

High Complexity Food Webs in Low-diversity Eastern Pacific Reef–Coral Communities

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ABSTRACT

Community-wide feeding interrelationships in a low-diversity coral reef off the Pacific coast of Panamá (Uva Island reef) demonstrate complex pathways involving herbivore, strong corallivore, and carnivore interactions. Four trophic levels with 31 interguild links are identified in a generalized food web, and documented feeding interrelationships with 287+ species links are portrayed in a coral–corallivore subweb. The importance of trophic groups changes greatly with time, from unknown causes over annual to decadal-scale periods, and during very strong El Niño–Southern Oscillation events such that intermittent intense herbivory by echinoids (*Diadema*) and corallivory by gastropod mollusks, the crown-of-thorns sea star *Acanthaster*, hermit crabs, and fishes result in high levels of coral mortality and bioerosion of reef substratum. Intra-regional differences in species composition and abundances affecting food-web interactions are briefly described for nonupwelling (Uva Island) and upwelling areas (Pearl Islands) in Panamá. Seasonal

upwelling in the Pearl Islands results in high plankton productivity, which likely augments production in invertebrates, fishes, marine mammals, and seabirds, but these pathways still remain largely unquantified. The corallivore *Acanthaster* is absent from upwelling centers in Panamá and from upwelling and nonupwelling areas in the southern and central Galápagos Islands, and the highly destructive, facultative corallivore *Eucidaris galapagensis* occurs only in the latter offshore islands and at Cocos Island. Relatively recent declines in the abundances of manta rays, sharks, and spiny lobsters are correlated with, but not necessarily causally linked to, increasing fishing activities in the late 1970s to early 1980s. The extent to which the complex yet highly unstable Uva Island food web is representative of other eastern Pacific coral reef ecosystems remains to be investigated.

Key words: food web; coral reef; eastern Pacific; Panamá.

INTRODUCTION

With only about 8–10 zooxanthellate (reef-building) coral species present on any given reef, and three genera (*Pocillopora*, *Porites*, and *Pavona*) contributing dominantly to reef accretion in the eastern Pacific, the array and complexity of known trophic interactions are unexpectedly high in this low-diversity coral reef region. High-diversity coral reef

ecosystems in the Indo-West Pacific and Greater Caribbean biogeographic regions support from two to more than ten times the number of reef-building coral and fish species present on eastern Pacific coral reefs (Paulay 1997). Numerous direct and indirect feeding effects involving polychaetous worms, crustaceans, mollusks, echinoderms, and fishes have been identified during the last 30 years of coral community studies ranging from the Gulf of California to Ecuador (Barham and others 1973; Gilchrist 1985; Glynn 1973, 1974, 1976, 1977b, 1982a, 1982b, 1983a, 1983b, 1984, 1985a; Glynn and others 1979, 1982; Glynn and Colgan 1988;

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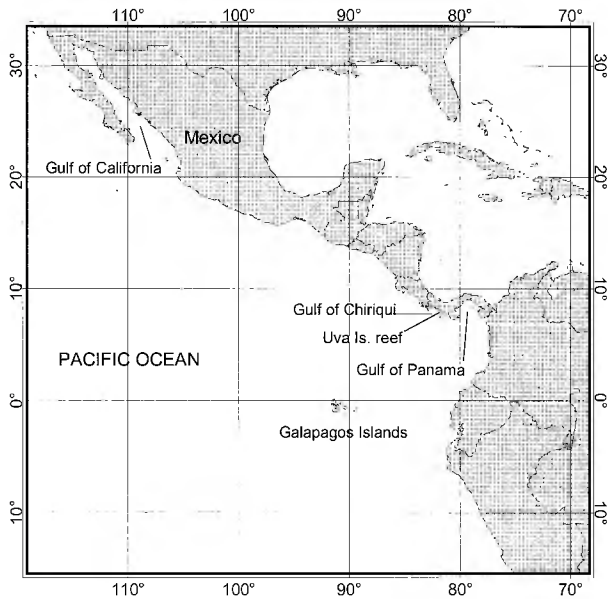


Figure 1 Eastern Pacific coral reef areas and location of Uva Island coral reef study site.

Guzmán 1988a, 1988b; Guzmán and López 1991; Guzmán and Robertson 1989; Reyes Bonilla and Calderón Aguilera 1999; Wellington 1982a). However, no comprehensive analysis of food-web relationships has yet been published for any coral reef community in the eastern Pacific.

I construct the first ecosystem-level food web of a coral reef in Panamá that my colleagues and I have continuously studied since 1970. This coral reef is located in the Gulf of Chiriquí (Figure 1), a nonupwelling environment supporting numerous small patch and fringing pocilloporid reefs. The reef is built predominantly by two frame-building coral species in the genus *Pocillopora* (*P. damicornis* and *P. elegans*), with secondary contributions from species in the genera *Porites*, *Gardineroseris*, *Pavona*, *Psammocora*, and *Millepora* (a hydrocoral). Unlike coral reefs in other regions, where crustose coralline algae are often abundant and contribute importantly as binding agents in framework construction, calcifying algae are generally unimportant to reef development in the eastern Pacific. The Uva Island patch reef covers about 2.5 ha and consists of a reef flat, reef slope, and seaward reef base at a maximum depth of approximately 6 m relative to mean low water (MLW) (Glynn and Maté 1997; Eakin 2001). Core drilling shows the reef framework to be 8–12 m thick, with a maximum age of about 5000 years (Glynn and Macintyre 1977). Strong seasonal patterns at Uva Island greatly influence environmental

conditions between the wet and dry seasons (Table 1).

Elevated sea temperatures associated with two exceptionally strong El Niño–Southern Oscillation (ENSO) events in 1982–83 and 1997–98 resulted in extensive reef–coral mortalities over most of the equatorial eastern Pacific (Glynn 1990, 2002; Glynn and Colgan 1992, Glynn and others 2001). ENSO-induced coral mortality in the Galápagos was 97% and 26% following 1982–83 and 1997–98, respectively. The Uva reef suffered about 75% overall coral mortality following the 1982–83 ENSO and about 13% from the 1997–98 ENSO. These disturbances need to be considered because they significantly altered the relative abundances of corals, the numerous species that prey on them, and the important links in the food-web design. It is also important to note that the magnitude of fluxes varies greatly over time, based on the presence of various species during a 30-year period. Several of these species have demonstrated marked variations in abundance, intermittently contributing significantly to food-web interactions or, when rare, scarcely having any effect.

COMMUNITY-WIDE FOOD WEB

Four trophic levels with 31 interguild links (including at least five intraguild pathways) have been identified in the Uva Island coral community (Figure 2). All nonreferenced, generalized, and species-specific pathways presented here and below for macrobiota and fishes are based on personal consumer–prey observations and gut-content analyses performed on field populations. Detritus, constituting particulate organic matter (for example, decaying organisms and feces), receives contributions from all reef biota and is consumed by decomposers and by suspension and deposit feeders. Decomposers such as microbes and species of meiofauna and microfauna are present in organic-rich sediment patches at the reef base, often encircling coral colonies and forming deposits in the internal structure of reefs where they accumulate in the highly porous basal reef framework. The organic matter content of sediments is also enriched by particulate fallout from river runoff and plankton advected onto the reef. Studies of meiofauna species undertaken on a Costa Rican reef found foraminifers, copepods, nematodes, and gastropods to predominate (Guzmán and others 1987), and this is expected for the Uva Island reef. This rich (largely microscopic) community demonstrates complex feeding interactions involving meiofauna that prey on microbes, and microfauna that consume meio-

Table 1 Physical Environmental Conditions Influencing Offshore Coral Reefs in the Gulf of Chiriquí, Panamá

Factor	Wet Season	Dry Season
Cloud Cover ^a median %	23.2–41.7	6.8–9.2
Rainfall mm ^b , mean annual = 2,598	423, maximum (Sep)	16, minimum (Feb)
Salinity, surface ^a Median (range)	28.0 (27.0–32.0)	34.0 (28.0–36.0)
Tides ^c semidiurnal, unequal mean spring range = 3.29 m	low water exposures near midnight low salinity stress from rainfall	low water exposures at midday intense solar exposure, heating, desiccation
Light Penetration ^b depth (m) of 10% surface radiation	10, minimum (Sep) 0.5 ^d –1.0 ^c (Jul-Sep)	37, maximum (Jan)
Sea Temperature (°C) ^{e,g} mean annual SST σ ~ 28°C	30–31, maximum (14 wk)	25 minimum (1 wk)
Nutrient Concentration ^b PO ₄ -P (μ g-at l ⁻¹) at 40 m depth	0.3, minimum (Oct, Nov)	1.1, maximum (Mar)

^aGlynn 1977b^bKwiecinski and Chial 1983^cU.S. Department of Commerce, calculated from tidal predictions for Balboa, Panamá^dGlynn unpublished observations^eDana 1975^fRenner 1963^gGlynn and others 2001

fauna; hence, the redirected arrow in trophic category 4 (Figure 2).

Reef waters in the Gulf of Chiriquí are often filled with phytoplankton and zooplankton, depending upon nutricline shoaling and nutrients advected to reefs via wet-season river discharge (L. D'Croz unpublished data). The sporadic abundance of plankton populations and ill-defined current movements around the Uva reef make this potential food source difficult to track and quantify. Phytoplankton and zooplankton are consumed by suspension feeders, such as sponges, sea anemones, polychaete worms, lithophage bivalves, vermetid gastropods, barnacles, porcelanid crabs, and brittle stars, and by zooplankton carnivores. These animals in turn contribute toward the organic matter content of sediments. Consumers of zooplankton include corals and a variety of fishes (*Paranthias colonus*, *Kyphosus elegans*, and damselfishes, mostly species of *Chromis*), and manta rays (*Manta birostris*). The relative contributions of zooplankton and photosynthates from algal endosymbionts toward the caloric intake of zooxanthellate corals are unknown in the eastern Pacific. However, Wellington (1982b), in a field study in the Pearl Islands (Panamá), demonstrated that maximum skeletal growth in two massive coral species (*Pavona clavus* and *Pavona gigantea*) was de-

pendent on the availability of zooplankton (> 95 μ m net mesh size), whereas the branching coral *Pocillopora damicornis* grew independent of zooplankton supply.

Turf and crustose coralline algae are most abundant on reef flats and in reef base habitats, whereas green frondose algae occur most commonly in the deeper reef base and talus slope zones. Reef slopes in forereef and backreef zones are dominated by nearly continuous stands of live *Pocillopora* spp. (Table 2). The occurrence of macroalgae is intermittent and may depend on nutrient concentrations arising from pycnocline shoaling and rivers and runoff as well as fluctuations in herbivore populations. When abundant, macroalgae such as *Caulerpa* spp. can overgrow and kill low-lying corals such as *Psammocora stellata* and *Porites panamensis* (Glynn and Maté 1997). Endolithic algae have been observed in coral skeletons but are unstudied, and little is known about their distribution and abundance in eastern tropical Pacific reefs. Reef flat turf algae are heavily grazed by large schools of scarid and acanthurid fishes that move into this zone at high water.

Zooxanthellate corals harbor both dinoflagellate endosymbionts and crustacean symbionts, the latter moving among colony branches or occupying shelters within coral skeletons. *Symbiodinium* clades C

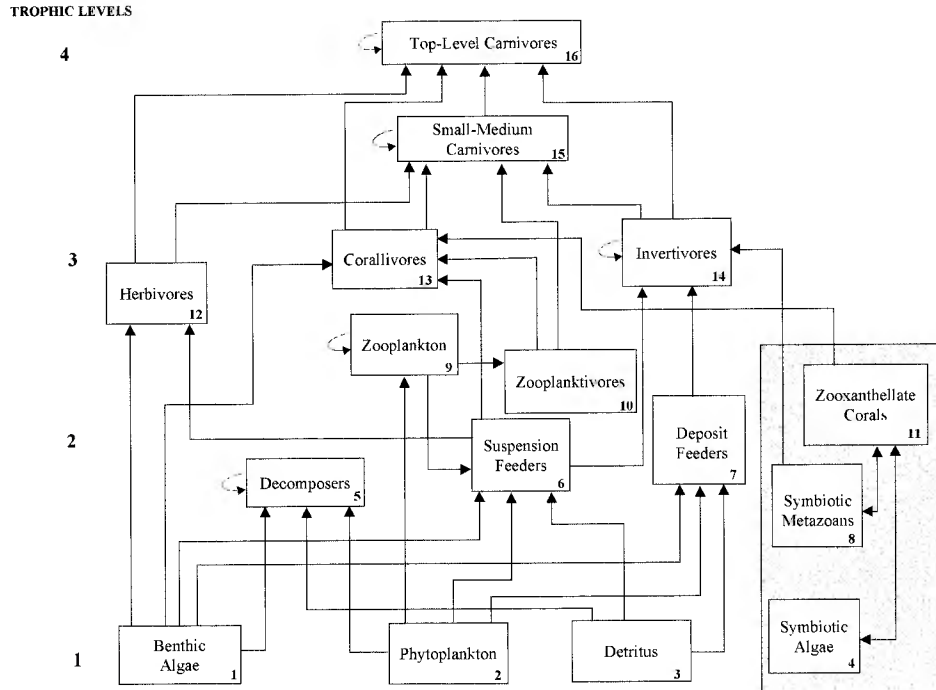


Figure 2 Conceptual coral reef food web at Uva Island, nonupwelling Gulf of Chiriquí, Panamá. Trophic level assignments follow Opitz (1996), which are from a modeling study of a Caribbean coral reef. The following categories are recognized: 1 benthic algae—algal turf, endolithic algae, crustose coralline algae, and macroalgae; 2 phytoplankton—femtoplankton to mesoplankton; 3 detritus—particulate organic matter; 4 symbiotic algae—*Symbiodinium* clades *A*, *C*, and *D*; 5 decomposers—microorganisms, meiofauna and microfauna; 6 suspension feeders—sponges, polychaete worms, lithophage bivalves, and barnacles; 7 deposit feeders—sea cucumbers, shrimp, and spiny lobster; 8 symbiotic metazoans—crabs, shrimp; 9 zooplankton—cnidarians, crustaceans, and various larval stages; 10 zooplanktivores—cnidarians, damselfishes, and manta rays; 11 zooxanthellate corals—scleractinian corals and hydrocorals; 12 herbivores—gastropods, echinoids, damselfishes, angelfishes, parrotfishes, kyphosids, acanthurids, and turtles; 13 corallivores—hermit crabs, gastropod mollusks, sea stars, and pufferfish; 14 invertivores—polychaete worms, octopus, hawkfish, jacks (*Caranx speciosus*), triggerfish, wrasses, and serranids; 15 small to medium carnivores—polychaete worms, crustaceans (*Hymenocera*, spiny lobster), puffers, balistids, eels, snappers, wrasses, groupers, jacks, and sharks; 16 top-level carnivores—sharks, barracuda, wahoo, snappers, groupers, and mackerels.

and *D* are present in scleractinian corals and *Symbiodinium* clade *A* in *Millepora* hydrocorals (Glynn and others 2001). At least 55 species of decapod crustaceans have been found on *Pocillopora damicornis* colonies alone in the Gulf of Panamá (Abele and Patton 1976). Some of these directly graze coral polyps (Glynn 1983b), feed on coral mucus, remove food from polyps, or feed on fat bodies produced by the coral host (Stimson 1990).

Coral tissues (or tissues plus skeleton) are consumed by numerous corallivores, noted in more detail below. The diets of many corallivore species are not restricted; they also consume benthic algae, suspension feeders, and invertivores (here treated as noncoral consumers of various invertebrate taxa) that prey on crustaceans living symbiotically with corals. Resident invertebrate and fish carnivores feed on herbivores, planktivores, corallivores, and

invertivores. *Panulirus gracilis* (spiny lobster), here grouped with carnivores, largely feeds on the flesh of moribund and decaying organisms. Sea turtles, notably the olive Ridley (*Lepidochelys olivacea*) and the loggerhead (*Caretta caretta*), destroy live pocilloporid frameworks while searching for and feeding on sponges attached to the coral's dead subsurface skeletons. Finally, the largest transient carnivores, such as sharks, wahoo, mackerels, and tunas, prey on resident carnivores and consumers at lower trophic levels as well. Whitetip reef sharks, *Triaenodon obesus*, have also been observed to cause extensive breakage of pocilloporid frameworks while pursuing their prey sheltered in the reef (Jiménez 1996–97). Bird and mammal consumers have not been observed. Even when low water exposes the reef flats and causes massive mortality of invertebrates and fishes, no birds appear to feed on them.

Table 2 Uva Reef Benthic Cover and Abundances of the More Common Vagile Invertebrates and Fishes. Reef zone: RB, reef base; FR, fore reef; RF, reef flat; BR, back reef

Organism					Source
Benthic Cover (%)					
live <i>Pocillopora</i> spp.	0.23 (RB)	56.5 (FR)	7.6 (RF)	53.8 (BR)	Eakin 1996
filamentous algae	6.5 (RB)	3.6 (FR)	0.0 (RF)	14.0 (BR)	sampling 1988-1994
crustose coralline and fleshy algae	89.4 (RB)	38.4 (FR)	91.6 (RF)	32.0 (BR)	
Invertebrate Abundances					
Non-pocilloporid corals relative % abundance ^a	8.4 (RB)				Glynn 1974
<i>Diadema mexicanum</i> ind m ⁻²	58 ± 13 (RB)	21 ± 8 (FR)	< 1.0 (RF)	< 1.0 (BR)	Eakin 2001 ^b
<i>Acanthaster planci</i> ind ha ⁻¹ , entire reef	< 1.0 (RB)	6 ± 1 (FR)	< 1.0 (RF)	< 1.0 (BR)	Glynn unpublished data ^c
<i>Trapezia</i> spp. ^f	12.5 ± 2.3				Fong and Glynn 1998 ^d
<i>Alpheus lottini</i> ^f median ind colony ⁻¹	1.0 (0-2)	1.5-8.5 (FR)	3-9.5 (RF)		Glynn unpublished data ^c
<i>Hymenocera picta</i> ^g ind ha ⁻¹ , entire reef		2 (FR)	2 (RF)		Glynn 1976
<i>Pherecardia striata</i> ^h ind m ⁻² median ± c.l.	1-118				Glynn 1977a
	170 ± 95 RB				Glynn 1984
Fish Abundances					
mean ± 95% c.i. ha ⁻¹					Glynn unpublished data n = 27 transects sampled during 2000-2002
Balistidae	106.0 ± 15.8				RB, FR, and RF zones fish sizes ≥ 15 cm TL
Scaridae	100.0 ± 37.3				
<i>Arothron</i> spp.	66.2 ± 15.4				
Lutjanidae	39.8 ± 37.3				
Acanthuridae	34.2 ± 20.1				
Chaetodontidae + Pomacanthidae	30.0 ± 8.5				
Labridae	20.8 ± 8.3				
Serranidae	9.3 ± 5.1				
Diodontidae	2.3 ± 2.3				

^acalculated relative to live *Pocillopora* spp. cover^bsampling period, 1988-1994^csampling period, 2000-2002^dmaximum population density 1987, mean ± SE, sampling period 1983-1984^emean and range, sampling period 2000-2002^f*Pocillopora* spp. sampled in 1974^grange, sampled in 1976^hsampled in 1980

CORAL-CORALLIVORE SUBWEB

The coral-coralivore subweb depicts 287+ known interspecific links among coral prey, invertebrate and fish corallivores, invertivores, and top-level fish predators (Figure 3). This subweb includes only the chief reef-building corals (*Pocillopora* spp., *Pavona* spp., *Gardineroseris planulata*, and *Porites lobata*) and taxa that often contribute significantly to coral community cover (*Psammocora stellata* and *Millepora intricata*).

An undetermined but probably minor amount of feeding, by means of extracoelenteric digestion, occurs interspecifically among corals growing in close proximity. This kind of interaction is indicated between *Pocillopora* spp. and *Pavona* spp., where Wellington (1980) demonstrated that a feeding response initially dominated by *Pocillopora damicornis* was later reversed through the development of sweeper tentacles by *Pavona gigantea*.

The tissues of all scleractinian coral species are consumed by at least two corallivore species, but

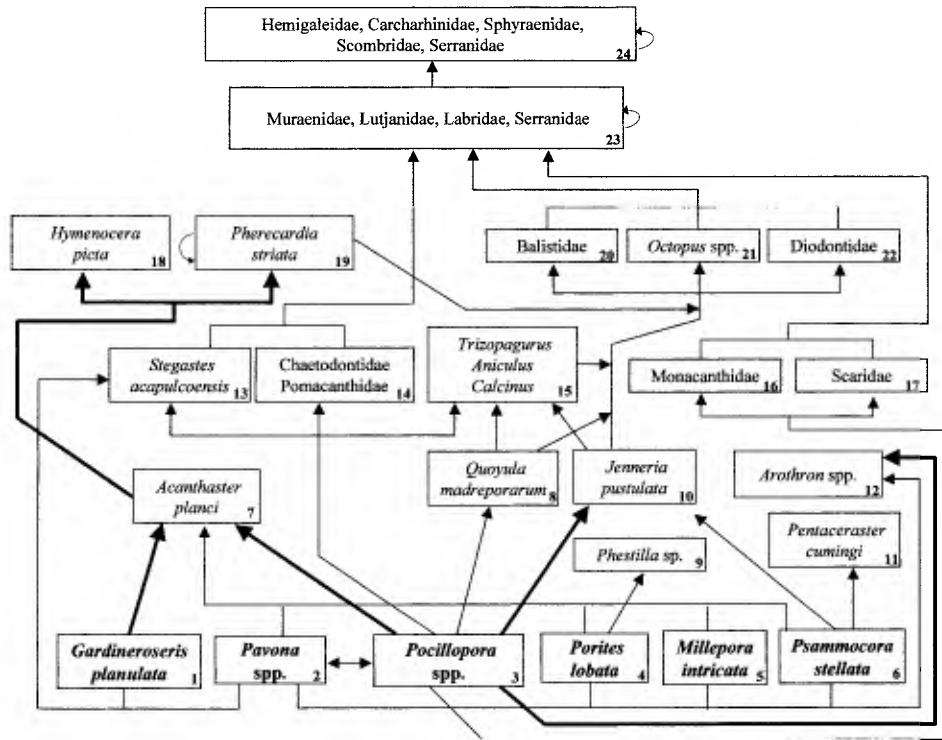


Figure 3 Documented feeding interrelationships among zooxanthellate scleractinian corals and hydrocorals, and corallivores and their predators at Uva Island, nonupwelling Gulf of Chiriquí, Panamá. Strong pathways are indicated by the thick arrows, denoting frequent prey consumption. Species identities: 1, *Gardineroseris planulata*; 2, *Pavona* spp. (*Pavona clavus*, *Pavona gigantea*, and *Pavona varians*); 3, *Pocillopora* spp. (*Pocillopora danicornis* and *Pocillopora elegans*); 4, *Porites lobata*; 5, *Millepora intricata*; 6, *Psammocora stellata*; 7, *Acanthaster planci*; 8, *Quoyula madreporarum*; 9, *Phestilla* sp.; 10, *Jenneria pustulata*; 11, *Pentaceraster cumingi*; 12, *Arothron* spp. (*A. mcleagris* and *A. hispidus*); 13, *Stegastes acapulcoensis*; 14, *Chaetodontidae* and *Pomacanthidae* (*Johnrandallia nigrirostris*, *Chaetodon humeralis*, *Holacanthus passer*, and *Pomacanthus zonipectus*); 15, hermit crabs (*Trizopagurus magnificus*, *Aniculus elegans*, and *Calcinus obscurus*); 16, *Monacanthidae* (*Aluterus scriptus* and *Cantherhinus dumerilii*); 17, *Scaridae* (*Scarus perrico* and *S. rubroviolaceus*); 18, *Hymenocera picta*; 19, *Pherecardia striata*; 20, *Balistidae* (*Sufflamen verres* and *Pseudobalistes naufragium*); 21, *Octopus* spp.; 22, *Diodontidae* (*Diodon holocanthus* and *Diodon hystrix*); 23, *Muraenidae* (*Gymnothorax castaneus* and *Gymnothorax dovii*), *Lutjanidae* (*Lutjanus viridis*, *Lutjanus argentiventris*, and *Lutjanus novcmfasciatus*), *Labridae* (*Bodianus diplotaenia*, *Novaculichthys taeniourus*, and *Thalassoma grammaticum*), and *Serranidae* (*Epinephelus panamensis* and *Epinephelus labriformis*); and 24, *Hemigaleidae* (*Triaenodon obesus*), *Carcharhinidae* (*Carcharhinus lucas*), *Sphyrnidae* (*Sphyrna ensis*), *Scombridae* (*Acanthocybium solandri*), and *Serranidae* (*Mycteroperca xenarcha*).

Pocillopora spp., which are the principal framework builders on Panamanian reefs, are preyed on by at least nine groups of consumers, some with multiple species. Pufferfishes (*Arothron*), parrotfishes (*Scaridae*), and filefishes (*Monacanthidae*) bite off colony branch-tips, and hermit crabs (*Trizopagurus*, *Aniculus*, and *Calcinus*) scrape skeletal surfaces, generating coarse to fine-grained calcareous sediments (Glynn and others 1972). Removing only tissues and leaving the skeleton intact are the gastropods *Jenneria pustulata* and *Quoyula madreporarum*, butterflyfishes and angelfishes, the damselfish *Stegastes acapulcoensis*, and *Acanthaster planci*, the crown-of-thorns sea star. Although damselfish nip and ingest coral tissues when establishing or enlarging algal

mats, the contribution of this food source toward the fish's dietary needs is unclear (Wellington 1982a). *Acanthaster* is a corallivore generalist, preying on nearly all coral taxa but consuming especially large amounts of *Pocillopora* and *Gardineroseris* (Glynn 1974). *Acanthaster* feeds more on small or broken branches of *Pocillopora*, which receive less protection by crustacean guards than large intact colonies (Glynn 1983a). Both adult and juvenile butterflyfishes and angelfishes nip and ingest *Pocillopora* polyps. They have not been seen feeding on other coral genera. *Jenneria* and *Acanthaster* can kill relatively large (approximately 30 cm in diameter) whole colonies of *Pocillopora*. Like the gastropod *Drupella* in the western Pacific, *Jenneria* sometimes

overwhelms *Pocillopora* with feeding aggregations exceeding 50–100 individuals on single 30-cm-diameter colonies.

Arothron spp. also bite off the branch tips of *Millepora intricata* and *Psammocora* spp., and remove centimeter-sized fragments from protuberances and ridges on the massive colonies of *Porites lobata* and *Pavona* spp. Balistids, notably *Pseudobalistes naufragium*, also bite 2- to 5-cm-diameter sections from *Porites* and *Pavona* corals, but in search of lithophagine bivalves that they extract and consume. Some of these fragments survive this breakage and produce new colonies, thus contributing to the asexual propagation of these corals (Guzmán 1988a). *Phestilla* sp., a small and secretive aeolid nudibranch, feeds on *Porites lobata* at night. The sea star *Pentaceraster cumingi* occasionally feeds on *Psammocora stellata* in reef slope and base zones with its everted stomach also digesting sponges and other metazoans attached to the coral colony's basal branches. No predators have been observed feeding on *Phestilla* sp. or *P. cumingi*.

Especially strong trophic pathways in this subweb, involving pocilloporid corals and *Gardineroseris planulata*, are supported by several studies. The consumption of *Pocillopora* spp. tissues by *Jenneria pustulata*, *Acanthaster planci*, and *Arothron meleagris* is notably high compared to that by hermit crabs, other gastropods and fishes, and other members of the corallivore guild [quantified by Glynn and others (1972) and Glynn (1973, 1976, 1977b, 1984, 1985a)]. From 1983 to 1985, *Jenneria* consumed about twice the amount of coral tissues as did *Acanthaster* and the latter about seven times that of *Arothron* (Glynn 1985a), but these values varied widely through time depending on the fluctuating abundances of corallivore populations. On the Uva reef, *Gardineroseris* is preferentially preyed on by *Acanthaster* (Fong and Glynn 2000). In turn, field and mesocosm studies (Glynn 1977b, 1984) indicate that *Acanthaster* abundance on the Uva reef is controlled by the harlequin shrimp *Hymenocera picta* and the polychaete worm *Pherecardia striata*. Shrimps and worms often feed on moribund *Acanthaster* and may, therefore, be scavengers rather than predators. Finally, several pathways from corallivores or corallivore consumers lead to higher-level resident carnivores such as eels and snappers, and ultimately to top-level transient carnivores such as groupers, wahoos, and sharks.

TEMPORAL AND SPATIAL VARIATIONS

As already noted, eastern Pacific coral reefs have been subject to significant declines in live coral

cover over the past 30 years, during periods of strong ENSO disturbances (Glynn and Colley 2001; Reyes Bonilla and others 2002). Corallivores and other consumers have also demonstrated significant fluctuations in abundances over this period. For example, *Acanthaster planci* ranged from 36 ind (14 ind ha⁻¹) on the Uva reef in 1972 (Glynn 1973) to 0 in 2001 (Fong and Glynn 1998; P. W. Glynn unpublished data). Also, *Jenneria pustulata* populations have ranged from 20,000 to 60,000 (8000–24,000 ind ha⁻¹) on the Uva reef in the 1970s (Glynn and others 1972; Oramas 1979) to 400,000 to 700,000 (160,000–280,000 ind ha⁻¹) in 1982 (Glynn 1985a). Tens of thousands of *Jenneria* were observed consuming whole large (approximately 30 cm in diameter) pocilloporid colonies in 1982. These abundances declined sharply following 1983, a likely result of elevated ENSO temperatures and coral mortality, and remained low from 1985 onward (Achurra Cardenas and Valdes Arauz 1980; Glynn 1985a; P. W. Glynn unpublished data). *Diadema mexicanum* mean population densities increased dramatically after 1983, from less than 5 ind m⁻² in reef base and forereef zones to 50 and 20 ind m⁻², respectively (Eakin 2001). These high densities began to decline in the mid 1990s, approaching pre-1983 levels by 2000, with the disappearance of shelter space due primarily to the erosive feeding activities of these sea urchins. In contrast to the aforementioned large changes in invertebrate numbers, mean *Arothron meleagris* abundances of 100–200 ind (40–80 ind ha⁻¹) on the Uva reef remained relatively constant for over 30 years (Glynn 1985a; Guzmán and Robertson 1989; P. W. Glynn unpublished data). Although *A. meleagris* feeds predominantly on *Pocillopora damicornis* at the Uva reef, it concentrates on *Porites lobata* at Caño Island, Costa Rica. The diets and feeding preferences of the puffer at different sites are not related in a consistent way to the relative abundances of coral prey or their fluctuations in abundance following major mortality events (Guzmán and Robertson 1989).

Notable, but poorly quantified, declines in abundances also have been observed in other consumer populations. In the 1970s, during each yearly research cruise to the Uva reef, 5–10 plankton-feeding *Manta birostris* could be seen gliding along the reef front during a 60-min dive. Often several (up to 13 ind) whitetip reef sharks and occasionally bull sharks, *Carcharhinus leucas*, were seen on the Uva reef in the 1970s. These species have been observed only rarely in the 1980s and 1990s, following shark-fishing activities off Uva Island in the late 1970s. The cryptic spiny lobster, *Panulirus gracilis*,

was abundant under massive corals and hidden in the pocilloporid frameworks in the early to mid-1970s, but virtually disappeared by the late 1970s and early 1980s, following large-scale extraction by commercial divers.

Variations in food webs occur spatially within the eastern Pacific, although most differences have not been well quantified. In Panamá, for example, some significant differences are evident between coral reefs located in the nonupwelling Gulf of Chiriquí (Uva Island reef) and the seasonally upwelling environment of the Gulf of Panamá. The productivity of primary producers (phytoplankton and benthic algae) and the production of their consumers (zooplankton, suspension feeders, and herbivores) are expected to increase during the upwelling season, and remain relatively high for some undetermined time thereafter. *Diadema mexicanum* attains a significantly larger test diameter in the upwelling Gulf of Panamá ($= 18.7 \pm 0.8$ mm, $n = 82$, Uva reef, 16 March 2002) and therefore probably demonstrates a higher per-capita rate of consumption in the former area. Also, *Acanthaster* is absent from the Gulf of Panamá, and *Jenneria* is apparently less abundant in the upwelling gulf than at Uva Island. Known only in the Galápagos Islands and at Cocos Island (Lessios and others 1999), the abundant and large grazing echinoid *Eucidaris galapagensis* has a strong effect on algal-covered carbonate surfaces. This sea urchin has bioeroded virtually all reef frameworks in the Galápagos Islands affected by the 1982–83 ENSO disturbance (Macintyre and others 1992; Glynn 1994; Reaka-Kudla and others 1997).

SUMMARY COMMENTS

A notable feature of the Uva Island trophic web is the large number of coral–corallivore pathways and the interannual variability of corallivory. At least eight invertebrate and 11 fish species consume corals on the Uva reef. This is probably attributable to the numerous consumer species that are adapted to feed on pocilloporid corals, which are notably abundant and among the main constructors of coral reefs in this region. Although a detailed subweb portraying invertebrate corallivore pathways is unavailable for other coral reef ecosystems, some perspective can be gained by comparing the fish corallivores summarized by Jones and others (1991) for reef areas ranging from the central to the western Pacific. The highest numbers of fish corallivores listed were for Hawaii and Okinawa (nine species), followed by the Marshall Islands (six species), and outer-slope habitats on the Great Barrier Reef (five

species). Thus, it is evident that the species-poor zooxanthellate coral fauna of eastern Pacific reefs is subject to intense predation by fish corallivores, possibly proportionately more so than in species-rich communities in the central and west Pacific.

Marked fluctuations in the population densities of *Acanthaster* and *Jenneria* result in highly variable rates of pocilloporid and agariciid coral mortalities (Glynn 1985a; Fong and Glynn 2001). Coral mortality resulting from ENSO warming also alters the relative abundances of coral prey and their spatial relationships relative to corallivore feeding activities (Glynn 1985b). Surviving coral populations may be subject to increased corallivory during and following such disturbances. Damselfish lawn expansion and accelerated bioerosion (largely by *Diadema*) of corals killed during ENSO disturbances cause rapid erosion and collapse of reef frameworks.

This attempt to portray a coral reef food web in the eastern Pacific underlines the complexity of feeding relationships in a low-diversity coral community, which will surely reveal additional intricacies with continuing studies. This exercise reveals that relatively little is known of the food-web links at the highest and lowest trophic levels, due in large measure to the mobility and sporadic feeding behaviors of large predators and the dynamic nature of plankton and suspended/dissolved organic matter supplies. Additional gaps in our knowledge relate to species consumption rates and changes in diet that occur during development. These research areas offer challenging opportunities that will require innovative approaches to map all critical trophic pathways, quantify energy and material flows, and determine the extent that consumers regulate coral community structure.

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