults. Consumption of coral tissues, which may occur at high rates (especially during corallivore population outbreaks), can be an important source of secondary production within reef ecosystems (Figure 1.10).

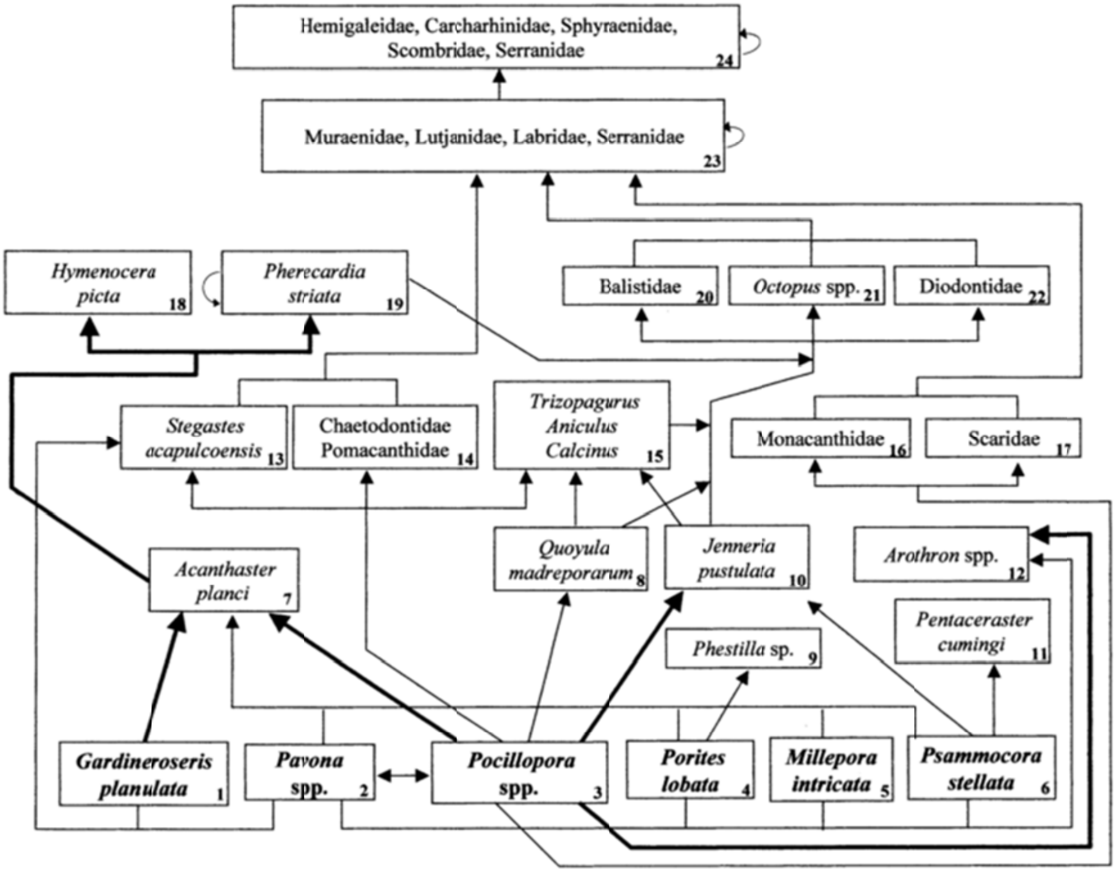

Figure 1.10. Simplified food web of coral supported trophic interactions at Uva Reef, Panamá. Boxes denote species or species groups and arrows indicate the direction of energy flow. Bolded pathways are especially strong (high energy flow) interactions (Glynn 2004).

Trophic connections between crypts and reef surfaces

The epibenthos, cryptos, and water column are interconnected habitats with the biota in each linked through numerous trophic interactions. The various means by which organic matter is captured outside of and used within reef crypts are described above. Benthic and water column communities energetically benefit from cryptofauna through the consumption of excretory products as well as through predation of adults and larvae (Ginsburg 1983). In the case of predation, surface consumers may gain access to the cryptos during the latter's nocturnal emergence as is the case with demersal reef plankton. They may wait and opportunistically prey upon briefly exposed organisms or they may physically disturb substrates in order to uncover prey hiding underneath. Finally, epibenthic and nektonic predators may themselves be intermittent members of the cryptos, capable of penetrating otherwise protective structures, and foraging within.

Reef cryptofauna are one of the most important food sources for fish communities on reef ecosystems (Vivien 1973; Peyrot-Clausade 1980). In a review encompassing reef ecosystems worldwide, Bakus (1966) observed that roughly 65% of coral reef fishes were carnivorous and many of these preyed upon cryptic invertebrates. Randall (1967) examined the gut contents of 212 fish species (5,526 individuals) from reef and inshore habitats in Puerto Rico and the Virgin Islands. He observed that arthropods and to a lesser extent annelids were the most important food source. While these doubtlessly included some epibenthic and holoplanktonic forms, it is likely that most of the prey items exhibited complete or semi-cryptic (e.g. demersal plankton) behaviors. Of the 56 families of coral reef fishes studied by Hiatt and Strasburg (1960) in the Marshall Islands, 10 are described by the authors as consuming primarily “fossorial” or burrowing forms of prey. Of the 25 dominant species of reef fishes in the Panamanian eastern Pacific, only four are strictly herbivorous (Dominici-Arosemena & Wolff 2006). Six species can be classified as feeding primarily on motile benthic invertebrates (cryptic or semi-cryptic) and the remainder are presumed to have diets that include cryptofauna.

While many nektonic fishes (e.g., barracudas) or even aquatic birds (e.g., herons) rely on chance encounters with briefly exposed cryptofauna, others have evolved adaptations that aid in the location and capture of their concealed prey (Steger 1987). Muraenid eels locate distant or hidden prey through sensitive olfactory structures (Bardach et al. 1959; Fishelson 1995) and are able to enter crypts due to their elongate slender bodies (Hobson 1974). Strong nektonic species including balistid fishes, sharks, and turtles may overturn corals, break apart frameworks, and disturb rubble in search of their coelobitic prey (Guzmán 1988; Jiménez 1997-1998; Glynn 2004). Thigmotactic and chemosensory barbels are employed by goatfishes (Mullidae) to riffle through reef rubble and sediments and locate cryptic food (Hobson 1974; Holland 1978; McCormick 1995). Planktivores and benthic invertivores that feed on nocturnally active and exposed cryptofauna, often have large eyes in order to visually detect their prey in the dark (Hobson 1991).

As previously mentioned in the “temporal variability” section, nocturnal emergence of demersal reef plankton and benthic cryptofauna is an important mechanism facilitating the connection of cryptic, epibenthic, and water column biota. In many reef areas, the majority of carnivorous reef fishes are nocturnal, taking advantage of nightly increases in prey availability (Vivien 1973). Families of fishes exhibiting this feeding behavior include the Apogonidae, Holocentridae, Lutjanidae, Priacanthidae, Scorpaenidae, and Serranidae. Their prey consists primarily of crustaceans (Hobson 1974) though polychaetes may be of importance as well (Vivien & Peyrot-Clausade 1974). Because of the difficulty of detection in low light conditions, most demersal reef plankton consumed by nocturnal planktivorous fishes are large and opaque (Hobson 1991). Regardless, the abundance and biomass of these plankton swarms are prodigious (Porter & Porter 1977) and of great trophic significance to reef fishes (Alldredge & King 1977).

McWilliams et al. (1981) have observed that the sizes of nocturnally emerging plankton are comparable to those reported by Porter (1974) to be consumed by

Montastraea cavernosa. Thus smaller demersal plankton are likely an important food source for corals though their contribution to a given coral's metabolism is likely species-specific (Alldredge & King 1977). Additionally, cryptic and demersal plankton may be of increased importance during bleaching events, as heterotrophy during reduced photosynthetic capability has been correlated to increased coral survivorship (Grottoli et al. 2006).

Given the strong trophic linkages between fishes and cryptic prey, it is not surprising that there are often significant correlations in distribution and abundance between the two. More invertivore fishes are found in areas of high cryptofauna abundances (Wolf et al. 1983) as their ability to feed may be dependent on the local biomass of their prey (Vivien & Peyrot-Clausade 1974). This relationship may explain the tendency of many non-corallivorous labrids to associate with areas of high coral cover (Bell & Galzin 1984). The fishes' motile invertebrate prey items are associated with live coral and thereby affect the distribution of their predators. Conversely, the numbers of cryptic prey have been inferred to be affected by the abundance of their predators. For example, abundances of brachyurans have been found to be negatively correlated with that of their grouper predators (Eggleston et al. 1998). A similar pattern was observed by Wolf et al. (1983) for motile stomatopods and polychaetes associated with artificial reefs and preyed upon by fishes. However, this relationship was found to break down for more secretive or less palatable taxa, which were presumably less affected by predation pressures. Reaka (1985) hypothesized that high motility was responsible for stomatopod populations experiencing greater effects from predation and that less motile cryptofauna remained sheltered and out of the reach of predators.

In addition to frameworks, investigations of fish predation pressure and cryptic prey abundances have also been conducted on reef sediment habitats. Despite robust experimental designs lasting up to two years, little effect of predation on sediment-dwelling cryptofauna has been observed (Jones et al. 1988; Jones et al. 1992). Given the secretive nature of the prey and the necessity for fishes to create discrete feeding scars to access them, it is likely that their effect on sediment infauna (and framework cryptofauna) is localized and therefore difficult to detect (McCormick 1995). More investigation is necessary and these feeding behaviors should not be overlooked.

Another way by which reef crypts and their biota influence surface flora and fauna is through nutrient regeneration. The high surface area of complex and anastomosing cryptic passages acts a filter for suspended matter and a biological catalyst for nutrient regeneration. Nitrogen, which is present in low concentrations in oligotrophic reef waters, is remineralized by meiofauna living within reef sediments and may be produced at rates of 1.60 mg N m^{-2} therein (Gray 1985). Excreted nitrogen is transformed into more bioavailable forms by nitrifying bacteria which live in close proximity. Framework cavities, where suspension feeders rapidly consumed bacterioplankton, have been shown to contribute 1.02 to 9.77 mmol NO_x m^{-1} (CSA) d^{-1} to reef surface waters and some if not all of this nutrient regeneration may occur within cavity sediments (Scheffers et al. 2004). Rasheed et al. (2002) have measured nutrient efflux from reef cavities corresponding to 14.5, 7.7, 0.9, and 1.3 mmol m^{-2} d^{-1} ammonium, nitrate, nitrite, and phosphate respectively. Compared to surface waters, well flushed cavities contained nutrient concentrations 1.2 to 2.3 times higher, while poorly flushed sediments contained nutrient concentrations 15 to 80 times higher. Yahel et al. (2006) calculated that endolithic suspension feeding fauna from surface reef rock, may effectively import 1.3 to 4.2 mmol N m^{-2} d^{-1} in the summer and spring months, respectively. Nitrates and nitrites are presumably incorporated into epibenthic plants and macroalgae, zooxanthellae within corals, and phytoplankton, which are in turn consumed by reef herbivores and corallivores.

Coral reef metazoan biodiversity and the importance of cryptofauna

Given the great biodiversity of coral reef ecosystems, their complex three-dimensional nature and their geographic limitation to tropical latitudes, it is of little surprise that they are considered the marine analogue of rainforests. The two ecosystems are often considered in parallel in discussions of species distributions, mechanisms of diversification, and maintenance of species diversity (Connell 1978; Volkov et al. 2007). Reviews, general introductions, and popular literature often refer to coral reefs as “the rainforest of the sea” in order to familiarize readers with their great biodiversity. It is perhaps a testament to the relatively understudied and underappreciated nature of the former ecosystem that we seldom if ever hear the converse statement that “rainforests are the coral reefs of the land.”

Of the 33 known metazoan phyla, 29 occur in coral reefs (exceptions are Xenoturbellida, Micrognathozoa, Onychophora, Pogonophora). Therefore with respect to metazoans, coral reefs are more phyletically rich than all terrestrial (11 phyla), freshwater (17 phyla) and most, if not all other marine ecosystems (Adrianov 2004). Over 13 years ago, the total number of described species from coral reef ecosystems was estimated to be roughly 93,000, a mere fraction of the presumed 618,000 to 9,477,000 total extant reef species (Reaka-Kudla 1997). While epibenthic taxa and fishes have received the most thorough systematic attention, the majority of coral reef biodiversity is due to the remarkable proliferation of the cryptofauna (Reaka-Kudla 1997; Mikkelsen & Cracraft 2001) . In fact, all prominent reef metazoan groups contain species that use reef crypts either for shelter or sustenance (Kobluk 1988). Therefore, in keeping with the aforementioned rainforest analogy, it is helpful to consider cryptofauna as the equivalent of the remarkably diverse rainforest beetles. In addition to their shared great biodiversity, both groups function as ecologically important herbivores, carnivores, and saprophytes and shelter within dominant structural taxa (trees vs. corals). This final characteristic, the hidden nature of most reef species, coupled with the remoteness and inaccessibility of reef ecosystems, is largely responsible for the great discrepancy between the numbers of described and the expected total richness of coral reef species. Both the magnitude of cryptic reef biodiversity and our lack of knowledge concerning its component taxa are staggering, necessitating further investigation.

The following review will cover reef species richness with a focus on the largest component of metazoan biodiversity, the cryptofauna. As many studies and species inventories from various reef ecosystems do not expressly describe the specific microhabitats or behaviors of the included taxa, it is difficult to say with certainty that all exhibit crypsis. However, most of the motile invertebrate reef phyla (e.g., Annelida, Arthropoda, Echinodermata, Mollusca, Sipuncula) are permanently or intermittently cryptic due to high predation and concomitant selective pressure on reef surfaces. Herein, it will be noted when examples are cited which are assumed to reference cryptofauna despite the lack of explicit statements referencing the subject’s cryptic behavior.

A brief history of coral reef biodiversity

Early work on coral reef biodiversity was conducted by naturalists who described animals dredged from reefs during extended marine expeditions (e.g., Alcock 1902, who describes cryptic associates of various Cnidaria and Porifera) and systematists who created detailed inventories and descriptions of species living within particular biogeographic regions (e.g., Rathbun 1926; reviewed in Glynn & Enochs, in press). While these works are of profound importance to the field and are often still used today in taxonomic work, they were somewhat limited in their ability to capture the multi-phyletic diversity that is a coral reef ecosystem. In the second half of the 20th century ecologists began to construct comprehensive reviews for entire reef ecosystems, addressing selected taxonomic groups (some cryptic) and even quantifying abundances and biomass in order to study their various trophic contributions (Odum & Odum 1955, Kohn 1987, Eniwetok Atoll; Taylor 1968, Mahe, Seychelles).

McCloskey's (1970) seminal study of the fauna associated with the branching *Oculina arbuscula*, though not from a tropical reef ecosystem, demonstrated the great abundance and diversity of cryptic metazoans associated with scleractinian corals. From eight coral colonies, McCloskey removed 56,616 individuals greater than 0.2 mm, comprising a total of 309 species belonging to 11 different phyla. In addition to highlighting species richness, McCloskey discussed the distribution, succession, and trophic potential of these organisms. Two years later, Grassle (1973) described how he had collected a single 4.7 kg colony of *Pocillopora damicornis* from a reef at Heron Island, GBR and found more than 2,000 metazoan associates greater than 0.25 mm.

These animals contained 1,441 polychaetes, belonging to 103 species as well as numerous amphipods, decapods, echinoderms, isopods, oligochaetes, ophiuroids, sipunculans, and tanaids. While previous studies had identified associates of pocilloporid corals (Patton 1966; Knudsen 1967), they had primarily been concerned with the large decapod fauna and were accordingly not as rich as those revealed by Grassle.

One of the first attempts to quantitatively study the biodiversity associated with multiple reef substrates was realized by Brander et al. (1971) at Aldabra Atoll and Watamu, Kenya. Though the terms cryptofauna and coelobite were not used, their sampling method of pulverizing reef carbonates, soaking them in water and formalin, and removing the associated fauna implies the cryptic nature of their subjects. Brander et al. (1971) used this methodology to calculate abundance and species densities for crustaceans, polychaetes, and echinoderms. They combined these data with rarefaction in order to compare the biodiversity associated with living and dead carbonates, to compare the biodiversity associated with seven coral species, as well as to compare different reef regions and geographic locations. The biological and physical characteristics of carbonate substrates were found to be important determinants of community biodiversity. Additionally, physical conditions and geographic location were important, and communities at offshore sites were less diverse.

Contemporary approaches to reef biodiversity research have followed several different avenues. Scientists have used replicate sampling of both artificial (Peyrot-Clausade 1977; Zimmerman & Martin 2004; Glynn 2006; Valles et al. 2006; Takada et al. 2007; Takada et al. 2008) and natural substrates (e.g., live and dead coral colonies; Abele 1976; Coles 1980; Caley et al. 2001; Enochs & Hockensmith 2008) to determine community composition, physical and biological determinants of species richness, as well as patterns in community succession. Other workers have used data from more thoroughly studied habitats (tropical rainforests, Reaka-Kudla 1997) or detailed quantitative examination of microcosm biota (Small et al. 1998) combined with species-area relationships to estimate the total number of coral reef species. Still others have used individual-based rarefaction of morphologically (gastropods, McClanahan 1989) and molecularly identified species (crustaceans, Plaisance et al. 2009) in order to compare coral reef sites or estimate overall species richness.

Importance of biodiversity

Before delving further into coral reef and cryptofauna biodiversity, it is important to first examine its intrinsic value. Superficially, biodiversity is nothing more than a numerical representation of the total number and relative abundances of species within a given area. Aside from vague references to "helping scientists find cures for cancer," it is essentially taken as gospel that biodiversity is "good" and its destruction is "bad." These are inherently anthropogenic concepts of morality, with little or no basis in science. There is, however, an emerging understanding that there are positive correlations between biodiversity and ecosystem function as well as biodiversity and anthropocentric/economic concerns.

The relationship between ecosystem diversity and stability has been hotly debated; however, recent experimental and descriptive studies suggest a positive correlation (Ives & Carpenter 2007). The pioneering work of Tilman and Downing (1994) has resulted in some of the best evidence for a positive relationship between ecosystem species richness and resistance/resilience to environmental perturbation. Using experimental plots of grass-land with different species richness, the authors calculated the yearly change in biomass during a multi-year drought period (Figure 1.11). Communities of greater species richness experienced less of a decrease in biomass during the drought (greater resistance) and were able to recover to pre-drought biomass levels quicker (greater resilience) following the drought. Using sessile marine organisms from the east coast of the US, Stachowicz et al. (1999) has shown that greater species richness is correlated with resistance to invasive taxa (Figure 1.12). The findings of these relatively short-term experiments are corroborated by long-term ecosystem patterns. For example, analysis of the fossil record indicates that reef ecosystem change over the past 500 million years is negatively correlated with the number of reef-building species (Figure 1.13, Kiessling 2005). As noted by the author, these data are especially indicative of a positive diversity-stability relationship, as the pattern holds across multiple disturbance types throughout a wide range of reef-building communities.

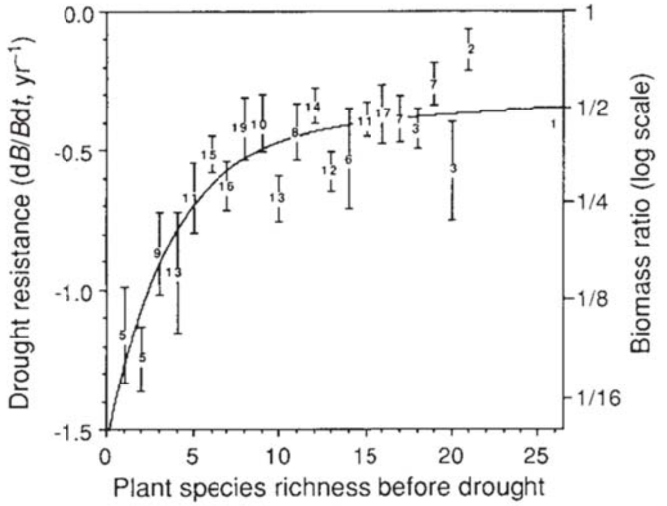

Figure 1.11. The relationship between species richness and resistance to drought in experimental grass plots (Tilman & Downing 1994).

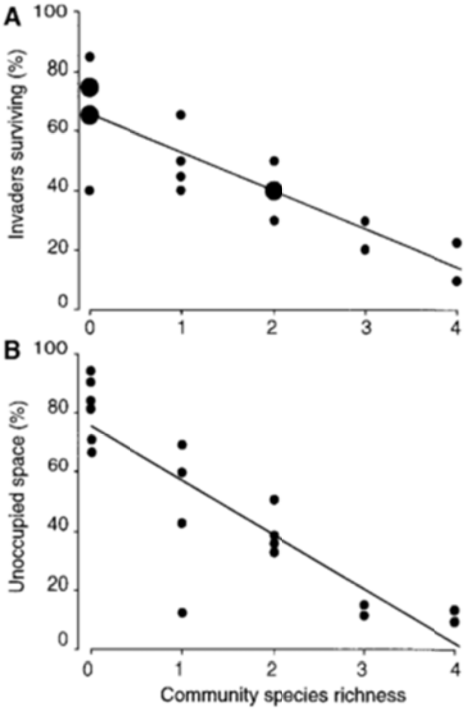

Figure 1.12. Relationship between species richness and resistance to invasive species in experimentally manipulated communities of marine sessile organisms (Stachowicz et al. 1999).

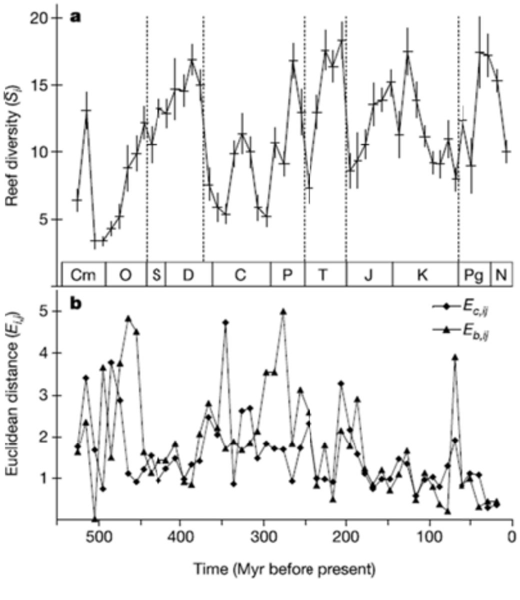

Figure 1.13. The correlation between reef biodiversity (a) and ecological change (b) (Euclidian distance) in constructional styles (diamonds) and reef types (triangles) between the plotted and subsequent time interval (Kiessling 2005).

General anthropocentric benefits of terrestrial and marine ecosystem biodiversity are reviewed by Lovejoy (1994). “Economic considerations,” including tourism, are the most applicable to reef ecosystems and have been extensively reviewed (see Brander et al. 2007). For example, in Hawaii alone, reefs are thought to be worth $350 million annually, with a total value of roughly $10 billion (Cesar & van Beukering 2004). The average value of coral reefs world-wide has been computed to be 6,075 $US ha^{-1} yr^{-1}; including 3,008 $US ha^{-1} yr^{-1} from recreation (diving and snorkeling), 2,750 $US ha^{-1} yr^{-1} from disturbance regulation (storms), 220 $US ha^{-1} yr^{-1} from fisheries, and 27 $US ha^{-1} yr^{-1} from raw materials (Costanza et al. 1997). Other anthropocentric valuations of coral reefs consider their biodiversity as a library of species potentially useful for future human applications. For example, various coral reef taxa are being investigated for their pharmaceutical value, and it is likely that secondary metabolites among unstudied reef species will have future medical applications (Carté 1996). Especially sensitive taxa, known as indicator species (e.g., corals), may help managers to indentify ecosystems impacted by pollution or environmental change. Areas of higher biodiversity may therefore be presumed to have a higher probability of containing species of future benefit to humanity.

Impediments to marine and reef biodiversity studies

To date, there are approximately 1.5 million terrestrial and 280,000 described marine species (Adrianov 2004). Of the latter, only 93,000 are estimated to be known from coral reef ecosystems (Reaka-Kudla 1997). Given that the ocean covers 70% of the

Earth's surface area and that marine phyletic richness is nearly three times that of terrestrial habitats, the question arises whether the disparity between known marine and terrestrial species is indicative of real-life patterns. The answer appears to be decidedly no.

Reasons for this incongruence are many (Mikkelsen & Cracraft 2001; Bouchet 2006), the most obvious being the physical barriers inherent in studying marine and reef biota. Collection of specimens from underwater habitats requires expensive equipment and training. Reef ecosystems are often located on remote offshore islands that, relative to many terrestrial habitats, are difficult to reach. Furthermore, while reefs are restricted to tropical latitudes, most scientific institutions involved in biodiversity work are located in temperate regions (Figure 1.14, Bouchet 2006). Compounding these problems is the relative paucity of properly trained systematists capable of making accurate identifications of previously described species as well as detailed descriptions of novel ones. This last issue is especially prevalent among the less-studied groups that form the bulk of the cryptofauna and by extension coral reef biodiversity (Figure 1.15, Bouchet 2006).

Because they are hidden and frequently imbedded in reef rock, collection of cryptofauna often requires destructive sampling practices. In the deep sea, seagrass beds, and rocky subtidal communities, it is possible to dredge, seine, or hand-collect the benthos. In reef environments, slow-growing and threatened corals form the majority of cryptic habitats and their mortality is often unjustifiable. Additionally, coral reefs are structurally heterogeneous. The composition and abundance of cryptofaunal communities are highly dependent on the morphology of the substrates that they occupy (see "substrate structure") and even minor differences in branch spacing between two coral colonies may have large ramification for cryptic occupants (Vytopil & Willis 2001). Because of this, replicate sampling necessary for statistically sound hypothesis testing, area-based richness extrapolations, or ecosystem-level population investigation is difficult (Hutchings 1974b).

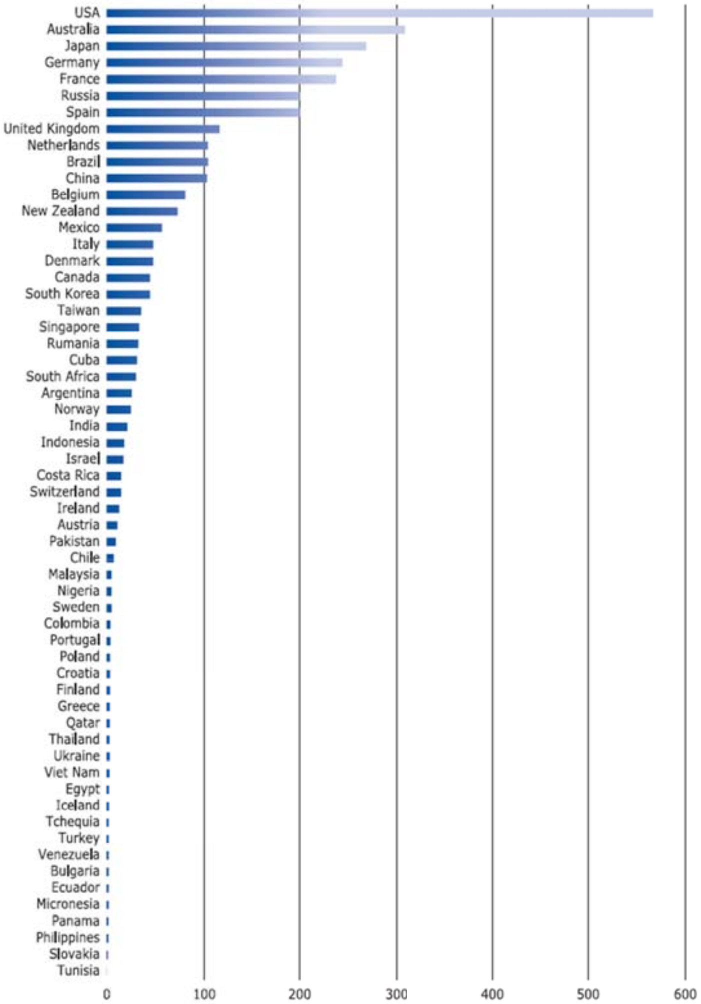

Figure 1.14. The number of new marine species described in 2002-2003 as a function of the first-author's national affiliation (Bouchet 2006).

New techniques of molecular barcoding may be useful in the identification of known species (Hebert et al. 2003), distinguishing morphologically cryptic taxa (Knowlton 1993), and also in the quantification of operational taxonomic unit richness (Plaisance et al. 2009). The use of artificial (framework proxies) and natural replicates (rubble fragments, corals) is allowing researchers to increase sampling effort. Coordinated systematic databases (e.g., itis.gov; marinespecies.org; fishbase.org) are providing workers with the means to check the validity of species names and quickly obtain relevant taxonomic, molecular, and ecological information. These advancements, together with recent scientific and public-awareness campaigns (e.g., UN International Year of Biodiversity; BioBlitz), will hopefully ameliorate many of the issues that have historically plagued marine and coral reef biodiversity work.

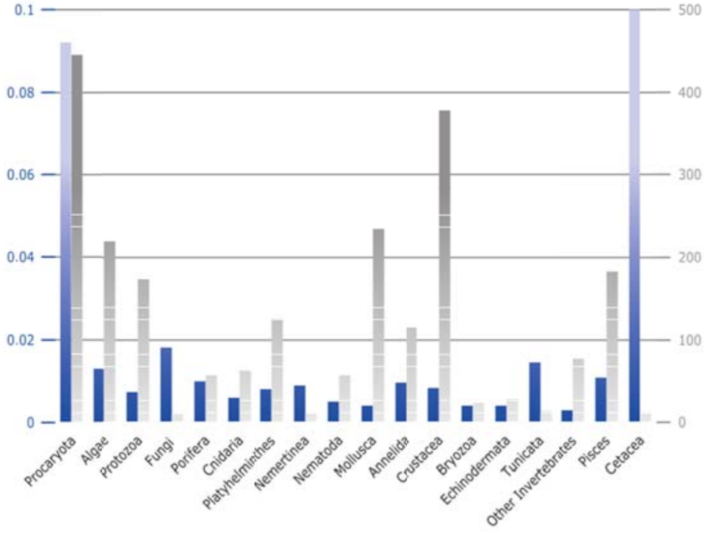

Figure 1.15. Numbers of authors involved in the description of major groups of marine taxa. Blue bar height denotes the number of authors working on a given taxon divided by the total number of species in the same taxon, thereby representing the relative effort or coverage, applied to each group (Bouchet 2006).

How many species?

Species descriptions and notes as to their distributions exist throughout a multitude of journals and volumes. Synonymies, misidentifications, and subspecies are not uncommon, making it difficult to interpret literature even after disparate sources have been compiled. Because no comprehensive and definitive inventory exists, it is difficult or even impossible to accurately state how many of the more than a million currently described species live on coral reefs. Given that we do not know exactly what is known, how then can we proceed to determine the unknown?

Species-area relationships ($S = cA^z$, where S is the number of species, A is area, and c and z are both constants) have been used to estimate the numbers of both described and undescribed reef species. Reaka-Kudla (1997) estimated that of the 318,000 described marine species at the time, 80% (219,000) were from coastal zones. She then used the assumption that tropical regions are twice as diverse as their temperate counterparts ($z = 0.265$ and 0.133 respectively) in order to calculate that there are 195,000 described tropical species. From this, along with a ratio of the area of tropical coastal habitats to coral reef habitats, and a species per area ratio of one to two (tropical coastal habitats to reefs); 93,000 described reef species was estimated, accounting for only 5% of the total number of described organisms.

Reaka-Kudla (1997) further estimated that there are 1.3 million species currently known from tropical rainforests (70% of all species, 90% of terrestrial species) and hypothesized that the true number is conservatively 2 million and possibly as high as 20 million. For each of these three rainforest species richness scenarios, she estimated the total number of coral reef species. These calculations were made using areal estimates of coral reef and rainforest cover worldwide along with the assumption that species-area relationships are identical between coral reefs and tropical rainforests (identical c and z values). If all rainforest species were already identified (1.3 million species), she calculated that there should be 618,000 reef species. Given that there are likely a total of 2 to 20 million rainforest species, she estimated that there should be between 948,000-9,477,000 coral reef species.

Small et al. (1998) took the opposite approach, preferring to start at a small-scale and using the species-area relationship to extrapolate to regional and world-wide scales. The authors identified 532 species, belonging to 96 orders and 27 phyla from a single 5.0 m^2 microcosm of a Caribbean coral reef. They then used the estimated area of Caribbean coral reefs (23×10^9 m^2) and the suggested z value of 0.25 (Reaka-Kudla 1997) to calculate a Caribbean-wide estimate of 138,394 reef species. They cite Paulay (1997) in their assumption that Caribbean reefs contain 1/12 of the total number of reef species and estimate that world-wide coral reef species richness is at least 2,162,603. This number was further refined by taking into account approximate numbers of unidentified fauna (30%) as well as the number of species that presumably were eliminated during the seven year maturation of the microcosm (20±10%). The authors finally arrived at an estimate of 2.6 million reef species, not including bacteria, viruses, and parasites.

Both of these methodologies are dependent on very large assumptions concerning the relationship between area and species richness (parameterization of c and z). Despite Small et al. (1998) adopting the same equation and identical z parameter as Reaka-Kudla (1997), their estimates differ greatly (2.6 vs. 0.5 million species respectively). This disparity is even greater considering that Reaka-Kudla's much lower "total species richness” is based on an estimate of world-wide reef area that was approximately 26 times greater than that of Small et al. Rectifying this discrepancy (using Reaka-Kudla’s reef area and the calculations of Small et al.) elevates Small et al.’s estimate to 3.2 million, more than three times that of Reaka-Kudla.

Bouchet (2006) estimated total marine biodiversity by multiplying the presumed number of species from well-studied European waters by a variety of European/world-wide taxon-specific ratios. Bouchet recognized that this methodology is not appropriate when using ratios of groups of organisms, whose European fauna are either over or under represented relative to other regions (e.g., Euphausiacea). However, extrapolations based on fishes and brachyurans yield estimates of world-wide marine species richness of 50,000-570,000 and 1.4-1.6 million species respectively.

Grassle and Maciolek (1992) collected 233 0.9 m^2 box-cores from deep-sea habitats ranging from 1.5 km to 2.5 km depth. These yielded 90,677 individuals belonging to 798 species, 171 families, and 14 phyla. Approximately the same number of samples from additional sites along a 176 km transect increased the overall species count to 1,597. After a rapid initial increase, they observed the addition of roughly 100 species every 100 km (Figure 1.16). Given that the deep sea (>1 km depth) is roughly 3×10^8 km^2, one novel species per km^2 would result in 3×10^8 species in the deep sea alone. They qualify this number with the observation that deeper oligotrophic deep-ocean regions have densities of individuals that are more than an order of magnitude lower and they finally arrive at a “conservative” estimate of 10 million deep-ocean species.

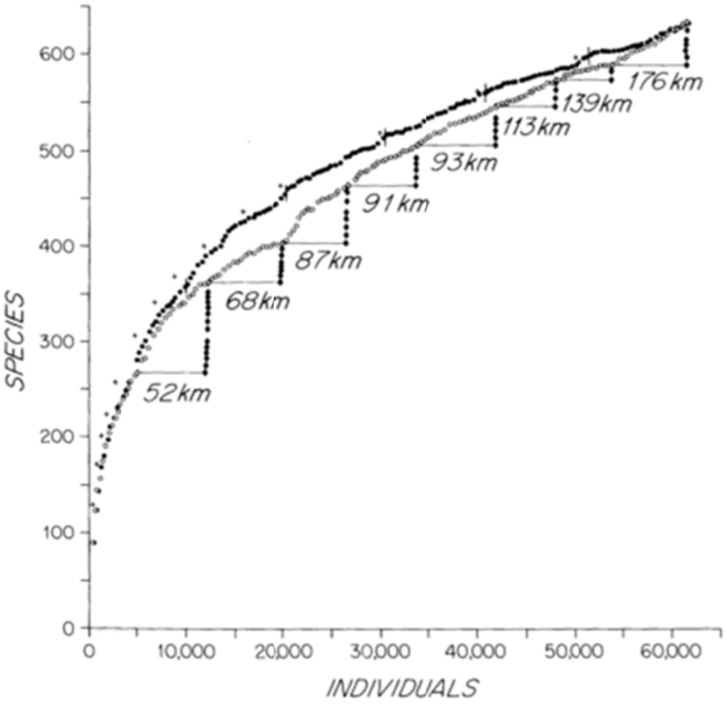

Figure 1.16. Species per number of individuals collected from deep sea box cores. Open circles, within-station samples combined over time and arranged according to distance along a 176 km transect. Horizontal lines indicate the total number of species collected at each successive station/distance. Plus symbols indicate rarefaction curves for all combined samples and station. Closed diamonds and closed circles are not relevant for the purposes of this paper (Grassle & Maciolek 1992).

May (1994) referred to the aforementioned workers as "marine chauvinists," hypothesizing that the 85:15 ratio of described terrestrial to marine taxa was likely indicative of real world patterns. Based on Grassle and Maciolek's (1992) observation that roughly half of their species were new to science, May (1992) hypothesized that the true number of marine species was probably twice that of the total described, approximately 500,000. Regardless of who is correct, all of the aforementioned estimates of both reef and marine biodiversity are dependent on assumptions that have not been rigorously tested. It is therefore clear that further inquiry is necessary in order to rectify current discrepancies.

Analysis of coral reef cryptofauna using new molecular techniques has indicated that species richness is much higher than previous estimates have revealed. For example, Barber and Boyce (2006) used DNA barcodes (700 bp sequences of mitochondrial cytochrome c oxidase subunit-1 gene) from 189 coral reef stomatopod larvae and identified 22 OTUs. Of the 10 OTUs that belonged to the well-known western Pacific gonodactylid and protosquillid stomatopods, at least three were new to science. Of those collected from the Red Sea (four OTUs), at least two were undescribed species. The authors thereby conclude that despite the relatively well-studied nature of this reef cryptofauna group, current numbers of described species underestimate the true richness by 50 to 150%.

Reefs and cryptofauna, why so much biodiversity?

What aspects of reef ecosystems, their biota and their environment allow this exceptional level of biodiversity? What mechanisms encourage and maintain a great number of species to be able to live in close proximity? Moreover, what is unique about reef crypts that has led to their occupation by rich assemblages of biota throughout contemporary Holocene reefs as well as within ancient reef structures as far back as the Lower Cambrian, 535 million years ago (Wood 1999)?

Several hypotheses have been offered attempting to explain both the origin and maintenance of coral reef biodiversity (Connell 1978; Huston 1985; Paulay 1997). Within these discussions, relatively little emphasis has been placed on reef cryptofauna despite their incredible richness and occupation of a unique habitat. Selected mechanisms of special relevance to reef cryptofauna are discussed below.

The intermediate disturbance hypothesis was first proposed by Grime (1973) and later applied to reef systems by Connell (1978). Inherent in the idea is the concept of competitive exclusion; given a limiting resource and time, some species will dominate over others. Following a disturbance and the mortality of preexisting biota, previously limiting resources become accessible. Diversity increases as more and more species utilize the readily available resource. As densities increases and as the resource becomes limiting, competitively dominant taxa exclude weaker species, thereby decreasing diversity. Therefore, in this example, there is an intermediate period, after initial post-disturbance colonization and before the establishment of a climax community, where diversity is highest. In general, high frequencies/magnitudes of disturbance will lead to low diversity assemblages of rapidly colonizing species while low frequency/magnitude disturbances lead to low diversity communities of competitively dominant species. Intermediate frequencies/levels of disturbance lead to maximum community richness.

Many studies have observed patterns in coral diversity that reflect those predicted by the intermediate disturbance hypothesis (Figure 1.17; Grigg & Maragos 1974; Connell 1978; Rogers 1993; Aronson & Precht 1995). Competitive exclusion, resulting in lower diversity climax communities is known from cryptofauna (see “colonization and succession”), most notably from those associated with coral rubble. Meesters et al. (1991) as well as Gischler and Ginsburg (1996) have observed a correlation between rubble stability and size and used this relationship as a disturbance proxy. Sub-rubble communities outside of an intermediate size/disturbance threshold were less diverse. Other factors including rubble consolidation, and depth related wave-sheltering further corroborated this hypothesis.

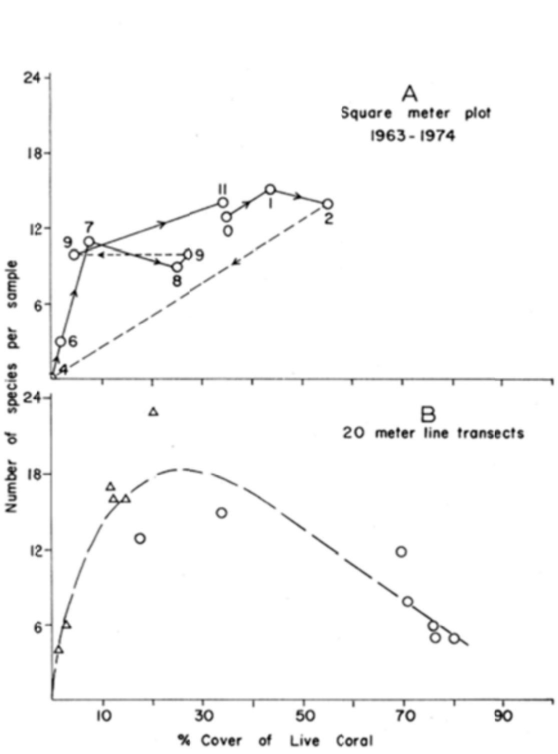

Figure 1.17. Coral cover and species richness at Heron Island, GBR. A., Changes in species richness and % coral cover in a single 1 m^2 plot over 11 years. Numbers indicate years following initial sampling and vectors show yearly changes. Dashed vectors are years experiencing significant hurricane disturbances (1967, 1972). B., Species richness of corals as a function of % live coral along a 20 m transect 3 to 4 months following the 1972 hurricane (Connell 1978).

Competitive network theory was first proposed by Jackson and Buss (1975) in order to explain the diversity of well-protected cryptic reef communities. It was subsequently demonstrated by Buss and Jackson (1979) using sessile cryptofauna living underneath corals from Jamaican reefs. In contrast to the intermediate disturbance hypothesis, competitive network theory postulates that diversity may be maintained in the absence of disturbance if competition follows nonlinear hierarchies. If three species A, B, and C coexist in the same niche space, A is competitively dominant over B and B is dominant over C; diversity may be maintained if C can outcompete species A. Competitive network and intermediate disturbance theories are not mutually exclusive and the relative importance of each likely depends on the taxa involved as well as the nature of their physical habitat. While studies by Buss and Jackson (1979) and Jackson (1977) have observed nearly complete surface occupation of reef crypts, Meesters et al. (1991) noted that sub-rubble communities have large amounts of free space. Therefore, it is unlikely that in this less protected habitat competition reaches a level where non-transitive networks are important mechanisms of biodiversity maintenance.

Ecological neutral theory was proposed by Hubbell (2001) as a modification of Kimura's (1985) model for genetic drift. Neutral theory treats all organisms as equal, with the same chance of dying, reproducing, immigrating, emigrating, etc. In addition, if the space occupied by an individual from one species is vacated (i.e. death), another individual (possibly a different species) will immediately fill in that space. Differences in species abundances between locations, their distributions, are therefore the product of demographic stochasticity. Divergence in community similarity is due to drift. While the assumptions of neutral theory are clearly incorrect given the high diversity of organism life histories, they give rise to species distributions that are remarkably similar to those in real life.

In contrast to neutral theory's supposition that species distributions are the result of chance dispersal, niche theory holds that species are found in a given area because they are specifically adapted to live there. Organisms cannot coexist unless intraspecific competition is higher than interspecific competition. Because of this, organisms partition themselves out in n-dimensional space where n is a number of niche axis's (space, time, food type, etc.). Finer specialization (restricted range in n-dimensional space) will lead to the possibility of a greater number of species in a given space. According to this model, diversity can lead to diversity as more organisms can create more niches for more species to fill.

With respect to cryptic fauna, Black and Prince (1983) examined variability in decapod communities associated with *Pocillopora damicornis* across latitudinal gradients off western Australia. There was similarity between communities in all study areas and no significant difference with latitude. In fact, cryptic communities associated with living pocilloporid corals in the IWP are most likely similar to those in the eastern Pacific as territorial *Trapezia* spp. exist in both. This suggests firm niche development and occupation by these coral associates.

Cryptofaunal communities associated with dead substrates are more speciose and less similar than their live-coral counterparts. This may be due in part to greater niche diversity as the co-occurrence of bryozoans, algae, sponges, and other encrusting taxa would facilitate the occupation of species that specialize on each of these different habitat resources. Conversely, live corals may simply offer harsher environments, inhospitable to most cryptic reef taxa. On average, non-coral-dwelling cryptofauna likely have greater niche overlap, displaying less specialization than their coral-associated counterparts. Many cosmopolitan cryptic taxa are opportunistic feeders, utilizing scavenging and omnivorous strategies.

Connolly et al. (2005) examined species abundance distributions of fishes and corals at different spatial scales across the Pacific. Niche theory postulates a log-series species abundance distribution (high proportion of very rare species), which is in contrast to the null hypothesis of a log-normal species distribution. Connolly et al. (2005) observed species distributions similar to a log-linear plot; however, there was poor sampling of rare species, leading to a “veiling” of the true log-normal population distribution. Furthermore, Connolly et al. (2005) used surface area and biomass to approximate resource use for corals and fish, respectively. While resource use was also distributed log-normally in relation to species, it was not on the same scale as abundance, suggesting that the relationship between species and resource use is not direct. Their results therefore do not support the predictions of niche theory.

Dornelas et al. (2006) pointed out that many models can be fitted to localized species abundance distributions and that it might be better instead to test the multi-scale predictions of a given model. She recognized that niche theory will ultimately give rise to communities of greater similarity than those predicted by neutral theory and she tested this across coral communities at island, regional, and Pacific-wide scales. She found that communities were more variable and less similar than could be explained by either niche partitioning or the demographic stochasticity of the neutral theory. She concluded that differences in community composition were due to spatio-temporal stochasticity, the occurrence of random environmental perturbations affecting localities and communities differentially.

Reef biodiversity under climate change and human impacts

Concerns over the impacts of global climate change and overfishing on coral reef ecosystems have been focused primarily on corals and coral reef fishes. While these taxa are ecologically important in reef ecosystems, they contribute relatively little towards species richness. Given that cryptofauna form the majority of reef metazoan biodiversity and are important components of substrate and trophic dynamics, it is imperative that coral reef scientists widen their scope in order to examine how these communities will respond to the singular conditions facing both coral reef ecosystems and the world as a whole.

Our current basic understanding indicates that coral mortality will have negative consequences for cryptofauna biodiversity, especially those organisms intimately associated with living corals. Coral bleaching and habitat degradation have been shown experimentally to increase predation pressure on fishes sheltering within coral substrates (Coker et al. 2009) and to negatively affect the richness, abundance (Caley et al. 2001), and biomass (Enochs & Hockensmith 2008) of cryptic coral occupants.

While a parallel relationship between the decline of corals and their obligate symbionts is fairly clear, the impacts that coral death will have on more cosmopolitan coelobites are vastly more complex. Enochs and Hockensmith (2008) observed significant decreases in cryptofauna richness (l^{-1} habitat) six months after coral mortality. However, after one year, the number of species per liter of substrate was not statistically different. This was likely due in part to changes in the sizes of sampled corals. Living corals grew and dead corals decreased in size as they were eroded. Despite similar richness/volume carbonate relationships in both scenarios, the reduced availability of carbonate substrate as the result of coral mortality and bioerosion could lead to fewer species. Had the authors used rarefaction in order to standardize sample size, rather than the somewhat contentious method of dividing by coral volume, it is likely that they would have observed greater biodiversity associated with dead coral substrates. Nonmetric multidimensional scaling of coral-associated species assemblages revealed that different living coral colonies were occupied by more similar cryptofauna communities than dead. Greater inter-colony similarity suggests that at a reef-wide scale, living corals would host depauperate faunal assemblages compared with more heterogeneous dead substrates.

Therefore following mass coral mortality, coral symbiont abundances and diversity would be expected to precipitously decline. Newly available dead coral substrates will likely be colonized by diverse assemblages of sessile biota that was previously outcompeted by corals. Biodiversity could remain elevated as associates of these new substrates would likely continue to flourish in spite of, and perhaps due to declines in coral cover. Collapse of coral reef biodiversity and ecosystem function may follow as bioerosion progresses. Decreases in or cessation of coral growth could tip the tenuous balance of reef carbonate dynamics into a net erosional state, ultimately leading to decreases in substrate complexity and habitat destruction. This process would be accelerated due to the erosional behavior of many of the organisms that may colonize following coral mortality. Major declines in biodiversity and ecosystem function would therefore parallel the disappearance of habitat, as initiated by coral death, rather than the immediate death of coral tissues per se.

The restricted ranges and high endemicity of reef faunas make them especially susceptible to extinction (Roberts et al. 2002). Currently no reef species are known to have become globally extinct, however regional coral extinctions are known and many fish and coral species are threatened (Munday 2004; Carpenter et al. 2008; Glynn 2011). Given the numbers of undescribed reef species, the probability of the disappearance of a species before it is known to science (a centinelan extinction) is high. Carlton et al. (1999) used species-area relationships and Reaka-Kudla's estimates of total described reef species to calculate that a 5% reduction in reef habitat area would lead to the extinction of roughly 1,000 known reef species. Given Reaka-Kudla’s conservative estimate of 950,000 total reef species (described and undescribed), a 30% decline in reefs over the next 10 to 20 years would lead to the extinction of 10 to 12 thousand species.

These estimates assume that reef species are completely restricted to reef habitats. This is likely untrue as many reef species, including fishes and cryptofauna are known from other habitats (Knowlton 2001). Cosmopolitan cryptofauna may therefore take refuge in non-reef habitats during times of reef-ecosystem duress and may effectively be less susceptible to extinction than corals themselves.

In an era of global change, it is of the utmost importance that we accelerate efforts to document, describe, and catalog unknown reef species before they face global extinction. Furthermore, it is imperative that we continue to investigate the ecological roles of the described reef biota, especially those of the understudied cryptofauna. Only with an understanding of this important and speciose community can we hope to accurately predict and responsibly manage the dynamics of reef ecosystems in a rapidly changing world.

Table 1.1. The richness of selected reef and coral associated cryptofauna.

Taxon	Geographic Location	Habitat	Richness	Sample size	Source	Notes
Annelida						
Polychaeta	Enewetak Atoll	Windward refe bench	79 spp., 24 fam. [1]	6,931 indiv.	Bailey-Brock et al. 1980	
Polychaeta	Aldabra Atoll, Seychelles	Coral area	33 spp [1]	393 indiv.	Brander et al. 1971	
Polychaeta	Watamu, Kenya	Coral area	50 spp. [1]	219 indiv.	Brander et al. 1971	
Polychaeta	Lizard Island, GBR	Coral blocks	144 spp.	+40,000 indiv.	Hutchings 1985	
Polychaeta	Cozumel Island, Mexico	Dead coral	42 spp. 19 fam.	148 idiv.	Ochoa-Rivera et al. 2000	
Polychaeta	Tuléar, Madagascar	Reef flat	118 spp.	5,500 indiv.	Peyrot-Clausade 1974	
Polychaeta	NE Gulf of Acaba, Jordan	0.2 - 0.5 diameter reef cavities	14 taxa	~4.0 m^2	Wunsch et al. 2000	
Polychaeta	Curaçao and Bonaire	Below coral rubble	18 spp.	3.35 m^2	Meesters et al. 1991	
Polychaeta	Heron Island, GBR	4.7 kg *Pocillopora damicornis*	103 spp.	1,441 indiv.	Grassle 1973	
Polychaeta	North and South Carolina, USA	*Oculina arbuscula*	89 spp.	8 coral heads	McCloskey 1970	
Arthropoda						
Crustacea	Paynes Bay, Barbados	*Madracis mirabilis*	94 spp.	2,750 indiv.	Lewis & Snelgrove 1990	5 site endemics
Crustacea	Brighton, Barbados	*M. mirabilis*	79 spp.	1,302 indiv.	Lewis & Snelgrove 1990	6 site endemics
Crustacea	Bank Reef, Barbados	*M. mirabilis*	79 spp.	1,846 indiv.	Lewis & Snelgrove 1990	
Crustacea	Barbados	*M. mirabilis*	130 spp.	8,409 indiv.	Snelgrove & Lewis 1989	mean of 6 colonies
Crustacea	Reef flat Shaab Baraja, Sudan	*Stylophora pistillata*	18.7 spp.	124 indiv.	Edwards & Emberton 1980	
Crustacea	Aldabra Atoll, Seychelles	Coral area	17 spp [1]	62 indiv.	Brander et al. 1971	
Crustacea	Watamu, Kenya	Coral area	30 spp. [1]	106 indiv.	Brander et al. 1971	Spp criteria was 5% similarity cytochrome oxidase subunit I
Crustacea	Northern Line Iss., Moorea	*Pocillopora* coral heads	135 spp.	403 indiv.	Plaisance et al. 2009	
Cirripedia	North and South Carolina, USA	*O. arbuscula*	6 spp.	8 coral heads	McCloskey 1970	
Amphipoda	North and South Carolina, USA	*O. arbuscula*	31 spp.	8 coral heads	McCloskey 1970	
Amphipoda	Heron and One Tree Reef, GBR	*P. damicornis*	4 spp.	40 coral heads	Austin et al. 1980	
Copepoda	Heron and One Tree Reef, GBR	*P. damicornis*	3 spp.	40 coral heads	Austin et al. 1980	
Copepoda	North and South Carolina, USA	*O. arbuscula*	1 sp.	8 coral heads	McCloskey 1970	
Cumacea	North and South Carolina, USA	*O. arbuscula*	1 sp.	8 coral heads	McCloskey 1970	
Decapoda	North and South Carolina, USA	*O. arbuscula*	21 spp.	8 coral heads	McCloskey 1970	
Decapoda	Heron and One Tree Reef, GBR	*P. damicornis*	~62 spp., +10 fam.	40 coral heads	Austin et al. 1980	
Decapoda (symbiotic)	Hawaii	*Pocillopora meandrina*	12 spp.	18 corals	Coles 1980	
Decapoda (nonsymbiotic)	Hawaii	*P. meandrina*	115 spp.	18 corals	Coles 1980	

Table 1.1. Cont.

Taxon	Geographic Location	Habitat	Richness	Sample size	Source	Notes
Decapoda	Pearl Islands, Panamá	*P. damicornis*	55 spp.	1,107 indiv.	Abele & Patton 1976	1107 individuals drawn randomly from 4724
Decapoda	Uva Island, Panamá	*P. damicornis*	37 ± 2	1,107 indiv.	Abele 1976	817 individuals unidentified
Isopoda	North and South Carolina, USA	*O. arbuscula*	3 spp.	8 coral heads	McCloskey 1970	
Ostracoda	North and South Carolina, USA	*O. arbuscula*	2 spp.	8 coral heads	McCloskey 1970	
Pycnogonida	North and South Carolina, USA	*O. arbuscula*	6 spp.	8 coral heads	McCloskey 1970	
Stomatopoda	Heron and One Tree Reef, GBR	*P. damicornis*	1 sp.	40 coral heads	Austin et al. 1980	
Tanaidacea	North and South Carolina, USA	*O. arbuscula*	2 spp.	8 coral heads	McCloskey 1970	
Brachyura and Anomura	Tuléar, Madagascar	Dead coral blocks	120 spp.	1,807 indiv.	Peyrot-Clausade 1981	
Caridea and Panaeoidea	central GBR	*Pocillopora verrucosa* (live)	21 spp.[1]	6,467 indiv., 270 corals	Preston & Doherty 1990	listed as agile shrimps
Caridea and Panaeoidea	central GBR	*P. verrucosa* (dead)	28 spp.[1]	25,324 indiv. 1,080 corals	Preston & Doherty 1990	listed as agile shrimps
Porcellanidae, Majoidea, Xanthoidea	Bahias de Huatulco, Mexico	*Pocillopora* reef	47 spp., 27 genera	8,826 indiv.	Ramirez Luna et al. 2002	17 site endemics
Xanthoidea	Southern Taiwan	*P. damicornis*	25 spp.	356 indiv.	Chang et al. 1987	
Xanthoidea	Southern Taiwan	*P. verrucosa*	21 spp.	444 indiv.	Chang et al. 1987	
Brachiopoda						
Brachiopoda	North and South Carolina, USA	*O. arbuscula*	1 sp.	8 coral heads	McCloskey 1970	
Bryozoa						
Bryozoa	NE Gulf of Acaba, Jordan	0.2 - 0.5 diameter reef cavities	13 taxa	~4.0 m^2	Wunsch et al. 2000	
Bryozoa	Curaçao and Bonaire	Below coral rubble	41 spp.	3.35 m^2	Meesters et al. 1991	
Chordata						
Osteichthyes	North and South Carolina, USA	*O. arbuscula*	2 spp.	8 coral heads	McCloskey 1970	
Pisces	Lizard Island, GBR	Coral reef	44 spp., 8 fam.	1,042 indiv.	Depczynski & Bellwood 2005	
Pisces	Heron and One Tree Reef, GBR	*P. damicornis*	14 spp., 5 fam.	40 coral heads	Austin et al. 1980	
Tunicata	North and South Carolina, USA	*O. arbuscula*	3 spp.	8 coral heads	McCloskey 1970	
Ascidiacea	NE Gulf of Acaba, Jordan	0.2 - 0.5 diam. reef cavities	23 taxa	~4.0 m^2	Wunsch et al. 2000	listed as Ascidia
Ascidiacea	Curaçao and Bonaire	Below coral rubble	65 spp.	3.35 m^2	Meesters et al. 1991	

Table 1.1. Cont.

Taxon	Geographic Location	Habitat	Richness	Sample size	Source	Notes
Cnidaria						
Hydrozoa	NE Gulf of Acaba, Jordan	0.2 - 0.5 diam. reef cavities	4 taxa	~4.0 m^2	Wunsch et al. 2000	
Hydroidolina	Curaçao and Bonaire	Below coral rubble	2 spp.	3.35 m^2	Meesters et al. 1991	listed as Hydroida
Octocorallia	NE Gulf of Acaba, Jordan	0.2 - 0.5 diam. reef cavities	8 taxa	~4.0 m^2	Wunsch et al. 2000	
Octocorallia	Curaçao and Bonaire	Below coral rubble	1 sp.	3.35 m^2	Meesters et al. 1991	
Actinaria	Curaçao and Bonaire	Below coral rubble	4 spp.	3.35 m^2	Meesters et al. 1991	
Scleractinia	Curaçao and Bonaire	Below coral rubble	11 spp.	3.35 m^2	Meesters et al. 1991	
Scleractinia	NE Gulf of Acaba, Jordan	0.2 - 0.5 diam. reef cavities	20 taxa	~4.0 m^2	Wunsch et al. 2000	
Stylasteridae	Curaçao and Bonaire	Below coral rubble	1 sp.	3.35 m^2	Meesters et al. 1991	
Echinodermata						
Echinodermata	Aldabra Atoll, Seychelles	Coral area	3 spp	5 indiv	Brander et al.1971	
Echinodermata	North and South Carolina, USA	*O. arbuscula*	5 spp.	8 coral heads	McCloskey 1970	
Asteroidea	Aldabra Atoll, Seychelles	*Porites nigrescens*	3 spp.	40 coral colonies	Sloan 1982	
Echinoidea	Aldabra Atoll, Seychelles	*P. nigrescens*	5 spp.	40 coral colonies	Sloan 1982	
Holothuroidea	Aldabra Atoll, Seychelles	*P. nigrescens*	1 sp.	40 coral colonies	Sloan 1982	
Ophiuroidea	Aldabra Atoll, Seychelles	*P. nigrescens*	14 spp.	40 coral colonies	Sloan 1982	
Ophiuroidea	Heron and One Tree Reef, GBR	*P. damicornis*	5 spp., 4 fam.	40 coral heads	Austin et al. 1980	
Mollusca						
Mollusca	New Caledonia	28 reef stations, 14 other	2,738 spp. [1]	127,652 indiv.	Bouchet et al. 2002	
Mollusca	NE Gulf of Acaba, Jordan	0.2 - 0.5 diam. reef cavities	4 taxa	~4.0 m^2	Wunsch et al. 2000	
Mollusca	Santa Marta, Colombia	Reef localities	263 spp. [1]	7 reefs, 8 years	Díaz et al.1990	
Bivalvia	Curaçao and Bonaire	Below coral rubble	2 spp.	3.35 m^2	Meesters et al. 1991	
Bivalvia	North and South Carolina, USA	*O. arbuscula*	41 spp.	8 coral heads	McCloskey 1970	listed as Pelecypoda
Gastropoda	Heron and One Tree Reef, GBR	*P. damicornis*	7 spp.	40 coral heads	Austin et al. 1980	
Gastropoda	North and South Carolina, USA	*O. arbuscula*	34 spp.	8 coral heads	McCloskey 1970	
Prosobranchia	Kenya	Coral reef	135 spp., 25 fam. [1]	~ 9,000 indiv.	McClanahan 1989	
Conidae	Enewetak atoll	Windward reef platform	8 spp. [1]	688 indiv.	Kohn 1987	
Muricidae	Enewetak atoll	Windward reef platform	7 spp. [1]	526 indiv	Kohn 1987	
Conus	Thailand and Indonesia	Fringin reefs	48 spp. [1]	1,350 indiv.	Kohn & Nybakken 1975	62 spp represented by Dead shells

Table 1.1. Cont.

Taxon	Geographic Location	Habitat	Richness	Sample size	Source	Notes
Nemertea						
Nemertea	North and South Carolina, USA	*O. arbuscula*	7 spp.	8 coral heads	McCloskey 1970	
Platyhelminthes						
Platyhelminthes	North and South Carolina, USA	*O. arbuscula*	7 spp.	8 coral heads	McCloskey 1970	
Porifera						
Porifera	Bonaire, Netherlands Antilles	reef cavities	92 spp.	1,245 indiv.	Kobluk & Van Soest 1989	
Porifera	NE Gulf of Acaba, Jordan	0.2 - 0.5 diam. reef cavities	133 taxa	~4.0 m^2	Wunsch et al. 2000	
Porifera	Curaçao and Bonaire	Below coral rubble	199 spp.	3.35 m^2	Meesters et al. 1991	
Sipuncula						
Sipuncula	Carrie Bow Cay, Belize	Reef rock and rubble	8 spp.	1,133 indiv.	Rice & Macintyre 1982	
Sipuncula	Bocas del Toro, Panamá	Coral rubble	14 spp.	5 days	Schulze 2005	
Sipuncula	North and South Carolina, USA	*O. arbuscula*	3 spp.	8 coral heads	McCloskey 1970	

Chapter 2: Responses of reef biodiversity to coral mortality and habitat degradation

Coral reefs are widely considered to be the most biodiverse marine ecosystem. Containing 29 of the 33 known metazoan phyla and an estimated 2.6 million species, they are more phyletically rich than all terrestrial ecosystems and likely more species rich than all except tropical rainforests (Small et al. 1998; Adrianov 2004). Within coral reef ecosystems, biodiversity is so staggeringly high that close examination of a single coral head may reveal 103 species of polychaete worms and a five m^2 mesocosm can contain as many as 534 species (Grassle 1973; Small et al. 1998).

The more conspicuous fishes and corals account for only a small fraction of reef faunal richness. Most of the species comprising reef ecosystems live within the cracks, crevices, and cavities of carbonate frameworks (Reaka-Kudla 1997; Mikkelsen & Cracraft 2001). These animals are known collectively as the cryptofauna or coelobites. In addition to comprising the majority of reef biodiversity, they are integral components of reef food webs, capturing suspended plankton from surrounding waters (Richter et al. 2001), recycling detritus (Depczynski & Bellwood 2003), grazing on algae (Klumpp et al. 1988), and providing food to the epibenthos and nekton (Vivien 1973; McWilliam et al. 1981). Their members include corallivores (Rotjan & Lewis 2008) as well as symbiotic species which deter coral predators and clean surface tissues (Glynn 1980, 1983). Additionally, cryptic biota can bind and stabilize unconsolidated corals (Wulff & Buss 1979) as well as chemically and physically erode carbonate structures (Glynn 1997), both important processes in the persistence of coral reef frameworks.

The permanence of reef structures is very much in question. In recent years, climate change, ocean acidification, overfishing, predator outbreaks and disease have all lead to global declines in coral cover and the loss of coral reef habitat (Glynn 1973; Jackson et al. 2001; Harvell et al. 2002; Hughes et al. 2003; Baker et al. 2008; Manzello et al. 2008; Alvarez-Filip et al. 2009). Considering the enormity of this species repository, the present frequency and severity of coral mortality, and the predicted levels of habitat destruction, it is of paramount importance that we understand the cryptic component so that we may more accurately interpret and manage the dynamics of entire reef ecosystems.

Preliminary evidence suggests that coral bleaching and mortality may have severe detrimental impacts on coral-associated cryptofauna populations. Fishes sheltering within *Pocillopora damicornis* colonies experience increased predation pressure following the bleaching, mortality, and overgrowth of their hosts (Coker et al., 2009). Bleaching of *Stylophora pistillata* colonies has been shown to reduce the richness and abundance of decapod associates (Caley et al. 2001). Furthermore, coral mortality may lead to a reduction in the density of cryptofauna biomass (per unit volume), possibly due to the unavailability of coral-derived food sources (e.g., tissues, mucus, fat bodies; Enochs & Hockensmith 2008). While highly informative, the aforementioned studies have been conducted at small spatial and temporal scales. Large-scale ecosystem-level analysis, rather than single-colony community shifts, is necessary in order to determine the effects of widespread coral mortality and habitat destruction.

To date, ecosystem-scale analyses of coral reef cryptofauna have been hampered by overwhelming levels of biodiversity as well as complex reef topographies and heterogeneous reef substrates, both of which give rise to patchy and variable community distributions. On the Pacific coast of Panamá, coral reef structures are composed primarily of monogeneric stands of *Pocillopora*, mostly *P. damicornis*. These frameworks are horizontally homogeneous relative to other reef ecosystems yet retain the structural complexity conducive to abundant cryptofauna populations. Furthermore, analysis of biogeographic patterns across multiple phyla reveals that reef ecosystems in the eastern Pacific are among the most depauperate in the world (Roberts et al. 2002). The simplicity of these reef ecosystems makes them ideally suited for inquiry into the dynamics of cryptic reef biodiversity.

Materials and methods

Study site

This study was conducted at Playa Larga Reef (8°38'0.75"N 79°1'47.90"W) off the NE shore of Isla Contadora, in the Pacific Gulf of Panamá (Figure 2.1). The reef is approximately 12 hectares and is located within a bay on the Northeast of the island. It is composed primarily of *Pocillopora damicornis*, however there is a 1,300 m^2 (1.1% of the total reef area) patch of *Porites lobata* colonies on the shallow inland margin of the reef. Zonation and *P. damicornis* framework structures are discussed below.

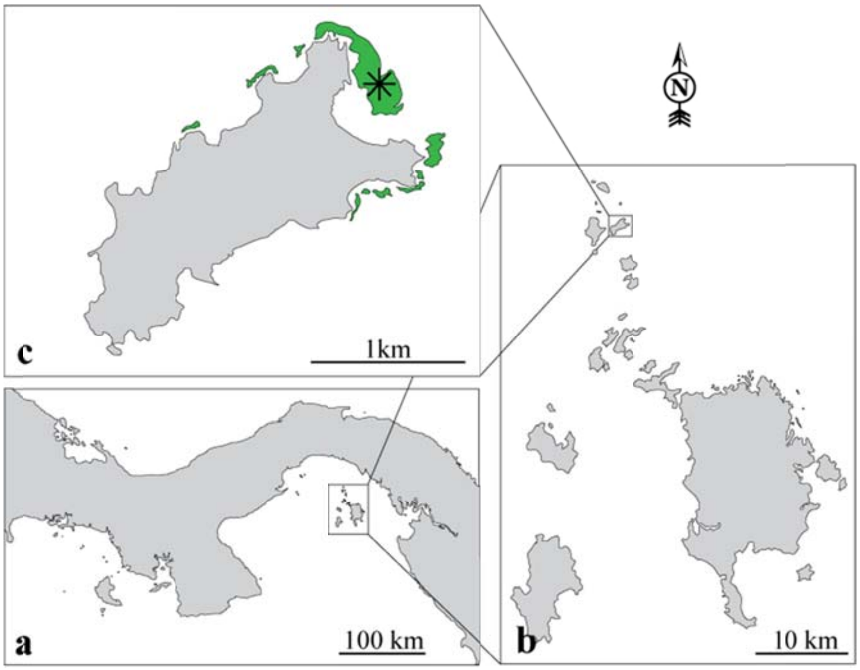

Figure 2.1. a, Panamá; b, Pearl Islands; c, Isla Contadora with reef formations in green, Playa Larga Reef denoted with a star.

Habitat map

Pocilloporid reefs in the Gulf of Panamá contain contiguous zones of similar coral cover and framework composition. These zones form discrete boundaries, making it possible to identify and map their location and shape. A total of four zones were recognized. Three zones consisted of consolidated frameworks: Low Degradation Framework (LDF), >80% coral cover; Medium Degradation Framework (MDF), 20-80% coral cover; Low Degradation Framework (LDF), <20% coral cover; and one of unconsolidated rubble surrounding the reef framework. The margins of zone formations, greater than 10 m diameter, were logged with a handheld Garmin GPSMAP76S (2,975 waypoints) and plotted in ArcGIS. Waypoints were connected in ArcGIS in order to create polygons of reef zones. Using Hawth's Analysis Tools v. 3.27, random sampling points were placed within each zone.

Sampling

The position of each random point was located in the field with GPS and a 1 m^2 quadrat was placed at each site. Quadrats that were not within the desired zone (due to inaccuracies of the GPS) were moved to the nearest area of correct benthic composition. Five 0.25 m^2 photoquadrats were taken, one in the center of the site quadrat as well as one within each 0.25 m^2 corner. Sampling of communities associated with live and dead coral substrates was conducted between October 17 and November 21, 2008. The number of samples and methodologies used to collect dead coral substrates are given in Figure 2.2 and described below.

Zone	LDF	MDF	HDF	Rubble
Live coral	n=24	n=25	n=20	n=45
Dead coral	n=20	n=25	n=19	n=47
Method	Core	Hand	Hand	Scoop

Figure 2.2. The number of samples collected for live and dead coral substrate within each zone. “Method” refers to how dead coral substrates were sampled from the reef.

Live coral

A representative *Pocillopora damicornis* colony, close to the center of the quadrat, was enclosed in a plastic bag and brought to the surface. In areas of contiguous coral cover, it was often impossible to completely surround a colony with the plastic bag while it was still in growth position. Fragments of the sampled coral were removed and placed quickly in the bag while underwater. Because of the cryptic nature of the communities sampled, few animals swam away from their live-coral substrates during sampling. If associates were observed to escape, the sample was returned to the sampling site and not included in analysis. Colonies were defaunated over 2 mm mesh using forceps and saltwater flushing. For corals large enough to render the use of forceps impractical, it was necessary to fragment the colony. All collected metazoans were preserved in 70% EtOH for further identification and analysis. Living corals and coral fragments were returned to the reef.

Dead coral (frameworks)

Due to differences in substrate structure across the four reef zones, it was necessary to employ different methodologies to sample communities associated with dead coral materials (Figure 2.2). Motile cryptic metazoans were again removed using forceps and flushing over a 2 mm mesh screen. All collected organisms were preserved in 70% EtOH. After cryptic organisms were removed, the skeletal volume of each dead coral sample was measured. Buoyant weights were obtained by suspending each sample in seawater (to minimize the mortality of minute sessile biota). Buoyant weight was subtracted from aerial weight and the volume of the water displaced by the submerged skeleton was calculated using the specific gravity of the water (measured by refractometer).

Rubble

The margins of a 0.25 m^2 area in the center of each quadrat were cleared and rubble was removed down to the coarse sand layer. Living corals within this area were relocated to outside the margins of the quadrat. A flexible mesh sheet was attached to the top of a ~0.5 m wide shovel and a flap of excess mesh was left along the anterior margin. Rubble within the 0.25 m^2 area was quickly collected into the scoop and the mesh was folded over the entrance to prevent the escape of sampled animals. Upon collection, rubble was emptied into a plastic bag underwater and the sealed bag was brought to the surface for further analysis.

High/medium degradation framework

Living coral was removed from a 0.125 m^2 section of the quadrat. Habitat depth, defined as the distance from the sediment/framework interface to the epibenthic framework surface, was measured using a ruler. All dead framework materials within the 0.125 m^2 were removed by hand and quickly sealed within a plastic bag. Those few organisms that were observed to escape were noted.

Low degradation framework

The presence of reef framework structures in growth position and the thickness of the cryptic habitat (up to 85 cm) necessitated a minimally invasive methodology that could sample deep within the framework. The high porosity and weak interdigitating structure of the carbonate allowed for the quick penetration of a core in order to capture both frameworks and framework-associated organisms. Living coral was removed from the site to be cored and a three cm diameter aluminum core was hammered through the reef framework and into the fine sand below. The top of each core was capped, sealed with electrical tape underwater, and the depth of the core was measured. The combination of a top cap and bottom sediment plug sealed the reef carbonates within the core during removal. Once the core was free of the framework, the bottom was immediately capped and sealed with electrical tape. Cores were brought to the surface and extruded. Fine sediments and framework materials were separated. The volume of fine sediments obtained in the core was measured using a graduated cylinder. The depth of sediments cored was calculated from their volume divided by the surface area of the core. Calculated sediment depth was subtracted from the core depth to determine habitable framework depth.

Sample processing

Preserved specimens were separated into vials and identified to the lowest possible taxonomic level. Specimen identification was facilitated through the creation of a photographic species database, containing descriptions and images of important/distinguishing morphological features. Taxonomists (listed in the acknowledgements) were consulted. In many cases high-resolution digital images were sufficient for identification. For smaller taxa with less distinguishable morphologies, it was necessary to ship voucher specimens to the appropriate taxonomists in order to make or confirm identifications.

Fragmentation of several more-fragile taxa occurred and effort was made to avoid double-counting specimens. Accordingly, the following criteria for determination of an individual was applied: Annelida (Polychaeta), presence of prostomium and mouthparts; Arthropoda (Crustacea), presence of head, including rostrum and one or more eyestalks; Chordata, presence of complete body; Echinodermata (Asteroidea), presence of disc; Echinodermata (Echinoidea), majority of test present; Echinodermata (Holothuroidea), mouth present; Echinodermata (Ophiuroidea), more than half of disc present; Echiura, presence of prostomium; Mollusca (Bivalvia), presence of two valves; Mollusca (Cephalopoda), presence of complete individual; Mollusca (Caenogastropoda, Patellogastropoda, Vetigastropoda), presence of a shell and body tissues; Mollusca (Heterobranchia), whole individual present; Platyhelminthes (Polycladida), more than half of body present; Sipuncula, presence of anal shield or introvert. Because abandoned gastropod shells may be occupied by a variety of non-molluscan species, it was necessary to closely examine each shell to determine the presence/identity of its occupants. Those specimens with significant fouling on their aperture, holes in the body whorl, an absence of an otherwise conspicuous operculum, or those where pagurid chelae were observed within the aperture, were broken apart for further identification. Species with translucent shells were examined over a bright light and those individuals with abnormal internal body morphologies were removed from their shells for closer examination.

The abundances of individuals within sample vials (unique identification and sample site) were transformed into a species-sample matrix using Matlab routines. Organisms which were only identifiable to broad taxonomic groupings inclusive of other more finely identified specimens (e.g. Caridea spp. inclusive of *Alpheus lottini*) were eliminated from further analysis of richness. All remaining taxa are herein referred to as operational taxonomic units (OTUs).

Benthic composition

The benthic composition of each quadrat was determined using the Coral Point Count with Excel Extension (CPCe) software package (Kohler & Gill 2006). Twenty points were applied randomly to the 0.25 m^2 center image of each quadrat and the substrate under each point was recorded (*Pocillopora*, *Psammocora*, *Porites*, *Pavona,* sediment, bare reef rock, crustose coralline algae, filamentous algae, other. The percent cover from each sample site within each zone (LDF, n = 24; MDF, n = 22; HDF, n = 20; rubble, n = 46) was averaged in order to determine the mean benthic composition of each zone.

Richness estimators

OTU-sample matrices were analyzed using the EstimateS software package (Colwell 2009). Individual-based (Coleman) rarefaction was conducted for OTUs associated with living corals and dead coral substrates in order to standardize sample size. To estimate species richness at infinite sample size, asymptotic models were fitted to the plots using the GraphPad Prism v5.03 software package. Four convex models (Monod, Equation 2.1; negative exponential, Equation 2.2; asymptotic regression, Equation 2.3; rational function, Equation 2.4) and two sigmoidal models (Chapman-Richards, Equation 2.5; cumulative Weibull, Equation 2.6). The use and efficacy of these models are reviewed by Flather (1996), Tjørve (2003) and Thompson et al. (2003).

Equation 2.1. Monod model

$$y = a\left(\frac{x}{b + x}\right)$$

Equation 2.2. Negative exponential model

$$y = a(1 - e^{-bx})$$

Equation 2.3. Asymptotic regression model

$$y = a - bc^{-x}$$

Equation 2.4. Rational function model

$$y = \frac{a + bx}{1 + cx}$$

Equation 2.5. Chapman-Richards model

$$y = a(1 - e^{-bx})^{c}$$

Equation 2.6. Cumulative Weibull distribution model

$$y = a\left(1 - e^{-bx^{c}}\right)$$

To compare the richness of cryptic metazoans associated with dead coral substrates across the four reef zones, both individual (Coleman) and sample-based (Mao Tau) rarefaction curves were plotted and fitted with the aforementioned models (Equations 2.1-2.6). Nonparametric estimators of total species richness within each zone were calculated. These included abundance-based coverage estimators (ACE, Equation 2.7), incidence-based coverage estimators (ICE, Equation 2.8), Chao1 (Equation 2.9) and Chao2 (Equation 2.10) estimators (classic methodologies), first- (Equation 2.11) and second-order jackknife estimators (Equation 2.12), and bootstrap estimators (Equation 2.13). For a review of these estimators see Colwell & Coddington (1994), Chazdon et al. (1998), Chao (2004), and Colwell et al. (2004). Finally, Michaelis-Menten (MM) richness estimators were computed two ways (MMMeans and MMRuns, Colwell 2009) and plotted for each zone. With MMMeans, the MM richness estimator is calculated once for each additional number of samples, based on the number of species (MaoTau). MMRuns calculates the mean of a large number of MM estimates from randomly chosen samples at each incrementally increasing number of within zone samples (1 to Total).

Equation 2.7. Abundance-based coverage estimator (ACE). S_{abund}, number of species with more than 10 individuals; S_{rare}, number of species with 10 or fewer individuals; S_{obs}, number of total species observed; F_i, number of species with a total of i individuals across all samples.

$$(a) S_{ace} = S_{abund} + \frac{S_{rare}}{\mathrm{C_{ace}}} + \frac{F_1}{\mathrm{C_{ace}}} \gamma_{ace}^2$$

$$(b)\ S_{obs} = S_{rare} + S_{abund}$$

$$(c) C_{ace} = 1 - \frac{F_1}{N_{rare}}$$

$$(d)\ N_{rare} = \sum_{i=1}^{10} iF_i$$

$$(e)\ \gamma_{ace}^2 = \max\left[\frac{\mathrm{S_{rare}}}{\mathrm{C_{ace}}} \frac{\sum_{\mathrm{i=1}}^{10} \mathrm{i(i-1)F_i}}{(\mathrm{N_{rare}})(\mathrm{N_{rare}} - 1)} - 1{,}0\right]$$

Equation 2.8. Incidence-based coverage estimator (ICE). S_{freq}, number of species found in more than 10 samples; S_{infr}, number of of species found in 10 or fewer samples; Q_j, number of species occurring in j samples.

$$(a) S_{ice} = S_{freq} + \frac{S_{infr}}{\mathrm{C_{ice}}} + \frac{Q_1}{\mathrm{C_{ice}}} \gamma_{ice}^2$$

$$(b)\ S_{obs} = S_{\mathrm{inf}r} + S_{freq}$$

$$(c) C_{ace} = 1 - \frac{Q_1}{N_{infr}}$$

$$(d)\ N_{\mathrm{inf}r} = \sum_{i=1}^{10} jQ_{ij}$$

$$(e)\ \gamma_{ace}^2 = \max\left[\frac{\mathrm{S_{infr}}}{\mathrm{C_{ice}}} \frac{\mathrm{m}_{infr}}{\mathrm{m}_{infr-1}} \frac{\sum_{\mathrm{j=1}}^{10} \mathrm{j(j-1)Q_j}}{\left(\mathrm{N}_{infr}\right)^2} - 1{,}0\right]$$

Equation 2.9. Chao 1 estimator. S_{obs}, number of total species observed; F_1, number of species represented by one individual across all samples; F_2, number of species represented by two individuals across all samples (doubletons).

$$\hat{S}_{Chao1} = S_{obs} + \frac{F_1^2}{2F_2}$$

Equation 2.10. Chao 2 estimator. S_{obs}, number of total species observed; Q_1, number of species found in only one sample; Q_2, number of species found in only two samples.

$$\hat{S}_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$$

Equation 2.11. First-order jackknife estimator. S_{obs}, number of total species observed; Q_1, number of species found in only one sample; m, number of samples.

$$S_{jack1} = S_{obs} + Q_1 \frac{m-1}{m}$$

Equation 2.12. Second-order jackknife estimator. S_{obs}, number of total species observed; Q_1, number of species found in only one sample; Q_2, number of species found in only two samples; m, number of samples.

$$S_{jack2} = S_{obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right]$$

Equation 2.13. Bootstrap estimator. S_{obs}, number of total species observed; P_k, number of samples containing species k, divided by the total number of samples (m).

$$S_{boot} = S_{obs} + \sum_{k=1}^{S_{obs}} (1-P_k)^m$$

Results

Habitat map

Four zones were identified and mapped. An elongate zone of LDF was found to approximately parallel the shore (Figure 2.3b). A shallow reef flat of intermediate coral cover (MDF) was present on the protected leeward margin (Figure 2.3c). Large, low coral cover patches (FL, Figure 2.3d) were present throughout the MDF zone and it is likely that the limited coral growth and flat topography of this area is due to mortality associated with areal exposure during extreme low tides (Eakin & Glynn 1996). Coral rubble was found surrounding the reef and was especially prevalent on the fore-reef and LDF margins (Figure 2.3e). Corals present within this zone were largely unattached coralliths sensu Glynn (1974). The mean percent coral cover within each zone corresponded to the original guidelines for zone delineation; however, the LDF zone contained slightly less than 80% live coral (Figure 2.4, Table 2.1). Mean habitable framework depth was significantly higher (Tukey's test, $p < 0.05$) in the LDF zone ($\bar{x} = 0.60$ m) than in the MDF ($\bar{x} = 0.15$ m) and HDF ($\bar{x} = 0.12$ m) zones, which were not significantly different. Frameworks in the HDF zone, however, were significantly more eroded than in the MDF and LDF zones, with a mean percent porosity of 74.6 compared with 93.5 and 91.7 percent porosity, MDF and LDF respectively. Depths and porosities were not recorded in the rubble zone, which was approximately planar, consisting of a thin veneer of dead coral fragments overlying fine sediment.

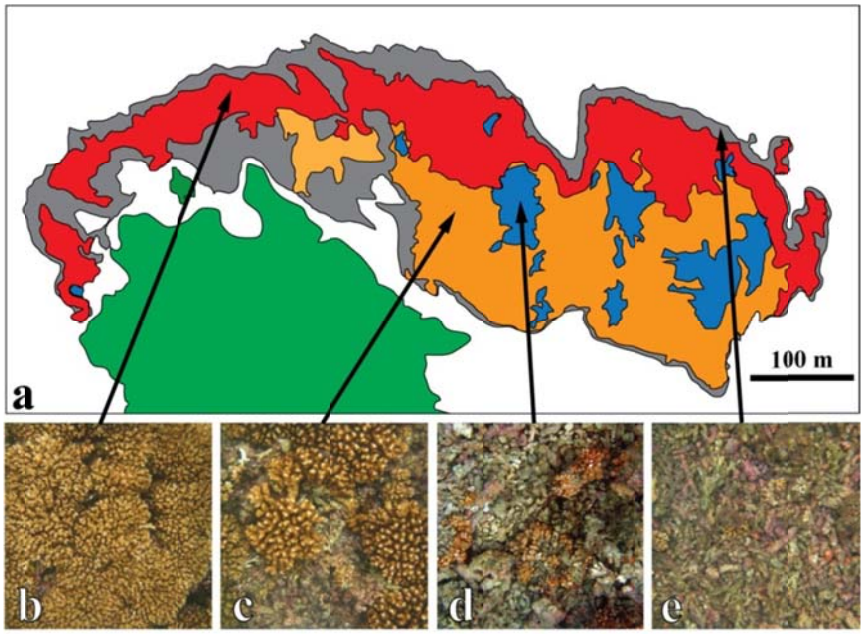

Figure 2.3. a, Playa Larga Reef; b, low degradation framework (LDF, red); c, medium degradation framework (MDF, orange) ; d, high degradation framework (HDF, blue); e, rubble (gray).

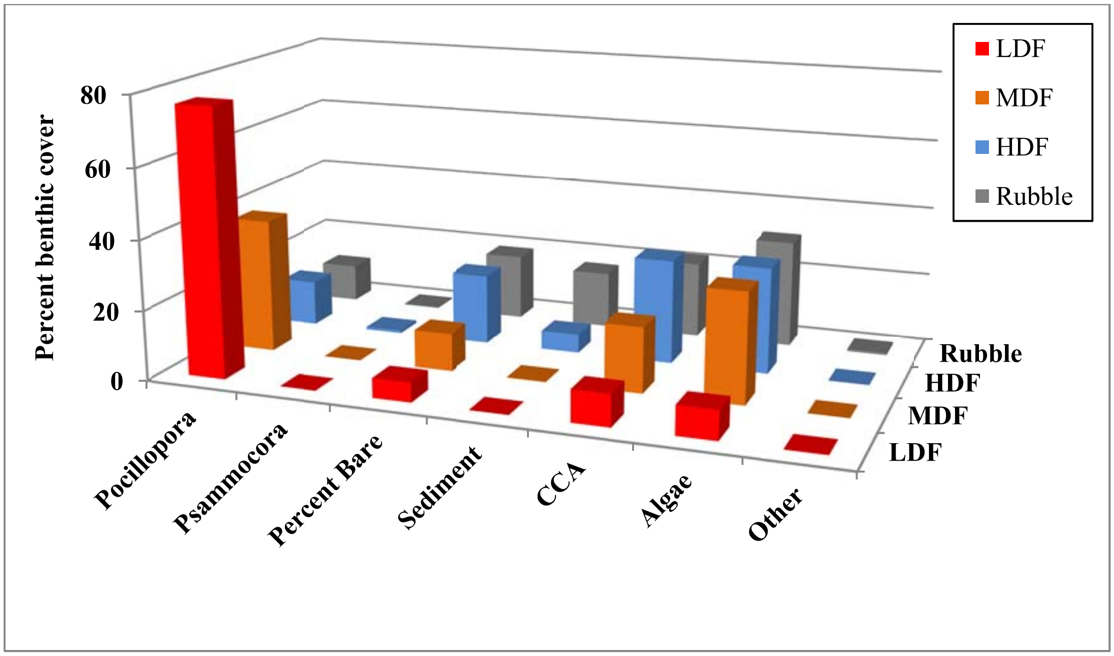

Figure 2.4. Mean percent benthic cover within the four zones of the Playa Larga Reef.

Table 2.1. Area of zones present at Playa Larga Reef. ± 95% confidence interval in parentheses. Note: one HDF point removed due to anomalous depth and void space values.

	Habitat								**Framework**	
	Area (m^2)	**Percent *Pocillopora***	**Percent *Psammocor***	**Percent Bare**	**Percent Sediment**	**Percent CCA**	**Percent Algae**	**Percent Other**	**Depth (m)**	**Percent Void space**
LDF	36324	76.67 (9.21)	0	5.63 (5.07)	0	9.17 (3.87)	8.33 (5.69)	0.21 (0.43)	0.60 (0.08)	91.7 (0.92)
MDF	41433	38.41 (9.76)	0	10.91 (6.07)	0.23 (0.47)	18.86 (6.52)	31.59 (7.99)	0	0.15 (0.03)	93.5 (1.80)
HDF	11089	13 (8.23)	0.75 (1.15)	20.25 (8.33)	5.5 (6.21)	30 (9.96)	30.5 (11.46)	0	0.12 (0.04)	75.1 (5.44)
Rubble	31586	10.87 (4.31)	0.33 (0.49)	19.02 (4.89)	16.3 (6.72)	21.96 (5.35)	30.87 (6.59)	0.65 (0.97)	Na Na	Na Na

Community composition

A total of 289 OTUs were identified, belonging to eight different phyla (Table 2.2, see Appendix 1 for the classification scheme employed). Mollusca was the richest phylum, comprising 132 OTUs, 88 of which were identified to the species level. A total of 77, 32, and 24 OTUs were identified belonging to Arthropoda, Annelida, and Echinodermata, respectively. Comparisons of richness across phyla are complicated by differences in identification effort. It is expected that morphologically cryptic species are present within multiple phyla and that the observed number of OTUs are indicative of their relative real-word diversity. However, OTU counts within Annelida and Echiura most likely under-represent true richness more than other phyla.

Arthropoda was the most abundant phylum associated with both living and dead coral substrates, accounting for 84.33% and 57.53% of individuals, respectively (Figure 2.5). Accordingly, with respect to individuals, all other phyla were proportionally more important on dead coral substrates than on live corals. The relative importance of each phylum was identical for living and dead coral (Arthropoda > Mollusca > Echinodermata > Annelida > Sipuncula > Platyhelminthes > Echiura > Chordata), with the single exception of Mollusca and Echinodermata associated with live corals, which were switched yet only differed by 0.01%.

Table 2.2. Number of identified taxonomic categories within each phylum. OTUs represents operational taxonomic units.

Phylum	Class	Order	Family	Genus	Species	OTUs
Annelida	1	0	16	18	6	32
Arthropoda	1	6	30	43	46	77
Chordata	1	2	5	2	2	5
Echinodermata	4	8	15	14	16	24
Echiura	0	0	0	0	0	1
Mollusca	4	8	49	81	88	132
Platyhelminthes	1	1	0	0	0	11
Sipuncula	2	3	4	3	3	7
TOTAL	14	28	119	161	159	289

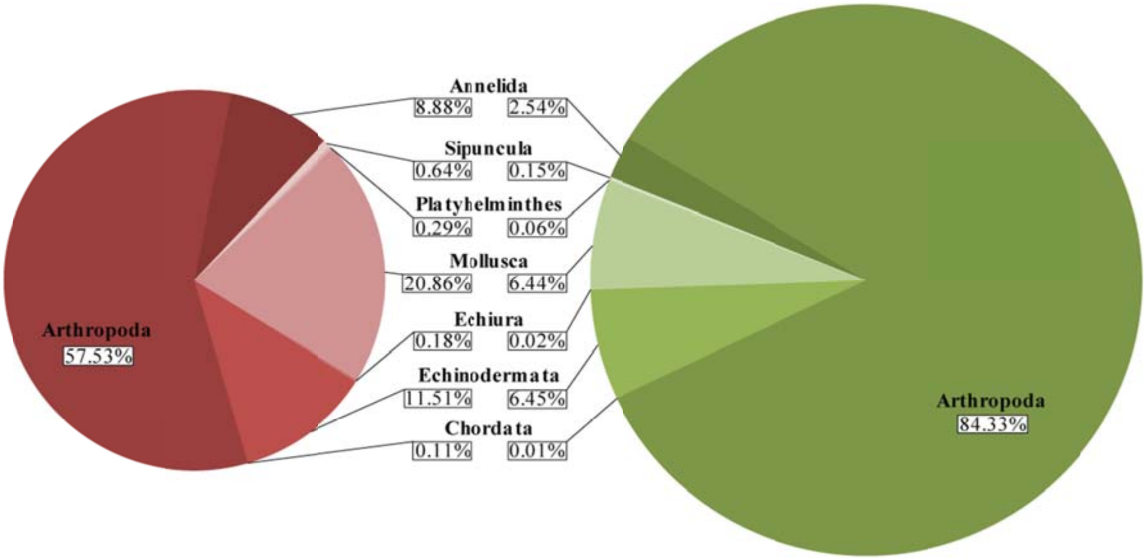

Figure 2.5. Relative abundance of individuals within a given phylum associated with dead (red) and living coral (green). The areas of the pie charts are proportional to the total density of individuals associated with a given substrate.

Relatively few OTUs were found to have distributions favoring live coral substrates (Appendix 2). However, many of those OTUs associated with living coral displayed greater densities (per volume substrate) than those collected from dead frameworks. Especially prevalent live coral associates included the decapod crustaceans *Fennera chacei*, *Harpiliopsis spinigera*, *Alpheus lottini*, and *Trapezia* spp. (Appendix 2a). All are previously known to be obligate symbionts of *Pocillopora*. Prominent associates of both live and dead coral substrates included the decapods *Psidia magdalenensis*, *Petrolisthes haigae*, *Thor* cf. *algicola*, *Teleophrys cristulipes*, *Heteractaea lunata*, *Pagurus* sp. A, *Palaemonella* spp., as well as the ophiuroids *Ophiothrix spiculata* and *Ophiactis savignyi* (Appendix 2a,b). Though less abundant than live coral associates as well as more cosmopolitan taxa, notable obligate dead coral associates included the decapods *Lophopanopeus maculatus*, *Alpheus* cf. *normanni*, *Pilumnus pygmaeus*, the stomatopod *Neogonodactylus zacae*, and the chiton *Acanthochitona hirudiniformis* (Appendix 2f).

Community richness

Live vs. dead coral substrates

Individual-based rarefaction revealed greater numbers of OTUs associated with dead coral substrates than live coral colonies (Figure 2.6). The differences between the minimum and maximum asymptotic OTU richness estimate was great for both dead (108.8 OTUs) and live coral communities (107.0 OTUs), but there was no overlap between the live vs. dead models. With live coral communities, the cumulative Weibull model gave the highest richness estimate followed by the Chapman-Richards, rational function, Monod, asymptotic regression, and negative exponential models, in order of decreasing asymptotic OTU value. The relative order of asymptotes as predicted by models fitted to dead coral associated communities was identical with the exception of the Chapman-Richards and rational function models, which were switched. All models, with the exception of the Monod and negative exponential, had R^2 values greater than 0.99 when fitted to communities associated with both substrates.

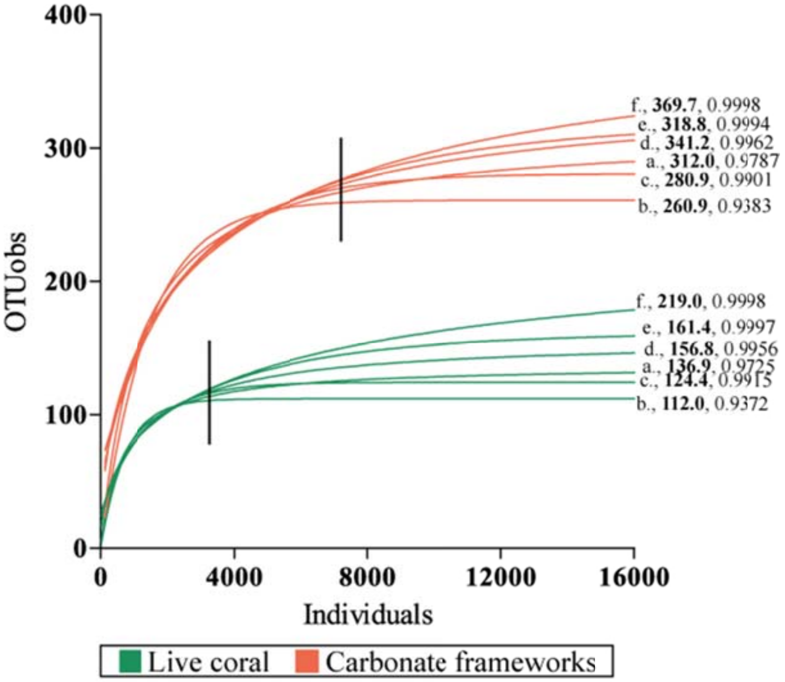

Figure 2.6. Individual-based rarefaction (Coleman) curves of communities associated with live coral (green) and dead coral substrates (red), fitted with a, Monod model; b, negative exponential model; c, asymptotic regression model; d, rational function model; e, Chapman-Richards model; f, cumulative Weibull distribution model. Bold numbers following model letters represent the asymptote of the respective function. The R^2 value of each fitted function is to the right of the asymptote. Vertical lines represent total individuals collected. Values to the right are extrapolations.

Inter-zone differences in the richness of dead coral associated cryptofauna

All methods of diversity estimation, including both individual-based (Figure 2.7; Table 2.3) and sample-based rarefaction fitted with asymptotic functions (Figure 2.8; Table 2.4), nonparametric estimators (Figure 2.9; Table 2.5), and MM richness estimators (Figure 2.10), consistently applied to dead coral communitys collected from different zones, showed a progressive decline in community richness from Rubble to HDF to MDF and finally to LDF, with the single exception of the MMRuns (Figure 2.10b). Across zones, cryptofauna diversity is negatively correlated with percent coral cover and positively correlated with framework degradation. The most depauperate zone (LDF) is characterized by large contiguous stands of living *Pocillopora*, wich cover deep frameworks in growth position. Higher levels of diversity are found in the MDF zone, which has shallower eroded frameworks and lower amounts of coral due to periodic mortality from aerial exposure. Coelobite richness is higher still in HDF patches, which are even more eroded and have even lower cover. Finally, cryptofauna richness is highest in the most disturbed reef environment, where rubble fragments from dead and broken corals accumulate.

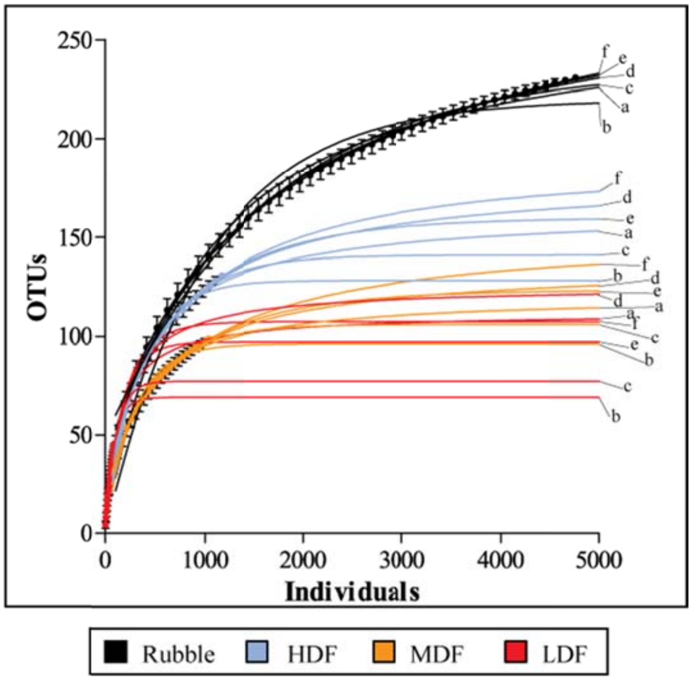

Figure 2.7. Individual-based rarefaction (Coleman curves) of communities associated with coral rubble and reef framework structures. Rubble (black), HDF (blue), MDF (orange), and LDF (red) zones, fitted with a, Monod model; b, negative exponential model; c, asymptotic regression model; d, rational function model; e, Chapman-Richards model; f, cumulative Weibull distribution model. Error bars, SD around the mean.

Table 2.3. Asymptotic estimated total species richness for zones as projected by six types of functions fitted through individual-based rarefaction (Coleman curves). R^2 value in parentheses.

	Rubble		HDF		MDF		LDF	
Monod	265.9	(0.9855)	163.2	(0.9905)	120.7	(0.9866)	111.7	(0.9994)
Negative exponential	219.7	(0.9526)	128.2	(0.9709)	95.79	(0.9634)	68.67	(0.9989)
Asymptotic regression	235.7	(0.9942)	141.0	(0.9970)	105.9	(0.9966)	76.93	(0.9998)
Rational function	289.0	(0.9985)	182.0	(0.9990)	136.4	(0.9988)	125.4	(0.9999)
Chapman-Richards	259.4	(0.9997)	159.6	(0.9996)	123.3	(0.9998)	96.84	(1.0000)
Weibull distribution	289.3	(0.9999)	180.6	(0.9998)	144.6	(0.9999)	107.5	(1.0000)

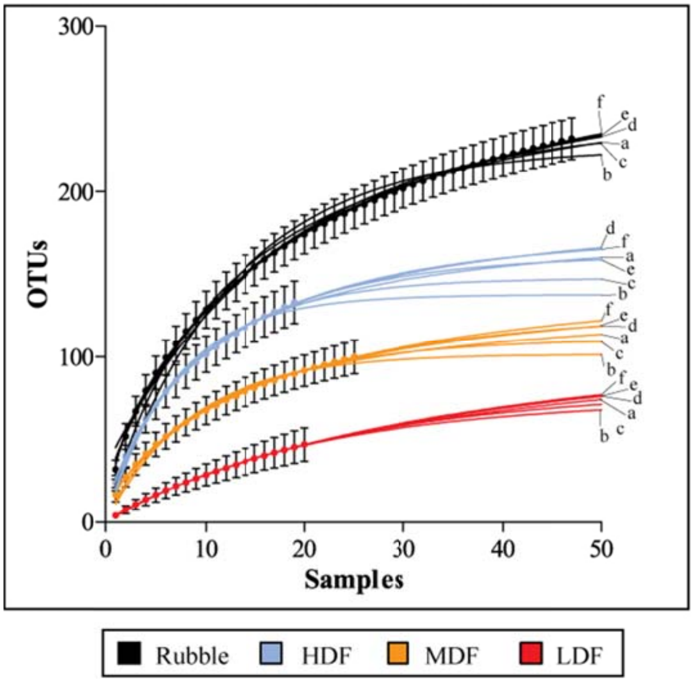

Figure 2.8. Sample-based rarefaction (Mao Tau) curves of communities associated with dead coral substrates in the rubble (black), HDF (blue), MDF (orange), and LDF (red) zones, fitted with a, Monod model; b, negative exponential model; c, asymptotic regression model; d, rational function model; e, Chapman-Richards model; f, cumulative Weibull distribution model. Error bars show ± 95% confidence interval around the mean.

Table 2.4. Asymptotic estimated total species richness for zones as projected by six types of functions fitted through sample-based rarefaction (Mao Tau). R^2 value in parentheses.

	Rubble		**HDF**		**MDF**		**LDF**	
Monod	284.9	(0.9935)	185.8	(0.9975)	135.3	(0.9946)	122.4	(0.9997)
Negative exponential	226.2	(0.9764)	137.6	(0.9906)	101.8	(0.9847)	74.2	(0.9994)
Asymptotic regression	240.7	(0.9964)	147.7	(0.9981)	111.1	(0.9978)	80.7	(0.9999)
Rational function	304.3	(0.9989)	198.3	(0.9995)	149.0	(0.9993)	132.4	(0.9999)
Chapman-Richards	263.1	(0.9996)	161.9	(0.9996)	126.9	(0.9998)	95.2	(1.0000)
Weibull distribution	286.2	(0.9999)	174.2	(0.9998)	142.0	(0.9999)	102.1	(1.0000)

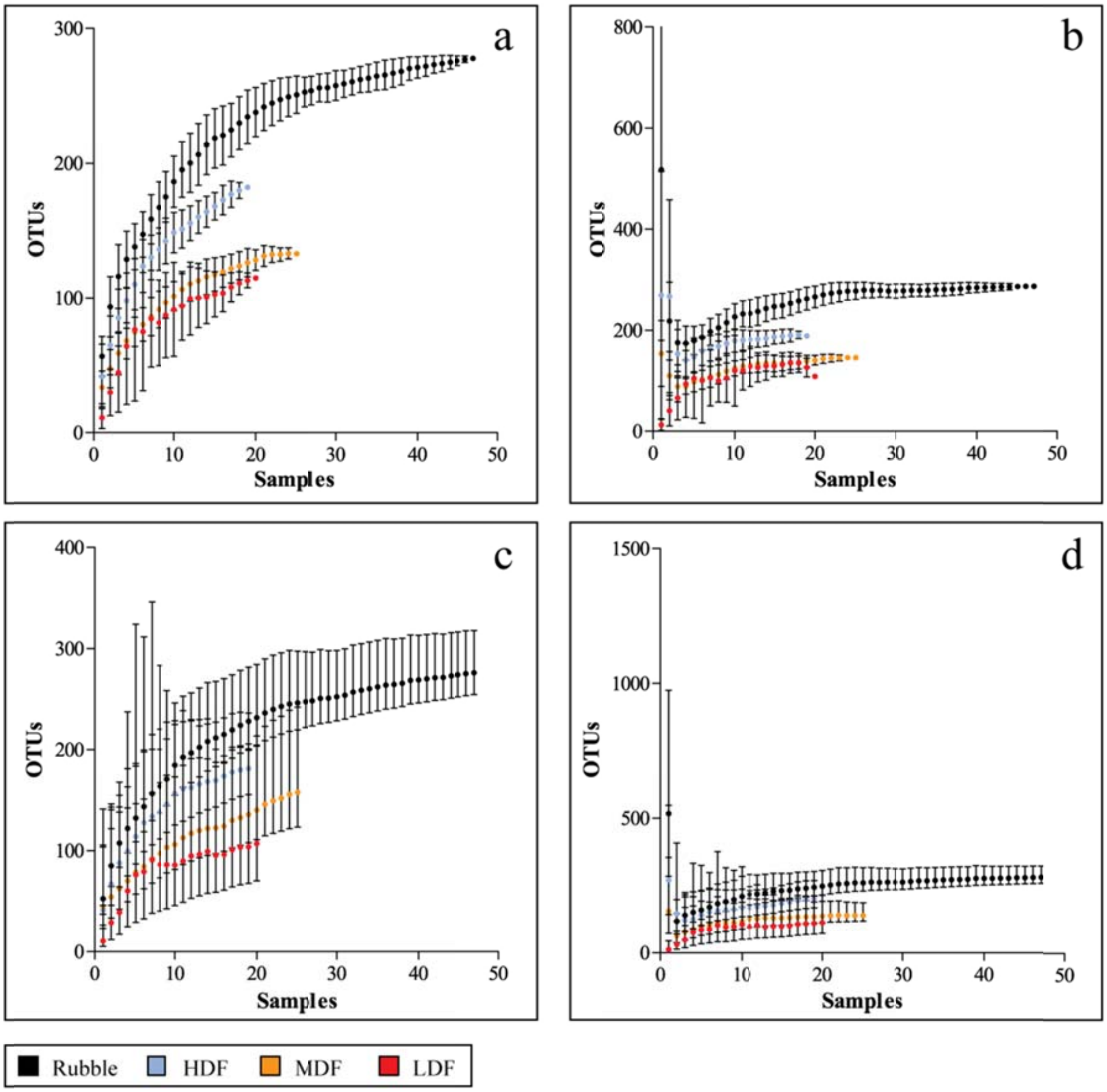

Figure 2.9. Nonparametric richness estimators of dead coral associated communities by zone. a., ACE; b., ICE; c., Chao1; d., Chao2; e., Jack1; f., Jack2; g., Bootstrap. All error bars are ± 1 standard deviations, except for those in Chao1(d) and Chao2(e) are ± 95% confidence intervals.

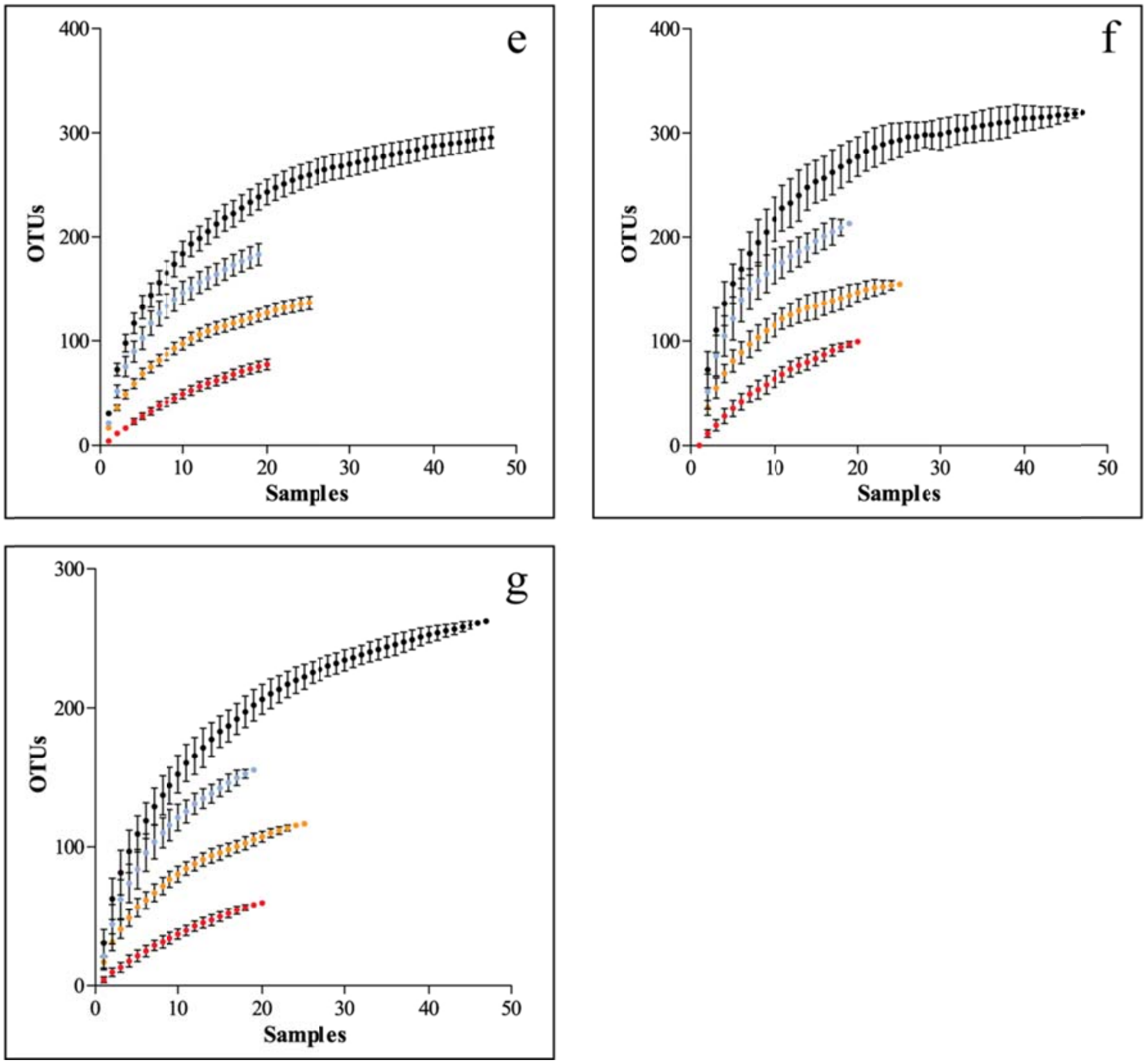

Figure 2.9. *Cont.*

Table 2.5. Nonparametric estimates of total species richness and actual species observed within each zone.

	Rubble	**HDF**	**MDF**	**LDF**
ACE	277.78	182.2	132.9	114.9
ICE	287.15	189.1	145.9	108.6
Chao1 [a]	276.0 (317.8, 254.6)	181.4 (236.3, 155.7)	157.8 (242.2, 123.4)	107.1 (203.8, 70.0)
Chao2 [a]	280.5 (322.4, 258.0)	199.9 (268.3, 166.1)	138.0 (185.1, 117.0)	111.0 (212.7, 71.7)
Jack1 [b]	295.6 (10.1)	183.2 (10.4)	136.5 (6.2)	77.4 (5.1)
Jack2	319.5	212.9	154.7	99.4
Bootstrap	262.4	155.3	116.6	59.6
Sobs	227	133	100	47

[a] Parens are upper and lower 95% confidence intervals respectively

[b] Parens are standard deviation.

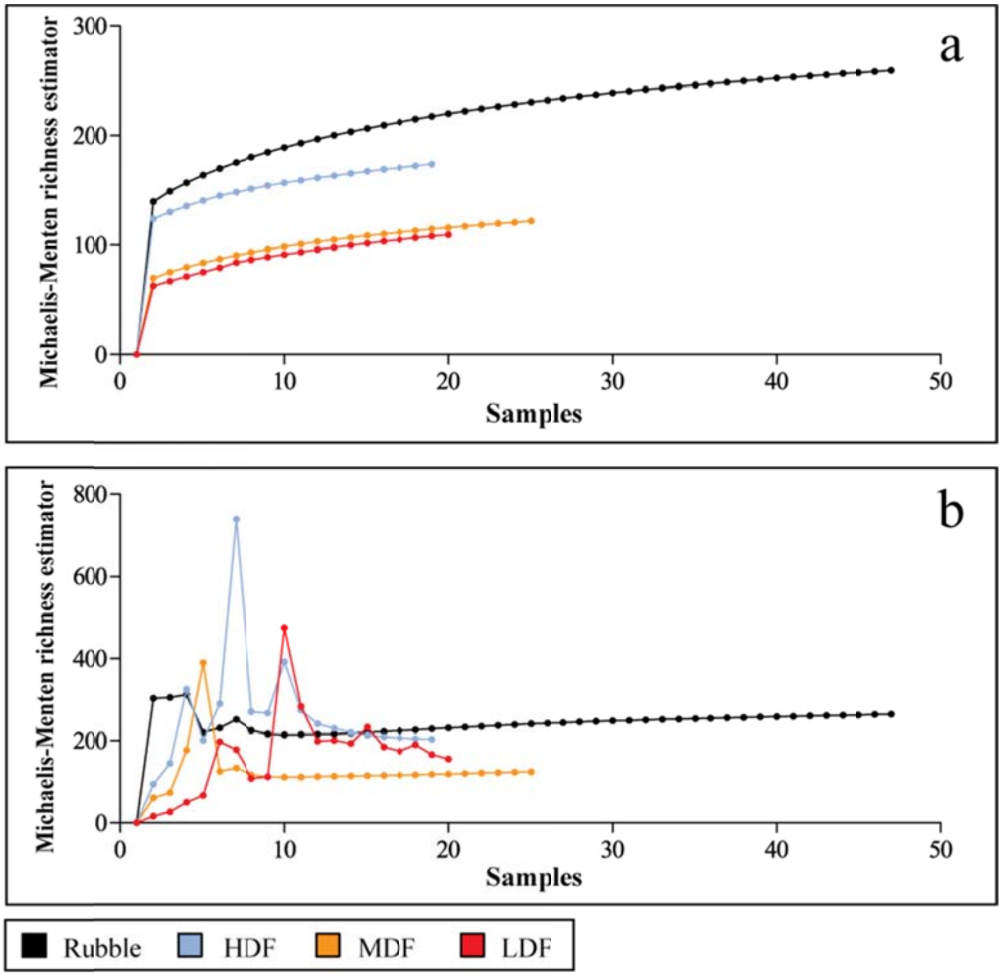

Figure 2.10. Michaelis-Menten richness estimators of communities associated with dead coral substrates by zone. a., MMMeans, estimators computed once for each successive number of species (Mao Tau) and samples; b., MMRuns, mean of estimators computed for multiple randomizations of the indicated number of samples.

Discussion

Live vs. dead coral substrates

Cryptofauna communities associated with living *Pocillopora damicornis* are less rich than those associated with dead coral (framework) materials (Figure 2.6). This is consistent with the findings of Coles (1980) who observed that nonsymbiotic decapod cryptofauna are more diverse than obligate *Pocillopora meandrina* associates. Additionally, Enochs and Hockensmith (2008) observed that communities associated with *P. damicornis* were more dissimilar following coral mortality, suggesting that live coral habitats support less species-rich cryptofauna.

This pattern of higher diversity associated with dead coral substrates is not surprising considering the number and variety of defensive mechanisms employed by corals (Lang & Chornesky 1990). Living coral tissues contain specialized stinging cells (cnidocytes) and shed large quantities of mucus, both of which may act to deter potentially sheltering organisms (Kirsteuer 1969). Those animals that do thrive within living corals often exhibit morphologies and behaviors which minimize and even capitalize on their hosts' defenses (Patton 1974, 1994). Some species are known to directly feed on coral mucus (Knudsen 1967) as well as coral tissues (Rotjan & Lewis 2008). Many cryptic coral symbionts are crustaceans, with chitinous exoskeletons that may reduce sensitivity to nematocyst stings. They exhibit adapted mouthparts for feeding in coral environments and walking legs ideal for grasping coral surfaces (Bruce 1976).

The higher community richness associated with dead coral may be explained by greater niche diversity. While living pocilloporid corals provide protection and food (tissue, mucus, fat-bodies, gametes), dead coral is colonized by a myriad of sessile flora and fauna which are in turn utilized as shelter and nutriment by diverse motile cryptofauna. Algae and encrusting fauna may thrive on bare substrates, thereby encouraging occupation by herbivores and grazing carnivores, respectively. Sediments that are normally cleared by living coral tissues can accumulate on dead coral surfaces, providing food for deposit feeders (Preston & Doherty 1994). Dead coral susbtrates are more often colonized by endolithic bioeroders which may increase substrate complexity over short time periods, providing structurally diverse habitats for nestling fauna

(McCloskey 1970; Moran & Reaka-Kudla 1991). Therefore, “diversity begets diversity” in that a greater number of food sources and shelter types encourage more diverse coelobite communities.

It is likely that this study underestimates differences in species richness between live and dead coral-associated communities. As *Pocillopora* colonies grow, their bases, interstices, and sheltered undersurfaces die, thereby creating habitat without living coral tissues. These hidden dead carbonate surfaces are known to be occupied by a variety of organisms including anemones, holothurians, polychaetes, and sipunculans (Abele & Patton 1976). Additionally, many *Pocillopora* colonies experience partial mortality on their surfaces, which subsequently become overgrown by other organisms, including algae and sponges. Motile cryptofauna occupying these surfaces may not be able to tolerate living coral tissues and therefore should not be considered live coral associates. Because coral colonies were sampled in their entirety, all of these organisms were included in the live coral rarefaction. Had organisms associated with dead colony surfaces been removed, it is likely that the live coral cryptofauna would have been more impoverished (i.e., depressed asymptotic coral associated richness, Figure 2.6). Accordingly, it is expected that there would be reduced overlap in OTU substrate preferences as observed in Appendix 2a,b,c.

Caley et al. (2001) observed a decrease in the diversity of cryptofauna associates following experimentally induced mortality of host *Stylophora pistillata* colonies. Their findings suggest that coral mortality is detrimental to biodiversity. This is likely true over short time scales (two months in their study), especially when considering symbiotic taxa. Immediately following coral mortality, obligate symbionts would die due to the cessation of their food supply and neutralization of their protective coral shelter. Furthermore, cryptically colored associates may become more conspicuous and therefore preyed upon (Coker et al. 2009). However, data herein suggest that over longer time periods (more than a few months), following the establishment of other benthic flora and fauna, coelobite communities become increasingly speciose.

Zone differences

The pattern of increasing OTU richness from LDF to MDF, HDF, and rubble zones is consistent with the predictions of the intermediate disturbance hypothesis (Grime 1973; Connell 1978). Relatively undisturbed areas are characterized by living blankets of monogeneric stands of *Pocillopora,* occupied by an impoverished community of symbiotic cryptofauna. Taxa that would otherwise be able to occupy dead frameworks are excluded due to an effective barrier of living coral tissue, feeding coral polyps, and territorial live coral symbionts. Disturbance creates open spaces that are occupied by a diverse suite of sessile benthic biota and a rich array of cryptic motile associates. At some high level of habitat destruction, coral mortality and bioerosion, it is expected that coral rubble will be broken into fine sediments (course sands to silt) that will negatively affect biodiversity (Bailey-Brock et al. 2007).

Non-parametric estimators may be correlated with sample size at small sample sizes, but it is likely that the number of OTUs observed in this study were sufficiently high to reduce this bias. For instance, Chao estimators are considered to strongly correlate with sample size until the total number of OTUs observed is equal to the square root of two times the actual number of taxa (Colwell & Coddington 1994). In the most poorly sampled zone (LDF), 47 OTUs were collected, corresponding to a strong sample size correlation (according to the aforementioned relationship) if the true OTU richness of the LDF zone is in excess of 1,104 OTUs. In the most heavily sampled zone (Rubble, 227 OTUs) this corresponds to 25,764 OTUs. These numbers are likely greatly in excess of the true number of cryptofauna OTUs present on Playa Larga Reef. Given this, along with the ubiquity of the observed pattern across multiple established sample-standardizing and diversity-estimating methodologies, it is likely that the reported trends are indicative of real-world patterns. Future work should evaulate the applicability of trends reported herein to other reef communities outside of the eastern Pacific.

Implications

Given the frequency of mass bleaching events, disease and predator outbreaks, as well as physical ecosystem destruction, it is important to examine the theoretical effects that widespread coral mortality may have on reef ecosystem biodiversity. Consider a hypothetical “classically healthy” reef ecosystem of high coral cover that experiences complete coral mortality due to some biological or environmental perturbation. Local extinction of obligate symbionts would likely parallel the death of their hosts, possibly displaying a lag of weeks or months. Biodiversity would therefore dip, though not severely due to the relatively depauperate nature of obligate coral symbionts. The majority of cryptofauna species would likely continue to occupy reef substrates and a protracted period of elevated biodiversity is probable. Newly available dead coral substrates would be colonized by an increasingly diverse flora and fauna and thereby elevate species richness. Taphonomic alteration of dead coral substrates could lead to numerous and complex reef crypts, encouraging the prolonged occupation of coelobite communities. Only after erosion has reduced framework complexity to levels too low to provide habitat to nestling taxa would ecosystem richness precipitously plummet (e.g., from rubble to sand and silt).

Parallels with terrestrial forests are striking. In temperate woodlands, a large proportion of species (roughly 20-25%) are saproxylic, meaning that they rely on dead wood for food or shelter (Speight 1989; Siitonen 2001). Such organisms are equivalent to the cryptic reef taxa, sheltering within and burrowing into dead coral carbonates. Managed forests have lower abundances of dead wood and therefore fewer habitats for these cryptic forest taxa. Similarly, continuous stands of living coral with few dead coral habitats have reduced coelobite diversity. Within natural forests, smaller size classes of dead wood are occupied by more diverse communities per unit volume (Schiegg 2001; Heilmann-Clausen & Christensen 2004; Norden et al. 2004), mirroring the higher cryptofauna richness observed in highly eroded reef substrates. Maintenance of dead and rotting wood materials is considered to be crucial in preserving forest biodiversity (Nilsson et al. 2001; Siitonen 2001) and it is likely that dead corals are equally or even more important in reef ecosystems.

Considering that biodiversity has been linked to resistance to invasive species (Stachowicz 1999), long-term ecosystem stability (Kiessling 2005), as well as short term stability and recovery from environmental perturbations (Tilman & Downing 1994), it is important that we adopt coral reef management strategies that support species richness. Metrics of ecosystem health based on percent coral cover are limited at best. Communities associated with areas of 100% living coral are likely less diverse and by extension may be less healthy than those in more heterogeneous reef environments. Intermediate levels of coral mortality provide substrates necessary for diverse and healthy reef communities.

I propose that habitat heterogeneity and substrate structure may be better determinants of biodiversity than live coral cover, in that the bulk of reef biodiversity depends on cryptic habitats within dead frameworks for shelter. Coral cover is important for reef biodiversity in that calcification must exceed erosion in order to maintain reef frameworks and to supply rubble habitats. Recent evidence suggests a long-term (35 year) decline in the structural complexity of Caribbean coral reefs (Alvarez-Filip et al. 2009). If this trajectory is maintained, it may ultimately have devastating consequences for coral reef biodiversity and ecosystem health.

Chapter 3: Coral reef cryptofauna abundance and biomass, live versus dead coral substrates: trophic implications

Coral reef ecosystems contain elevated abundances of metazoans and high biomass relative to surrounding ecosystems. The majority of this biomass is hidden out of site, sheltered within the cracks and cavities of reef frameworks (Ginsburg 1983). These cryptic taxa are known collectively as cryptofauna or coelobites and their members belong to every major reef metazoan group with the exception of Mammalia (Kobluk 1988). A single living coral colony may contain more than 2,000 cryptic individuals belonging to numerous species within the phyla Annelida, Crustacea, Echinodermata, and Sipuncula (Grassle 1973). Within reef rocks, cryptic polychaetes alone may reach abundances of 127,900 m^{-2} and a biomass of 93.4 g m^{-2} dry weight (Brock & Brock 1977). Inside protected damselfish territories, small crustacean and molluscan cryptofauna may exist at densities of more than 5,200 m^{-2} and 570 m^{-2}, respectively (Klumpp et al. 1988).

Coral reefs maintain high biomass despite their location in oligotrophic waters due in part to efficient nutrient capture and recycling. Cryptofauna are of vital importance to these trophic functions and by extension entire reef ecosystems. Suspension feeding coelobites have been observed to capture 0.9 g C m^{-2} d^{-1}, accounting for approximately 22% of gross reef metabolism (Richter et al. 2001). The biomass of one cryptic suspension feeding phylum, Porifera, may in some localities exceed that of all surface suspension feeders by two orders of magnitude (Richter et al. 2001). Echinoids, which are one of the most effective herbivorous grazers within reef ecosystems (Carpenter 1986), often remain cryptic during the day, emerging at night to forage on algal encrusted reef surfaces. Cryptic micrograzing crustaceans, mollusks, and annelids have high grazing rates at local scales, e.g., 2.145 g C m^{-2} d^{-1} inside damselfish territories (Klumpp et al. 1988), and may even reduce algal proliferation on live coral colonies (Coen 1988). Deposit feeding and detritivorous coelobites are instrumental in recycling organic byproducts and decaying matter back into reef food webs. They are important consumers of coral mucus (McCloskey 1970) and fish feces (Rothans & Miller 1991). Cryptic carnivores include fishes (Depczynski & Bellwood 2003; Glynn 2006), mollusks (Kohn 1983), annelids (Ott & Lewis 1972), and crustaceans (Reaka 1987) as well as numerous other metazoan phyla. These taxa prey on motile nektonic, epibenthic, and other cryptic species or may graze on sessile animals including corals.

Coelobites are one of the principal food sources of coral reef fishes (Vivien 1973; Peyrot-Clausade 1980). Cryptic species were well represented among the gut contents of many of the 5,526 reef fishes from 212 species collected by Randall (1967) from the West Indies. The most important prey items belonged to the phyla Arthropoda and Annelida and many if not most are known to exhibit cryptic behaviors. Reef fishes may wait until cryptofauna emerge from reef substrates (Steger 1987; Hobson 1991) or break apart and forage within framework shelters (Guzman 1988; Hobson 1974).

Cryptofauna may benefit corals through their cleansing of tissue surfaces (Glynn 1983), removal of competitive algae (Coen 1988), and their defensive aggression towards harmful corallivores (Glynn 1980). Additionally, there is evidence that some species of corals may directly feed on cryptofauna and demersal reef plankton, which shelter in reef crypts during the day and emerge at night (Porter 1974; Hutchings & Weate 1977; Alldredge & King 1977). During times of reduced photosynthetic capability, such as during stressful bleaching events, some corals may rely on heterotrophy to survive (Grottoli et al. 2006).

Increased incidences of coral bleaching and mortality, coupled with declines in coral cover and framework complexity, may have widespread implications for coral reef cryptofauna (Gardner 2003; Hughes et al. 2003; Alvarez-Filip et al. 2009; Baker et al. 2008). Evidence suggests that coral bleaching and mortality may lead to increased predation on cryptic occupants (Coker et al. 2009). Following coral death, metabolic byproducts that are normally fed upon by cryptic symbionts may become no longer available, ultimately leading to reduced abundances (Caley et al. 2001) and lower biomass of associated fauna (Enochs & Hockensmith 2009). Nonsymbiotic fauna (e.g., fishes) that associate with dead coral frameworks may be less abundant and more depauperate among degraded and eroded substrates (Glynn 2006).

Given these short-term and small-scale patterns it is likely that widespread coral mortality and framework erosion will have profound effects on cryptofauna populations and, by extension, coral reef trophodynamics. It is therefore important to examine cryptofauna on a reef-wide scale to determine baseline magnitudes as well as to investigate conditions and/or substrates conducive to supporting these communities. Sampling cryptofauna associated with reef habitats subject to varying degrees of stress and degradation will allow predictions of reef ecosystem response to climate change that exceed the limitations of single-taxon declines (e.g., corals or fishes).

In this study we examine cryptofauna abundances and biomass associated with both live and dead coral substrates. The relationship between the size of living corals and their cryptic associates is explored. Cryptofauna communities associated with dead coral framework materials are examined across a gradient of reef degradation. Finally, sample statistics are extrapolated to a reef-wide scale in order to determine the relative importance of different substrates and to examine the likely responses of cryptofauna populations to coral mortality and framework erosion.

Materials and methods

Basemap creation, reef zone identification (LDF, low degradation framework; MDF, medium degradation framework; HDF, high degradation framework; rubble), cryptofauna sampling, and taxon-specific criteria for counting individuals are detailed in Chapter 2. Unlike Chapter 2, higher-level taxonomic identifications were sufficient for analysis, and individuals were included in abundance totals regardless of their status as operational taxonomic units (OTUs). Similarly, fragments of specimens which were not counted as complete individuals were included in biomass totals. All cryptofauna samples were lightly blotted to remove excess alcohol and then weighed using an analytical balance. Wet weight was converted into ash-free dry weight (AFDW) using the conversion factors compiled in Appendix 3.

Abundances and biomass were divided into trophic groups according to Appendix 4 and references therein. Trophic groups were constructed based on the exploitation of a common food source as well as similar feeding behaviors (see Simberloff & Dayan 1991). It is recognized that these categories are anthropogenic, include many exceptions and ultimately fail to capture the true diversity of trophic interactions. Regardless, their construction simplifies the complexity of coral reef trophodynamics and facilitates an understanding of important energy sources. Therefore, carnivorous predators (CP) are defined as taxa that eat other motile metazoans, while carnivorous grazers (CG) refer to those species that feed on sessile animals. Carnivorous multiple strategies (CM) includes taxa that feed on both sessile and motile animal species. Herbivorous grazers (HG) consume sessile plant biota and detritivorous deposit feeders (DD) feed on organic deposits and detritus. Organisms utilizing suspension feeding (SU) were not separated according to diet due to the inherent difficulties in identifying food sources as well as the omnivorous diets of many of the constituent taxa. Regardless, the suspension feeding behavior is ecologically relevant and sufficiently unique to merit its categorization as a trophic group. Finally, it was necessary to create both an opportunistic grazer (OG) and an opportunistic omnivore category (OO) due to the variable diets and indiscriminate food preferences of many coral reef organisms.

Live coral abundances

Two diagonally situated 0.25 m^2 photoquadrats from within each of the 1 m^2 sample quadrat were selected from the MDF (total 44) and HDF (total 40) zones and a single 0.25 m^2 photoquadrat was obtained from the center of each of the rubble sample quadrats. All *Pocillopora* colonies not touching the quadrat margins were counted and their planar surface area was measured using CPCe. The circular diameter of each coral was calculated from the planar surface area (Equation 3.1). Corals were separated into size-classes (3.0 cm increments of diameter) and the number of colonies within each class was tallied. The frequency of corals within each size-class was corrected for bias due to edge effects according to the Zvuloni et al. (2008) “type I” correction factor (Equation 3.2). Colonies with centers inside photoquadrats (one per sample site) were counted to estimate coral density within MDF, HDF, and Rubble zones. Coral density was multiplied by the total area of each zone (calculated from the GIS basemap) to estimate overall numbers of corals. The corrected frequency of each coral size-class within each zone was multiplied by the estimated total number of corals within each zone in order to estimate the total abundance and density of each coral size-class.

Equation 3.1. The diameter of corals computed from planar surface area. D, diameter; A, area measured with CPCe.

$$D = 2\sqrt{\frac{A}{\pi}}$$

Equation 3.2. Correction factor (α) multiplied by observed frequency of corals with a diameter (D) in size-class i. Quadrat of width R_W and length R_L.

$$\alpha_i = \frac{R_W R_L}{(R_W - D_i)(R_L - D_i)}$$

Cryptofauna associated with live coral

The relationship between coral size-class and cryptofauna associates is exponential. The Log_{10} abundance and biomass of *Pocillopora* associates was plotted against the diameter of their host coral colonies (n = 62) collected from the MDF, HDF, and rubble zones. Linear functions were fitted to these points and the resulting log-linear equations were converted back into functions directly relating community abundance and biomass to diameter. The estimated abundance and biomass of individuals for each size-class were multiplied by the number of corals within that size-class in order to estimate the overall population size of cryptic metazoans associated with living corals.

At high diameter size-classes the estimated abundance and biomass of cryptofauna associates became improbable (Figure 3.1, dashed line). Consequently, for coral size-classes larger than those sampled (> 21 cm), the mean number of individuals per surface area of coral (collected from the LDF zone) was used to estimate the abundance of associates (Figure 3.1, solid line). This relationship was used for 24, 27, 30, and 33 cm diameter corals in the MDF zone and 24 cm corals in the HDF and rubble zones. Switching to this methodology at larger size classes is justifiable geometrically as coral morphology becomes more appropriately approximated as a laterally expanding plane rather than an outwardly growing sphere (Figure 3.1). Furthermore, it is admissible ecologically as planar and spheroidal colonies have been shown to provide dissimilar habitats to their occupants, resulting in differently structured cryptofaunal communities (Lewis & Snelgrove 1990).

In the MDF, HDF, and rubble zones, the estimated mean number and biomass of cryptofauna per coral colony was calculated by multiplying the frequency of each coral size-class (for a given zone) by the estimated cryptofauna community at that size class and then adding all of the subsequently weighted values. This value was multiplied by the mean density of corals per m^2 in order to estimate the density of cryptofauna associated with live coral per m^2 reef. The resulting planar cryptofauna densities were multiplied by zone areas in order to estimate zone-wide cryptofauna population parameters.

In the LDF zone, the mean percent cover of living *Pocillopora* was multiplied by the spatial extent of the zone to determine the surface area of living coral. This was multiplied by the planar density of live coral associates in order to calculate the total number of cryptic metazoans associated with living coral in the LDF zone.

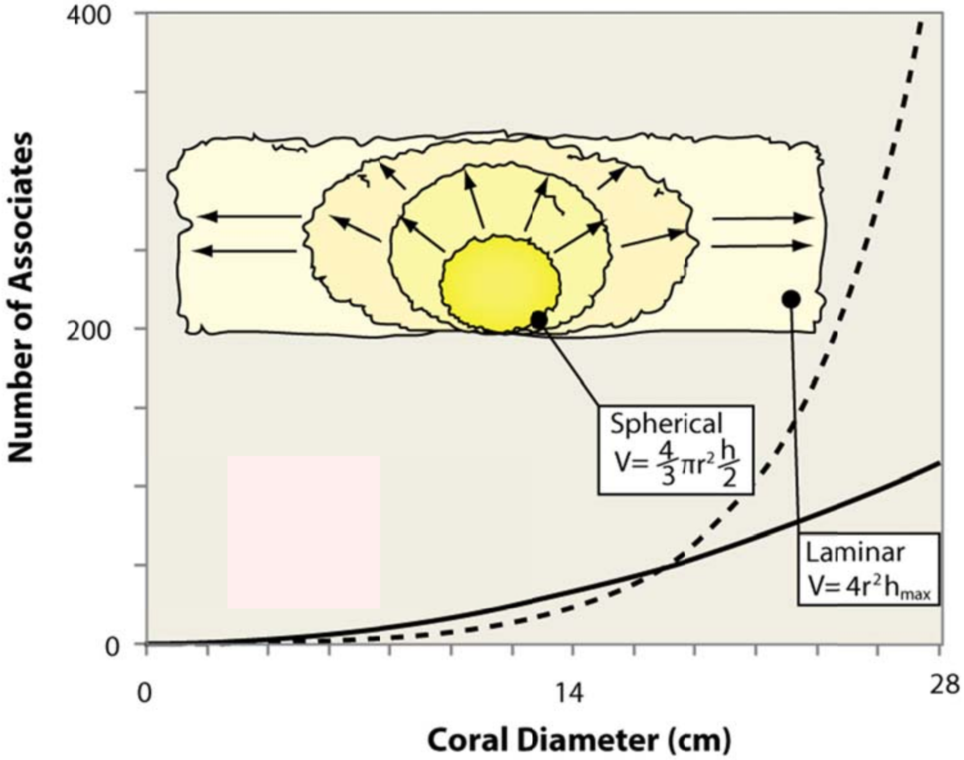

Figure 3.1. Predicted abundance of metazoans associated with a *Pocillopora* colony of a given diameter. Dashed line shows the exponential increase of cryptofauna as predicted by the size-class-based spherical growth function. Solid line shows the more gradual increase as predicted by the density-based laminar growth function.

Cryptofauna associated with dead coral (frameworks)

The density of cryptic metazoans associated with dead coral substrates was standardized per surface area and per skeletal volume for each of the four reef zones. Zone-specific densities were multiplied by the surface area of each zone to estimate the total abundance of individuals associated with dead coral substrates.

Results

Benthic composition

The area, percent benthic cover, estimated number of corals, habitat depth and percent void space of each zone are given in Table 3.1. Mean framework depth was significantly higher (Tukey's test, $p < 0.05$) in the LDF zone (0.60 m) than in the MDF (0.15 m) and HDF zones (0.12 m), which did not differ significantly. Dead coral substrates within the HDF zone were significantly more eroded (Tukey's test, $p < 0.05$) with a lower percent porosity (75.1%) than in LDF (91.7%) and MDF (93.5%) zones.

Table 3.1. The area, percent benthic cover, estimated number of corals, habitat depth and porosity of reef zones at Playa Larga Reef. 95% confidence intervals in parentheses. Note: one anomalous HDF value removed for depth and void space calculations.

Zone	**Area (m^2)**	**% *Pocillopora***	**%*Psammocora***	**%Bare**	**%Sediment**	**% CCA**	**% Algae**	**% Other**	**Tot. corals $*10^6$**	**Depth (m)**	**% Void space**
LDF	36324	76.67	0	5.63	0	9.17	8.33	0.21	Na	0.60	91.7
		(9.21)		(5.07)		(3.87)	(5.69)	(0.43)		(0.08)	(0.92)
MDF	41433	38.41	0	10.91	0.23	18.86	31.59	0	1.28	0.15	93.5
		(9.76)		(6.07)	(0.47)	(6.52)	(7.99)		(0.23)	(0.03)	(1.80)
HDF	11089	13	0.75	20.25	5.5	30	30.5	0	0.21	0.12	75.1
		(8.23)	(1.15)	(8.33)	(6.21)	(9.96)	(11.46)		(0.06)	(0.04)	(5.44)
Rubble	31586	10.87	0.33	19.02	16.3	21.96	30.87	0.65	0.82	Na	Na
		(4.31)	(0.49)	(4.89)	(6.72)	(5.35)	(6.59)	(0.97)	(0.24)	Na	Na

Live coral abundances

The Zvuloni et al. (2008) "type I" correction factor shifted coral size-frequency distributions towards larger size-classes, deemphasizing the proportion of small diameter corals (Figure 3.2). The six cm diameter size-class consistently accounted for the highest proportion of coral, followed by the three and nine cm size-classes. Gradual decreases in frequency were observed in size-classes larger than six cm. The largest corals (33 cm size-class) were observed in MDF and the largest size-class recorded in HDF and rubble zones was 24 cm.

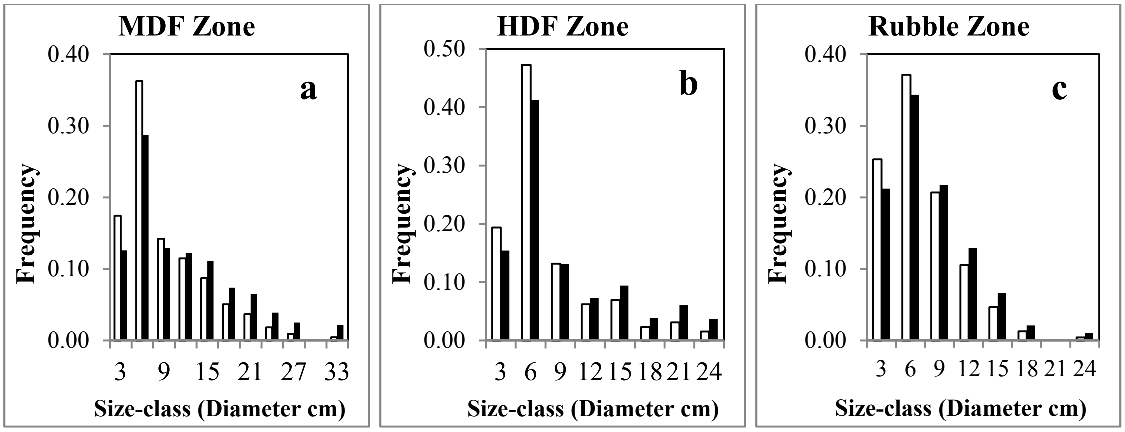

Figure 3.2. Size-frequency distribution of live *Pocillopora* colonies in MDF (a), HDF (b), and Rubble (c) zones. Open bars are uncorrected frequencies, calculated from colonies completely within 0.25 m^2 photoquadrats. Colored bars are corrected with the Zvuloni et al. (2008) "type I" correction factor.

Communities associated with live corals of different sizes

The planar density of abundances and biomass of cryptofauna associated with live coral is greater for larger size-class colonies (Figure 3.3). Linear regression of abundance and biomass (AFDW) data resulted in $abund = 10^{0.10895*Diam-0.1657}$ and $mass = 10^{0.1565*Diam-0.229}$ with R^2 values of 0.6822 and 0.6608, respectively (Figure 3.4). One outlying data point was removed from the biomass calculations due to the presence of a large holothurian. Abundance and biomass densities from coral in LDF, as well as HDF and MDF corals 24 cm and larger, were determined from 10 LDF corals, where the planar surface area was known. Mean abundance and biomass was 2145.75 indiv. m^{-2} (95% CI = 365.35) and 26.59 g m^{-2} (95% CI = 11.23), respectively.

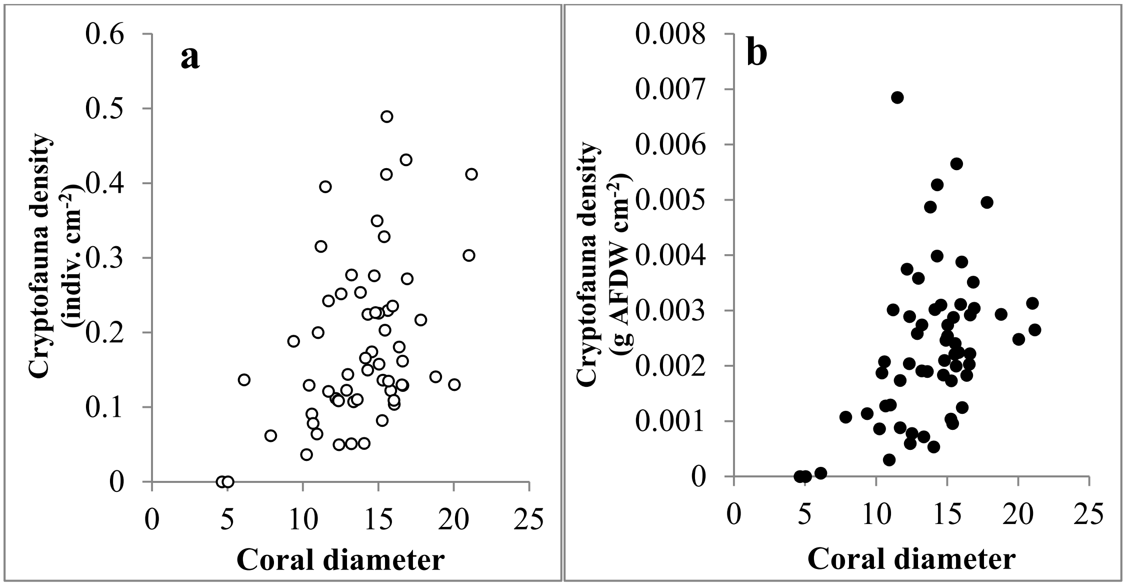

Figure 3.3. Abundance (a) and biomass (b) of live coral associated cryptofauna per colony area.

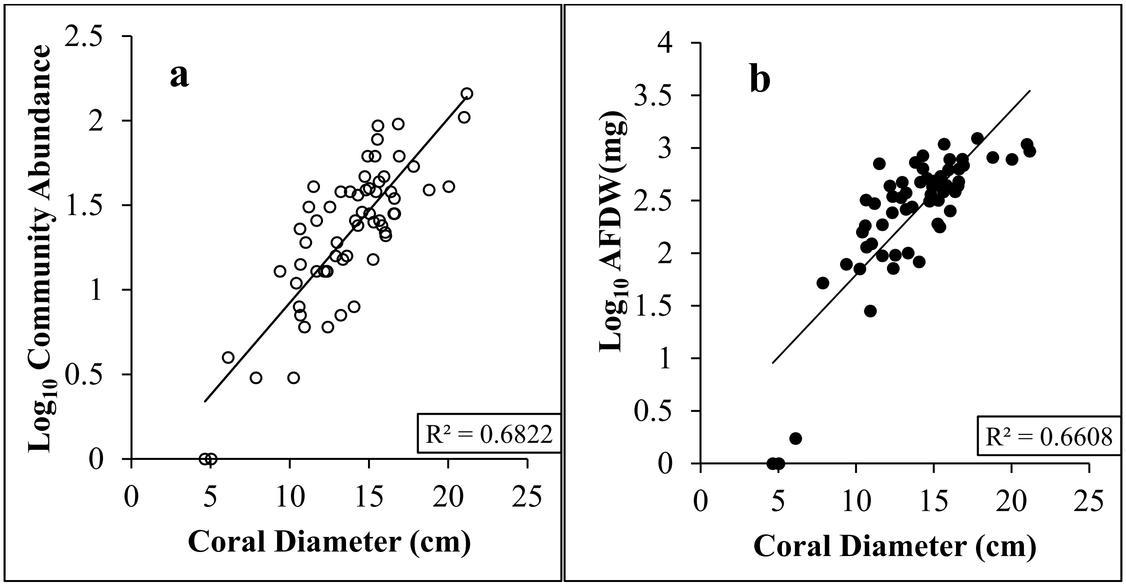

Figure 3.4. Log abundance (a) and biomass (b) of associates plotted against coral diameter and fitted with a linear function.

The total abundance and biomass of cryptofauna associated with live *Pocillopora* along with the proportion per size-class of coral was estimated within MDF (Table 3.2), HDF (Table 3.3), and rubble (Table 3.4) zones. The estimated density (per planar reef area) of cryptofauna abundance (a) and biomass (b) associated with each coral size-class is plotted in Figure 3.5. Despite relatively low frequencies of occurrence, higher size-class corals support higher proportions of cryptic individuals and biomass. Corals in the 24 cm diameter size-class had low frequencies of occurrence yet accounted for the greatest proportion of within-zone abundance and biomass with the exception of the MDF 33 cm size-class.

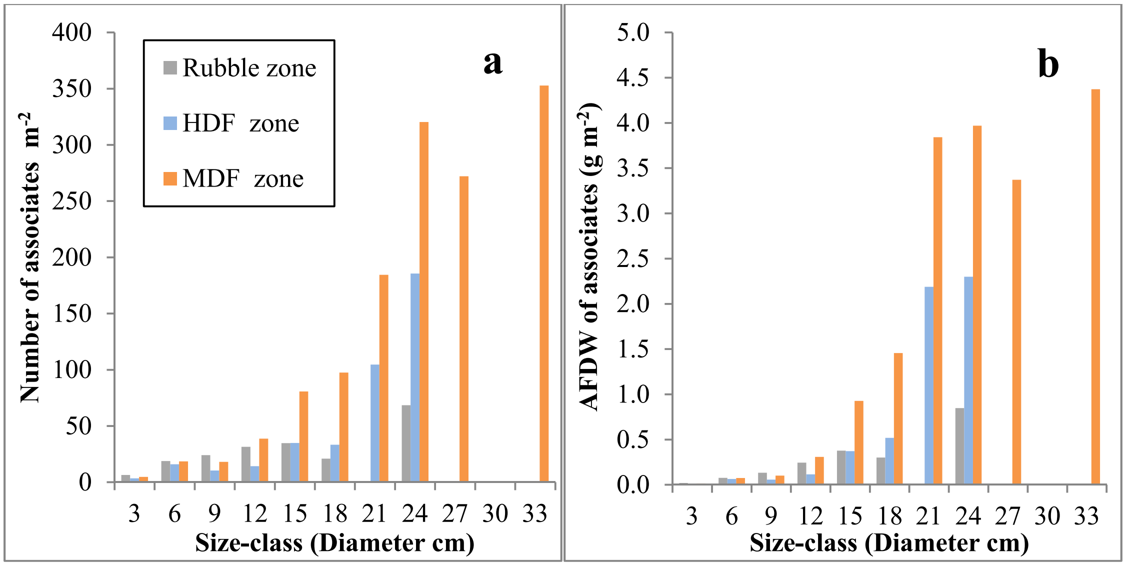

Figure 3.5. The estimated abundance (a) and biomass (b) of cryptofauna associated with different size-classes of live corals within MDF, HDF and rubble zones.

Table 3.2. MDF, estimated frequency and abundance of *Pocillopora* size-classes (3 cm increments) and the estimated abundance and biomass of cryptofauna associated with that size-class colony (col.). Community parameters for size-classes marked with “a” are calculated from planar densities, all other values calculated from regression of cryptofauna associated with spheroidal colonies. Values per m^2 are determined by multiply the mean number of colonies of a given size-class per m^2 by the estimated cryptofauna associated with that size-class. Reef-wide extrapolations calculated by multiply cryptofauna densities per m^2 by the planar area of the MDF zone.

Coral				**Est. cryptofauna col.$^{-1}$**		**Est. cryptofauna m^{-2}**		**Est. reef-wide total**	
Size class	**Mean diam.**	**Corr. freq.**	**Mean col. m^{-2}**	**Abund.**	**AFDW (mg)**	**Abund.**	**AFDW (mg)**	**Abund. (millions)**	**AFDW (kg)**
3	2.20	0.13	4.00	1.19	3.74	4.75	14.98	0.20	0.62
6	4.36	0.29	9.13	2.04	8.14	18.59	74.32	0.77	3.08
9	7.42	0.13	4.12	4.40	24.58	18.10	101.22	0.75	4.19
12	10.68	0.12	3.89	9.94	79.41	38.71	309.16	1.60	12.81
15	14.00	0.11	3.53	22.88	262.91	80.77	928.11	3.35	38.45
18	16.38	0.07	2.34	41.63	621.09	97.58	1455.91	4.04	60.32
21	19.43	0.06	2.06	89.45	1863.51	184.43	3842.32	7.64	159.20
24^a	22.11	0.04	1.24	258.73	3206.25	320.29	3969.19	13.27	164.46
27^a	25.41	0.03	0.80	341.73	4234.92	272.10	3371.94	11.27	139.71
30^a	na	na	na	0.00	0.00	0.00	0.00	0.00	0.00
33^a	31.23	0.02	0.68	516.30	6398.24	352.81	4372.19	14.62	181.15
Total						**1388.12**	**18439.33**	**57.51**	**764.00**

Table 3.3. HDF, estimated frequency and abundance of *Pocillopora* size-classes (3 cm increments) and the estimated abundance and biomass of cryptofauna associated with that size-class colony (col.). Community parameters for size-classes marked with “a” are calculated from planar densities, all other values calculated from regression of cryptofauna associated with spheroidal colonies. Values per m^2 are determined by multiply the mean number of colonies of a given size-class per m^2 by the estimated cryptofauna associated with that size-class. Reef-wide extrapolations calculated by multiply cryptofauna densities per m^2 by the planar area of the HDF zone.

Coral				**Est. cryptofauna col.$^{-1}$**		**Est. cryptofauna m^{-2}**		**Est. reef-wide total**	
Size class	**Mean diam.**	**Corr. freq.**	**Mean col. m^{-2}**	**Abund.**	**AFDW (mg)**	**Abund.**	**AFDW (mg)**	**Abund. (millions)**	**AFDW (kg)**
3	2.22	0.15	2.96	1.19	3.77	3.53	11.15	0.04	0.12
6	4.34	0.41	7.91	2.03	8.10	16.06	64.09	0.18	0.71
9	7.22	0.13	2.51	4.18	22.85	10.49	57.39	0.12	0.64
12	10.78	0.07	1.41	10.20	82.43	14.35	115.93	0.16	1.29
15	13.32	0.09	1.81	19.29	205.67	34.88	372.01	0.39	4.13
18	16.74	0.04	0.73	45.53	706.52	33.40	518.21	0.37	5.75
21	19.47	0.06	1.16	90.20	1886.17	104.67	2188.55	1.16	24.27
24[a]	22.30	0.04	0.70	263.32	3263.19	185.63	2300.46	2.06	25.51
Total						**403.01**	**5627.80**	**4.47**	**62.41**

Table 3.4. Rubble zone, estimated frequency and abundance of *Pocillopora* size-classes (3 cm increments) and the estimated abundance and biomass of cryptofauna associated with that size-class colony (col.). Community parameters for size-classes marked with “a” are calculated from planar densities, all other values calculated from regression of cryptofauna associated with spheroidal colonies. Values per m^2 are determined by multiply the mean number of colonies of a given size-class per m^2 by the estimated cryptofauna associated with that size-class. Reef-wide extrapolations calculated by multiply cryptofauna densities per m^2 by the planar area of the rubble zone.

Coral				**Est. cryptofauna col.$^{-1}$**		**Est. cryptofauna m^{-2}**		**Est. reef-wide total**	
Size class	**Mean diam.**	**Corr. freq.**	**Mean col. m^{-2}**	**Abund.**	**AFDW (mg)**	**Abund.**	**AFDW (mg)**	**Abund. (millions)**	**AFDW (kg)**
3	2.19	0.21	5.52	1.18	3.73	6.52	20.55	0.21	0.65
6	4.50	0.34	8.93	2.11	8.56	18.84	76.49	0.60	2.42
9	7.31	0.22	5.65	4.27	23.60	24.14	133.33	0.76	4.21
12	10.44	0.13	3.36	9.38	73.01	31.49	245.14	0.99	7.74
15	13.47	0.07	1.73	20.05	217.48	34.73	376.77	1.10	11.90
18	16.05	0.02	0.55	38.25	550.04	20.92	300.79	0.66	9.50
21	na	na	na	0.00	0.00	0.00	0.00	0.00	0.00
24^a	21.98	0.01	0.27	255.81	3170.09	68.47	848.53	2.16	26.80
Total						**205.11**	**2001.60**	**6.48**	**63.22**

Cryptofauna densities

Live coral colonies supported significantly more abundant cryptofauna communities per liter substrate ($\bar{x}$ = 126.8 indiv. l^{-1}) than dead coral substrates ($\bar{x}$ = 61.7 indiv. l^{-1}; t-test 1-tail, $p < 0.001$; Figure 3.6). Additionally, live corals supported significantly greater coelobite biomass per liter substrate ($\bar{x}$ = 1.6 g AFDW l^{-1}) than dead coral habitats ($\bar{x}$ = 0.6 g AFDW l^{-1}; t-test, 1-tail, $p < 0.001$; Figure 3.6).

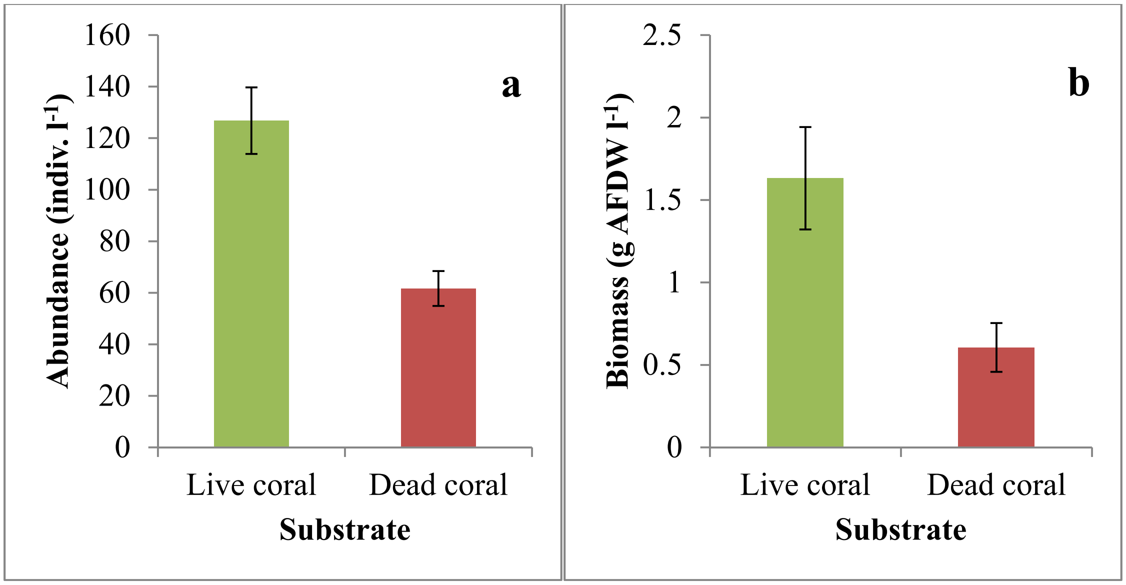

Figure 3.6. The mean abundance (a) and biomass (b) of cryptofauna communities associated with live (green) and dead coral (red), per liter substrate. Error bars ± 95% confidence interval

The abundance and biomass of cryptofauna per liter dead coral substrate were significantly affected by zone characteristics (1-way ANOVA, $p < 0.001$; Table 3.5; Figure 3.7). Post hoc analysis of volumetrically standardized data revealed that MDF contained significantly greater abundance and biomass densities than all other zones (Tukey’s test, $p < 0.001$) and LDF contained significantly lower densities of individuals (not biomass) than rubble ($p < 0.001$).

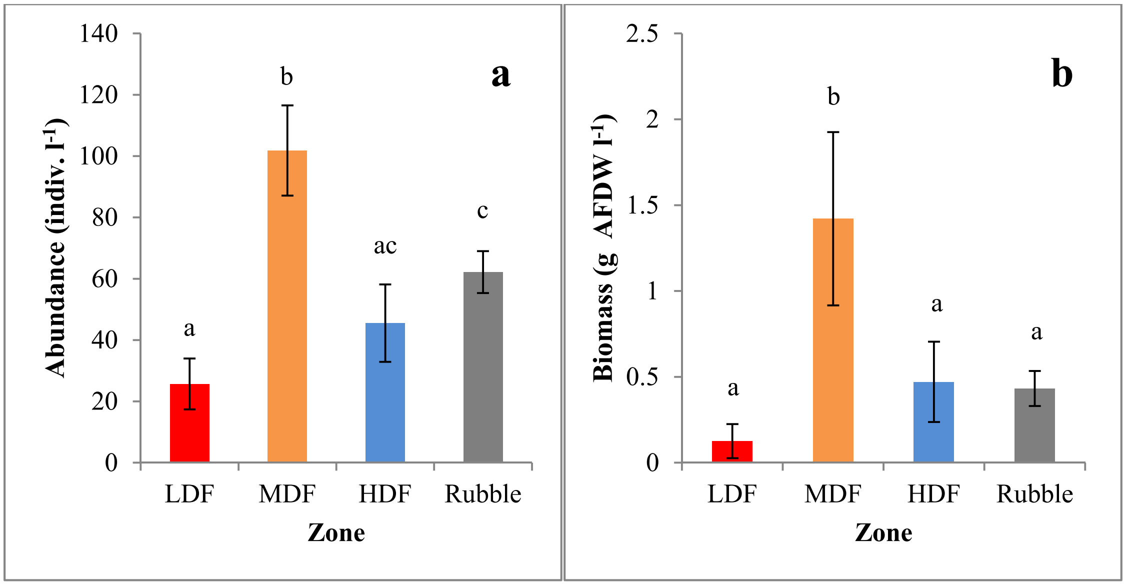

Figure 3.7. Abundance (a) and biomass (b) of metazoans associated with dead coral substrates in the LDF (red), MDF (orange), HDF (blue), and Rubble (gray) zones, per l substrate. Error bars ± 95% confidence interval. Zones that do not share letters are significantly different (Tukey's test, $p < 0.05$).

There was a significant zone effect on area-standardized, dead coral associated cryptofauna biomass and abundance (1-way ANOVA, $p < 0.001$; Table 3.5; Figure 3.8). Post hoc (Tukey's) tests revealed that LDF area-standardized community abundances were significantly greater than that of MDF ($p = 0.046$) and rubble ($p < 0.001$). Cryptofauna abundances and biomass densities in the HDF zone were significantly greater ($p < 0.001$ and $p = 0.002$, abundance and biomass respectively) than in the rubble zone and MDF cryptofauna biomass per unit area was greater than that in rubble ($p = 0.005$). For comparison, estimated zone-specific planar densities of live coral associated cryptofauna are shown in Figure 3.8 and given in Table 3.5. Densities of cryptofauna decrease across zones of increasing degradation, paralleling percent coral cover.

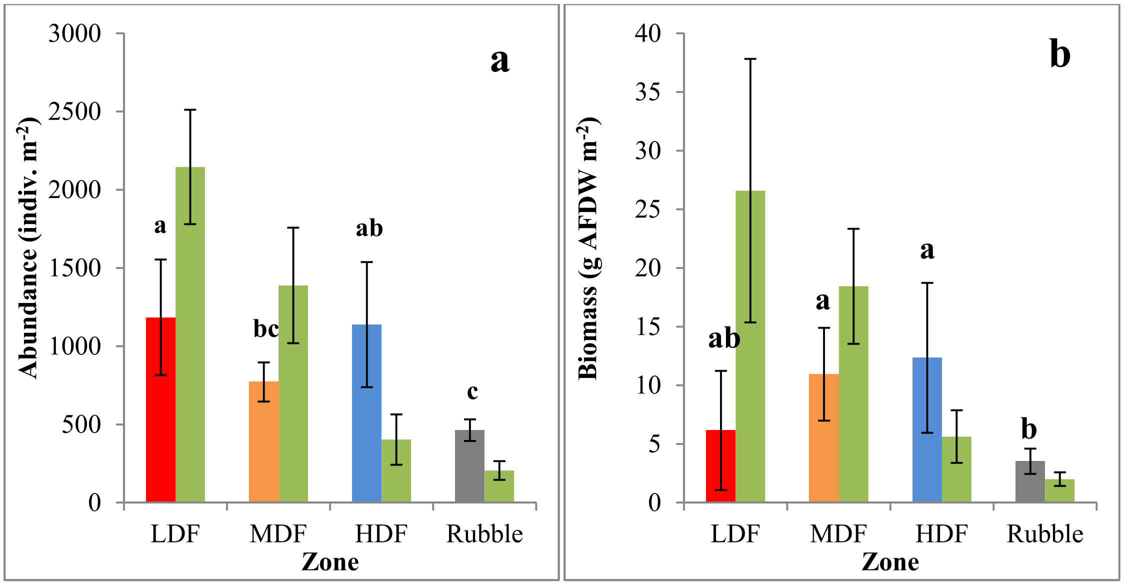

Figure 3.8. Abundance (a) and biomass (b) of metazoans associated with live coral (green) and dead coral substrates in the LDF (red), MDF (orange), HDF (blue), and Rubble (gray) zones, per m^2 planar surface reef area. Error bars on dead coral substrates are ± 95% confidence intervals. Dead coral substrate values that do not share letters are significantly different (Tukey's test, $p < 0.05$). LDF coral values are the mean cryptofauna per planar surface area of coral and error bars are ± 95% confidence intervals. MDF, HDF, Rubble live coral values represent the mean number of corals per m^2 in each zone times the estimated mean number of cryptofauna associated with live coral colonies, calculated from the size-frequency distribution of corals within each zone and the estimated number of individuals associated with each size class. Error bars on MDF, HDF, Rubble live coral values are ± 95% confidence intervals of coral density within each zone multiplied by the estimated mean number of cryptofauna per live coral colony in that zone.

Reef-wide extrapolations of cryptofauna associated with live and dead coral

Extrapolation of cryptic community densities across zones revealed elevated abundances associated with live (146.40 million indiv.) than dead coral substrates (102.22 million indiv.), and much greater biomass associated with live (1,856 kg AFDW) than dead coral habitats (925 kg AFDW; Table 3.5). LDF and MDF are estimated to contain the majority of individuals (77.94 and 57.51 million indiv., respectively) and biomass (966 and 764 kg AFDW, respectively) associated with live coral (Table 3.5, Figure 3.9). Dead coral materials in the LDF zone are estimated to shelter the greatest abundance of individuals (43.02 million), followed by MDF (31.95 million), rubble (14.63 million), and then HDF (12.62 million; Table 3.5; Figure 3.9a). Dead coral frameworks in the MDF zone shelter the most biomass (764 kg AFDW), followed by those in LDF (741 kg AFDW), rubble (78 kg AFDW), and HDF (65 kg AFDW), in that order (Table 3.5; Figure 3.9b).

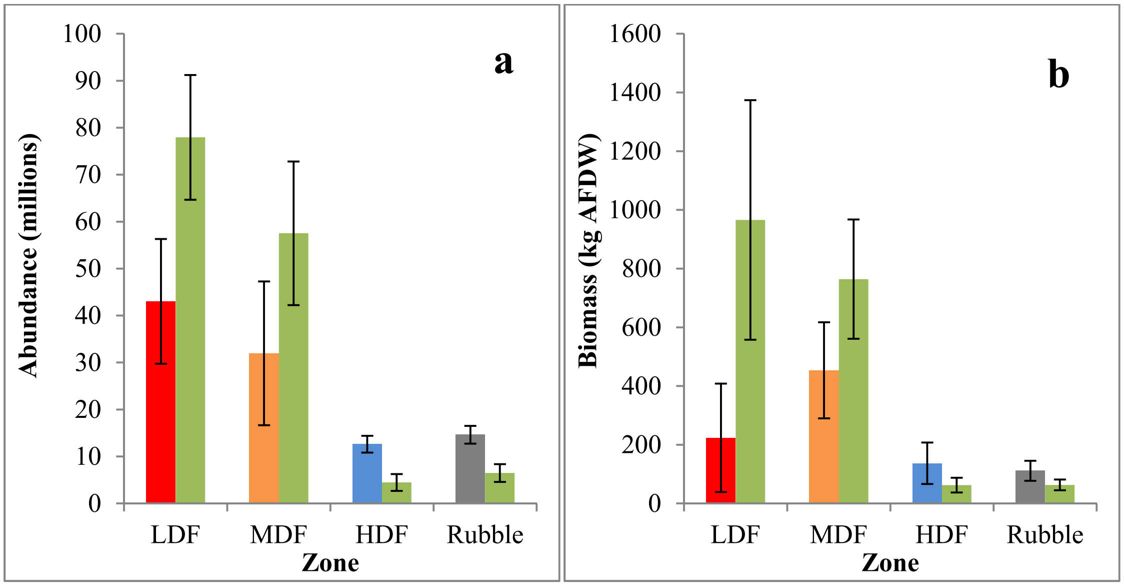

Figure 3.9. Estimated total abundance (a) and biomass (b) of cryptic metazoans associated with live coral (green) and dead coral (LDF, red; MDF, orange; HDF, blue; rubble, gray). Values calculated by multiplying densities (per m^2) and error bars in figure 3.8 by the planar area of each zone.

Table 3.5. Abundance and biomass of communities associated with dead coral substrate per l skeletal habitat, cryptofauna associated with live and dead coral per m^2 reef as well as estimated total abundance and biomass associated with live and dead coral. 95% confidence intervals in parentheses. Planar densities for cryptofauna associated with live coral calculated by multiplying the mean number of live coral colonies m^{-2} by the estimated mean community associated with a single coral in each zone, calculated from the zone-specific coral size frequency distribution. Confidence intervals for communities densities associated with live coral in the MDF, HDF, and rubble zones are ± 95% confidence intervals of live coral density within each zone multiplied by the estimated mean number of cryptofauna per live coral colony in that zone. Estimated reef-wide totals are calculated by multiplying the per m^2 values for each zone by the area of that zone.

	Cryptofauna l^{-1}		**Cryptofauna m^{-2}**				**Est. reef-wide total**			
	Dead coral		**Dead coral**		**Live coral**		**Live coral**		**Dead coral**	
Zone	**Indiv.**	**AFDW (mg)**	**Indiv.**	**AFDW (mg)**	**Indiv.**	**AFDW (mg)**	**Tot. indiv. (millions)**	**Tot. AFDW (kg)**	**Tot. indiv. (millions)**	**Tot. AFDW (kg)**
LDF	25.7	0.13	1184	6.15	2146	26.59	77.94	965.9	43.02	224
	(8.3)	(0.09)	(369.9)	(4.76)	(365.4)	(11.23)	(13.27)	(407.9)	(13.33)	(173)
MDF	101.8	1.42	771.2	10.95	1388	18.44	57.51	764.0	31.95	453
	(14.7)	(0.48)	(125.7)	(3.75)	(369.3)	(4.91)	(15.30)	(203.3)	(5.21)	(155)
HDF	45.5	0.47	1138	12.34	403	5.63	4.47	62.4	12.62	137
	(12.6)	(0.22)	(399.7)	(5.96)	(160.8)	(2.25)	(4.47)	(24.9)	(4.43)	(66)
Rubble	62.2	0.43	463.3	3.52	205	2.00	6.48	63.2	14.63	111
	(6.8)	(0.10)	(69.1)	(1.05)	(59.8)	(0.58)	(6.48)	(18.4)	(2.18)	(33)
Total							**146.40**	**1855.50**	**102.22**	**925**

Contribution of phyla and trophic groups to biomass

The proportion of biomass belonging to different phyla and trophic groups was not consistent across individual samples. When all samples of a given substrate were pooled, dead coral community biomass was more evenly distributed across phyla (Figure 3.10) and trophic groups (Figure 3.10) than that associated with live coral substrates. Live coral community biomass was dominated by Arthropoda (83.03%) whereas those associated with dead coral substrates were composed primarily of Echinodermata (36.02%), Arthropoda (32.85%), and Mollusca (25.04%). Live coral was dominated by opportunistic omnivores (77.77%) and dead coral habitats contained high proportions of opportunistic omnivores (28.78%), deposit feeding detritivores (20.04%), herbivorous grazers (17.3%) and carnivorous predators (16.05%).

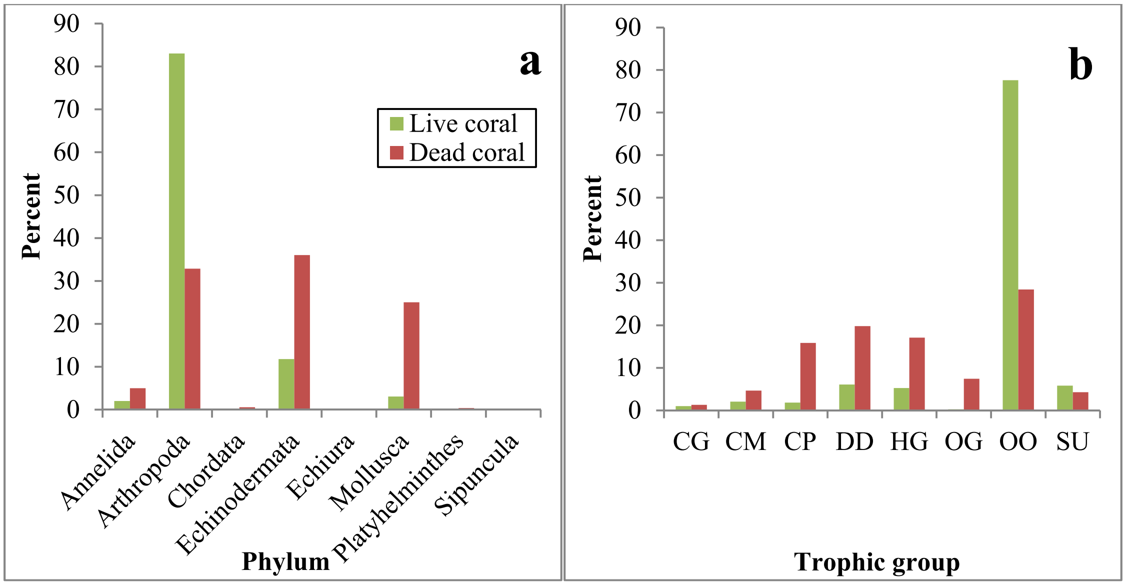

Figure 3.10. The proportion of collected cryptofauna biomass belonging to different metazoan phyla (a) and trophic groups (b) associated with live (green) and dead coral substrates (red). CM, carnivore multiple strategies; CP, carnivorous predator; DD, detritivore deposit feeder; HG, herbivorous grazer; OO, amnivore opportunistic; SU, suspension feeder.

Discussion

Live vs. dead coral habitats

Living corals support more than twice the biomass and cryptofauna abundances per volume substrate than dead corals. The findings of Caley et al. (2001) support this relationship as they observed declines in coral-associated cryptofauna abundances following the mortality of *Stylophora pistillata* colonies. Additionally, elevated abundances of demersal plankton have been recorded in association with living coral substrates relative to reef rock communities (Alldredge & King 1977). Enochs and Hockensmith (2008) found higher cryptofauna biomass associated with living rather than dead *Pocillopora damicornis* colonies, both six months and a year after coral mortality. They observed no significant differences in coelobite abundances six months after mortality and, in contrast to the data herein, higher abundances associated with dead coral substrates after 12 months. Whereas this study compared communities associated with a wide range of coral sizes and substrate volumes, the aforementioned paper focused on single coral colonies of intermediate size. Community abundances and biomass were standardized to theoretical spheroidal volume of each colony. It is likely that bioerosion of dead substrates and growth of living corals after 12 months resulted in changes in colony architecture regardless of spheroidal volume, thereby limiting the validity of their standardization methodology.

The high biomass and abundance of cryptofauna associated with live coral is due in part to the trophic benefits conferred by the host. A suite of primarily crustacean symbionts are specially adapted to feed on various metabolic products of their coral hosts, including mucus (Knudsen 1967) and fat-bodies (Stimson 1990), as well as nutrient-rich tissues (Rotjan & Lewis 2008). These taxa, which are largely classified as opportunistic omnivores in this study, account for the high proportions of Arthropoda and opportunistic omnivore biomass associated with live coral colonies (Figure 3.10). Coral food sources are not as readily available on dead coral substrates; however diverse benthic flora and fauna provide sustenance to a variety of nonsymbiotic taxa. This greater variety of food resources accounts for the more evenly distributed trophic groups on dead substrates (Figure 3.10b).

Additionally, live coral substrates may encourage elevated cryptofauna populations by sheltering them from predators. Besides the mosaic network of sheltering branches, defensive adaptations of the coral host include cnidocytes, mucus, and allelopathic chemicals. Animals indifferent to these otherwise repellant attributes would presumably inherit the benefits of their hosts' antipredatory mechanisms. Furthermore, many coral symbionts are cryptic in coloration and may camouflage themselves among a colony's branches. Indeed, Coker et al. (2009) observed more frequent predation events directed at coral symbionts immediately following the bleaching of their hosts. Predation was higher still after coral mortality and the subsequent fouling of the carbonate skeletons.

Despite their low frequency, large size-class colonies support disproportionately high abundances and biomass of cryptofauna. As such, coral cover alone is likely not a good indicator of cryptofaunal community abundance or biomass. Therefore, it is important to know the size-frequency distribution of the colonies in question as high abundances of small size-class corals would potentially support fewer cryptofauna than a single large size-class colony of equal surface area. By extension, it is expected that recovery of coral-associated cryptofauna populations following mass bleaching events will lag behind recruitment-related recovery of their hosts. Conversely, corals that reach a size whereby their shape becomes best approximated by a plane host cryptofauna communities of depressed abundance and biomass relative to their large spherical counterparts. Furthermore, some territorial coral symbionts (e.g., *Trapezia* spp.) may increase in abundance as the result of coral fragmentation (Caley et al. 2001). Reef areas composed of small, rather than large size-class corals may therefore support more territories and by extension, more territorial individuals. Given the depression of cryptofauna density at small and large size-classes, it is probable that there is some intermediate size of coral which supports the greatest amount of cryptic associates (biomass and abundances) per unit area.

Structure of dead coral habitats

Dead coral substrates in the LDF zone shelter significantly lower biomass and abundances of cryptofauna per volume substrate than those in the only other zone containing developed frameworks, MDF. The colonization and proliferation of coelobites within LDF is likely inhibited by the continuous barrier of live coral tissue which covers this cryptic habitat. Coral polyps have been observed to directly consume cryptofauna and it is likely that many non-symbiotic species are deterred by the various defensive mechanisms of live coral colonies (Hutchings & Weate 1977; Lang and Chornesky 1990). Because framework materials in the LDF zone are compact, it is probable that limited light penetration restricts algae and other potential photosynthetic food sources. During the course of this study, the day-time oxygen concentration of pore waters was measured. There was little reduction observed (data not shown), suggesting that frameworks are well-flushed and oxygen inhibition is likely not responsible for the vertical limitation of LDF cryptofauna. More investigation is necessary to determine if this holds true during the presumably hypoxic pre-sunrise hours and if the accumulation of noxious byproducts (e.g., ammonia) are possibly responsible for these patterns.

Significantly higher abundances and biomass of coelobites per liter substrate found within the MDF zone is likely due to the great availability of shelters as well as diverse food sources. Structurally complex frameworks, with porosity sufficient to encourage the settlement of photosynthetic and suspension feeding taxa would provide nutriment for motile cryptofauna. HDF and rubble zones contain relatively few cryptic individuals and less biomass per liter substrate, likely due to their low structural complexity and relatively thin habitat depth. Organisms within these habitats would therefore be more easily preyed upon by epibenthic and nektonic consumers. Whereas significant differences between communities standardized to surface area are obscured by the variability of framework depth in LDF, MDF and HDF zones, rubble still sheltered significantly lower densities of individuals than LDF and HDF zones and lower biomass per area than MDF and HDF zones. Again, this is likely due to its degraded and eroded nature resulting in low complexity and depressed sheltering capability.

Outlook and implications

Extrapolation of fine-scale cryptofauna population parameters to the whole reef level provides insight into how reef ecosystems may respond to mass coral mortality and framework erosion. Coral mortality, such as that experienced due to thermal bleaching, disease, or predator outbreaks, is expected to greatly impact the abundance and overall biomass of reef cryptofauna. If it is assumed that coral mortality results in the death of all live-coral associates, mass bleaching and coral mortality on the Playa Larga Reef could result in the elimination of roughly three fifths of cryptofauna individuals and two thirds of total cryptic biomass. This is likely an overestimate as non-obligate associates would presumably be able to survive to some degree. However, it is clear that overall community composition, abundances, and biomass would be greatly reduced. As these communities are trophically linked to epibenthic taxa and carnivorous reef fishes, it is expected that their standing stocks would be similarly stunted.

Reef ecosystems with less live coral cover, and those composed of coral morphologies not as conducive to abundant symbiont communities (e.g., massive corals), would likely experience a reduced effect of bleaching. Furthermore, it is noteworthy that abundant cryptofauna populations are found living within dead coral substrates, apparently unassociated with living coral. Therefore, it is expected that abundant cryptic communities may persist after coral mortality, continuing to play their important role in reef trophodynamics. Ultimately, bioerosion and framework destruction will lead to the collapse of cryptofauna populations as reef structures progressively lose their three-dimensional complexity and sheltering capability.

These findings are especially applicable to an understanding of reef fish dynamics following coral mortality. While populations of obligate corallivorous fishes decline following the death of their food source, facultative species exhibit decreases in abundances paralleling the deterioration of reef framework complexity (Graham et al. 2009). There are time-lags in reef fish declines following bleaching events (Graham et al.

2007) and it is possible that these trends are related to depressed cryptofauna biomass within framework crypts. Garpe et al. (2006) have observed that invertivore fish populations experience little effect from coral mortality, but instead decline following erosion of framework structures. It is likely that these fishes are dependent, in part, on the availability of reef crypts and cryptofauna, such that their abundances are correlated with that of their food source. Coral bleaching may even result in an immediate but discrete pulse of food availability as sheltering symbionts become more easily preyed upon by fishes (Coker et al. 2009). However, it is clear that if coral mortality events are frequent enough to result in net erosional reef ecosystems, cryptofauna and certain fish populations will tend towards collapse.

Chapter 4: Environmental determinants of cryptofauna community composition: an experimental analysis of coral cover, framework porosity, and flow

Coral reef cryptofauna describes organisms hidden from surface conditions in the cavities and recesses of reef framework structures. In many reef ecosystems, they are more species rich (Reaka-Kudla 1997) and comprise greater biomass (Ginsburg 1983; Richter et al. 2001) than the epibenthos and nekton. Their members include ecologically important suspension feeders (Richter & Wunsch 1999), predators (Reaka 1987; Glynn 2006), herbivores (Coen 1988), and detritivores (Rothans & Miller 1991) that are connected to surface communities through diverse trophic linkages. As with epibenthic reef communities (Done 1983), dynamic cryptofauna populations are affected by and distributed according to a variety of biological and environmental factors, though direct relationships and mechanisms are often unclear and unstudied.

Live coral substrates may support elevated cryptofauna biomass and different species assemblages than their dead coral counterparts (Coles 1980; Preston & Doherty 1990, 1994; Enochs & Hockensmith 2008). However, live coral tissues may inhibit the penetration of endolithic bioeroders (Hutchings 1985; Fonseca et al. 2006) and deter epilithic fauna sensitive to cnidae and mucus production (Kirsteuer 1969). This mucus, combined with adhering organics and other metabolic products of the coral, is used by a variety of cryptofauna for food and may be responsible for the elevated biomass of symbiont communities mentioned earlier (Stimson 1990). Corals release mucus at rates up to 4.8 l m^{-2} reef d^{-1}, potentially providing an important nutrient source for cryptic organisms not just inhabiting coral surfaces but on surrounding frameworks and sediments as well (McCloskey 1970; Wild et al. 2004). Despite this, Idjadi and Edmunds (2006) found no significant relationship between percent coral cover and the abundance of reef associated invertebrates. It is therefore not clear if corals elevate the metazoan biomass surrounding them.

Studies concerning the effects of substrate structure and porosity on cryptofauna communities have primarily focused on live corals and their associates. The work of Kirsteuer (1969), Edwards and Emberton (1980), as well as Vytopil and Willis (2001) have all shown a positive correlation between coral branch density and the abundance of sheltering cryptofauna. Similarly, Shirayama and Horikoshi (1982) found that coral morphology (e.g., massive vs. branching) is an important determinant of the composition of associated cryptic communities. While relationships between dead coral substrate structure and cryptofauna do exist, they are often complicated or obscured by extraneous factors (Hutchings & Weate 1977). Idjadi and Edmunds (2006) observed a positive correlation between topographic complexity and invertebrate diversity (many with cryptic behaviors), but not abundances. However, in extreme cases where bioerosion has severely limited shelter availability, the abundances and biodiversity of cryptic fishes may be depressed (Glynn 2006).

The effects of water movement on cryptic reef populations are similarly complicated by high variability as well as covariance with environmental conditions such as light and depth (Martindale 1992). Flushing may provide food to cryptic sessile suspension feeders (Buss & Jackson 1981) as well as sources of pelagic larvae; however high current velocities, such as those experienced during storms, may overturn and disturb cryptic shelters to the detriment of their occupants (Gischler & Ginsburg 1996).

The hidden nature of cryptic biota, their close association with ecologically sensitive structural taxa, as well as their high variability across different reef microhabitats all make replicate sampling of cryptofauna across environmental gradients difficult and in most instances impractical. To this end, workers have employed artificial substrates, often fashioned from rubble or framework materials. Peyrot-Clausade (1977) was one of the first to adopt this approach and used bags of coral fragments to investigate patterns in the colonization and succession of cryptofauna. A similar technique was employed by Glynn (Simulated Reef Framework, SRF, 2006) and Valles (Standard Monitoring Unit for the Recruitment of Fishes, SMURF, 2006) to examine the recruitment of cryptic fishes to artificial framework structures. Zimmerman and Martin (2004) described the construction of Artificial Reef Matrix Structures (ARMS), which included both natural (rubble) and artificial substrates (scrub pads, filter pads, concrete plates). Takada et al. (2007) examined succession of cryptic decapods and gastropods associated with baskets of coral rubble. Finally, Takada et al. (2008) examined multi-phyletic cryptic communities along a sediment gradient using a similar methodology.

To our knowledge, there are currently no studies that experimentally investigate the effects of flow, coral cover, and porosity on cryptic reef populations. Given the relevance of these factors to other reef communities (e.g., corals and fishes) and the often convoluted relationships with cryptofauna as shown by descriptive studies, it is necessary to employ experimental manipulations to examine the effects of environmental conditions on the functionally important and diverse cryptofauna.

Materials and methods

Two 20 x 20 m plots were located roughly 400 m apart at Playa Larga Reef (8°38'0.75"N 79°1'47.90"W), Isla Contadora, Pearl Islands, Panamá (Figure 4.1). Both sites were at similar depths and had comparable live coral cover (Figure 4.1). The exposed northern site (Figure 4.1a) was assumed to be subject to more water flow than the southern site (Figure 4.1b). Paired mechanical flow meters (General Oceanics model #2030R) were deployed at both sites for periods of roughly 24 hours to corroborate this assumption. Flow meters were placed at the SW corner of each site and positioned less than a meter above the reef.

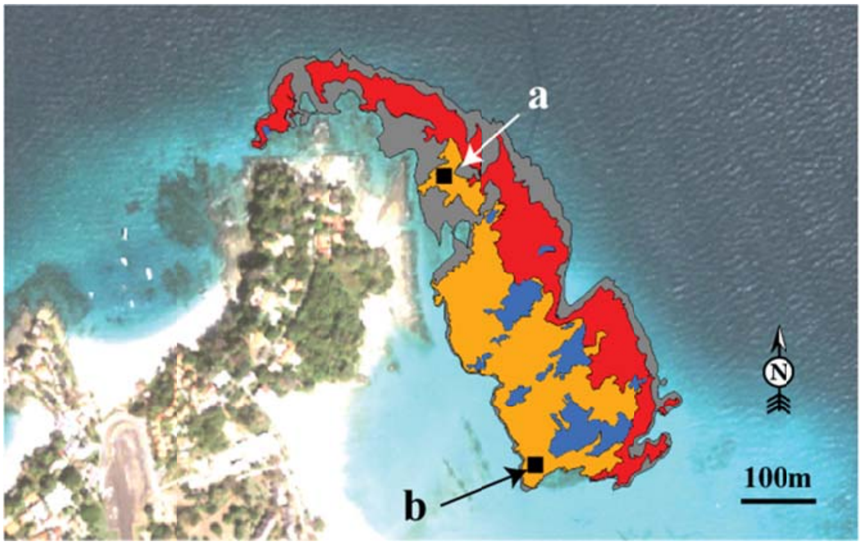

Figure 4.1. Playa Larga Reef at Isla Contadora, Pearl Islands. a, high flow site. b, low flow site. Red denotes high coral cover zone ($\bar{x} = 76.7\%$ coral cover, 36,300 m^2); orange is intermediate coral cover ($\bar{x} = 38.4\%$ coral cover, 41,400 m^2), blue is low coral cover ($\bar{x} = 13.0\%$ coral cover, 11,100 m^2), gray is a rubble margin with low abundances of mobile coralliths ($\bar{x} = 10.9\%$ coral cover, 31,600 m^2).

Artificial Reef Framework units (ARFs) were constructed from plastic mesh (~2.4 x 2.1 cm holes) held together with plastic cable ties to form open-topped cylinders, roughly 23 cm high and 28 cm in diameter. Each ARF “basket” was tagged and assigned treatment combinations of flow (fast vs. slow), porosity (high vs. low), and cover (live vs. dead coral). Unconsolidated dead coral rubble was removed from disturbed sections of the Playa Larga reef, cleaned of large sessile macrobiota, and allowed to sun dry for more than a week. ARFs were filled with small and large rubble in order to create low (Figure 4.2a) and high porosity treatments (Figure 4.2b) respectively. The volume of rubble within each ARF was measured with water displacement and adjusted so that treatments were consistent.

Twenty ARFs, 10 of each porosity treatment, were placed at each of the high and low flow sites. Within each site, ARFs were positioned according to randomly selected X and Y coordinates across a 20 x 20 m grid. ARFs were secured to rebar hammered into the substrate and large fragments of live and dead coral (collected from outside of the experimental plots) were affixed with heavy-test monofilament line to the open surface of the live and dead treatment ARFs, respectively (Figure 4.2c,d).

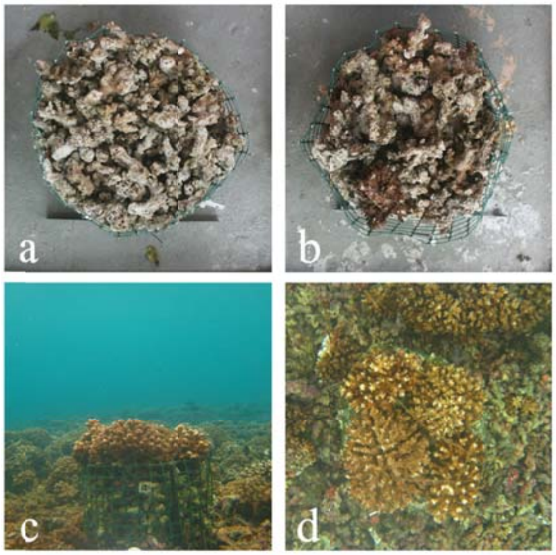

Figure 4.2. Porosity treatments (a, low; b, high) and live coral treatment of ARFs (c, side view; d, top view).

Flow at the high flow site ($\bar{x}$ = 13.4 cm s^{-1}) was consistently higher than the low flow site ($\bar{x}$ = 1.2 cm s^{-1}) when averaged over their roughly day-long deployment (Figure 4.3a). Porosity treatments were standardized to high ($\bar{x}$ = 76.2% void space, SD = 1.7) and low ($\bar{x}$ = 58.2% void space, SD = 1.3; Figure 4.3b). During the duration of the experiment, dead coral became detached from the surface of three fast flow/low porosity treatments. Cover treatments were partially removed from a single dead and two live coral slow current/low porosity treatments. These six perturbed cover treatments were included in further analysis as it was not known when the treatment substrate became detached. Additionally, all ARFs treated with living coral retained some of their original treatment, while those that lost all of their dead framework cover were themselves composed of dead framework.

A t-test of porosity treatments between flow sites following the run of the experiment revealed a significant difference (t-test, 2 tails, $p = 0.04$) between low porosity treatments. While natural variation in the volume of the ARF container (due to its flexibility) likely obscured the 2.66% lower mean porosity at the low flow site, a single anomalously low porosity replicate at the low flow site was not included in statistical tests (ANOVA and PERMANOVA) in order to eliminate potential bias.

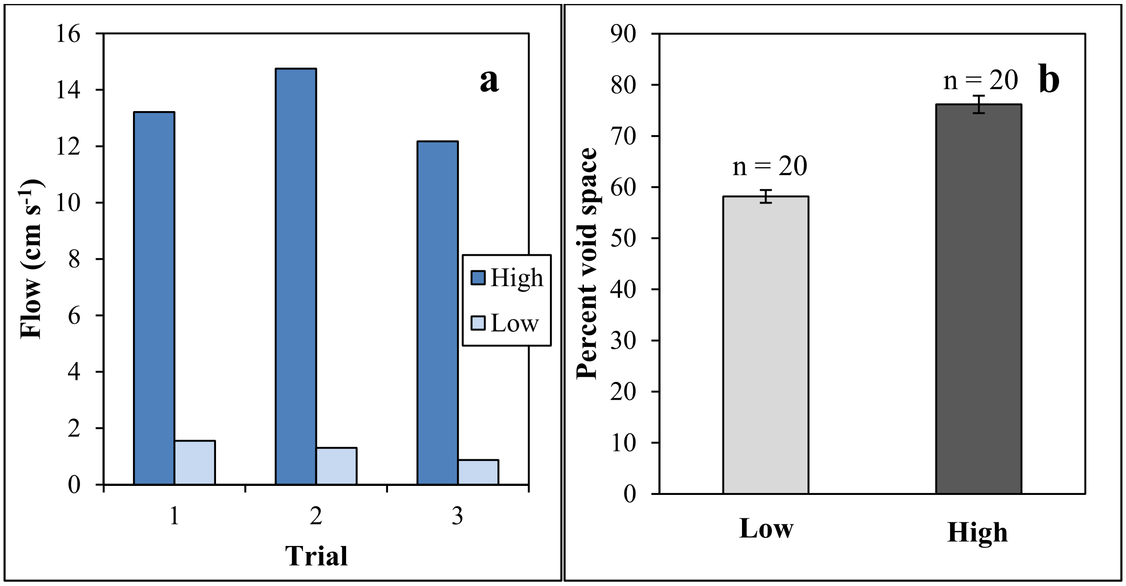

Figure 4.3. a, Flow speed at high and low flow sites obtained from paired current meters. Trial 1, Nov. 17-18; Trial 2, Nov. 19-20; Trial 3, Dec. 3-4. b, mean percent void space for high and low porosity treatments. Error bars show ± 1 standard deviation around the mean.

ARF units were deployed on September 22, 2008 and removed after approximately two months *in situ* (collected from November 26 to December 2). During collection, live and dead coral cover treatments were removed underwater and ARF units were placed in plastic buckets which were quickly brought to the surface. Few metazoans were observed to escape during ARF collection and those that did were noted. Water and ARF rubble was separated over a 2 mm mesh filter and all cryptofauna were removed from the surface of framework fragments with forceps. All specimens were preserved in 70% EtOH.

Individual organisms were counted and operational taxonomic units (OTUs) were identified according to the methodology of Chapter 2. Wet weights were recorded according to the methodology of Chapter 3 and converted to ash-free dry weights (AFDW) according to Chapter 3, Appendix 1. Specimens were assigned to trophic groups according to Chapter 3, Appendix 2 (CM, carnivore multiple strategies; CP, carnivore predator; DD, detritivore deposit feeder; HG, herbivore grazer; OG, omnivore grazer; OO, omnivore opportunistic; SU, suspension feeder).

Treatment-specific abundance and biomass data for each taxon was compiled into two OTU-sample data matrices using Matlab. Data matrices were loaded into the Plymouth Routines in Multivariate Ecological Research (PRIMER-E) with PERMANOVA+ software package (Anderson et al. 2008). Two sub-matrices were formed from each of the abundance and biomass data matrices by either filtering out non-OTUs or grouping all taxa into trophic groups irrespective of OTU status. Total abundances and biomass were calculated for each ARF as well as three biodiversity metrics (OTU richness, Fisher's ɑ, Shannon's H'($\log_e$)) and percent trophic group composition. Univariate sample parameters were analyzed with SPSS v17.0 using a 3-way ANOVA design. Biomass data was Log10 transformed and percent trophic group data were logit transformed in order to conform to the assumptions of homoscedasticity; though OG, HG, and DD were still found to have heterogeneous variances (Lavene's test).

Raw abundance and biomass data matrices were square root transformed and Bray Curtis similarity matrices were constructed. Non-metric multidimensional scaling (nMDS) plots of OTU-sample abundance and biomass matrices were constructed and dendrograms were created from group-averaged cluster analysis. Treatment centroids were ordinated in two-dimensional space using principal coordinate analysis (PCO) of OTU abundance and biomass data. The dimensionality of untransformed abundance and biomass data was reduced by consolidating taxa into trophic groups. The resulting data were square root transformed and ordinated using PCO. Trophic group vectors were superimposed onto the Euclidian space of the PCO plots in order to investigate their linear correlation (Pearson) with the ordination axes. Permutational Analysis of Variance (PERMANOVA) was conducted in order to test the significance of the three treatments and their interactions on the multivariate datasets without the constraints of homoscedasticity and normality inherent in the MANOVA test (Anderson 2001). Pseudo F-ratios were computed from 99,999 permutations.

Results

Taxa collected

A total of 180 OTUs were collected, 121 of which were identified to the species level. Collected cryptofauna belonged to six phyla, 10 classes, 22 orders, 33 superfamilies, 83 families and 118 unique genera. 10,297 specimens were assigned OTU status out of a total of 11,309 individuals collected. The remaining 1,012 individuals were included in abundance and biomass totals but not used to compute diversity indices. *Palaemonella* spp. was the most abundant OTU collected, accounting for 11.75% of the OTU specimens. The 25 most abundant species accounted for 87.37% of the individuals (Figure 4.4). These include 14 OTUs belonging to Crustacea, five to Gastropoda, two each to Holothuroidea, Ophiuroidea, and Polychaeta.

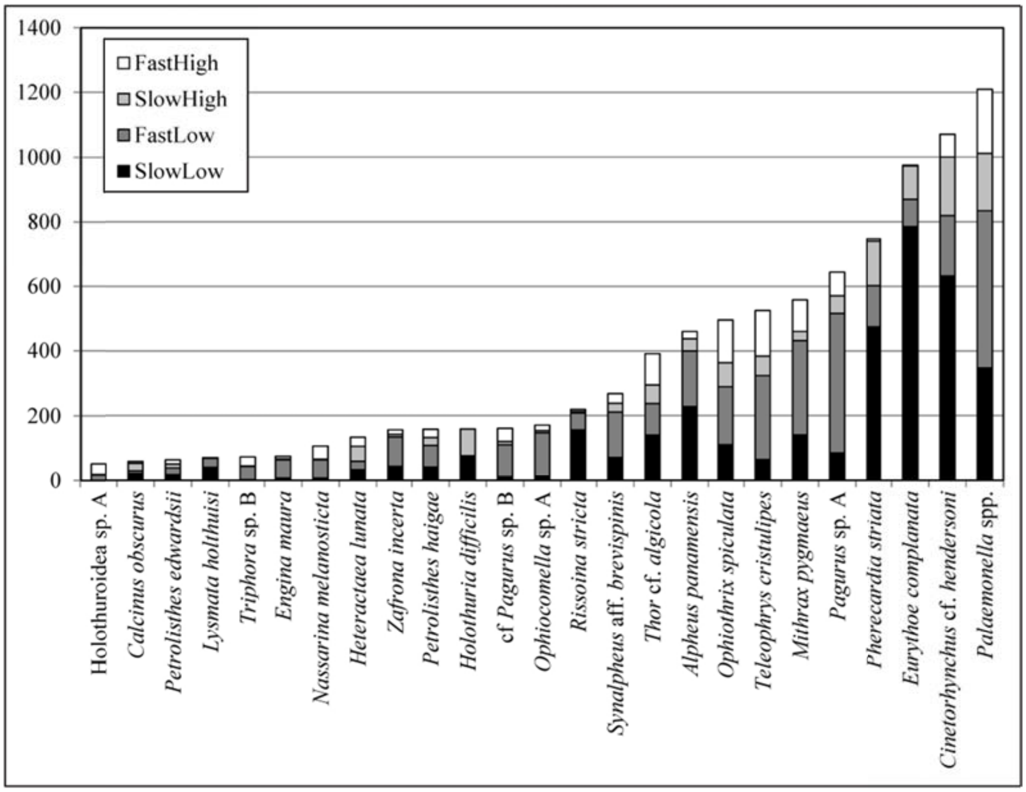

Figure 4.4. The number of individuals collected of each of the 25 most abundant OTUs from each of four unique combinations of flow and porosity treatments.

Univariate analysis

Univariate sample statistics for each of the eight unique treatment combinations are given in Table 4.1 and the *p* values from a 3-way ANOVA analysis of treatment and interactions effects are shown in Table 4.2. Porosity was found to have a significant effect on abundance, abundance per liter substrate, biomass, biodiversity (all metrics) as well as the percent CM and OO trophic groups. Low porosity treatments were associated with higher abundances, abundance per liter framework, biomass, and richness, yet Fisher's, and Shannon's, biodiversity indices were highest for high porosity treatments. Flow did not significantly affect cryptofauna OTU abundance. However, total biomass, biomass per liter substrate, all biodiversity indices, as well as percent CG, CM, HG, and SU trophic groups were all significantly affected. Biomass and biomass per liter framework were highest in slow flow environments, while all biodiversity indices were positively influenced by high flow. CM were more prominent in low flow environments while CG, HG, and SU biomass were proportionally more important under high flow conditions. Cover was not found to significantly affect any of the measured community statistics or terminal biodiversity metrics, however there was a significant ($p = 0.017$) effect on %CG biomass(lower on live coral treatments). Marginally significant interaction effects were obtained for cover and flow’s effect on total abundance ($p = 0.045$).

Table 4.1. Mean abundance, biomass, biodiversity and trophic composition for each ARF treatment combination. Parentheses denote standard deviation. Values computed from five replicates for each treatment combination with the exception of the Low, Slow, Live with four replicates (39 total).

Treatment			**Community**				**Biodiversity**			**Trophic composition, (%AFDW)** [a]							
Porosity	**Flow**	**Cover**	Total Abundance	Abundance frame^{-1} (indiv. l^{-1})	Biomass (g AFDW)	Biomass frame^{-1} (g AFDW l^{-1})	Richness	Fisher's α	Shannon's H'(loge)	%CG	%CM	%CP	%OG	%OO	%HG	%SU	%DD
Low	**Slow**	**Live**	451.3	76.0	5.7042	0.9588	38.0	10.28	2.58	0	56.2	11.1	0.2	15.0	4.8	3.9	8.4
			(55.3)	(10.2)	1.2957	(0.2184)	(4.3)	(1.62)	(0.18)	(0)	(11.6)	(11.9)	(0.1)	(7.1)	(2.7)	(1.7)	(15.2)
Low	**Slow**	**Dead**	399.6	66.4	5.8397	0.9701	36.8	10.31	2.66	0	40.7	24.3	0.1	20.3	5.1	5.8	3.3
			(45.3)	(8.2)	(1.6388)	(0.2716)	(4.3)	(1.47)	(0.04)	(0)	(11.5)	(15.6)	(0.1)	(9.8)	(2.7)	(3)	(7.4)
Low	**Fast**	**Live**	368.4	63.8	3.2959	0.5740	43.8	13.59	2.96	0.3	27.3	21	0.5	16	15.6	8.3	10.4
			(41.7)	(6.9)	(0.8023)	(0.1579)	(6.1)	(2.26)	(0.21)	(0.6)	(19.7)	(24.9)	(0. 3)	(10.3)	(7.3)	(4.7)	(3.5)
Low	**Fast**	**Dead**	423.6	71.5	3.4990	0.5908	43.4	12.59	2.96	1.4	19.1	26.5	0.3	16.6	15	12.6	4.7
			(79.2)	(12.8)	(1.2603)	(0.2124)	(6.2)	(1.94)	(0.13)	(2.8)	(16.7)	(21.5)	(0.1)	(5.5)	(3.9)	(13.1)	(6.4)
High	**Slow**	**Live**	147.0	41.4	3.0762	0.8742	30.4	12.08	2.81	0	20.6	17.1	7.6	31.8	4.8	7.3	9
			(37.2)	(10.8)	(1.1172)	(0.3452)	(6.2)	(2.55)	(0.18)	(0.1)	(9.5)	(24.6)	(17)	(13.8)	(1.8)	(5.3)	(7.5)
High	**Slow**	**Dead**	145.6	44.4	3.3660	1.0373	29.2	11.70	2.81	0	13.9	25.6	0	26.5	9.6	4.1	20.4
			(30.9)	(9.0)	(1.4466)	(0.4516)	(3.0)	(1.27)	(0.10)	(0)	(3.4)	(18.8)	(0)	(12.6)	(11.3)	(2.4)	(17.4)
High	**Fast**	**Live**	147.4	48.8	1.5099	0.4692	34.6	15.40	2.94	0.3	2.5	34	0.2	21.7	10.1	14.5	5.8
			(35.1)	(11.0)	(0.2755)	(0.0876)	(4.5)	(2.08)	(0.09)	(0.4)	(2.4)	(19.4)	(0.1)	(9.2)	(5.9)	(9.5)	(13)
High	**Fast**	**Dead**	187.0	55.0	1.8649	0.5400	39.8	17.56	3.04	2.4	2.3	22.4	8.1	20	18.1	6.6	1.4
			(86.8)	(27.6)	(0.5806)	(0.1270)	(9.8)	(3.88)	(0.15)	(4.8)	(1.9)	(13.1)	(13.2)	(7.7)	(13.8)	(4.9)	(3.2)

[a] CM, Carnivore multiple strategies; CP, Carnivorous predator; DD, Detritivore deposit feeder; HG, Herbivorous grazer; OO, Omnivore opportunistic; SU, Suspension feeder

Table 4.2. Univariate 3-way ANOVA *p* values for treatments and treatment interaction effects on cryptofauna abundance, biomass, biodiversity and trophic composition (% dry biomass). *P* values for significant effects in bold. n.s. is not significant. Biomass values $\log_{10}$ transformed. Trophic groups values logit transformed. Trophic groups marked with an asterix to not conform to the assumption of homogeneity of variance.

	Community				**Terminal biodiversity**			**Trophic composition (%AFDW)** [a]							
Treatment/interaction	Abundance (indiv.)	Abundance frame^{-1} (indiv. l^{-1})	Biomass (g AFDW)	Biomass frame^{-1} (g AFDW l^{-1})	Richness	Fisher's α	Shannon H'(loge)	%CG	%CM	%CP	%OG*	%OO	%HG*	%SU	%DD*
Porosity	**< .001**	**< .001**	**< .001**	n.s.	**< .01**	**< .01**	**< .05**	n.s.	**< .05**	n.s.	n.s.	**< .05**	n.s.	n.s.	n.s.
Flow	n.s.	n.s.	**< .001**	**< .001**	**< .01**	**< .001**	**< .001**	**< .05**	**< .05**	n.s.	n.s.	n.s.	**< .01**	**< .05**	n.s.
Cover	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**< .05**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Porosity * Flow	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**< .05**	n.s.
Porosity * Cover	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Flow * Cover	**< .05**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Porosity * Flow * Cover	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**< .05**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] CM, Carnivore multiple strategies; CP, Carnivorous predator; DD, Detritivore deposit feeder; HG, Herbivorous grazer; OO, Omnivore opportunistic; SU, Suspension feeder

Multivariate analysis

PERMANOVA revealed highly significant effects of flow and porosity as well as flow and porosity interaction effects on species- and trophic group-specific abundances and biomass (Table 4.3). Treatments of live versus dead coral were not significantly different.

Table 4.3. PERMANOVA *p* values for treatment and interaction effects on the abundance and biomass of species and trophic groups. Analysis for species based on OTUs only. Analysis for guilds based on all taxa assigned to guilds, regardless of OTU status. All data sets were square root transformed and analysis was based on symmetrical Bray Curtis similarity matrices. *P* values based on F-ratios constructed from 99,999 permutations. *P* values for significant effects in bold. n.s. is not significant.

	Species		**Trophic groups**	
Treatment/interaction	**Abundance**	**Biomass**	**Abundance**	**Biomass**
Flow	**< .0001**	**< .0001**	**< .0001**	**< .0001**
Porosity	**< .0001**	**< .0001**	**< .0001**	**< .0001**
Cover	n.s.	n.s.	n.s.	n.s.
Flow*Porosity	**< .0001**	**< .0001**	**< .0001**	**< 0.01**
Flow*Cover	n.s.	n.s.	n.s.	n.s.
Porosity*Cover	n.s.	n.s.	n.s.	n.s.
Flow*Porosity*Cover	n.s.	n.s.	n.s.	n.s.

Visualization of the data in two-dimensional Euclidian space with nMDS, resulted in relatively high stress levels (Figure 4.5; biomass, 0.18; abundances, 0.16), which is not surprising considering the high dimensionality of the original data (180 OTUs). Regardless, clustering of replicates was observed to correspond to porosity and flow treatments. Patterns are more apparent in the abundance data. High porosity treatments are less similar, clustering out at the >47% and >55% similarity level for fast and slow flow, respectively. All low porosity treatments cluster out at >53% similarity and within this, fast and slow treatments levels cluster at the >57% and >66% similarity level, respectively. There was more overlap between treatments when biomass data was considered. Several replicates of a given porosity/flow treatment combination were more similar to replicates of other porosity/flow treatment combinations than that of themselves. Patterns are still apparent, with all slow flow/low porosity treatments clustering at >59% similarity. Eight each of the high porosity treatments cluster at the >42% and >39% similarity level, slow and fast flow respectively. There are two groups of fast flow/low porosity treatments (5 replicates each; >51%, >52% similarity) though one is more similar to other slow flow/low porosity treatments.

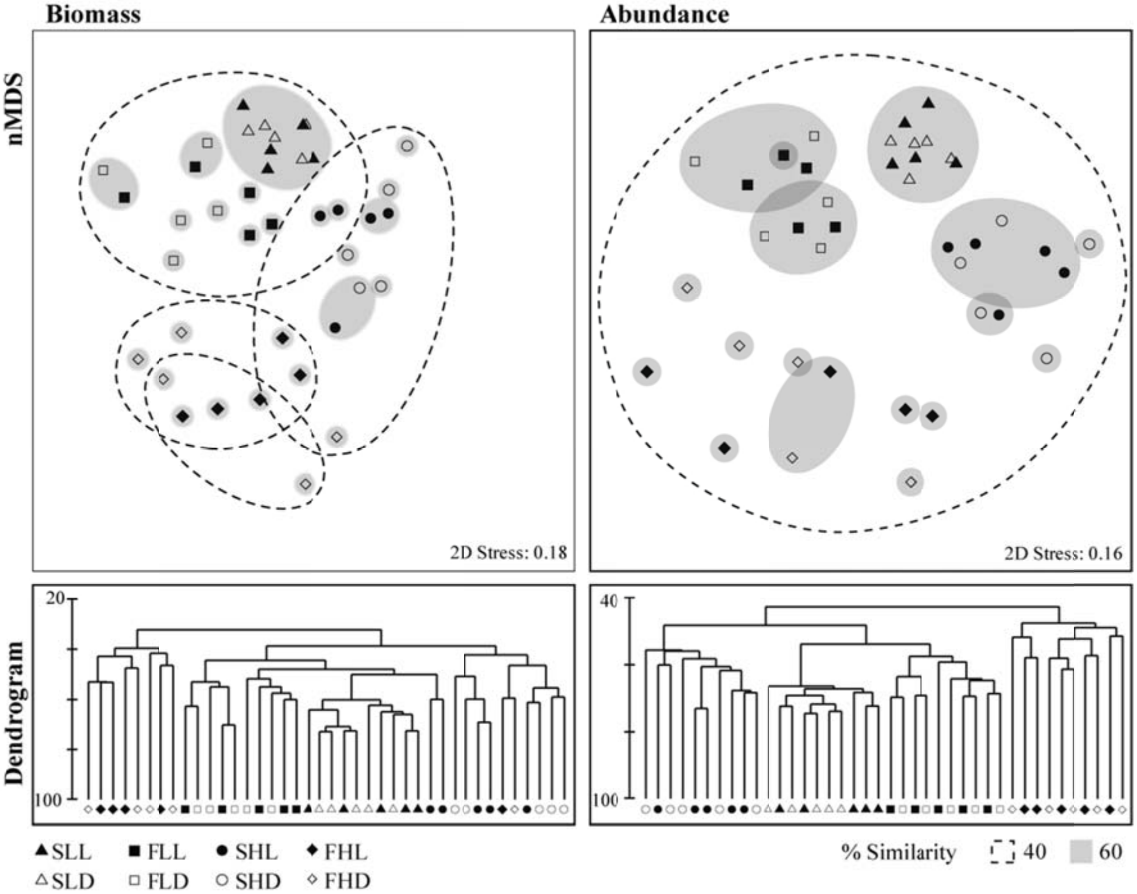

Figure 4.5. Two-dimensional nMDS plots of cryptofauna OTU biomass (stress = 0.18) and abundance (stress = 0.16) with corresponding dendrograms constructed from Bray Curtis similarity. Dashed and shaded regions in the nMDS plots represent 40 and 60% similarity, respectively. First letter represents current (S, Slow; F Fast), second letter represents porosity (L, Low; H, High), third letter represents coral cover (L, Live; D, Dead). All data were square root transformed.

Plotting the centroids of each treatment in two PCO dimensions, reveals similar patterns affecting both community biomass and abundance (Figure 4.6). In both plots, the majority of variation (PCO1) was between slow flow/low porosity and fast flow/high porosity treatments. There was little differentiation along the PCO1 axis between slow flow/high porosity, and fast flow/low porosity treatments. These instead showed separation along the PCO2 axis. Little separation was observed between live and dead coral cover treatments.

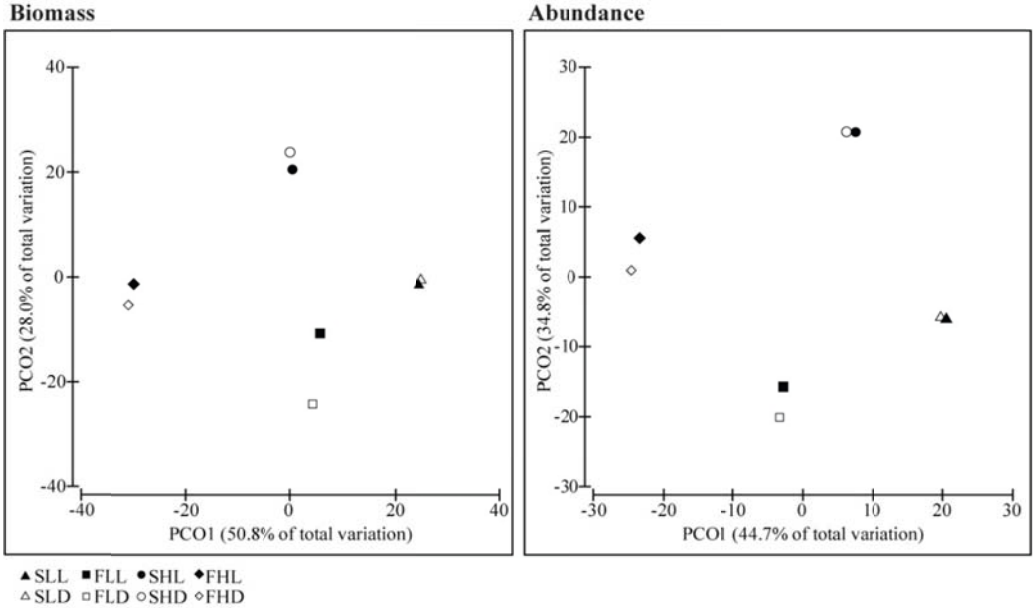

Figure 4.6. PCO plots of treatment centroids for cryptofauna OTU biomass and abundance. Biomass and abundance plots explain 78.8% and 79.5% of the variation, respectively. Three letter codes indicate treatments. First letter represents current (S, Slow; F Fast), second letter represents porosity (L, Low; H, High), third letter represents coral cover (L, Live; D, Dead). Data is square root transformed and distances are based on Bray Curtis similarity.

Reduction in data dimensionality through partitioning of specimens into trophic groups and subsequent ordination through PCO again reveals patterns in porosity and flow treatment combinations as well as linear correlation with specific trophic groups (Figure 4.7). Similar to the nMDS plots, patterns are less clear within biomass-derived ordination. Regardless, there is separation of the fast flow/high porosity treatments along PCO1, negative correlation between this treatment and CM and OO trophic groups, as well as weak positive correlation with the CG trophic group.

The trophic group abundance PCO plot shows clear differentiation between porosity treatments along PCO1 (47.9% of the variation) and separation of flow treatments along PCO2 (30.8% of the variation). Trophic group vectors reflect positive linear correlation with low porosity treatments. Again, the OO trophic group is negatively correlated with fast flow/high porosity treatment. CM is positively correlated with slow flow/low porosity treatments and the OG, HG, SU and CP groups appear to correlate with fast flow/low porosity treatments.

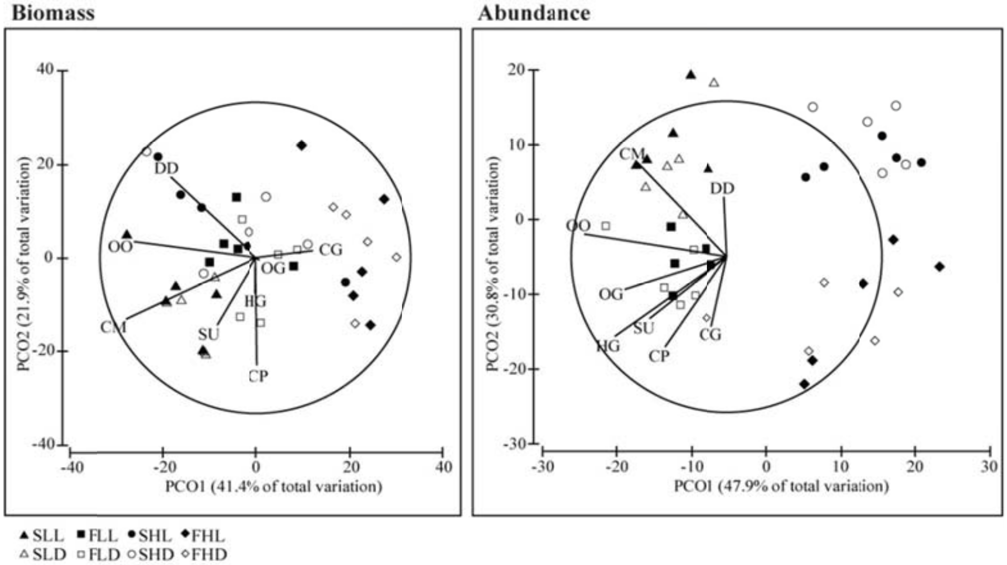

Figure 4.7. PCO plots of treatment replicates for the biomass and abundance of cryptofauna trophic groups. Biomass and abundance plots explain 63.3% and 78.7% of the variation respectively. Vector overlays represent linear correlation (Pearson) between a the transformed (square root) biomass or abundance of a given trophic group and the ordination axes (CM, Carnivore multiple strategies; CP, Carnivorous predator; DD, Detritivore deposit feeder; HG, Herbivorous grazer; OO, Omnivore opportunistic; SU, Suspension feeder). Vector length is proportional to the degree of correlation with length equal to the radius of the circle corresponding to a correlation of 1.0. Three letter codes indicate treatments. First letter represents current (S, Slow; F, Fast), second letter represents porosity (L, Low; H, High), third letter represents cover (L, Live; D, Dead). Data is square root transformed and distances are based on Bray Curtis similarity.

Discussion

Porosity

Framework porosity is an important determinant of cryptofauna community composition. Low porosity frameworks had greater abundances and biomass likely due to greater substrate surface area, habitat complexity, and possibly due to greater protection from pelagic predators. It is cautioned that the porosity treatments in this experiment do not represent the degradation of an individual piece of framework, as the fragmentation of the high porosity treatment would result in a low porosity habitat of smaller volume. Therefore, measurements of abundance and biomass apply to the characteristics of a habitat and not to its progressive destruction. However, standardization of these same community parameters to framework volume provides a metric that is more applicable to the loss of framework complexity as it is independent of the quantity of substrate within each treatment. Indeed, cryptofauna community abundances (but not biomass) are higher per volume substrate, suggesting that intermediate levels of framework degradation may lead to increases in community abundances.

While species richness was higher in the low porosity treatments, two computed diversity indices (α, H’) indicated greater biodiversity within high porosity treatments. This difference is likely due to higher numbers of individuals within low porosity ARFs. The incorporation of evenness, as done by these two diversity metrics, is therefore necessary to compare the two treatments. Higher cryptofauna diversity within high porosity treatments may be due to greater niche diversity. More open environments likely allowed greater light penetration and more access to suspended matter. These factors could have facilitated the settlement of sessile taxa utilized for shelter and sustenance by the motile cryptofauna collected in this study. This hypothesis is not statistically supported by the univariate ANOVA analysis of trophic guilds or by the correlation vectors of the PCO plots and it is therefore necessary to explore these ideas in greater depth. Other possible reasons for lower biodiversity in lower porosity treatments include small void sizes restricting the movement/occupation of larger/less agile taxa or reduced predation pressure leading to the proliferation of competitively dominant species.

It is cautioned that the depth of the habitat may influence both light penetration and particle deposition as well as the ease of access by cryptofauna prey and predators. Therefore, communities living in low porosity surface crypts or within relatively thin rubble veneers may experience conditions similar to deeper, more open reef recesses. In the former environments it is yet to be seen if cryptofauna diversity may be in fact higher than in deep porous habitats.

Flow

Slow flow environments are likely more conducive to the development and accumulation of cryptofauna biomass for a variety of reasons. Low flow environments often have greater sediment and organic matter deposition/retention, thereby leading to greater nutrient availability and more cryptofauna biomass. This hypothesis in not clearly supported by significant changes in the proportion of trophic groups, however decreases in HG and SU trophic groups may be sediment-related, due to covering of algae and clogging of filter apparatus, respectively. PCO plots reveal that DD trophic group vectors are correlated with low flow environments, which may represent an elevated detritivorous pathway corresponding to increased sedimentation. Alternatively, current- or wave-related disturbance could limit cryptofauna communities in high flow environments (Gischler & Ginsburg 1996). However, the applicability of this hypothesis is questionable due to the consolidated nature of the ARF unit bags. Regardless, in loose rubble environments substrate mobility may disturb cryptofauna, further exaggerating patterns observed in this study.

Higher richness and biodiversity within high flow environments may be explained by greater access to more species rich planktonic larvae sources. Alternatively, greater flushing may have led to higher diversity of sessile flora and fauna that might not have been able to tolerate greater sedimentation in low flow environments. Greater quantities and varieties of epilithic flora and fauna may have supported a higher diversity of motile cryptofauna. While this is difficult to discern from the biomass PCO plot, ordination of abundance data reveals 5 trophic group vectors positively correlated with high flow environments as opposed to 3 with low flow.

Coral cover

Considering that 56 to 80% of coral mucus may dissolve into surrounding seawater (Wild et al. 2004), it is not surprising that coral cover was not observed to affect cryptofauna communities occupying framework substrates below. It is conceivable that under abnormally calm and oligotrophic conditions, the role of mucus may be more important. However, in turbulent reef environments it is unlikely that live coral cover corresponds to elevated metazoan biomass in the frameworks immediately surrounding them. Coral tissues and mucus are undoubtedly an important source of nutriment for many reef organisms; however, it is likely that they must either be consumed directly from a colony's surface by micro or macrobiota, or from the water column and interstitial spaces by microorganisms. It is hypothesized that the trophic interactions involving the consumption of coral tissues and metabolic byproducts are either highly localized and limited to colony surfaces, or they are diffuse and spread out over large reef surface areas. These experimental results support the findings of Idjadi and Edmunds (2006) who found no effect of coral cover on local invertebrate abundances.

The single anomalous and marginally significant effect of coral cover on % CM biomass is difficult to explain as the CM trophic group contains both carnivorous predators and grazers. Of the 11 taxonomic groups assigned to this trophic group, 5 belong to the Polychaeta (Syllidae, Polynoidae, Phyllodocidae, Lumbrineridae, Chrysopetalidae, Amphinomidae). If this effect is not a type I error (false positive), it is likely due to these taxa, especially *Pherecardia striata* and *Eurythoe complanata* (Amphinomidae) which were especially prevalent within ARF replicates.

Interactions

Difficulties in explaining the effects of flow on cryptofauna populations may have been in part due to an interaction with porosity. While this is not reflected in the univariate ANOVA, PERMANOVA revealed a highly significant flow/porosity interaction effect on cryptofauna (OTUs and trophic groups) abundances and biomass. Additionally, fast flow/high porosity treatments tend to cluster more clearly in the nMDS and dendrogram plots. Considering the baffling nature of low porosity frameworks, this is not surprising. Presumably the occupants of low porosity crypts in faster flow environments would experience flow levels similar to low flow environments. High porosity/high flow environments were therefore unique in that their occupants were not as sheltered from the high flow conditions.

Implications

The results of this study may be considered from two different perspectives: 1. the spatial distribution of reef cryptofauna across environmental gradients and reef habitats, 2. how cryptofauna communities respond to ecosystem degradation. Coral reef cryptofauna are likely to be more abundant and of greater biomass in low porosity, low flow environments, similar to that in sheltered back-reef rubble piles or in deeper fore-reef rubble margins. In some areas, small broken coral fragments may be of greater importance in sheltering these communities than open, intact frameworks. Conservation efforts and management strategies designed to preserve ecosystem function and trophic pathways need to consider classically “less important” reef habitats such as eroded areas which may not have large amounts of live coral cover.

Similarly, bleaching and mass coral mortality may not have large immediate effects on framework-dwelling cryptofauna abundances, biomass and biodiversity. Abundances of these taxa may even rise during bioerosion of reef framework structures. However, over longer time periods, habitat loss and extreme decreases in structural complexity will likely lead to the elimination of these communities and by extension, other reef taxa which rely on them.

Chapter 5: Death brings life to eastern Pacific coral reef biodiversity

Coral reefs contain among the highest concentrations of species of any marine ecosystem and likely support the greatest number of metazoan phyla of any ecosystem on the planet (Adrianov 2004; Small et al. 2008). They are aptly considered ‘the rainforests of the sea,’ existing as vast and underexplored repositories of biological diversity. Cryptic coral reef organisms, termed the cryptofauna, are similar to the rainforest insects in that they make up the majority of animal biodiversity, a large proportion of biomass, and are important trophodynamic links vital to ecosystem function (Ginsburg 1983; Reaka-Kudla 1997).

Despite the importance of the coral reef cryptofauna, there is little quantitative evidence on how these communities respond to coral mortality and framework degradation. The general assumption is that coral reef biodiversity will decline drastically with the mortality of the ecosystem-engineering scleractinian corals (Knowlton & Jackson 2008; Glynn 2011). Indeed, those organisms that directly depend on live coral usually share its fate during a mortality event. For example, shortly after coral bleaching (< 2 months), the abundance and richness of cryptic decapod associates declines (Caley et al. 2001), and over longer intervals (1-2 yrs), community biomass does as well (Enochs & Hockensmith 2009), reflecting the subsequent mortality of these obligate live coral symbionts. Non-obligate commensals also experience an increase in predation because they become less camouflaged against the white background of bleached coral and more obvious to predators (Coker et al. 2009). However, these declines represent only a small fraction of the overall diversity found on reefs.

To begin to understand what happens to the remainder of the reef's biodiversity following coral mortality, we sampled cryptofauna communities from both live coral substrates and reef framework structures (dead coral) representing a gradient of increasing degradation and erosion (Figure 5.1). Biodiversity was greatest among reef framework structures, or the non-living coral 'rock' (Figure 5.2a). Dead coral that had undergone the most degradation (rubble) was the most species rich and richness decreased incrementally within each successively more intact reef framework structure (Figure 5.2b).

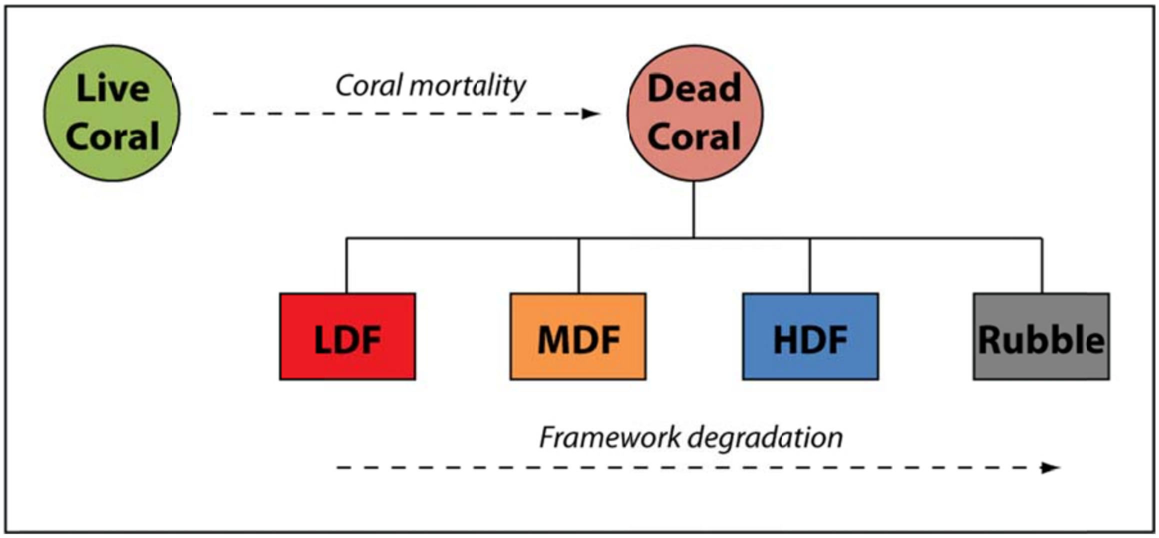

Figure 5.1. Substrates sampled and the degradation of skeletal materials following coral mortality. Dotted lines show processes responsible for their creation. LDF, low degradation framework; MDF, medium degradation framework; HDF, high degradation framework.

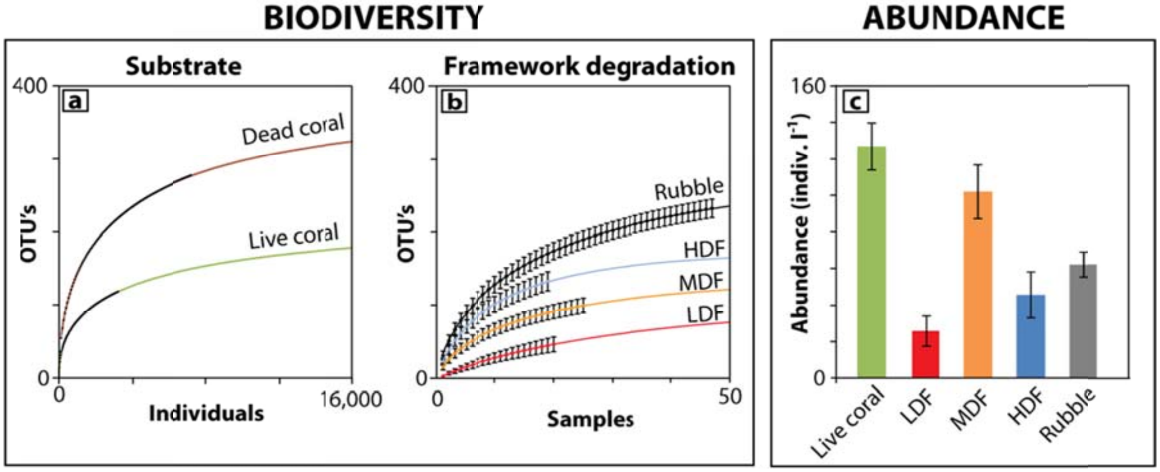

Figure 5.2. Species richness (number of operational taxonomic units, OTUs) and abundance of cryptofauna populations associated with live and dead coral substrates. a, Individual-based rarefaction (Coleman curves) of communities associated with live (green) and dead coral substrates (red), black lines represent number of individual operational taxonomic units (OTUs) sampled, fitted with colored Weibull cumulative distribution functions ($R^2 = 0.9998$ for both). b, Sample-based rarefaction (Mao Tau) for framework substrates in order of increasing degradation: LDF, low degradation framework; MDF, medium degradation framework; HDF, high degradation framework; Rubble. Fitted with Weibull cumulative distribution functions, $R^2 = 1.0000, 0.9999, 0.9998, 0.9999$, respectively). c, Mean abundance of cryptofauna per volume substrate associated with live coral, LDF, MDF, HDF, and Rubble. Error bars represent ± 95% confidence interval in both b and c.

These results are not surprising considering the myriad of defenses possessed by scleractinian corals (e.g., nematocysts, mesenterial filaments, allelopathic chemicals, mucus) and the need for closely associated taxa to be narrowly adapted to live within their unique habitat space (Patton 1974; Lang & Chornesky 1990). The entire existence of coral reefs is a result of the ability of corals to be domineering competitors, effectively excluding many other species. In contrast, dead coral frameworks and rubble support a more heterogeneous suite of sessile flora and fauna that encourage the occupation of diverse associates. Herein, differences in richness between live and dead substrates shown by rarefaction likely overestimate the biodiversity associated with live coral, as many of the colonies sampled contained areas of dead skeleton (e.g., dead basal branches). Therefore, the relative paucity of live coral associated species observed in this study would be even more pronounced had it been possible to exclusively sample live coral substrates.

The higher community richness associated with more degraded dead coral substrates is consistent with the predictions of the intermediate disturbance hypothesis (Grime 1973; Connell 1978). In low disturbance environments, contiguous stands of high coral cover restrict the recruitment and proliferation of the cryptofauna to the cracks and crevices in the frameworks below. However, in more degraded areas, such as rubble zones, cryptofauna diversity is elevated because there are fewer barriers to recruitment and more diverse benthic flora and fauna on which settling animals may thrive. At the highest levels of reef framework degradation, characterized by fine sediment and silt, cryptic macrofauna diversity is much lower than what occurs on a structural reef.

With respect to cryptofauna abundances, numbers of individuals were higher (per volume substrate) on living rather than dead coral (Figure 5.2c). Various metabolic byproducts and food sources are concentrated on the highly productive live coral colonies (tissues, mucus, fat bodies, captured plankton and particulate organic matter) and are exploited by a less diverse, yet more abundant suite of specialized organisms (Stimson 1990; Patton 1994; Rotjan & Lewis 2008). Intact, high-relief framework structures (‘low degradation framework’, LDF), contained the lowest abundances of individuals per volume substrate. The more degraded and eroded low-relief framework structures (‘high degradation framework’, HDF) and loose rubble zones with the least structural complexity, contained similar abundances of cryptofauna (Figure 5.2c). Substrates of intermediate degradation (‘medium degradation framework’, MDF) sheltered the most abundant cryptofaunal communities of all dead coral substrates. In these areas of intermediate degradation, structural relief provides habitat and shelter from predators, as well as a more heterogeneous substrate than the intact frameworks.

We propose the following conceptual model to illustrate how cryptofauna respond to coral mortality and reef structural degradation in the eastern Pacific (Figure 5.3). Mass coral mortality shifts the balance between calcium carbonate production and its breakdown such that the reef becomes a net-erosional system. Poor recovery of live coral will subsequently lead to decreases in accretion, framework complexity and rugosity, ultimately leading to a habitat of little or no relief.

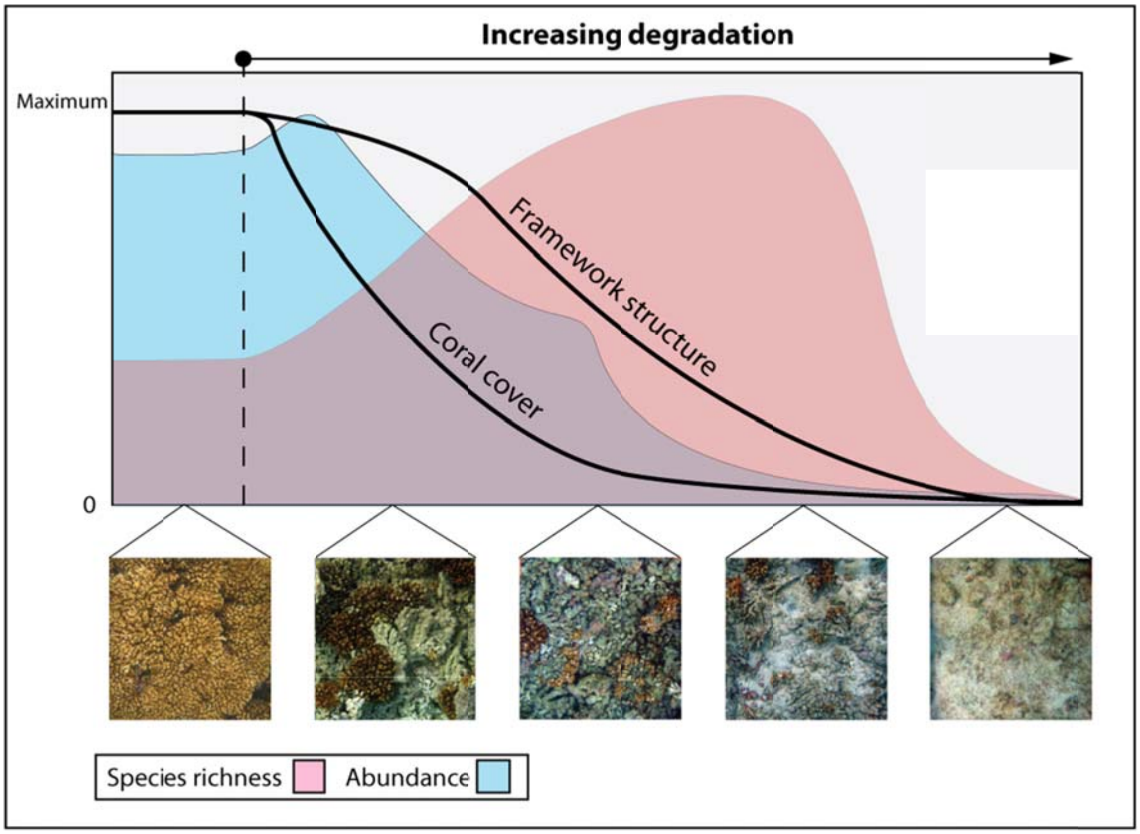

Figure 5.3. Response of coral reef cryptofauna richness and community abundance to declines in coral cover and framework structure with reef degradation.

Declines in coral cover coincide with an increase in cryptofauna species richness by freeing coral occupied space, thereby providing a mosaic of habitat niches on which a more diverse biota can proliferate. This more heterogeneous reef environment supports greater numbers of cosmopolitan taxa, rather than the limited subset of coral-specialist species found among live corals. The abundances of obligate live-coral associates mirror the decline of their hosts and food sources. Conversely, facultative associates persist long after coral mortality. These species depend primarily on the presence of reef framework habitat, and both their diversity and abundance will decrease only after reef framework structures and rubble are severely degraded to sand and silt.

The conceptual model proposed herein has important implications for the entire coral reef ecosystem. Declines in non-corallivorous reef fish populations often lag behind coral mortality by 3-4 years, paralleling the loss of framework structures (Garpe et al. 2006; Graham et al. 2007, 2009). Cryptofauna populations are known to be an important food source for reef fishes (Peyrot-Clausade 1980). Declines in cryptofauna abundances from the breakdown of reef framework structures may explain the concomitant declines in reef fishes several years after coral mortality events.

Coral reef frameworks in the Indo-West Pacific and Caribbean are constructed by a much more diverse suite of scleractinian corals compared to the low diversity eastern Pacific (Veron 2000), and these reefs likely contain more diverse communities of obligate symbionts. However, in these regions, as in the eastern Pacific, the relative number of obligate coral associates is low compared with more cosmopolitan taxa, highlighting the importance of dead coral substrates (Coles 1980). Furthermore, on reefs where massive coral morphologies are more prevalent, epilithic coral associates are likely depressed due to insufficient shelters (Shirayama & Horikoshi 1982). In these ecosystems, possibly more so than the eastern Pacific, dead coral substrates would host proportionally more species. In the short term, the erosion/degradation of geometrically simple massive colonies likely elevates habitat complexity and shelter as predicted by our model (Moran & Reaka 1988).

The existence of coral reefs as ‘rainforests of the sea’ is dependent on framework structures and their natural breakdown. Indeed, even those organisms that actively degrade reef frameworks, termed bioeroders, have the highest diversity among dead rather than live coral (Peyrot-Clausade et al. 1992). The most speciose cryptic communities are found in coral habitats in intermediate degrees of degradation, previously considered to have less importance to coral reef structure and function. Therefore, decreases in live coral cover, often cited as harbingers of reef degradation (Gardner et al. 2003), do not directly indicate declining biodiversity for all reef communities. In some cases, coral mortality may even result in increased cryptofauna richness. Instead, the most valid and alarming indicators of coral reef biodiversity and function are recent reports of long-term decreases in reef structural complexity and habitat loss (Alvarez-Filip et al. 2009). To conserve coral reef biodiversity in a period of global reef decline, it is imperative that management plans expand their scope to include all habitats associated with coral reefs, even eroded rubble, as these will be the refugia for a large share of reef-associated species.

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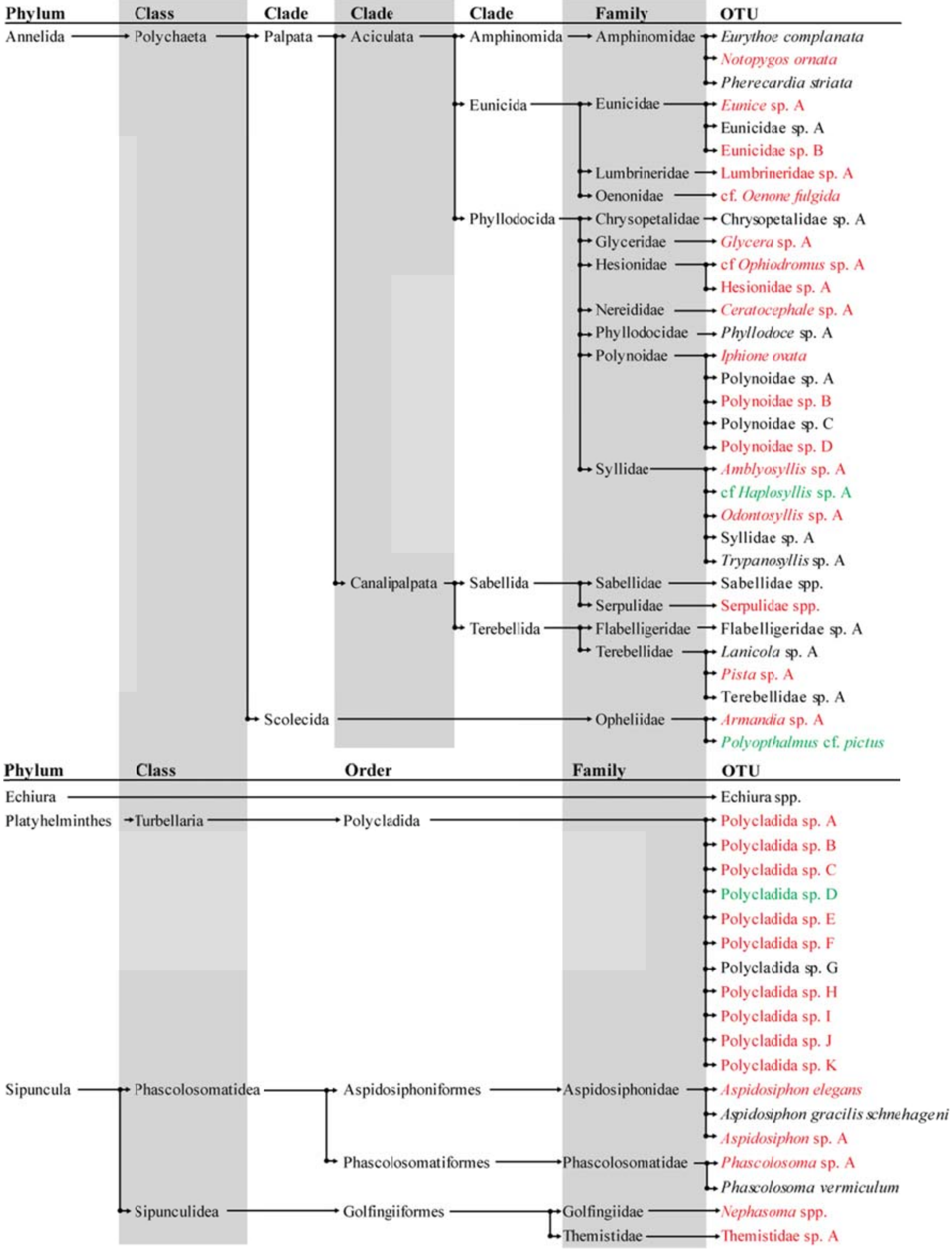
Appendices

Appendix 1. Classification scheme utilized for OTUs. Red, OTUs exclusively associated with dead coral materials. Green, exclusively associated with living coral. Black, associated with both substrates.



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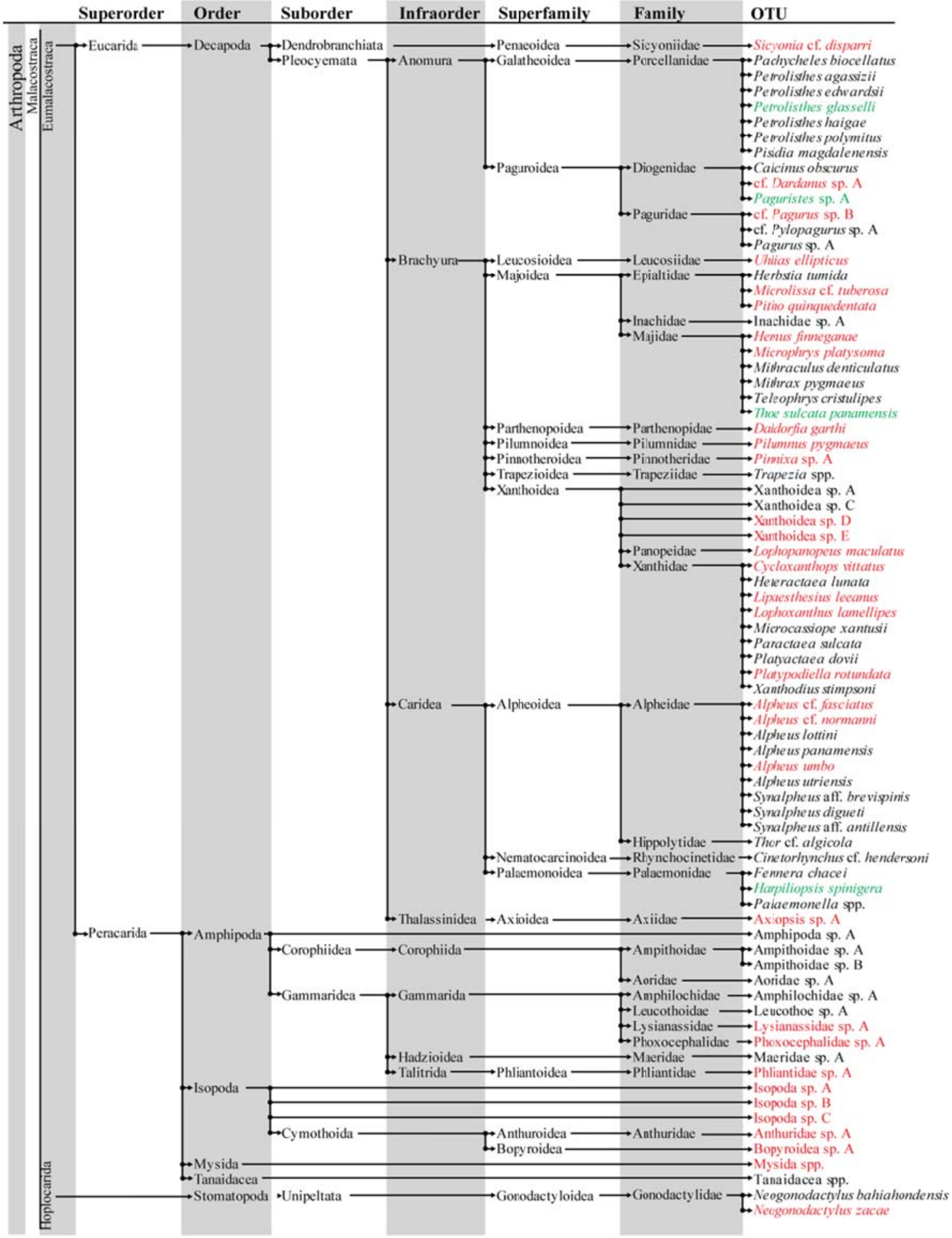
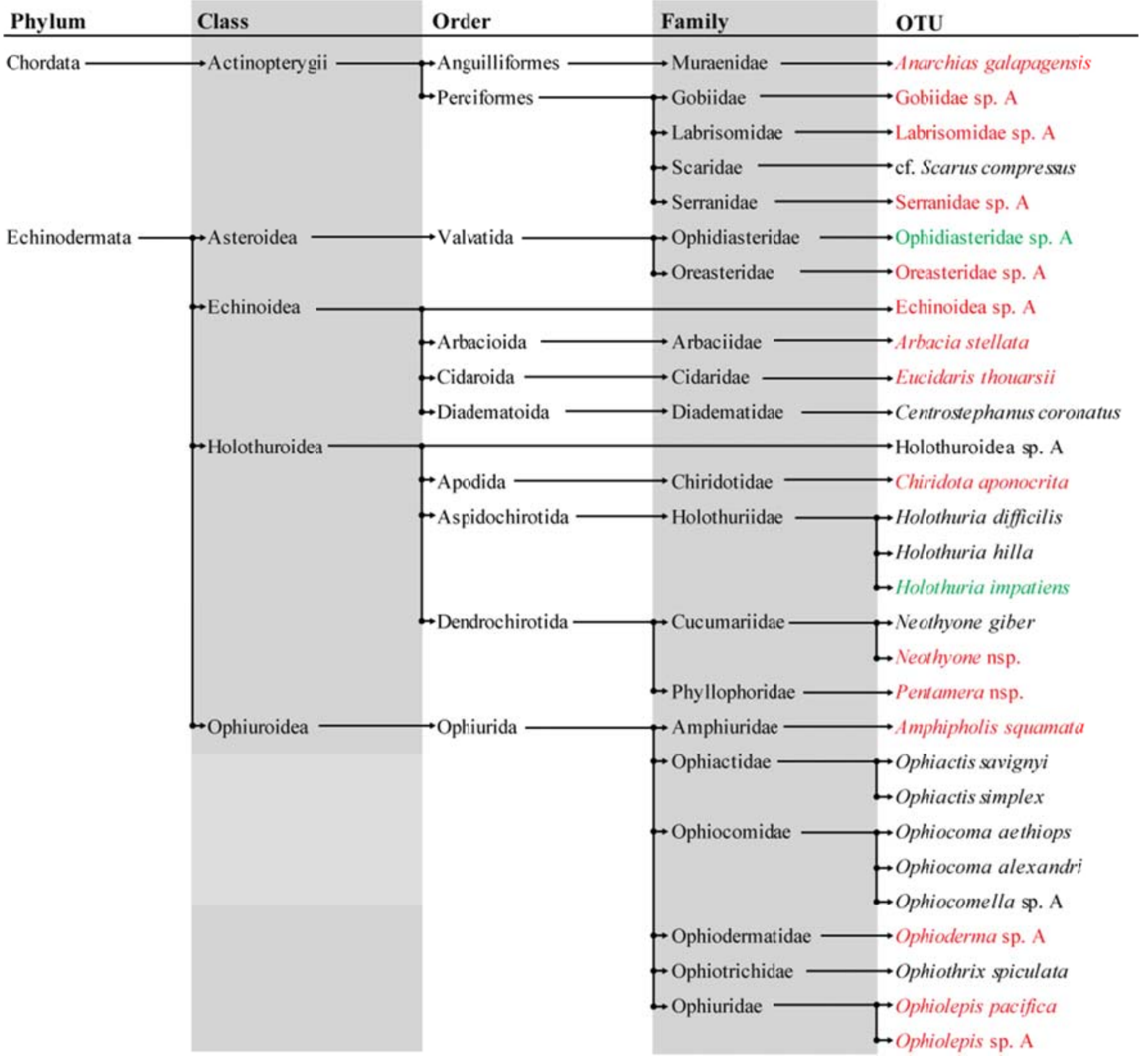


			Superorder	Order	Suborder	Infraorder	Superfamily	Family	OTU
Arthropoda	Malacostraca	Eumalacostraca	Eucarida	Decapoda	Dendrobranchiata		Penaeoidea	Sicyoniidae	*Sicyonia* cf. *disparri*
					Pleocyemata	Anomura	Galatheoidea	Porcellanidae	*Pachycheles biocellatus*
									Petrolisthes agassizii
									Petrolisthes edwardsii
									Petrolisthes glasselli
									Petrolisthes haigae
									Petrolisthes polymitus
									Pisidia magdalenensis
							Paguroidea	Diogenidae	*Calcinus obscurus*
									cf. *Dardanus* sp. A
									Paguristes sp. A
								Paguridae	cf. *Pagurus* sp. B
									cf. *Pylopagurus* sp. A
									Pagurus sp. A
						Brachyura	Leucosioidea	Leucosiidae	*Uhlias ellipticus*
							Majoidea	Epialtidae	*Herbstia tumida*
									Microlissa cf. *tuberosa*
									Pitho quinquedentata
								Inachidae	Inachidae sp. A
								Majidae	*Herbstia finneganae*
									Microphrys platysoma
									Mithraculus denticulatus
									Mithrax pygmaeus
									Teleophrys cristulipes
									Thoe sulcata panamensis
							Parthenopoidea	Parthenopidae	*Daldorfia garthi*
							Pilumnoidea	Pilumnidae	*Pilumnus pygmaeus*
							Pinnotheroidea	Pinnotheridae	*Pinnixa* sp. A
							Trapezioidea	Trapeziidae	*Trapezia* spp.
							Xanthoidea		Xanthoidea sp. A
									Xanthoidea sp. C
									Xanthoidea sp. D
									Xanthoidea sp. E
								Panopeidae	*Lophopanopeus maculatus*
								Xanthidae	*Cycloxanthops vittatus*
									Heteractaea lunata
									Lipaesthesius leeanus
									Lophoxanthus lamellipes
									Microcassiope xantusii
									Paractaea sulcata
									Platyactaea dovii
									Platypodiella rotundata
									Xanthodius stimpsoni
						Caridea	Alpheoidea	Alpheidae	*Alpheus* cf. *fasciatus*
									Alpheus cf. *normanni*
									Alpheus lottini
									Alpheus panamensis
									Alpheus umbo
									Alpheus utriensis
									Synalpheus aff. *brevispinis*
									Synalpheus digueti
									Synalpheus aff. *antillensis*
								Hippolytidae	*Thor* cf. *algicola*
							Nematocarcinoidea	Rhynchocinetidae	*Cinetorhynchus* cf. *hendersoni*
							Palaemonoidea	Palaemonidae	*Fennera chacei*
									Harpiliopsis spinigera
									Palaemonella spp.
						Thalassinidea	Axioidea	Axiidae	*Axiopsis* sp. A
			Peracarida	Amphipoda					Amphipoda sp. A
					Corophiidea	Corophiida		Ampithoidae	Ampithoidae sp. A
									Ampithoidae sp. B
								Aoridae	Aoridae sp. A
					Gammaridea	Gammarida		Amphilochidae	Amphilochidae sp. A
								Leucothoidae	Leucothoe sp. A
								Lysianassidae	Lysianassidae sp. A
								Phoxocephalidae	Phoxocephalidae sp. A
						Hadzioidea		Maeridae	Maeridae sp. A
						Talitrida	Phliantoidea	Phliantidae	Phliantidae sp. A
				Isopoda					Isopoda sp. A
									Isopoda sp. B
									Isopoda sp. C
					Cymothoida		Anthuroidea	Anthuridae	Anthuridae sp. A
							Bopyroidea		Bopyroidea sp. A
				Mysida					Mysida spp.
				Tanaidacea					Tanaidacea spp.
		Hoplocarida		Stomatopoda	Unipeltata		Gonodactyloidea	Gonodactylidae	*Neogonodactylus bahiahondensis*
									Neogonodactylus zacae

Appendix 1. *Cont.*



Phylum	Class	Order	Family	OTU
Chordata	Actinopterygii	Anguilliformes	Muraenidae	*Anarchias galapagensis*
		Perciformes	Gobiidae	Gobiidae sp. A
			Labrisomidae	Labrisomidae sp. A
			Scaridae	cf. *Scarus compressus*
			Serranidae	Serranidae sp. A
Echinodermata	Asteroidea	Valvatida	Ophidiasteridae	Ophidiasteridae sp. A
			Oreasteridae	Oreasteridae sp. A
	Echinoidea			Echinoidea sp. A
		Arbacioida	Arbaciidae	*Arbacia stellata*
		Cidaroida	Cidaridae	*Eucidaris thouarsii*
		Diadematoida	Diadematidae	*Centrostephanus coronatus*
	Holothuroidea			Holothuroidea sp. A
		Apodida	Chiridotidae	*Chiridota aponocrita*
		Aspidochirotida	Holothuriidae	*Holothuria difficilis*
				Holothuria hilla
				Holothuria impatiens
		Dendrochirotida	Cucumariidae	*Neothyone giber*
				Neothyone nsp.
			Phyllophoridae	*Pentamera* nsp.
	Ophiuroidea	Ophiurida	Amphiuridae	*Amphipholis squamata*
			Ophiactidae	*Ophiactis savignyi*
				Ophiactis simplex
			Ophiocomidae	*Ophiocoma aethiops*
				Ophiocoma alexandri
				Ophiocomella sp. A
			Ophiodermatidae	*Ophioderma* sp. A
			Ophiotrichidae	*Ophiothrix spiculata*
			Ophiuridae	*Ophiolepis pacifica*
				Ophiolepis sp. A

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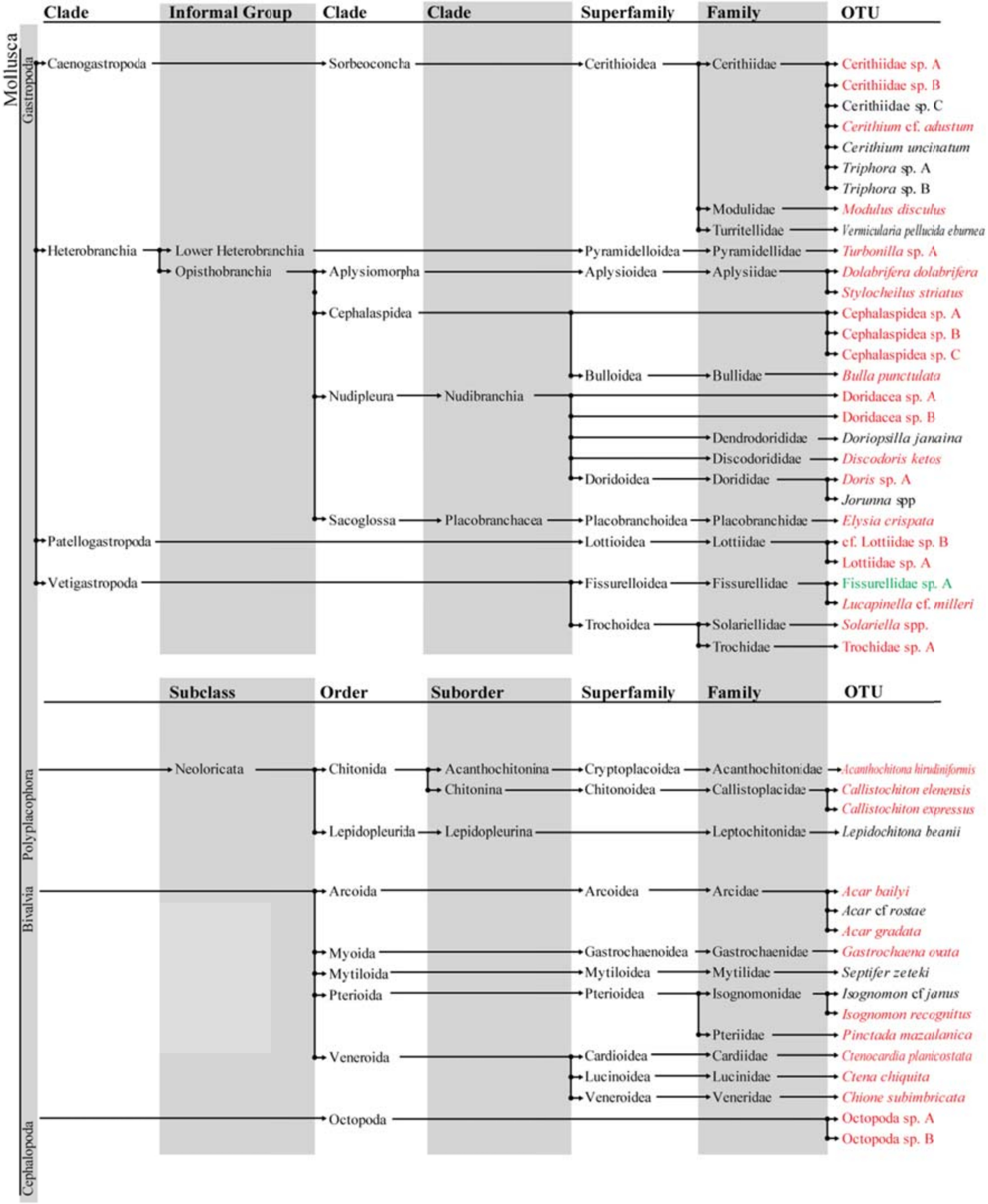

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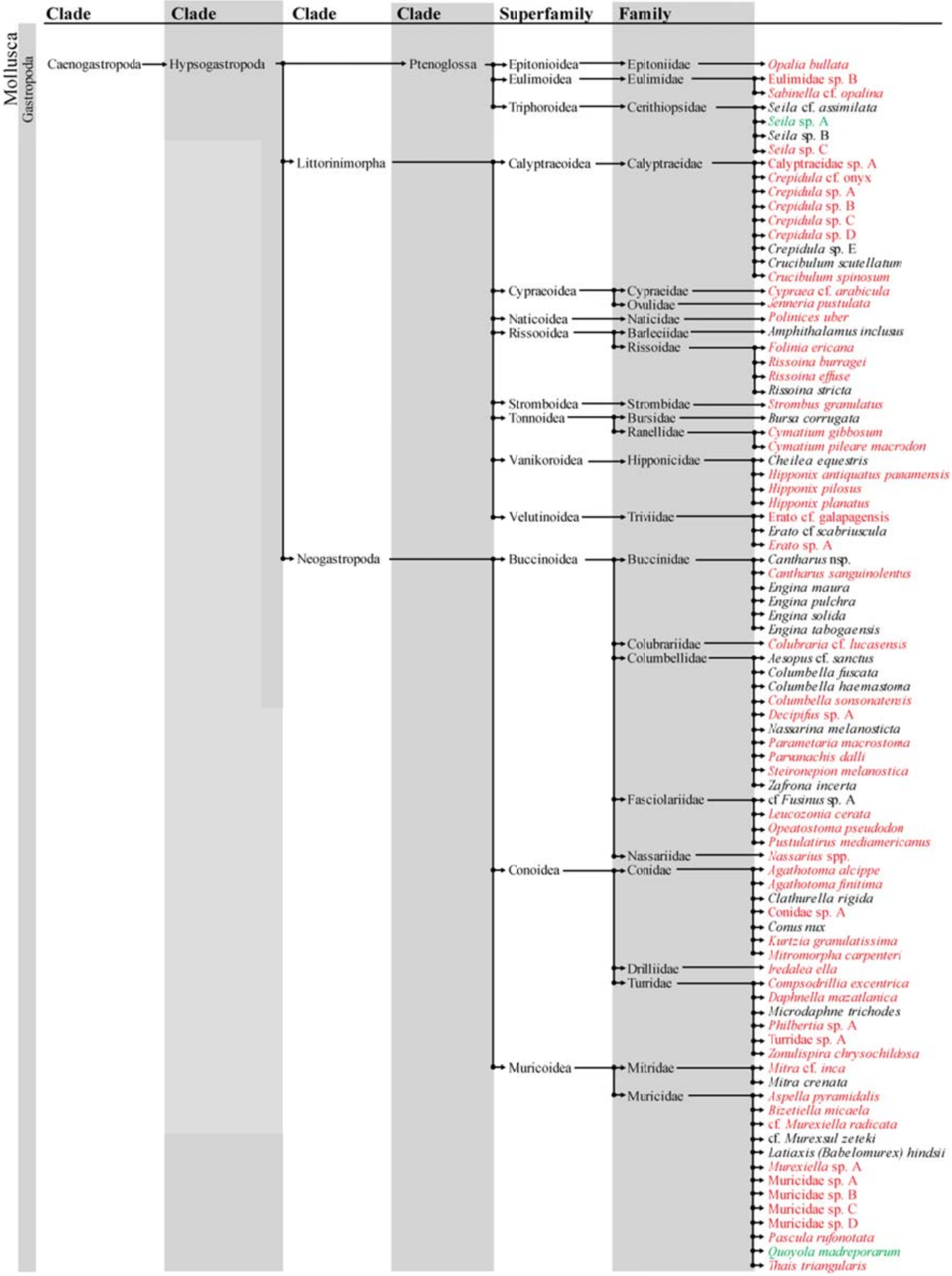
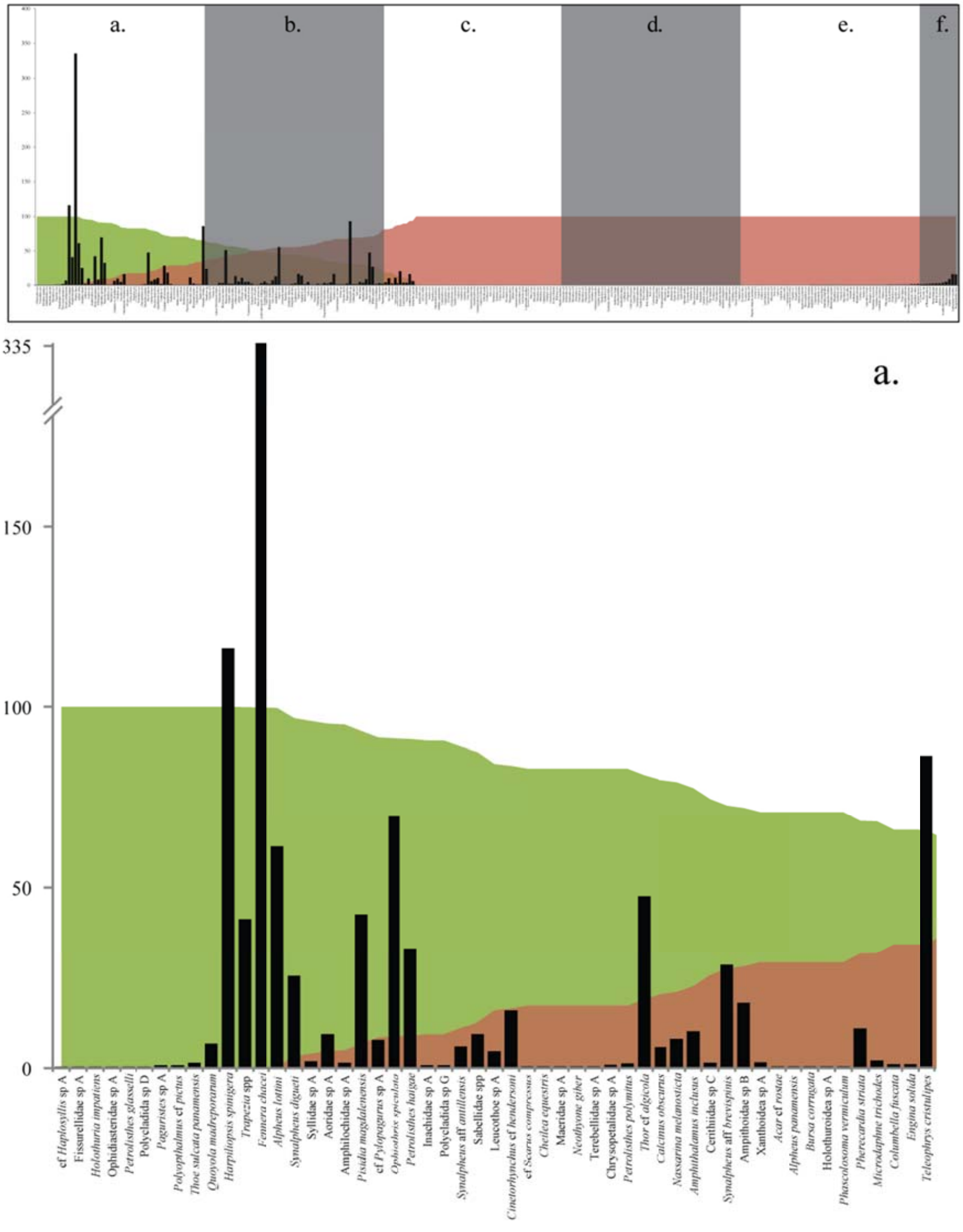


		Clade	Clade	Clade	Clade	Superfamily	Family	
Mollusca	Gastropoda	Caenogastropoda	Hypsogastropoda		Ptenoglossa	Epitonioidea	Epitoniidae	*Opalia bullata*
						Eulimoidea	Eulimidae	Eulimidae sp. B
								Sabinella cf. *opalina*
						Triphoroidea	Cerithiopsidae	*Seila* cf. *assimilata*
								Seila sp. A
								Seila sp. B
								Seila sp. C
				Littorinimorpha		Calyptraeoidea	Calyptraeidae	Calyptraeidae sp. A
								Crepidula cf. onyx
								Crepidula sp. A
								Crepidula sp. B
								Crepidula sp. C
								Crepidula sp. D
								Crepidula sp. E
								Crucibulum scutellatum
								Crucibulum spinosum
						Cypraeoidea	Cypraeidae	*Cypraea* cf. *arabicula*
							Ovulidae	*Jenneria pustulata*
						Naticoidea	Naticidae	*Polinices uber*
						Rissooidea	Barleeiidae	*Amphithalamus inclusus*
							Rissoidae	*Folinia ericana*
								Rissoina burragei
								Rissoina effuse
								Rissoina stricta
						Stromboidea	Strombidae	*Strombus granulatus*
						Tonnoidea	Bursidae	*Bursa corrugata*
							Ranellidae	*Cymatium gibbosum*
								Cymatium pileare macrodon
						Vanikoroidea	Hipponicidae	*Cheilea equestris*
								Hipponix antiquatus panamensis
								Hipponix pilosus
								Hipponix planatus
						Velutinoidea	Triviidae	Erato cf. galapagensis
								Erato cf *scabriuscula*
								Erato sp. A
				Neogastropoda		Buccinoidea	Buccinidae	*Cantharus* nsp.
								Cantharus sanguinolentus
								Engina maura
								Engina pulchra
								Engina solida
								Engina tabogaensis
							Colubrariidae	*Colubraria* cf. *lucasensis*
							Columbellidae	*Aesopus* cf. *sanctus*
								Columbella fuscata
								Columbella haemastoma
								Columbella sonsonatensis
								Decipifus sp. A
								Nassarina melanosticta
								Parametaria macrostoma
								Parvanachis dalli
								Steironepion melanostica
								Zafrona incerta
							Fasciolariidae	cf *Fusinus* sp. A
								Leucozonia cerata
								Opeatostoma pseudodon
								Pustulatirus mediamericanus
							Nassariidae	*Nassarius* spp.
						Conoidea	Conidae	*Agathotoma alcippe*
								Agathotoma finitima
								Clathurella rigida
								Conidae sp. A
								Conus nux
								Kurtzia granulatissima
								Mitromorpha carpenteri
							Drilliidae	*Iredalea ella*
							Turridae	*Compsodrillia excentrica*
								Daphnella mazatlanica
								Microdaphne trichodes
								Philbertia sp. A
								Turridae sp. A
								Zonulispira chrysochildosa
						Muricoidea	Mitridae	*Mitra* cf. *inca*
								Mitra crenata
							Muricidae	*Aspella pyramidalis*
								Bizetiella micaela
								cf. *Murexiella radicata*
								cf. *Murexsul zeteki*
								Latiaxis (Babelomurex) hindsii
								Murexiella sp. A
								Muricidae sp. A
								Muricidae sp. B
								Muricidae sp. C
								Muricidae sp. D
								Pascula rufonotata
								Quoyola madreporarum
								Thais triangularis

Appendix 2. Substrate affinity and relative density OTUs. Green and red represent association with live and dead coral, respectively. Total individuals collected from live and dead coralsubstrates were first divided by the respective total substrate volume to avoid bias of unequal substrate collection. Black bars show mean individuals per 10 kg live coral + mean individuals per 10 kg dead coral. Letters (a-f) denote the enlarged panel corresponding to the shrunken diagram (top).



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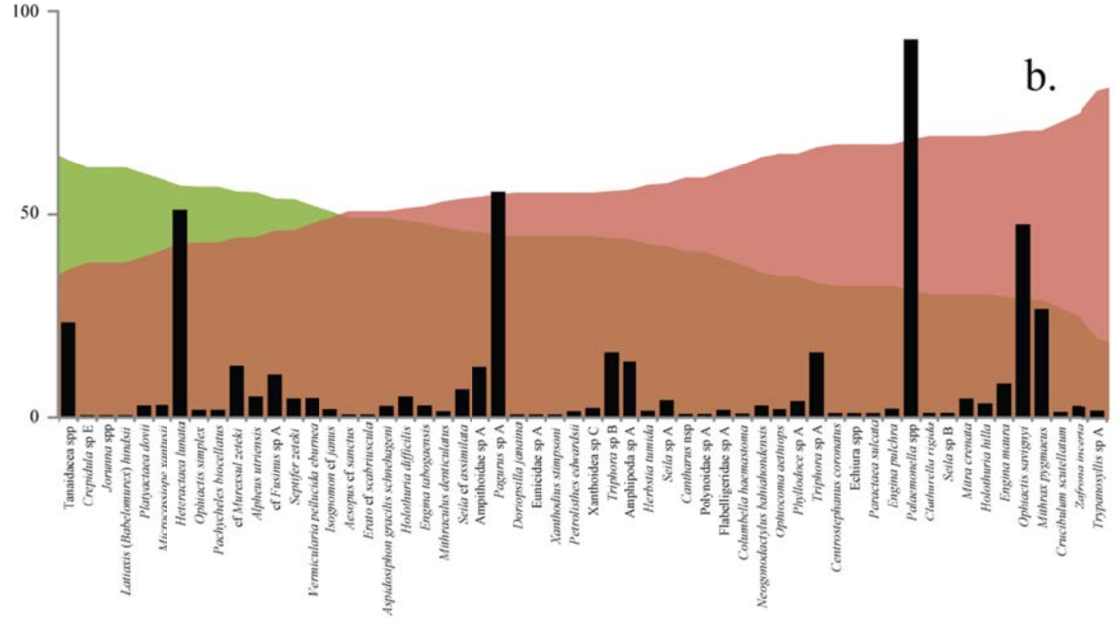

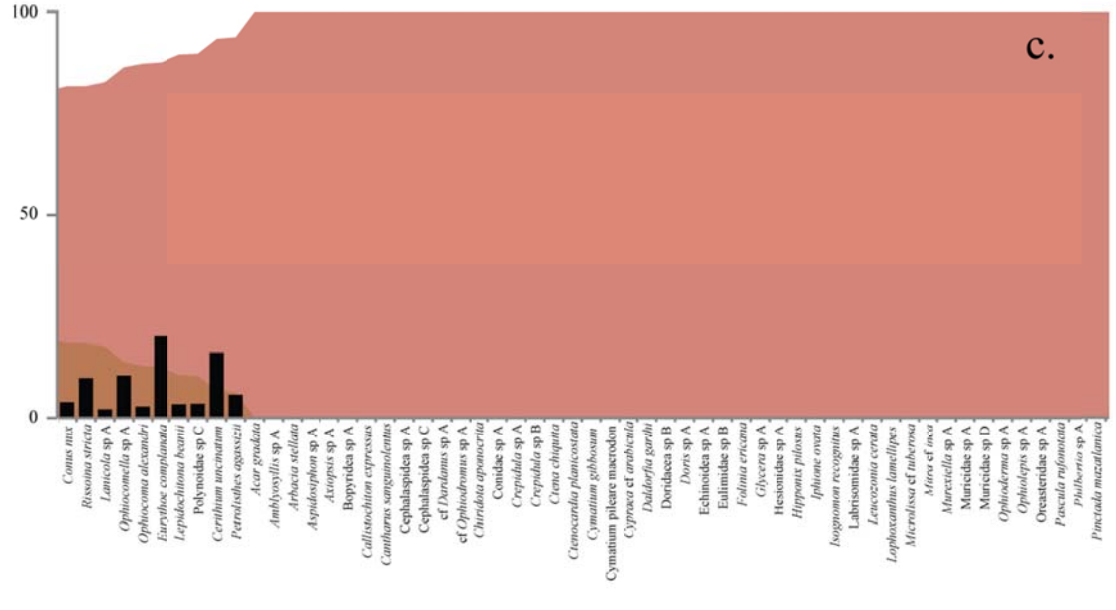

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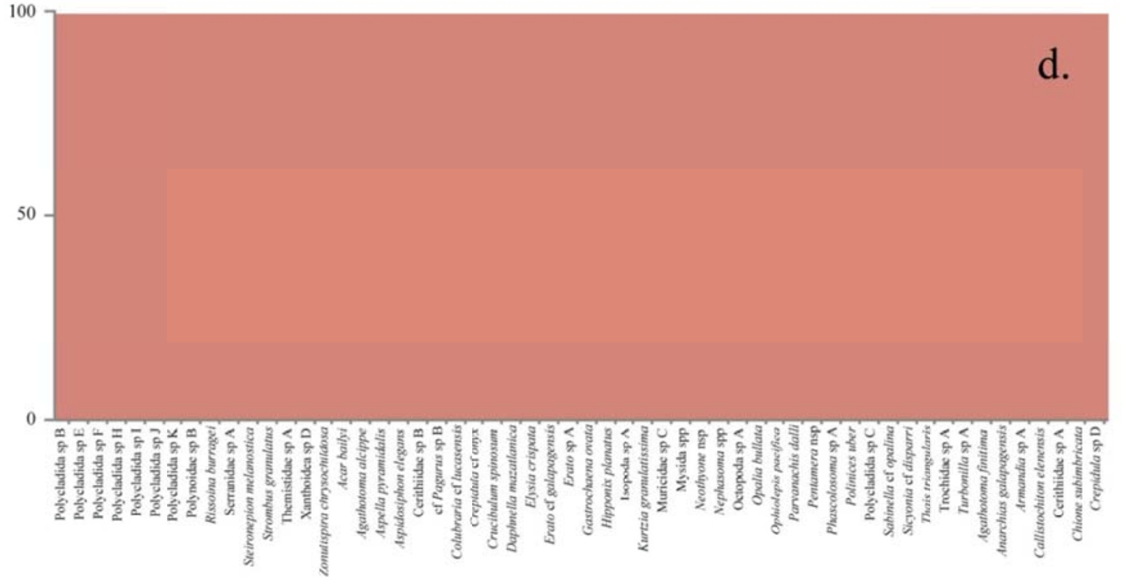

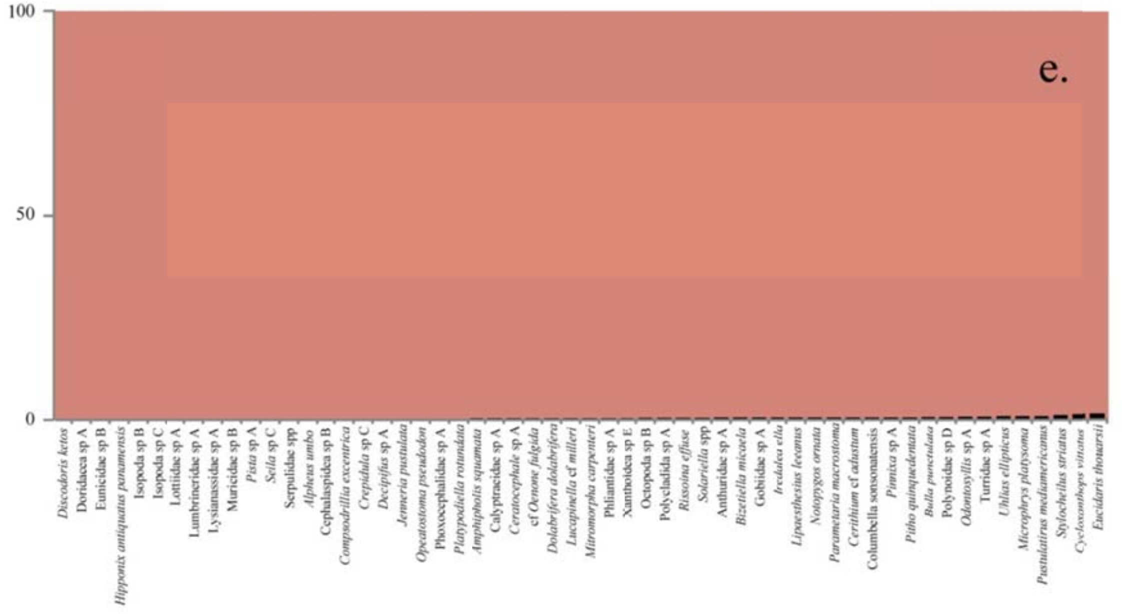

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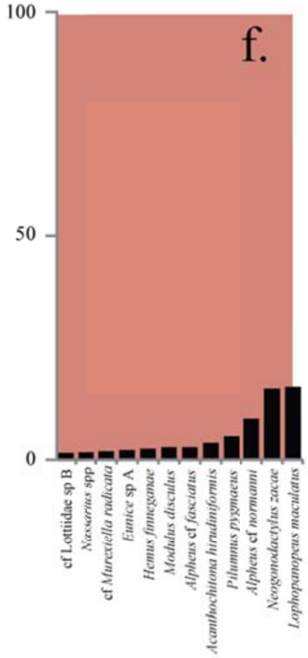

Appendix 3. Ash free dry weight, wet weight conversions.

Phylum	**Taxon**	**Mean%**	**N**	**SPP**	**Ref**
Annelida	Polychaeta	16.0	93	>83	1
Mollusca	Prosobranchia [a]	7.5	11	14	1
	Opisthobranchia (shelled) [b]	13.8	3	2	1
	Opisthobranchia (non-shelled) [c]	17.2 [d]	na	na	1
	Polyplacophora	27.2	1	3	1
	Bivalvia	5.5	66	47	1
	Cephalopoda	21.4	5	5	1
Arthropoda	Crustacea [e]	15.6	35	>27	1,2
	Amphipoda	16.0	14	>12	1
	Decapoda	16.5	17	11	1
	Isopoda	14.2	1	1	1
	Mysida	15.5	2	2	1
	Stomatopoda	10 [f]	1	1	3
Echinodermata	Tanaidacea	14.4	1	1	2
	Asteroidea	11.2	8	4	1
	Ophiuroidea	7.4	12	8	1
	Echinoidea	3.5	8	6	1
	Holothuroidea	10.9	3	3	1
Sipuncula	Sipuncula	11.2	3	2	1
Platyhelminthes	Turbellaria	25.2	1	1	1
Echiura	Echiura	10.0	1	1	4
Chordata	Ophidiiformes [g]	20.9	1	1	4
	Perciformes [h]	20.5	32	>=21	4
	Gobiidae	18.1	11	>=7	4
	Muraenidae	23.3	5	>=1	4
	Scorpaenidae	19.7	4	2	4
	Serranidae	20.3	3	3	4

[a] for Gastropoda spp, Hypsogastropoda, Lower Heterobranchia, Neritomorpha, Patellogastropoda, Sorbeoconcha, Vetigastropoda
[b] for Cephalaspidea
[c] for Anaspidea, Nudibrancia, Pleurobranchomorpha, Sacoglossa
[d] Calculated by multiplying dry weight to wet weight ratio by ash-free dry weight to wet weight ratio
[e] Mean value for all considered crustacea
[f] Approximate value
[g] for Bythitidae, value from Ophidiidae
[h] for Apogonidae, Labrisomidae, Scaridae; value from Gobiidae, Lutjanidae, Sciaenidae, Serranidae

References

1., Ricciardi & Bourget 1998; 2., Dall et al. 1991; 3., Griffiths & Blaine 1988; 4., Vinogradov 1953;

Appendix 4. Trophic group assignments of collected taxa. CM, Carnivore multiple strategies; CP, Carnivorous predator; DD, Detritivore deposit feeder; HG, Herbivorous grazer; OO, Omnivore opportunistic; SU, Suspension feeder.

Taxon	Guild	Ref	Notes
Annelida			
Amphinomidae	CM	1	
Chrysopetalidae	CM	1	Probably similar to non-jawed Amphinomidae
Eunicidae		1	Members belong to multiple guilds: CG, CP, HG
Flabelligeridae	DD	1	May also utilize suspension feeding
Glyceridae	CP	1	Primarily carnivores, may practice detritivory and copraphagy
Hesionidae	CP	1,2	Smaller interstitial species diatoms, bacteria, etc.
Lumbrineridae	CM	1	Primarily predators and scavengers, some species may utilize hervivory and detritivory
Nereididae	OO	1	
Oenonidae		1	Poorly known
Opheliidae	DD	1,2	
Phyllodocidae	CM	1	Primarily a predator but may also scavenge
Polynoidae	CM	1	
Sabellidae	SU	1	
Serpulidae	SU	1	
Syllidae	CM	1	Primarily grazes on sessile taxa but may feed on motile prey as well
Terebellidae	DD	1	
Arthropoda			
Amphipoda			
Ampithoidae	HG	3	
Aoridae	OO	4	May utilize suspension and deposit feeding though very important in herbivory
Gammaridea (unless noted)	OO	5,6	Many are herbivorous, see 5 and references therein
Lysianassidae	CM	7,8	Deep water, probably principal diet but 8 and references therein describe detrital sources
Decapoda			
Axiidae			
Axiopsis	HG	9	Scavenges seagrass
Caridea	OO		All included taxa belonged to the OO category
Alpheidae	OO	10,11,12	
Hippolytidae	OO	10,13,14	
Palaemonidae	OO	10,14,15,16	
	OO	17	
Rhynchocinetidae			
Dromiidae	OO		Feeding behaviors assumed to be similar to Xanthoidea
Epialtidae	HG	18	
Inachidae (unless noted)	OO	19	
Stenoryhnchus	SU	20	
Majidae	HG	21,22,23,24	Other feeding strategies and sources exist though herbivory is likely dominant. *T. crisutlipes* based on one observation.
Paguroidea	OO	25,26	Not all collected genera mentioned in literature
Panopeidae	OO	27	

Appendix 4. *Cont.*

Taxon	Guild	Ref	Notes
Parthenopidae	CP	28	
Pilumnidae	OO	12	
Pinnotheridae	OO	29	
Porcellanidae	SU	25,27,30,31	
Sicyoniidae	CP	32	
Trapeziidae	OO	10	
Xanthoidea	OO	33,34	
Leucosiidae	CM	35	Predation and scavenging
Isopoda (unless noted)	CM	36	Collected specimens are similar to Cirolanidae
Anthuridae spp		37	Diverse feeding types, likely differ across genera
Bopyroidea	CG	38	
Mysida	OO	39,40	
Stomatopoda	CP	31	
Tanaidacea	DD	41	Other feeding behaviours observed but deposit feeding is likely dominant
Chordata			
Apogonidae	CP	42	
Bythitidae	CP	43	Proportionally insignificant quantities of fleshy algae found in gut
Gobiidae	CP	42,43	Proportionally insignificant quantities of fleshy algae found in gut
Labrisomidae	CP	42	
Muraenidae	CP	42	
Scorpaenidae	CP	42	
Serranidae	CP	42	
Scaridae	HG	42	
Echinodermata			
Asteroidea			
Ophidiasteridae	OO	44	Feed on epibenthic films and encrusting biota
Oreasteridae	OO	44	Graze on epifauna, detrital feeders, or may utilize predation
Echinoidea			
Arbacia	OG	45,46	
Centrostephanus coronatus	OG	47,46	
Echinoidea sp A (Irregular)	DD	46,48,49	
Eucidaris thouarsii	OG	46,50	
Holothuroidea			
Apodida, Aspidochirotida	DD	51	
Dendrochriotida	SU	51,52	
Ophiuroidea			
Amphipholis squamata	SU	53	May also utilize deposit feeding
Ophiactis	SU	53	
Ophiocomidae (unless noted)	SU	53	Some species engage in predation, scavenging, deposit feeding and browsing.
Ophiocoma	OO	53	Suspension, deposit, scavenging and predation observed

Appendix 4. *Cont.*

Taxon	**Guild**	**Ref**	**Notes**
Ophioderma	OO	53	Predation, scavenging, deposit feeding observed
Ophionereis	SU	53	Infrequent accounts of deposit feeding and scavenging recorded
Ophiothrix	SU	53	May also exhibit predation, scavenging and deposit feeding
Ophiolepis	OO	53	Observed to scavenge, deposit feed and browse
Echiura			
Echiura	DD	54	
Mollusca			
Bivalvia	SU		All families collected in this study are suspension feeders
Arcidae	SU	55	
Cardiidae	SU	55	
Gastrochaenidae	SU	56	
Isognomonidae	SU	56	
Lucinidae	SU	56	
Mytilidae	SU	56	
Pteriidae	SU	56	
Veneridae	SU	56	
Cephalopoda			
Octopoda	CP	57	
Gastropoda			
Aplysiidae	HG	58	
Barleeiidae	HG	56	
Buccinidae	CP	55,59	
Bursidae	CP	56,58	
Calyptraeidae	SU	58,60	
Cephalaspidea	CP	58	
Cerithiidae	HG	55	
Cerithiopsidae	CG	55	Often parasitic
Colubrariidae	CP	55	
Columbellidae			
Aesopus	CP	56	
Parametaria	CP	56	
Decipifus	CP	56	
Nassarina	CP	55,56	
Paravanchis	CP	56	
Columbella	HG	59	
Steironepion	CP	56	
Zafrona	OG	61	
Conidae	CP	55	
Cypraeidae	OG	55,59	Herbivory but likely uncommon
Drillidae	CP	62	
Epitoniidae	CG	56,58	Often parasitic
Eulimidae	CG	56,60	Parasitic
Fasciolariidae	CP	55,56	
Fissurellidae	HG	56	
Hipponicidae	SU	55,63	
Lottiidae	HG	56	

Appendix 4. *Cont.*

Taxon	Guild	Ref	Notes
Mitridae	CP	55,56	
Modulidae	HG	56	
Muricidae (unless noted)	CP	56	
Coralliophila	CG	56	
Quoyula madreporarum	CG	64	
Nassariidae	CP	56	
Naticidae	CP	56	
Nudibranchia	CG	58	
Olividae	CP	56	
Ovulidae	CG	64	
Pleurobranchidae	CM	58	
Pyramidellidae	CG	56	
Ranellidae	CP	56	
Rissoidae	HG	56	
Sacoglossa	HG	60	
Solariellidae	DD	65,66	May utilize herbivory
Strombidae	OG	56	
Triviidae	CG	60	
Trochidae	HG	56,59	May utilize carnivory, but likely infrequent
Turridae	CP	56	
Turritellidae	SU	55	
Polyplacophora	HG	67,62,68	
Platyhelminthes			
Polycladida	CM	69	
Sipuncula			
Sipuncula	DD	70	

1 Fauchald & Jumars 1979; 2 Penry & Jumars 1990; 3 Poore et al. 2008; 4 Taylor & Brown 2006; 5 Klumpp et al. 1988; 6 Zimmerman et al. 1979; 7 Hargrave 1985; 8 Fanelli et al. 2009; 9 Griffis & Suchanek 1991; 10 Patton 1974; 11 Castro 1971; 12 Gore et al. 1978; 13 A. Baeza pers. comm.; 14 Rothans & Miller 1991; 15 Barry 1965; 16 Glynn pers. comm.; 17 Burkenroad 1939; 18 Hultgren & Stachowicz 2008; 19 Ambrose & Anderson 1990; 20 Barr 1975; 21 Kilar & Lou 1986; 22 Hazlett & Rittschof 1975; 23 Engstrom 1984; 24 Gotelli et al. 1985; 25 Abele 1976; 26 Thomassin 1974; 27 Knudsen 1964; 28 Zipser & Vermeij 1978; 29 Pearse 1913; 30 Kropp 1981; 31 Hickman & Zimmerman 2000; 32 Kennedy et al. 1977; 33 Saisho et al. 1983; 34 Morris et al. 1980; 35 Schembri 1982; 36 Shafir & Field 1980; 37 Kensley 1998; 38 Chopra 1923; 39 Mullin & Roman 1986; 40 Roman et al. 1990; 41 Holdich & Jones 1983; 42 Froese & Pauly 2010; 43 Prochazka 1998; 44 Jangoux 1982; 45 Cobb & Lawrence 2005; 46 De Ridder & Lawrence 1982; 47 Vance 1979; 48 Moore 1966; 49 Reese 1966; 50 Glynn et al. 1979; 51 Roberts & Bryce 1982; 52 Hickman 1998; 53 Warner 1982 and references therein; 54 Brusca 1980; 55 Diaz et al. 1990; 56 Budd et al. 2001 and references therein; 57 Ambrose 1986; 58 Behrens & Hermosillo 2005; 59 Taylor & Reid 1984; 60 Graham 1955; 61 deMaintenon 1999; 62 Taylor 1984; 63 Yonge 1953; 64 Glynn 2004; 65 Hickman & McLean 1990; 66 Hickman 1980; 67 Lubchenco et al. 1984; 68 Jörger et al. 2008; 69 Newman & Cannon 2003; 70 Pearse et al. 2002