

Impact of coral predators on tropical reefs

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ABSTRACT: It is well known that herbivores have numerous and diverse impacts on plant and algal fitness, community structure and ecosystem function. The importance of corallivory as a selective force, however, has been underestimated. Corallivores, or consumers of live coral tissue, employ a wide variety of feeding strategies and can be obligate or facultative coral feeders. Our literature review reveals a complex array of corallivores across the globe, represented by 11 families of fishes and 5 invertebrate phyla and totaling over 160 species known to consume scleractinian corals worldwide. Importantly, although these corallivores span a wide taxonomic range, we found that they have been reported to feed on relatively few genera of hard corals, specifically, on only 28 scleractinian genera worldwide. Damage by corallivores ranges from minor to lethal, but there is a growing body of evidence to support that even limited removal of tissue or skeletal structures has growth and/or fitness consequences for a scleractinian coral colony. In light of increasing reef stressors and diminishing coral populations, we suggest that the role of corallivores in reef trophodynamics is more complex than appreciated previously.

KEY WORDS: Coral reef resilience · Herbivory · Trophodynamics

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INTRODUCTION

Coral reefs are among the most diverse ecosystems on earth, rivaled only by tropical rainforests in species diversity and abundance (reviewed by Reaka-Kudla 1997). Scleractinian corals are the major architects of tropical reefs, acting as ecosystem engineers (*sensu* Jones et al. 1994) and providing the structural framework for a highly diverse assemblage of marine organisms. It is well established that corals worldwide are increasingly threatened by abiotic stressors, including changes in seawater temperatures (Jokiel & Coles 1977, 1990) and storms (Knowlton et al. 1990, Bythell et al. 1993, Alvarez-Filip & Gil 2006). Likewise, much attention has been given to other stressors, including overfishing (Myers & Worm 2003) and disease (Sutherland et al. 2004), which can be caused by biotic or abiotic factors and also contribute to coral reef decline. Direct consumption of live coral, or corallivory, represents another biotic stressor that can adversely affect coral fitness and accelerate rates of coral decline (Knowlton et al. 1990, Rotjan et al. 2006), yet little

attention has been paid to the role corallivores might play in maintaining or conserving coral reef ecosystems.

Judging the impact of corallivory on tropical reefs has been controversial because many corallivores cause little apparent damage to corals, although a few species are known to cause severe damage. A variety of organisms consumes living coral, including fishes, annelids, crustaceans, echinoderms, and mollusks. Previous reviews on corallivory by Carpenter (1997), Glynn (1990b), and Robertson (1970) have focused mainly on invertebrates. Robertson (1970) provides an excellent description of corallivorous prosobranch gastropods. Hixon (1997) reviewed both direct and indirect effects of fishes on corals, including corallivorous butterflyfish, whose feeding habits have been well described (e.g. Harmelin-Vivien 1989). Even though most general discussions of reef trophic interactions have ignored the importance of corallivory, the identities and impacts of corallivores have been carefully investigated for a few specific locations, such as in the Galapagos (Glynn et al.

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1983) and Panama (Glynn et al. 1972, Glynn 2004). However, because no comprehensive review of the impact of corallivores on tropical reefs exists, the importance of corallivory as a selective force has likely been underestimated.

In this review, we provide a comprehensive description of known vertebrate and invertebrate corallivores, their foraging modes, and their rates of coral consumption. Since scleractinian corals are considered to be the major reef-builders, we focus exclusively on scleractinian corallivores. We describe major shifts in the relative importance of different corallivore groups across biogeographic regions. We provide a categorization of major predators as obligate versus facultative coral feeders, and examine whether they specialize on particular scleractinian coral genera. We review evidence concerning the impact of corallivory on the growth and fitness of reef-building corals. We conclude by discussing critical areas for future research necessary for an understanding of the changing role of corallivores and corallivory in reef trophodynamics and reef resilience.

CLASSIFICATION OF CORALLIVORE FEEDING STRATEGIES

Corallivores differ in their feeding strategies, with different consequences for coral prey. 'Mucus-feeders' consume only coral mucus without removing any other live coral tissue or underlying skeleton. Corallivores that remove coral tissue without damaging the underlying calcium carbonate skeleton are known as 'browsers' (Hiatt & Strasburg 1960). Bellwood & Choat (1990) distinguished two feeding modes for parrotfish that we apply here to all corallivores: 'excavators', which feed by removing live coral tissue with major portions of the underlying skeleton, and 'scrapers', which remove live coral tissue while taking only little of the accompanying skeleton. These four categories can be used to classify the feeding strategies used by a wide variety of invertebrates and fish corallivores.

Some corallivores may also act as bioeroders (consumers of dead coral substrate), and these terms are sometimes used interchangeably. However, this distinction is important because corallivores directly affect live coral and so are likely to have stronger effects on coral fitness. Bioeroders are known to play an important role in coral reef dynamics, re-shaping reef topography by eroding dead skeletons of mound-building corals, and weakening colony structure of live branching corals (reviewed by Hutchings 1986, Sammarco 1996). However, because bioeroders do not consume live coral tissue, they are not considered further in this review.

MAJOR VERTEBRATE CORALLIVORES

The first evidence of vertebrate corallivory was provided by Darwin (1842) from the HMS 'Beagle' in the Indian Ocean, where he recovered live coral from the stomachs of two *Scarus* parrotfish species. However, vertebrate corallivory received little attention until Cousteau (1952) made detailed behavioral observations of parrotfish feeding on live corals. Since then, accumulated studies have reported 114 species of vertebrates, representing 11 families of osteichthyan fishes, known to at least occasionally consume live corals (Appendix 1). The corals most commonly grazed by fishes include the genera *Acropora*, *Pocillopora*, *Montipora*, and *Porites*. Interestingly, we found that only 18 of the 111 known coral genera (listed in Veron 2000), a mere 16.2%, have been reported to be even occasionally consumed by corallivorous fishes (Appendix 1). This suggests that either observational data are incomplete, or that many coral genera have evolved effective means of deterring predation.

Vertebrate corallivores use each of the coral feeding strategies described above (see also Appendix 1). Approximately half of the 114 corallivorous fishes are butterflyfishes (Chaetodontidae), browsers that remove individual coral polyps with long, fleshy lips (Motta 1988, 1989) without damaging the underlying skeleton. In contrast, all other piscine corallivores such as parrotfish, puffers, triggerfish, filefish, wrasses, and damselfish have the ability to remove skeletal material along with coral tissue, and thus are either excavators or scrapers. The feeding habits of Indo-Pacific parrotfishes have been relatively well studied (Bellwood & Choat 1990), and corallivory is restricted to a few large excavating species that possess jaw structures capable of exerting large forces on their cutting edge. Caribbean parrotfish use two distinct grazing behaviors called focused biting and spot-biting (Bruckner et al. 2000): in the former, individual fish repeatedly bite a single area, resulting in extensive coral tissue and skeletal loss (Fig. 1A), whereas in the latter, feeding consists of shallow bites that are widely scattered over the colony surface (Fig. 1B). Identifying grazing scars can be difficult; both focused and spot-biting scars have been mistaken for disease lesions (Bruckner & Bruckner 1998a,b, 2000). Although focused biting (Fig. 1C) on live coral has been implicated in territorial marking by adult terminal phase males of the stoplight parrotfish *Sparisoma viride* (Bruggemann et al. 1994, van Rooij et al. 1995), spot-biting does not appear to be associated with territoriality (Bruckner et al. 2000). Parrotfish grazing behavior may differ geographically, since focused biting is common in some Caribbean locations, e.g. Puerto Rico (Bruckner & Bruckner 1998c), but comparatively rare

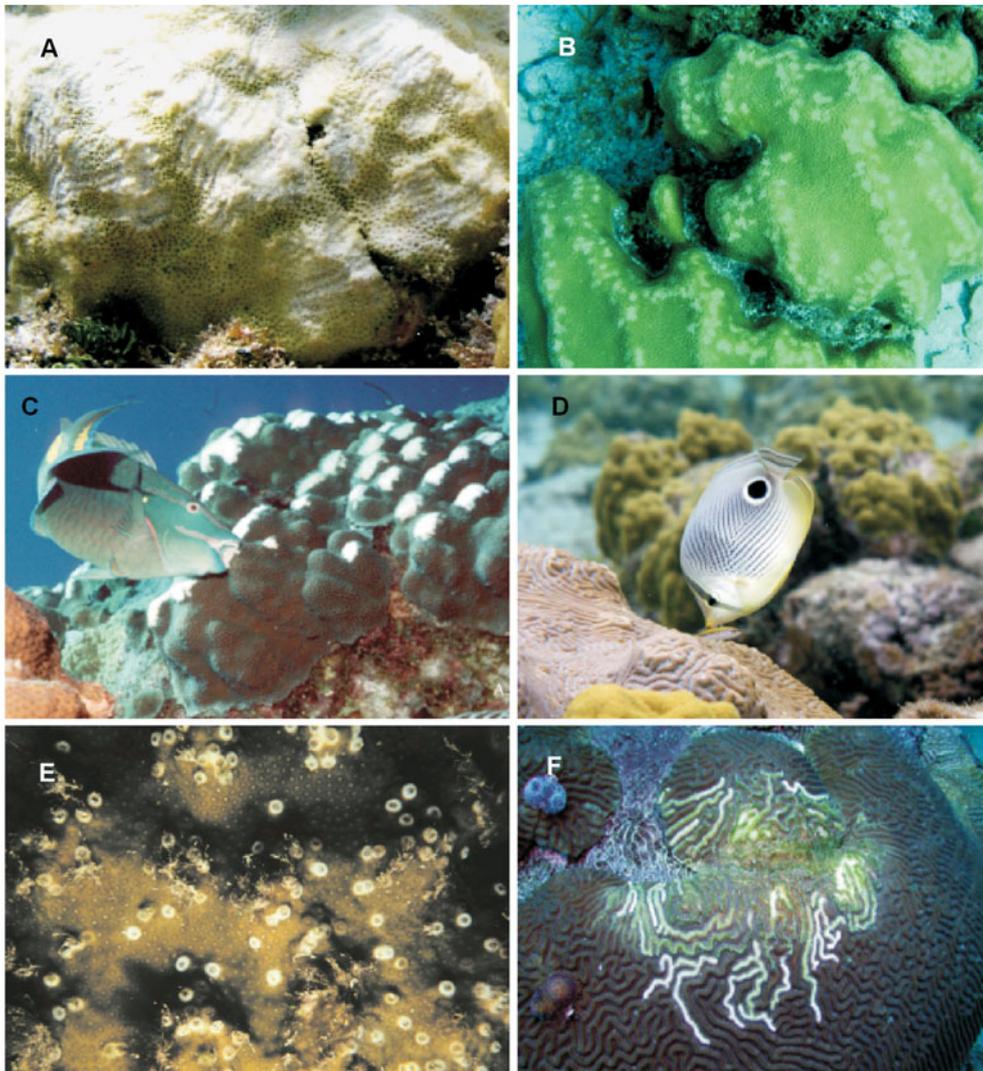


Fig. 1. Grazing impacts of Caribbean vertebrate corallivores. (A) Focused biting by the parrotfish *Sparisoma viride* on a *Porites astreoides* colony in a Belizean backreef habitat (image by R. Rotjan). (B) Spot-biting by *S. viride* on *Montastraea* spp. corals off Belize (image by R. Rotjan). (C) Terminal-phase *S. viride* in the act of grazing *M. franksi* (image by A. Bruckner). (D) The four-eye butterflyfish (*Chaetodon capistratus*) grazing on a *Diploria clivosa* colony off Belize (image by R. Rotjan). (E) Chimneys on a *Montastraea* colony caused by damselfish grazing (image by A. Bruckner). (F) Algal garden growing on *Colpophyllia natans* after *Stegastes* damselfish have removed live coral tissue in the Flower Garden Banks in the Gulf of Mexico (image by E. Borneman)

in others, e.g. Belize (reported only for a single coral species by Rotjan & Lewis 2005).

The Indo-Pacific giant humphead parrotfish *Bolbometopon muricatum* is by far the largest consumer of live coral tissue and skeletal material, although it is a facultative corallivore. It has been estimated that a *B. muricatum* population can consume 13.5 kg live coral $m^{-2} yr^{-1}$ (Bellwood et al. 2003). These parrotfish also contribute to reef bioerosion, breaking down >5 t of structural reef carbonates per year (Bellwood et al. 2003). Although largely non-selective, *B. muricatum* avoids Montipera species (Hoey & Bellwood 2008) and instead prefers fast-growing acroporid and pocillo-

porid corals (Bellwood et al. 2003), and thus may help to promote overall coral diversity by maintaining space for slower-growing coral species. This parrotfish species is likely to have a large influence on coral growth, mortality, and reproductive fitness, although additional studies are needed to investigate its ecological role on Pacific reefs.

Butterflyfishes are also major coral predators (Fig. 1D), consuming tissue but generally not removing coral skeleton (Randall 1967, Randall et al. 1996, Randall 2005). Many butterflyfishes remove single coral polyps using small forceps-like mouths, whereas others scrape coral mucus and polyps with wide, shovel-shaped

mouths (Motta 1988). Overall, 53 species of butterflyfish are known to consume live coral, and 14 of these are obligate coral-feeders. Consumption rates vary among species, but average 7 bites min^{-1} . Chaetodontids consume a wide variety of coral genera, but appear to focus on *Porites*, *Acropora*, *Agaricites*, *Pocillopora*, and *Montipora* corals (Appendix 1). Many butterflyfish are also highly territorial (Roberts & Ormond 1992) and graze coral colonies within their territories repeatedly (Reese 1989, Roberts & Ormond 1992). This chronic tissue removal might be expected to deplete colony resources, reducing nutrient content, growth, and reproductive output, although the effects of chronic butterflyfish corallivory have yet to be studied in detail for scleractinians. There are some data showing butterflyfish can remove substantial biomass and lower reproductive output in gorgonian corals (Lasker 1985). For example, in the San Blas Islands, Panama, *Chaetodon capistratus* was estimated to remove an average of 378 polyps d^{-1} from the gorgonian *Plexaura homomalla* and 100 polyps d^{-1} from *Pseudopterogorgia americana* gorgonians. At some sites, *C. capistratus* selectively grazed *Plexaura* spp. colonies with ripe gonads (Lasker 1985). It is known that, among scleractinians, the butterflyfish *C. unimaculatus* has a major influence on the abundance and distribution of *Montipora verrucosa* in Hawaii; caging experiments demonstrate that *C. unimaculatus* feeding restricts vertical growth of those corals (Cox 1986). Similarly, growth, zonation, and distribution of *Pocillopora damicornis* in Guam are impacted by piscine corallivores; transplant experiments suggest that these corals are restricted to shallow lagoon habitats due to feeding by chaetodontid and balistid fishes (Neudecker 1979). Nonetheless, several studies have documented a positive relationship between the density of obligate corallivorous butterflyfish and coral cover of their preferred prey species (Cox 1994, Findley & Findley 2001), suggesting that frequent tissue removal by butterflyfish does not necessarily impact coral fitness negatively.

Damsel-fishes are also highly territorial, but they remove coral tissue mainly to promote growth of algal gardens (Fig. 1E,F) (Kaufman 1977), which these fish use for food and mate-attraction (Randall 1967, Brawley & Adey 1977). Grazing by the damselfish *Stegastes* (formerly *Eupomacentrus*) *planifrons* on acroporid corals promotes coral skeletal growth into a distinctive, chimney-like structure characterized by a rounded lip on a raised column (Fig. 1E) (Kaufman 1977). Similar structures have been found on Pleistocene acroporid fossils, implying that damselfish biting live coral is not a recent phenomenon (Kaufman 1981). *S. planifrons* is known to cause ridge mortality on *Diploria* spp. corals (Proppe 1998), as well as partial mortality in Acropid coral fragments (Bruckner & Bruckner 2001). Colony areas where damselfish have removed coral tissue are

subsequently colonized by algal turf and macroalgae, which may have consequences for corals beyond tissue loss and energy needed for repair. Faster-growing algae compete with corals for light and space (reviewed by McCook et al. 2001), and direct contact with algae can enhance harmful microbial activity (Smith et al. 2006) and trigger coral disease (Nugues et al. 2004). On the other hand, damselfish aggressively guard their algal mats from herbivores, and this territorial behavior often deters grazing by corallivores as well (Glynn et al. 1983).

MAJOR INVERTEBRATE CORALLIVORES

There are 51 known species of invertebrate corallivores, including annelids, arthropods, echinoderms and mollusks; of these, only 16 are known to be obligate corallivores (Appendix 1). Invertebrates employ a range of strategies for feeding on coral (Fig. 2). Crabs of the genera *Tetralia* and *Trapezia* consume mostly coral mucus (Stimson 1990). Such mucus removal is not likely to have major negative effects as corals regularly slough off mucus into the water column, although mucus-feeding has been shown to disrupt coral microbial communities (Ducklow & Mitchell 1979). Other invertebrate browsers on corals include the crown-of-thorns seastar *Acanthaster planci*, which feeds by everting its stomach to digest coral tissue without damaging skeletons (Fig. 2A) (Birkeland & Lucas 1990). Many other invertebrate corallivores, for example the sea urchin *Eucidaris thouarsii* in Panama (Glynn et al. 1983), are scrapers that contribute to reef bioerosion by removing both tissue and underlying coral skeleton.

Among invertebrate predators, the seastar *Acanthaster planci* is perhaps the most influential. On Pacific reefs, it periodically reaches high population densities capable of destroying large reef tracts (Pearson & Endeane 1969, Moyer et al. 1982, Moran 1986, Colgan 1987, Birkeland & Lucas 1990, Turner 1994, Cumming 1999). The causative factors responsible for these population outbreaks are not well-understood, although this has been the subject of much research (Vine 1971, Birkeland 1982, Birkeland & Lucas 1990, Houk et al. 2007). Hypotheses for these outbreaks abound and include over-fishing, pesticide use, atomic testing, rain forest depletion, global climate change, and over-population (reviewed by Sapp 1999). Regardless of the cause, it has been estimated that a single *A. planci* individual can consume 5 to 6 m^2 live coral yr^{-1} (Birkeland 1989), and densities during outbreaks can reach 4 to 6 ind. m^{-2} (reviewed by Carpenter 1997). *A. planci* aggregations often cause nearly 100% coral mortality in a localized area (reviewed by Carpenter 1997). *A. planci* is a facultative corallivore that prefer-

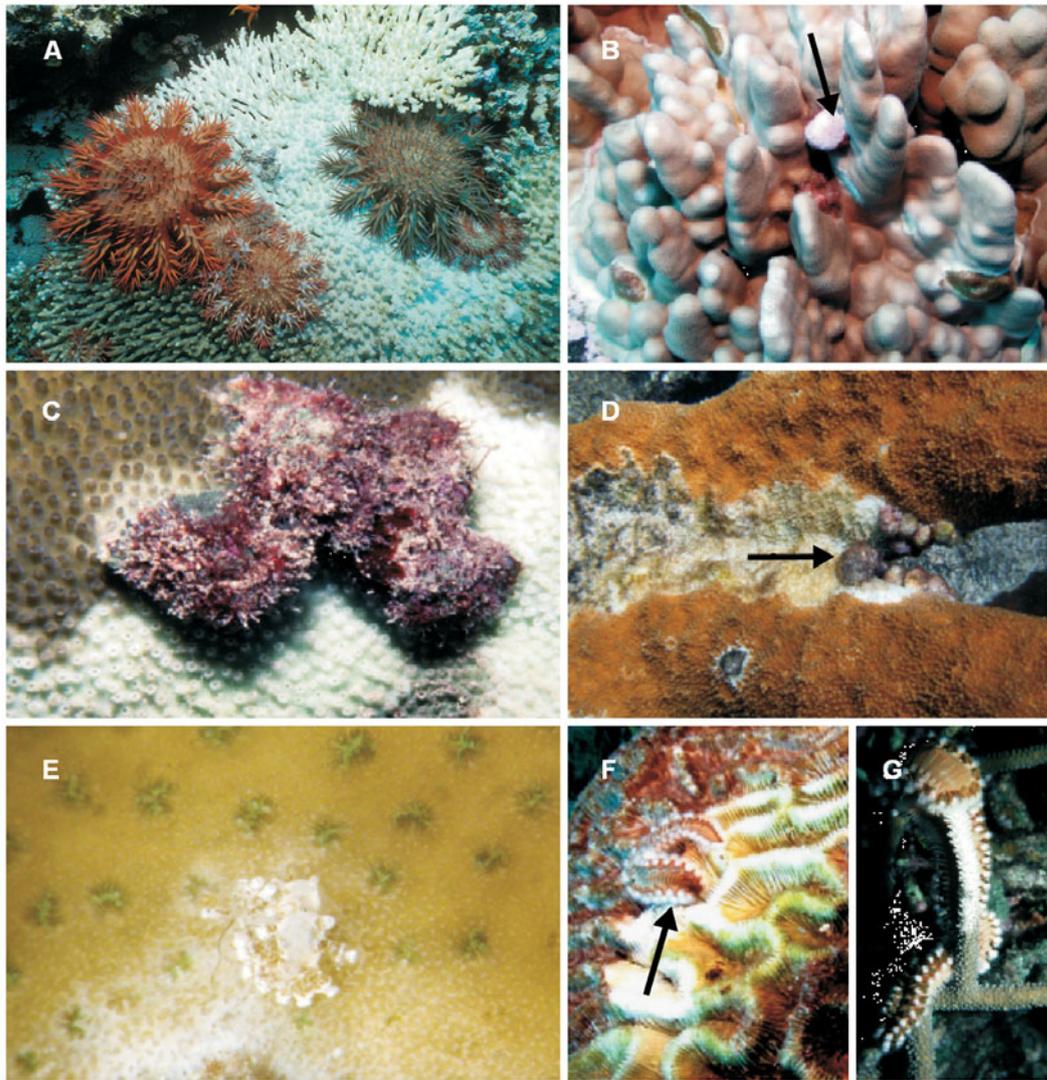


Fig. 2. Grazing on corals by various invertebrate corallivores. (A) Extensive coral tissue removal by *Acanthaster planci* (white coral skeleton remaining) off Tiran Island, Egypt (image by B. Furlan). (B) Snails of *Drupella* spp. feeding on live coral off Palau (image by E. Borneman). (C) *Coralliophila abbreviata* feeding on *Acropora palmata* colonies (image by A. Bruckner). (D) *C. abbreviata* coralivory off Mona Island, Puerto Rico (image by E. Borneman). (E) Nudibranch feeding on *Montipora digitata* tissue (image by E. Borneman). (F) *Hermodice carunculata* fireworm feeding on a *Diploria* spp. coral colony off Mona Island, Puerto Rico (image by E. Borneman). (G) *H. carunculata* feeding on an *Acropora cervicornis* colony (image by A. Bruckner). Arrows in B,D,F point to corallivores

entially consumes *Pocillopora* corals in Hawaii (Chess et al. 1997), but prefers *Montipora* and *Acropora* coral species almost everywhere else (Colgan 1987, Pratchett 2001). Following a large outbreak in Guam, *A. planci* prey preferences influenced reef community dynamics by temporarily shifting coral dominance to non-preferred corals (such as *Porites* spp. and *Leptastrea* spp.) until the reef recovered (Colgan 1987). Corallivorous snails of the genus *Drupella* (Fig. 2B) also periodically form aggregates of thousands of individuals (reviewed by Moyer et al. 1982 and Turner 1994). *Drupella* spp. are obligate corallivores that specialize on acroporid corals, primarily fast-growing

Acropora and *Montipora* spp. (Morton et al. 2002). Aggregations of *Drupella* spp. consumed an area of live coral covering 35 m² in Toga Bay, Japan, over a period of 2 mo, and were considered responsible for a 35% decline in live coral cover over 2 yr (reviewed by Turner 1994). Due to a *Drupella* spp. outbreak on Ningaloo Reef (Western Australia), live coral cover was reduced by up to 86% in some reef habitats in less than a decade (Ayling & Ayling 1987). Thus, localized population outbreaks of both *A. planci* and *Drupella* spp. can rapidly and severely reduce coral survival, although some reefs subsequently recover (e.g. Glynn 1973, Colgan 1987).

In the Caribbean, the snail *Coralliophila abbreviata* appears to be an obligate coral feeder, since even after starvation, this corallivore would not consume algae, fish, or crustacean tissue (Ward 1965). *C. abbreviata* is known to consume 26 species of scleractinian coral (Miller 1981, Bruckner 2000), and is commonly found feeding on *Acropora* (Fig. 2C,D), *Agaricia*, and *Montastraea* spp. (Hayes 1990a, Bruckner 2000, Miller 2001, Baums et al. 2003). However, *C. abbreviata* does not seem to prefer one coral prey species over another (Hayes 1990b). Abiotic stressors, such as hurricanes, have been shown to concentrate corallivore populations, resulting in localized areas of rapid and high acroporid coral mortality (Knowlton et al. 1990). Furthermore, corallivory by *Coralliophila* spp., combined with other reef stressors such as herbivore reduction and/or hurricanes lowers reef resilience and has been implicated in contributing to phase shifts from coral-dominated to algal-dominated reefs (Knowlton et al. 1990).

On Galapagos reefs, the sea urchin *Eucidaris thouarsii* can reach densities of 10 to 50 ind. m⁻² (Glynn et al. 1979), and these corallivores caused extensive coral mortality and reduced reef resilience during an El Niño event (Glynn 1990a). These urchins are facultative corallivores specializing on *Pocillopora* and *Pavona* species, but crustose coralline algae are another major dietary component (Glynn et al. 1983). *E. thouarsii* does not regularly consume live coral in regions outside the Galapagos, although occasional corallivory has been reported in Panama (Glynn et al. 1983).

In contrast to the uniformly negative effects of most corallivores, some invertebrate predators are mutualists that provide net benefits to corals. The xanthid crabs *Tetralia* and *Trapezia* spp. feed on mucus and coral tissue (Knudsen 1967, Stimson 1990, Rinkevich et al. 1991), but guard their acroporid and pocilloporid coral hosts against more damaging corallivores such as *Acanthaster planci* (Glynn 1980, 1987, Pratchett 2001). Pocilloporid corals guarded by crabs have greater chances of survival when exposed to predation by *A. planci* compared to corals experimentally deprived of their crustacean symbionts (Glynn 1983). The shrimp *Alpheus lottini* also defends its coral hosts while having little negative impact on corals because it consumes only mucus (Glynn 1980). Finally, crabs of the genus *Trapezia* also enhance coral health by clearing fine sediments from coral surfaces. Stewart et al. (2006) showed in a field study that, when mutualist crabs (*Trapezia*) were removed, 45 to 80% of *Acropora hyacinthus* and *Pocillopora verrucosa* died within a month. Corals hosting crabs experienced no mortality under the same conditions, grew faster, and had lower sediment load and less tissue bleaching compared to corals without crabs (Stewart et al. 2006).

PATTERNS OF CORALLIVORY

Looking broadly across biogeographic regions, vertebrate corallivores clearly outnumber invertebrate species in almost every region of the world (Fig. 3). Reefs in the Pacific and Indian Oceans have more corallivore species compared to the Caribbean. This circumtropical pattern of species diversity has been previously noted for butterflyfishes, which have similarly few species in the tropical Atlantic and Eastern Pacific than the Indo-Pacific (Findley & Findley 1989). In addition, we found that reefs in the Indo-Pacific, Oceania, and along the Great Barrier Reef, Australia, host more obligate corallivore species than Atlantic reefs (Fig. 3), which can possibly be explained by the lower coral diversity and older reefs of the Atlantic (Veron 1995). Worldwide, the majority of 161 known corallivores are facultative coral feeders, with only ~25% feeding exclusively on live coral (Table 1). However, although live coral constitutes only a minor portion of the diet for most species, even low levels of corallivory can have potentially major consequences for corals.

Corallivores can be either specialists, consuming mainly one or a few coral genera, or generalists, consuming many coral genera. For example, the crab *Tetralia cavimana* is found exclusively on *Acropora* spp. (Glynn 1987), whereas the parrotfish *Sparisoma viride* feeds on a variety of coral genera including *Montastraea*, *Porites*, *Siderastraea*, and *Colpophyllia* spp. (Bruckner & Bruckner 1998c, Garzon-Ferreira & Reyes-Nivia 2001, Reyes-Nivia et al. 2004, Rotjan & Lewis 2006). With almost 100% overlap in preferred coral genera between invertebrates and vertebrates, it appears that corallivores across the globe selectively feed on only a few coral families. Thus, all corallivores may be considered specialists to some degree because most coral species are avoided.

CONSEQUENCES OF CORALLIVORY

Coral growth

Corallivory causes coral tissue damage and/or loss, which can have direct negative effects on coral colony growth and survival. First, tissue loss requires reallocation of resources to tissue regeneration at the expense of new colony growth (reviewed by Henry & Hart 2005). Colonies respond to damage by initiating regeneration and repair, which is very energy intensive for neighboring polyps (Meesters et al. 1994), and probably for the colony as a whole (Henry & Hart 2005). In *Montastraea annularis*, 1 cm² of artificial lesions suppressed colony growth by 32% over a

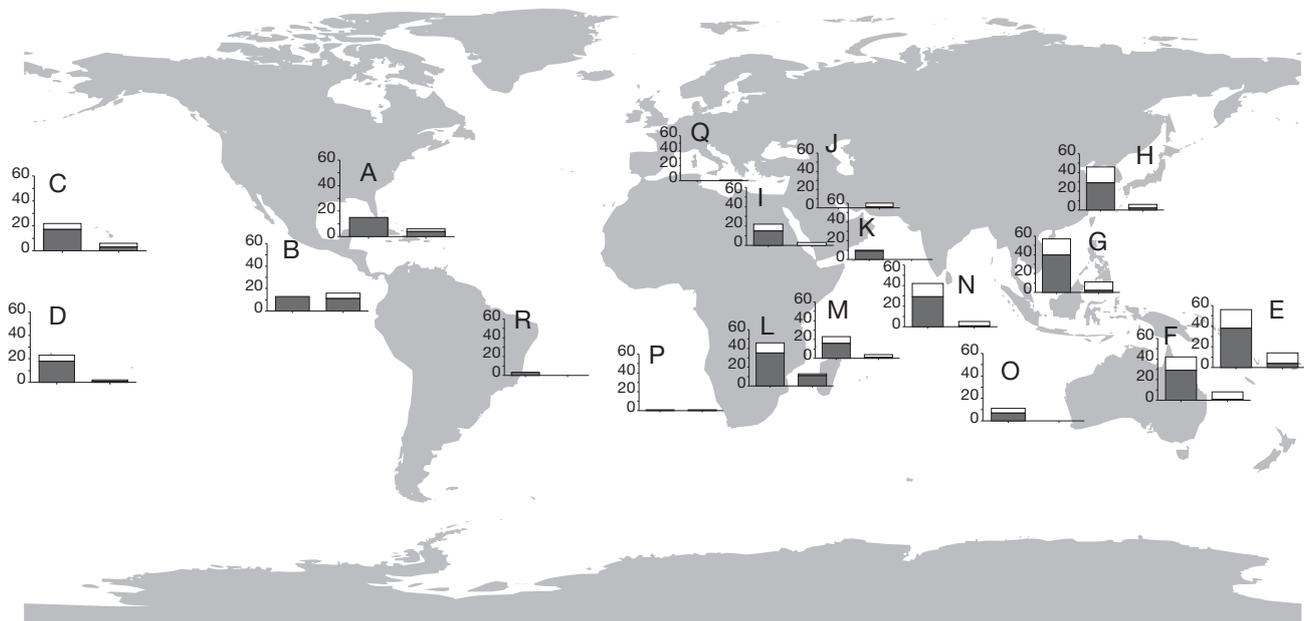


Fig. 3. Geographic distribution of corallivores. Stacked bars compare the number of obligate (□) to facultative (■) corallivorous species, either vertebrate (left bar) or invertebrate (right bar). y-axis on all graphs is no. of species. Letters represent geographic distribution of coral reef regions: (A) Caribbean and Bermuda, (B) Far Eastern Pacific (Galapagos and Panama), (C) Hawaii and the Johnston Atoll, (D) South Pacific (Tahiti, Pitcairn Islands, Marquesas), (E) Oceania (Guam, Micronesia, Marshall Islands American Samoa, French Polynesia, Cook Islands, Palau, Papua New Guinea, Fiji, New Caledonia, Tonga, Samoa, Solomon Islands, Palmyra Atoll, Jarvis Island, Tuvalu, Tokelau, Northern Mariana Islands), (F) Australia and the Great Barrier Reef, (G) Indo-Pacific (Cocos-Keeling Islands, Philippines, Singapore, Thailand, Indonesia, Malaysia, Paracel Islands), (H) Asian Pacific (Japan, South Korea, Taiwan, Hong Kong), (I) Red Sea, (J) Persian Gulf, (K) Arabian Sea (Oman), (L) African-Indian Ocean, (M) Southwest Indian Ocean (Seychelles, Mauritius, Reunion Islands), (N) Indian Ocean (Maldives, Sri Lanka, India), (O) Western Australia, (P) Southern Atlantic Ocean, (Q) Mediterranean Sea, (R) eastern South America (Brazil). Geographic distributions taken from Randall et al. (1996) and Randall (2005), and as specified by specific studies (Appendix 1) documenting incidents of corallivory. Note: Regions Q and P do have some corallivores, but literature about these regions is scarce, so we have reserved graph space to indicate that more corallivores are likely

2-mo regeneration period, and new growth continued to be suppressed for at least 30 d after regeneration stopped (Meesters et al. 1994). Considerably greater impacts on colony growth would be expected as a consequence of multiple tissue lesions (Henry & Hart 2005), which is typically the case in piscine corallivory. Regeneration costs are related to lesion length or perimeter (the area bordering live tissue); regenerative capacity does not change with overall colony size (Meesters et al. 1994, Oren et al. 1997). Thus, even though larger colonies presumably have larger energy stores and more resources, the likelihood of recovery from damage is approximately equal among differently sized colonies.

Initial lesion size plays an important role in recovery potential, which is the likelihood that a coral will fully regenerate following tissue damage. For example, *Porites astreoides* in the Caribbean successfully repairs 1 cm² lesions approximately 50% of the time, whereas it does not completely re-grow tissue over 5 cm² lesions, either artificially-induced, or from parrotfish grazing (Bak & Steward-Van Es 1980, Rotjan & Lewis

2005). Other coral species recover more quickly or more fully from smaller lesions than from larger ones (Bak & Steward-Van Es 1980, Lester & Bak 1985, Oren et al. 1997, Croquer et al. 2002). In some cases, corals can completely recover from small grazing scars (e.g. Sanchez et al. 2004). Regeneration rates vary across coral species (Meesters et al. 1996), and are also dependent on environmental factors such as temperature (Lester & Bak 1985, Meesters & Bak 1993), depth (Meesters et al. 1997, Nagelkerken et al. 1999), location (Nagelkerken et al. 1999), and sedimentation rates (Croquer et al. 2002).

Lesion shape can also play an important role in recovery potential. Oren et al. (1997) found that removal of a single coral polyp (imitating butterflyfish feeding) leads to a ~60% chance of recovery over a 90-d period. The same study also evaluated regeneration of tissue over parallel elongated lesions with 6 polyps removed per area and found 65% lesion recovery over 90 d (Oren et al. 1997). In theory, this parallel lesion pattern resembles scars from parrotfish grazing; however, these artificial lesions did not cause any

skeletal damage, whereas real parrotfish feeding scars remove some portion of the underlying substrate. Strikingly, lesions resembling invertebrate grazing scars had the lowest recovery rate (~16% regenerated tissue over 90 d). Thus, it seems that single-polyp, linear, and small ($\leq 2\text{cm}^2$) tissue-only lesions have best rates of regeneration, whereas circular or square lesions have the least (Bak & Steward-Van Es 1980, Oren et al. 1997). Furthermore, tissue loss with accompanying skeletal damage has lower regenerative success than tissue damage alone (Bak & Steward-Van Es 1980, Bak 1983, Croquer et al. 2002). These results suggest that any damage, even at the single-polyp level, initiates a regeneration procedure (with likely costs to overall colony growth or reproduction), and that regeneration of grazing scars is far from guaranteed. In the case of corallivory, tissue loss is likely to occur in multiple places on a colony simultaneously, and is likely to be chronic as many corallivores repeatedly graze the same colonies (Tricas 1989, Rotjan 2007). Thus, coral regeneration capabilities estimated from lesions inflicted at a single time point can give only a best-case scenario for tissue regeneration following the removal of tissue by corallivory.

Coral reproduction

Corallivory can also have direct consequences for coral reproductive potential (Henry & Hart 2005). Corals have limited energy stores that are partitioned among growth, regeneration, and reproduction (Bak 1983, Harrison & Wallace 1990). Energetically expensive reproduction is often compromised in favor of tissue regeneration processes (Szmant-Froelich 1985, Rinkevich & Loya 1989, Harrison & Wallace 1990, Van Veghel & Bak 1994). Van Veghel & Bak (1994) conducted a careful study of *Montastraea annularis*, *M. faveolata*, and *M. franksi* and found that colonies inflicted with artificial lesions ~10 wk prior to spawning showed a reduced reproductive effort (fertility, fecundity, fewer gonads per polyp, and fewer eggs per gonad) in neighboring polyps, compared to polyps located 20 cm away from the lesion area on the same colony. Furthermore, regenerated polyps had no reproductive activity, and polyps near regenerating tissue often had eggs of differing sizes (mature and immature), whereas distant polyps had only mature eggs (Van Veghel & Bak 1994). Similarly, Rotjan (2007) examined *Montastraea annularis* corals that had been recently grazed by parrotfishes (within 1 wk of spawning) and found that parrotfish preferentially remove polyps with high reproductive potential (Rotjan 2007). Interestingly, they also found that intact portions of grazed colonies had fewer eggs per gonad and gonads

per polyp than intact colonies (i.e. colonies without visible signs of corallivory). Since grazed colonies tend to be grazed repeatedly (Rotjan 2007), such chronic grazing requires constant regenerative efforts that would likely lead to lower reproduction rates. Taken together, these studies suggest that corallivory directly reduces coral reproduction by removing polyps with large numbers of mature eggs and gonads, and indirectly reduces reproduction in adjacent polyps which have to devote energy to tissue regeneration rather than reproduction.

Indirect effects of corallivory

Damage to colonies by corallivory can also have indirect consequences, such as the facilitation of algal competitors. Algal colonization does not necessarily prevent coral tissue regeneration, but unless regeneration occurs quickly, the likelihood of coral re-growth is severely reduced (Bak & Steward-Van Es 1980, Bak 1983, Meesters & Bak 1993, Oren et al. 1997). If a coral colony can complete the majority (at least 75%) of its regeneration within the first 70 d following damage, full recovery is likely (Bak & Steward-Van Es 1980). If tissue regeneration is incomplete, persisting portions of the colony become susceptible to colonization by spatial competitors such as algae, sponges, or other colonial invertebrates (e.g. zoanthids) (Bak & Steward-Van Es 1980). For example, artificial lesions on *Montastraea cavernosa* increased susceptibility to overgrowth by the encrusting sponge *Rhaphidophlus venosus* in Santa Marta, Columbia (Aerts 2000). Furthermore, the process of regeneration may hinder coral immune responses. Corals typically defend themselves against endolithic fungi by encapsulation; however, Bents et al. (2000) found that, when acropid and pocilloporid coral colonies were in the process of regenerating, they were less effective at preventing fungal infections. Future investigations might examine interactions between damage from corallivory and coral immunity to various diseases, as this is an issue likely to become increasingly important in coral reef conservation.

Although loss of coral tissue is the most obvious consequence of corallivory, corallivores can also negatively impact coral growth and fitness in other ways. The bearded fireworm *Hermodice carunculata* (Fig. 2F) is believed to serve as a vector for spreading coral disease agents, such as the bacterium *Vibrio shiloi* (Sussman et al. 2003). Similarly, field experiments in the Florida Keys have shown that the snail *Coralliophila abbreviata* infects *Acropora palmata* corals with white syndrome (Williams & Miller 2005). The corallivorous nudibranch *Phestilla* spp. has also

been implicated as a potential disease vector in Australia; following nudibranch grazing, coral fragments were colonized by various microbes, e.g. ciliates (*Paramoecium*) and bacteria (*Beggiatoa* spp.), leading to subsequent epidermal tissue loss (Dalton & Godwin 2006). Corallivorous fishes may also contribute to the spread of coral diseases. In laboratory studies, the Caribbean butterflyfish *Chaetodon capistratus* acted as a vector for black-band disease in the coral *Montastraea faveolata* via direct oral and/or indirect fecal transmission (Aeby & Santavy 2006). Parrotfish grazing scars on *Porites astreoides* colonies in Belize sometimes develop disease bands around the margins (R. D. Rotjan pers. obs.), but no quantification of this effect has yet been published. It is likely that other corallivorous fish species serve as occasional vectors for disease, but this remains an area for future investigation.

Some corallivores additionally exploit their coral prey by sequestering nutrients and symbionts from corals as they feed. The nudibranch *Phestilla sibogae* is known to incorporate coral photosynthetic endosymbionts (dinoflagellate zooxanthellae of the genus *Symbiodinium*) (Haramaty 1991), and the coral-feeding barnacle *Pyrgoma monticulariae* stimulates coral tissue growth into its aperture to facilitate direct feeding on coral nutrients and defenses (Ross & Newman 1969). This is not surprising, since many nudibranchs, sea hares, and other marine invertebrates are known to pilfer symbionts and defenses from a wide variety of prey, including Portuguese man o'war jellyfish, sponges, and soft corals (reviewed by Rudman 1986).

Some corallivores facilitate the destruction of corals by other corallivores. For example, predation by the gastropod *Coralliophila abbreviata* causes partial mortality in *Acropora palmata* colonies, and the feeding lesions then attract further corallivory by butterflyfish (*Chaetodon striatus* and *C. ocellatus*), which subsequently kills the colonies (Brawley & Adey 1982). Clearly, corallivores facilitating further corallivory is of potentially great concern, and much work remains to be done to understand these cascading consequences.

Synergies with other stressors

Corallivory can act in synergy with other stressors to further reduce coral growth, regeneration, and reproductive potential. Additional stressors can be either chronic or acute, and either natural or anthropogenic. Although coral stressors are becoming both more numerous and more severe, the interaction between corallivory and other stressors has not been well studied. Knowlton et al. (1990) found in Jamaica that a suite of coral predators, the snail *Coralliophila abbreviata*, the polychaete *Hermodice carunculata*,

the damselfish *Stegastes planifrons*, and the urchin *Diadema antillarum* significantly slowed the recovery of *Acropora cervicornis* after Hurricane Allen in 1980. Similarly, Rotjan et al. (2006) observed that chronic predation by parrotfishes on *Montastraea* spp. in Belize exacerbated the influence of abiotic stressors such as hurricanes and elevated seawater temperatures. Following a bleaching event in Belize, densities of zooxanthellae in colonies that had been grazed on by parrotfishes recovered slower, and their communities of zooxanthellae exhibited greater clade diversity (Rotjan et al. 2006). An interaction between partial colony mortality (functionally similar to corallivore grazing) and bleaching has also been demonstrated by Meesters and Bak (1993): they created artificial lesions on bleached and non-bleached *Montastraea annularis* colonies and found that bleached colonies exhibited less tissue growth, slower lesion recovery, slower tissue color restoration, and higher mortality. It is possible that coral reproduction may also be negatively affected by interactions between bleaching and corallivory, since bleaching (Szmant & Gassman 1990) and corallivory (Szmant-Froelich 1985, Harrison & Wallace 1990, Van Veghel & Bak 1994, Rotjan 2007) have known reproductive fitness costs. Taken together, these studies indicate that the synergistic effects of corallivory with other stressors may be important, especially given that coral stressors are on the rise: 2005 was the hottest year in recorded history (Hansen et al. 2005), hurricanes are increasing in intensity (Hoyos et al. 2006), and overfishing is contributing to the regular collapse of ecosystem food webs (Jackson et al. 2001). Much research remains to be done on the interaction of multiple stressors and their additive or synergistic consequences.

THE HERBIVORY–CORALLIVORY BALANCE

Corallivory, though destructive, has not historically been responsible for the collapse of coral reef ecosystems. Yet, as coral cover continues to decline (Gardner et al. 2003, Pandolfi et al. 2003, Lesser 2004), corallivory may play a new role; instead of acting as a bio-indicator of trouble (e.g. butterflyfish as bio-indicators of coral health), corallivores themselves may contribute to the problem. It should be noted that some common facultative corallivores, including scarid parrotfishes and the sea urchin *Diadema antillarum*, are also important herbivores. Herbivores are typically considered critical to the maintenance of healthy coral reefs (Hughes 1994), as their grazing activities indirectly benefit corals through preventing overgrowth by competitively superior macroalgae (Birkeland 1977, Lewis 1986, McClanahan & Muthiga 1998). Parrot-

fishes are perhaps the most important components of this herbivorous fish fauna, regularly consuming epilithic and endolithic algae from dead carbonate substrates (Mumby 2006). Similarly, *D. antillarum* normally scrapes algae growing on calcium carbonate structures using an extendable chewing apparatus. Yet since some parrotfishes and *D. antillarum* also consume live coral, these grazers are likely to play a more complex role in reef dynamics than has been appreciated previously.

Important members of herbivorous fish guilds include scarids (parrotfishes), acanthurids (surgeonfishes) and kyphosids (chubs). Among these herbivores, there is some functional trophic redundancy, i.e. some species have partly overlapping diets. Because algal turfs and macroalgae grow so rapidly, some trophic redundancy can greatly enhance reef ecosystem dynamics, as herbivores can act jointly to control the abundance of certain algal species. The mass-mortality of the mainly herbivorous sea urchins of the genus *Diadema* in 1983, for example, did not initiate a phase-shift to algal-dominated reefs in those regions where functionally redundant, herbivorous fishes were abundant (Bak et al. 1984). The resulting conservation philosophy has thus been to promote trophic redundancy by preserving all members of the herbivorous reef community (Mumby 2006, Mumby et al. 2006).

When major herbivores such as parrotfish and urchins also consume live coral, their role in reef trophodynamics becomes more complex. In the case of the Pacific parrotfish *Bolbometopon muricatum*, corallivory may keep fast-growing, weedy coral species in check, although the specific ecological role of *B. muricatum* has not yet been examined. In a healthy Caribbean reef ecosystem, the amount of live coral consumed by parrotfishes and urchins appears unlikely to be detrimental to coral reef ecosystems. However, as live coral cover declines worldwide (Gardner et al. 2003, Pandolfi et al. 2003), the dual roles played by some parrotfishes and urchins as both herbivores and corallivores will need to be re-evaluated. Current models of marine protected areas (MPAs) that advocate the conservation of parrotfish have underestimated the multifaceted trophic role of these fishes (as in Mumby 2006, Mumby et al. 2006). Specifically, they have not yet taken into account the potential direct impact that some parrotfish species may have through their consumption of live coral; in other words, they have not yet considered the herbivory/corallivory balance. Future models of reef trophodynamics should investigate possible thresholds, based on live coral abundance, where exclusive conservation of non-corallivorous herbivores offers a greater benefit to coral survival rather than conservation of the entire guild of reef herbivores.

THE INCREASING IMPORTANCE OF CORALLIVORY

The role of corallivory in decreasing reef resilience has not yet been examined, but may play an important new role in reef decline. As coral reefs suffer record losses in live coral cover due to changing ocean temperatures (Hoegh-Guldberg 1999, Ostrander et al. 2000, Aronson et al. 2002, Hughes et al. 2003), increasing storm intensities (Hughes 1994, Hoyos et al. 2006), disease (Richardson 1998, Harvell et al. 1999, Harvell et al. 2002, Rosenberg & Ben-Haim 2002, Sutherland et al. 2004), and increased pollution and eutrophication (Bell 1992, Lapointe 1997), the rate of coral decline may outpace the rate of corallivore decline. The relative impact of corallivory is likely to increase as coral cover decreases, with the potential for corallivory to negatively impact the fitness and survival of remaining reef corals. Future research is needed to re-evaluate the role of corallivores in reef trophodynamics and in reef-resilience models. Given that many facultative corallivores also play a major herbivorous role (e.g. parrotfishes, damselfishes, and the sea urchin *Diadema antillarum*), future studies might investigate the balance between beneficial herbivorous trophic contributions versus the detrimental corallivorous ones. Understanding this balance might help inform marine environmental managers about sustainable levels of corallivory, especially as live coral cover continues to decline.

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Appendix 1. Global list of vertebrate and invertebrate species known to consume live coral. Letter denotations for regions correspond to the map in Fig. 3. Feeding modes: obligate corallivores (O) eat exclusively live coral; facultative corallivores (F) have mixed diets that include some living coral. Consumption rate information varies, depending on the literature available (Appendix 2). In general, the table lists either the amount of coral removed per day (in g or cm²), number of bites min⁻¹, or % live coral in gut contents. Obligate corallivores for which there is no feeding information are assumed to have between 97 and 100% live coral found in gut contents. Feeding styles are classified based on the portion of coral removed: mucus (M), coral tissue (T), or skeleton (S). Coral prey are grouped by genera, listed with the first three letters of each genus. Numbers in parentheses represent the number of corallivores in each taxonomic grouping

Taxa	Region	Feeding mode	Consumption rate	Style	Coral prey	Literature cited
Invertebrates (51)						
<u>Annelida (1)</u>						
<i>Hermodice carunculata</i>	A, P, Q	F	12.9 cm ² d ⁻¹	T	Acr, Mil, Ocu, Por	1, 2
<u>Arthropoda, Crustacea (9)</u>						
<i>Alpheus lottini</i>	B, J	F		M	Poc	3
<i>Aniculus elegans</i>	B	F	1.24 g (dry wt) d ⁻¹	T, S	Poc	4
<i>Calcinus obscurus</i>	B			T, S		
<i>Pyrgoma monticulariae</i>	G, M, N	O		T		5
<i>Tetralia glaberrima</i>	E, F, J	O		T, M	Acr, Ser	6
<i>Tetralia cavimana</i>	F, I, J	O		T, M	Acr	7
<i>Trapezia cymodoce</i>	B, F, G, I, J	O	1.3–1.5 cm ² d ⁻¹	T, M	Poc, Sty	6, 8
<i>T. ferruginea</i>	B, E, F, G, J	O		M	Poc	4, 6, 9
<i>Trizopagurus magnificus</i>	B	F	10.3 mg d ⁻¹	T, S	Poc	4
<u>Echinodermata, Asteroidea (10)</u>						
<i>Acanthaster ellisii</i>	B	F	145 cm ² d ⁻¹	T	Pav, Poc, Por, Psa	10
<i>A. planci</i>	B, E, F, G, H	F	116–187 cm ² d ⁻¹	T	Acr, Gar, Monti, Poc	11–15
<i>Culcita novaguinaeae</i>	C, D, E, G, N	F	28 cm ² d ⁻¹	T	Acr, Poc	16
<i>C. schmideliana</i>	L	F		T	Acr, Gal, Gon	17
<i>Echinaster purpureus</i>	L	F		M	Por	17
<i>Linckia laevigata</i>	L	F		M	Por	17
<i>Nardoa variolata</i>	L	F		M	Por	17
<i>Nidorellia armata</i>	B	F		T	Pav	18
<i>Pentacaster cumingi</i>	B	F		T	Psa	12
<i>Pharia pyramidata</i>	B	F		T	Poc	10, 18
<u>Echinodermata, Echinoidea (11)</u>						
<i>Astropyga radiata</i>	L	F		T		19
<i>Diadema antillarum</i>	A	F		T, S	Acr, Aga, Mad, Monta, Por	20, 21
<i>D. setosum</i>	L	F		T		19
<i>Echinothrix calamaris</i>	L	F		T		19
<i>Eucidaris thouarsii</i>	B	F	0.47–1.83 g m ² d ⁻¹	T	Pav, Poc	11, 18, 22
<i>Echinometra mathaei</i>	E, L, M	F		T		19
<i>E. viridis</i>	A	F		T		23
<i>Echinoneus cyclostomus</i>	L	F		T		19
<i>Microcyphus rousseaui</i>	L	F		T		19
<i>Stomopneustes variolaris</i>	L	F		T		19
<i>Tripneustes gratillia</i>	L	F		T		19

Appendix 1 (continued)

Taxa	Region	Feeding mode	Consumption rate	Style	Coral prey	Literature cited
Mollusca (20)						
<i>Aeolidia edmondsoni</i>	C	O		T	Por	24
<i>Phestilla melanobranchia</i>	E, G, F	O			Tur	25, 26
<i>P. minor</i>	E, L	O			Por	27
<i>P. sibogae (P. lugubris)</i>	C, E, F, G	O	6.4 cm ² d ⁻¹	T	Por	27, 28
<i>Coralliophilla abbreviata</i>	A	O	0.08–16 cm ² d ⁻¹	T	Acr, Aga, Col, Dic, Dip, Eus, Fav, Hel, Mad, Mea, Monta Myc, Por Sid	29–32, 83
<i>C. violacea</i>	D, E, G, N		0.25 cm ² d ⁻¹	T	Por	25, 33
<i>C. caribaea</i>	A			T	Acr, Por	31, 34
<i>Drupella cornus</i>	C, E, F, H, I, N	O	2.6 cm ² d ⁻¹	T	Acr, Monti, Poc, Por, Ser, Sty	25, 35–38
<i>D. elata</i>	G, H	O		T	Acr, Monti, Poc, Por	37, 39
<i>D. fragum</i>	E, H	O		T	Acr, Monti, Poc, Ser, Sty	35, 37, 39, 40
<i>D. rugosa</i>	E, F, G, H	O	137–229 min d ⁻¹	T	Acr, Monti, Poc, Ser, Sty	37, 39, 40
<i>Epitonium ulu</i>	C			T	Fun	41
<i>Habromorula spinosa</i>	H					42
<i>Jenneria pustulata</i>	B	O	0.8 g d ⁻¹	T	Poc, Por, Sid	4
<i>Latiaxis hindsii</i>	B			T	Poc	18, 43
<i>Muricopsis zeteki</i>	B			T	Poc	18, 43
<i>Pedicularia decussata</i>	A			T	Sol	44
<i>Philippia radiata</i>	C	F		T	Por	45
<i>Quoyula madreporarum</i>	B, E, G, L, M, N	O		T	Monti, Poc, Por, Ser, Sty	25, 46
<i>Q. monodonta</i>	B, E, M	O	0.64 cm ² d ⁻¹	T	Monti, Poc, Por, Ser, Sty	43
Vertebrates (114)						
Chordata, Tetraodontiformes						
Tetraodontidae (8)						
<i>Arothron hispidus</i>	B, C, E, K, L, M, N	F		T, S	Poc	4, 47, 48
<i>A. meleagris</i>	B, C, D, E, G, H, K, L	F	10.13 – 16.38 g d ⁻¹	T, S	Acr, Poc, Por, Pav, Psa, Monti	4, 11, 48–50
<i>A. nigropunctatus</i>	E, F, H, I, K, L, M, N	F	1.73 bites min ⁻¹	T, S	Acr, Pav, Poc, Por	47, 51, 52
<i>A. stellatus</i>	D, E, F, G, H, I, K, L, M, N	F		T, S		47, 48
<i>Canthigaster amboinensis</i>	B, C, D, E, F, G, H, M, N	F	3.7 % live coral diet	T, S		48, 53
<i>C. jactator</i>	C	F	1.0 % gut contents	T, S		53
<i>C. solandri</i>	C, E, G, K, L, M, M, N	F	11.1 % live coral diet	T, S		53–55
<i>C. valentini</i>	B, E, F, G, H, L, N	F	0.06 – 3 bites min ⁻¹	T, S	Pav, Poc, Por	52
Balistidae (7)						
<i>Balistapus undulatus</i>	D, E, F, G, I, L, M, N	F	1.87 bites min ⁻¹	T, S	Pav, Poc, Por	47, 48, 52
<i>Balistes polyepis</i>	B, C	F		T, S	Pav, Por	4
<i>B. vetula</i>	A, P	F	0.2 % gut contents	T, S		56
<i>Balistoides viridescens</i>	G, M, N	F		T, S		47
<i>Melichthys niger</i>	A, B, C, E, G, H, L, M, N	F	0.6 % gut contents	T, S	Col	56
<i>Rhinecanthus aculeatus</i>	G, I, K, L, M, N	F		T, S		48
<i>Sufflamen verres</i>	B	F		T, S	Poc, Por, Pav	4
Monacanthidae (5)						
<i>Amanses scopas</i>	E, F, G, H, I, L, N	O		T, S		48
<i>Cantherhines dumerilii</i>	B, D, E, F, G, L, M, N	F		T, S	Acr, Poc, Monti, Lep, Por	47, 48, 50
<i>C. pullus</i>	A	F	0.7 % gut contents	T, S		56
<i>C. sandwichiensis</i>	C, D	F		T, S		48
<i>Oxymonacanthus longirostris</i>	E, F, G, H, L, M, N	O	10.5 bites min ⁻¹	M, T	Acr	47, 48, 51, 57

Appendix 1 (continued)

Taxa	Region	Feeding mode	Consumption rate	Style	Coral prey	Literature cited
Chordata, Perciformes						
<u>Gobiidae (1)</u>						
<i>Gobiodon citrinus</i>	E, F, G, H, I, L, N	O	99% gut contents	T, M	Acr	51
<u>Labridae (8)</u>						
<i>Coris aygula</i>	G, N, O	F	0.13 bites min ⁻¹	T	Pav, Poc, Por	52
<i>Diproctacanthus xanthurus</i>	E, F, G	F		T, S		47
<i>Gomphosus caeruleus</i>	N	F	0.13 bites min ⁻¹	T	Pav, Poc, Por	52
<i>Labrichthys unilineatus</i>	E, F, G, H, L, M, N	O	1.9 bites min ⁻¹	T, S	Acr, Monti	47, 48, 51, 58
<i>Labropsis australis</i>	E, F	O		T, S		47, 48
<i>L. polynesica</i>	E	O		T, S		48
<i>L. xanthonota</i>	E, F, G, H, L, N	O		T, S		48
<i>Thalassoma lunare</i>	E, F, G, H, I, L, N	F	0.13 bites min ⁻¹	T	Pav, Poc, Por	52
<u>Blennidae (1)</u>						
<i>Exallias brevis</i>	G, H, K, L, M, N	F	72% gut contents	T, S	Acr	47, 51
<u>Scaridae (21)</u>						
<i>Bolbometopon muricatum</i>	E, F, G, H, I, L, N	F	6.09 bites min ⁻¹	T, S	Acr, Poc, Por, Mont	47, 48, 59-61
<i>Calotomus carolinus</i>	B, C, D, E, F, G, H, L	F	0.13 bites min ⁻¹	T	Pav, Poc, Por	52
<i>Cetoscarus bicolor</i>	G, L	F	0.4 bites min ⁻¹	T, S	Por	62
<i>Chlororus gibbus</i>	I	F	1.1 bites min ⁻¹	T, S	Por	48, 62, 63
<i>C. microrhinos</i>	E, F, G, H	F		T, S		48, 63
<i>C. sordidus</i>	E, F, G, I, K, L, M, N	F	2.2 bites min ⁻¹	T, S		48, 62
<i>C. strongylocephalus</i>	G, L, N	F	0.26 bites min ⁻¹	T, S	Pav, Poc, Por	48, 52
<i>Scarus coelestinus</i>	A	F	0.2% gut contents	T, S		56
<i>S. frenatus</i>	E, F, G	F	< 1% live coral diet	T, S	Por	84
<i>S. guacamaia</i>	A	F		T, S		
<i>S. ghobban</i>	B, D, E, F, G, H, I, K, L	F		T, S	Por	
<i>S. perrico</i>	B	F		T, S	Poc	4
<i>S. perspicillatus</i>	C	F		T, S	Por	61
<i>S. rivulatus</i>	E, F, G, H, O	F	1.7 bites min ⁻¹	T, S	Por	62
<i>S. taeniopterus</i>	A	F		T, S	Mad, Por	64
<i>S. trispinosus</i>	R	F	0.8% live coral diet	T, S	Fav, Muss, Sid	49
<i>S. vetula</i>	A	F		T, S	Monta, Sid	64, 65
<i>S. viridifucatus</i>	L	F	0.2 bites min ⁻¹	T, S	Pav, Poc, Por	52
<i>Sparisoma aurofrenatum</i>	A	F	0.2% gut contents	T, S	Monta, Por, Mad	56, 64, 65
<i>S. amplum</i>	R	F	8.1% live coral diet	T, S	Fav, Muss, Sid	49
<i>S. viride</i>	A	F	25 cm ² d ⁻¹	T, S	Col, Por, Monta, Sid, Dip, Aga	65-67
<u>Pomacanthidae (2)</u>						
<i>Centropyge multispinus</i>	L	F	0.2 bites min ⁻¹	T	Pav, Poc, Por	52
<i>Pomacanthus semicirculatus</i>	E, F, G	F	0.13-0.26 bites min ⁻¹	T	Pav, Poc, Por	52
<u>Pomacentridae (7)</u>						
<i>Cheilopriion labiatus</i>	F, G, H	F	93% gut contents	T, S	Acr	51
<i>Neoglyphidodon melas</i>	I, G	F		T		51
<i>Pomacentrus leucostictus</i>	A	F	1.5% gut contents	T		56
<i>P. variabilis</i>	A	F	1.7% gut contents	T		56
<i>Plectroglyphidodon dickii</i>	D, E, F, G, H, L	F	37% gut contents	T	Acr, Poc	51
<i>P. johnstonianus</i>	C, D, F, G, H, L	F	96% gut contents	M, T	Acr	51
<i>Stegastes planifrons</i>	A	F	0.6% gut contents	T	Acr, Monta	56, 68
<u>Zanclidae (1)</u>						
<i>Zanclus canascens/cornutus</i>	B, C, D, E, F, G, L, M, N	F	0.53 bites min ⁻¹	T, S	Pav, Por, Poc	52
<u>Chaetodontidae (53)</u>						
<i>Chaetodon aculeatus</i>	A	F	0.43 bites min ⁻¹	T	Aga, Monta, Sid	69
<i>C. andamanensis</i>	K, M, N	O		T	Acr	70
<i>C. aureofasciatus</i>	E, F, O	F		T		47, 71
<i>C. auriga</i>	E, G, H, I, L, N	F	18-60% gut contents	T		47, 51, 71, 72
<i>C. auripes</i>	H	F	12% gut contents	T		51
<i>C. austriacus</i>	I	O	4.4-6.4 bites min ⁻¹	T	Acr, Fav, Monti, Poc, Por, Ser, Sty	71, 73-75

Appendix 1 (continued)

Taxa	Region	Feeding mode	Consumption rate	Style	Coral prey	Literature cited
<i>C. baronessa</i>	E, F, G, H	O		T	Acr	47, 51
<i>C. bennetti</i>	D, E, F, G, H, L, M	O		M, T		47, 51
<i>C. capistratus</i>	A	F	5.4 bites min ⁻¹	T	Aga, Sid, Mad, Myc	69, 71
<i>Chaetodon citrinellus</i>	C, D, E, G, H, L, M, N	F	15–19% gut contents	T		47, 51, 71, 72
<i>C. ephippium</i>	C, D, E, G, H	F	19–26% gut contents	T		51, 71, 72
<i>C. falcula</i>	L	F	0.26 bites min ⁻¹	T	Pav, Poc, Por	52, 71
<i>C. flavirostris</i>	D, E, F	F		T		47, 48
<i>C. guttatissimus</i>	L	F		T		71
<i>C. kleinii</i>	C, E, G, H, I, L, N	F	3% gut contents	T		47, 51, 71
<i>C. larvatus</i>	I	O	10 bites min ⁻¹	T		76
<i>C. lineolatus</i>	E, G, I, L, N	F		T		47
<i>C. lunula</i>	E, F, G, L, N	F	0.2 bites min ⁻¹	T	Pav, Poc, Por	47, 52, 71
<i>C. lunulatus</i>	C, E, F, G, H, O	O		T		48
<i>C. madagascariensis</i>	L	F		T		71
<i>C. melannotus</i>	E, F, G, H, I, L, N	F	42% gut contents	T		47, 51, 71
<i>C. mertensii</i>	D, E, F, G, H, L	F		T		71
<i>C. mesoleucos</i>	I	F	6 bites min ⁻¹	T		76
<i>C. meyeri</i>	F, G, H, L, M, N	O		T		47, 48
<i>C. multicinctus</i>	C	F	21.8 bites min ⁻¹	T	Poc, Por	71, 77
<i>C. ocellatus</i>	A	F		T	Acr	31
<i>C. octofasciatus</i>	G, H	O		T	Acr	78
<i>C. ornatissimus</i>	E, F, G, N, O	O	2.08–5.62 bites min ⁻¹	M, T	Monti, Poc, Por	51, 71, 79
<i>C. oxycephalus</i>	G, N, O	F		T		47
<i>C. pelewensis</i>	D, E, F	F	58.9% gut contents	T		47, 71, 72
<i>C. plebeius</i>	E, G, H, O	O		T	Acr	47, 51, 71
<i>C. punctatofasciatus</i>	M, N	F		T	Poc	47, 80
<i>C. quadrimaculatus</i>	C, D, E, G, H	T	27.5% gut contents	T	Poc	48, 71, 72
<i>C. rafflesii</i>	E, F, G, H, N	F	10% gut contents	T		47, 51
<i>C. rainfordi</i>	F	F		T		71
<i>C. reticulatus</i>	E, F, G, H	O		T		47, 71
<i>C. semilarvatus</i>	G, H, I, N	O	6 bites min ⁻¹	T		76
<i>C. smithi</i>	D	F		T		48
<i>C. speculum</i>	E, F, G, H, N, O	F	75% gut contents	T		47, 51
<i>C. striatus</i>	A	F		T	Acr	31
<i>C. triangulum</i>	N	O		T		71
<i>C. trichrous</i>	D	F		T		48
<i>C. trifascialis</i>	C, E, G, H, I, L, M	O	4.58–10.74 bites min ⁻¹	T	Acr, Poc, Por, Monti	51, 71, 78, 81
<i>C. trifasciatus</i>	C, D, E, G, H, I, L, M	O	1.1–3.1 bites min ⁻¹	T	Acr, Pav, Poc, Por, Monti	47, 51, 52, 71, 79
<i>C. ulietensis</i>	E, G, H	F	10–69% gut contents	T		51, 72
<i>C. unimaculatus</i>	C, D, E, G, H, L, N, O	–	4.9–7.2 bites min ⁻¹	T	Monti, Poc	47, 51, 71, 82
<i>C. vagabundus</i>	E, G, H, L, M, N	F	8–18% gut contents	T		51, 71, 72
<i>C. xanthocephalus</i>	L	F		T		71
<i>Forcipiger flavissimus</i>	B, E, L	F	6.2% gut contents	T		72
<i>Heniochus chrysostomus</i>	D, E, F, G, H, O	F	7.1% gut contents	T		47, 48, 72
<i>H. intermedius</i>	I	F	1.3 bites min ⁻¹	T		76
<i>H. singularus</i>	E, G, H	F		T		48
<i>H. varius</i>	E, F, H, N, O	F		T		48

Appendix 2. References (Author, year) corresponding to reference numbers in Appendix 1

No.	Corresponding reference	No.	Corresponding reference	No.	Corresponding reference
1	Sussman et al. (2003)	29	Miller (2001)	58	McIlwain & Jones (1997)
2	Witman (1988)	30	Baums et al. (2003)	59	Choat (1991)
3	Glynn (1980)	31	Brawley & Adey (1982)	60	Bellwood et al. (2003)
4	Glynn et al. (1972)	32	Ward (1965)	61	Randall (1974)
5	Ross & Newman (1969)	33	Oren et al. (1998)	62	Bellwood & Choat (1990)
6	Knudsen (1967)	34	Miller (1981)	63	Bellwood (1995)
7	Glynn (1987)	35	Cumming (1999)	64	Frydl (1979)
8	Rinkevich et al. (1991)	36	Kita et al. (2005)	65	Rotjan & Lewis (2006)
9	Castro (1978)	37	Turner (1994)	66	Rotjan & Lewis (2005)
10	Dana & Wolfson (1970)	38	Ayling & Ayling (1987)	67	Bruckner & Bruckner (1998a)
11	Reyes-Bonilla & Calderon-Aguilera (1999)	39	Moyer et al. (1982)	68	Kaufman (1977)
12	Glynn (2004)	40	Morton et al. (2002)	69	Neudecker (1985)
13	Colgan (1987)	41	Bosch (1965)	70	Kuiter & Debelius (1999)
14	Chess et al. (1997)	42	Yokochi (2004)	71	Harmelin-Vivien (1989)
15	Pearson & Endean (1969)	43	Guzman (1988)	72	Harmelin-Vivien & Bouchon-Navaro (1983)
16	Glynn & Krupp (1986)	44	Dall (1889)	73	Wrathall et al. (1992)
17	Thomassin (1976)	45	Robertson et al. (1970)	74	Alwany et al. (2003)
18	Glynn et al. (1983)	46	Keen (1958)	75	Righton et al. (1998)
19	Herring (1972)	47	Randall et al. (1996)	76	Zekeria et al. (2002)
20	Bak & van Eys (1975)	48	Randall (2005)	77	Tricas (1989)
21	Glynn (1988)	49	Francini-Filho et al. (2008)	78	Sadovy & Cornish (2000)
22	Glynn et al. (1979)	50	Jayewardene & Birkeland (2006)	79	Reese (1977)
23	Griffin et al. (2003)	51	Sano et al. (1984)	80	Neudecker (1979)
24	Ostergaard (1955)	52	McClanahan et al. (2005)	81	Irons (1989)
25	Robertson (1970)	53	Allen & Randall (1977)	82	Cox (1986)
26	Dalton & Godwin (2006)	54	Acero & Rivera (1992)	83	Bruckner (2000)
27	Ritson-Williams et al. (2003)	55	Harmelin-Vivien (1979)	84	Hoey & Bellwood (2008)
28	Haramaty (1991)	56	Randall (1967)		
		57	Barlow (1987)		

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