Corallivory in the Eastern Pacific

10

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Abstract

Eastern Pacific reef ecosystems are home to a diverse assemblage of corallivorous fishes and invertebrates. It is therefore not surprising that there is a rich history of research on corallivores in the eastern Pacific. In fact, much of what is known today on the topic of corallivory has built upon studies from the eastern Pacific region. Here we review the progression of our understanding of eastern Pacific corallivory and corallivores. We discuss the behavior and ecology of these specialized consumers, dividing our analysis into the larger conspicuous taxa such as the crown-of-thorns sea star (*Acanthaster planci*) and the guineafowl puffer (*Arothron meleagris*), as well as into the smaller cryptic species such as the pustulate egg shell (*Jenneria pustulata*) and coral crustacean guards (*Trapezia* spp., *Alpheus lottini*). The majority of species that consume coral tissues are facultative corallivores, feeding on corals only incidentally. Both the negative and positive interactions of corallivores to their prey/hosts are reviewed. We address detrimental direct consumption of coral and how it can ultimately influence growth form, species distributions, population structure, and the asexual reproduction of corals. We examine the cleaning behavior of some corallivorous species as well as their territorial tendencies, which may potentially lead to the exclusion of more lethal coral predators. Despite the high diversity of corallivore taxa, no population outbreaks have been observed in the eastern Pacific; coral colony growth rates and reef accretion proceed apace. Finally, we explore the far-reaching implications of the corallivore feeding strategy, touching on the connections that ultimately link coral biomass with higher trophic levels and the rest of the reef ecosystem.

Keywords

Corallivory • *Acanthaster* • *Arothron meleagris* • Food webs • Coral mortality

10.1 Introduction

Where there are reef-building corals, there are nearly always animals present that feed on them. The coral-consuming guild is known collectively as corallivores. This is, admittedly, a broad categorization, encompassing species that not only feed on the tissues of adult coral colonies, but also on metabolic byproducts such as mucus, fat bodies, and larvae. Taxa exhibiting corallivorous behavior are phyletically diverse, including species belonging to Platyhelminthes, Annelida, Arthropoda, Chordata, Echinodermata, and Mollusca. They exhibit a wind range of morphologies and feeding behaviors, from jawed fishes that scrape away

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tissues and skeleton (e.g., Scaridae, Tetraodontidae) to those that remove individual coral polyps (e.g., Chaetodontidae), from sea stars that evert their stomach and digest underlying coral tissues (e.g., Acanthasteridae) to crabs that use setose appendages to scrape the surface of living corals to remove mucus, tissues, and organic deposits (e.g., Trapeziidae). While many of these animals naturally occur at low densities, dynamic fluctuations in population size may result in "outbreaks," potentially leading to devastating consequences for coral cover and reef health (e.g., Colgan 1987). As such, corallivores are of paramount importance to reef ecology and conservation. Reviews of corallivorous reef taxa, their behavior and feeding mechanisms, as well as the impacts that they have on corals and coral reef ecosystems can be found in Robertson (1970), Endean (1976), Glynn (1982, 1983a, 1988, 1990), Carpenter (1997), Cole et al. (2008), Rotjan and Lewis (2008), and in Glynn and Enochs (2011). Here we focus primarily on the corallivores of the eastern Pacific, including literature on pan-Pacific species from other regions when relevant.

The corallivore feeding strategy is especially prominent in the eastern Pacific, where the proportion of described corallivorous species (from Rotjan and Lewis 2008) to known coral species is much higher than all other reef regions (Fig. 10.1). While a more species rich corallivorous fauna exists in other areas (e.g., Indo-Asian Archipelago, 73 spp.), these regions also contain a greater number of coral species. Therefore, the biogeography of corallivores and corals in the eastern Pacific is unique, in that species feeding on corals have been favored, while corals themselves have not. This trend may be influenced by the exceptionally depauperate nature of the eastern Pacific coral fauna. It is of note, however, that the eastern Pacific contains more corallivorous species than nine of the 16 reef regions from which data are presented, suggesting that this pattern is not due to the lower numbers of coral species alone. We hypothesize that the prominence of fast growing (Guzmán and Cortés 1989a) nutritionally rich *Pocillopora* spp. (Stimson 1990), that contribute importantly to the coral communities and reefs in this region, have conferred a competitive advantage to species utilizing corallivory as a feeding method. Whereas various hydrographic (e.g., upwelling) and climatic (ENSO) phases have limited the diversity of corals in the eastern tropical Pacific, the persistence, and in some cases proliferation, of *Pocillopora* have provided an abundant food source for corallivores and contributed to their prevalence.

Given the richness of corallivore species, the remote, understudied nature of many eastern Pacific coral reef sites,

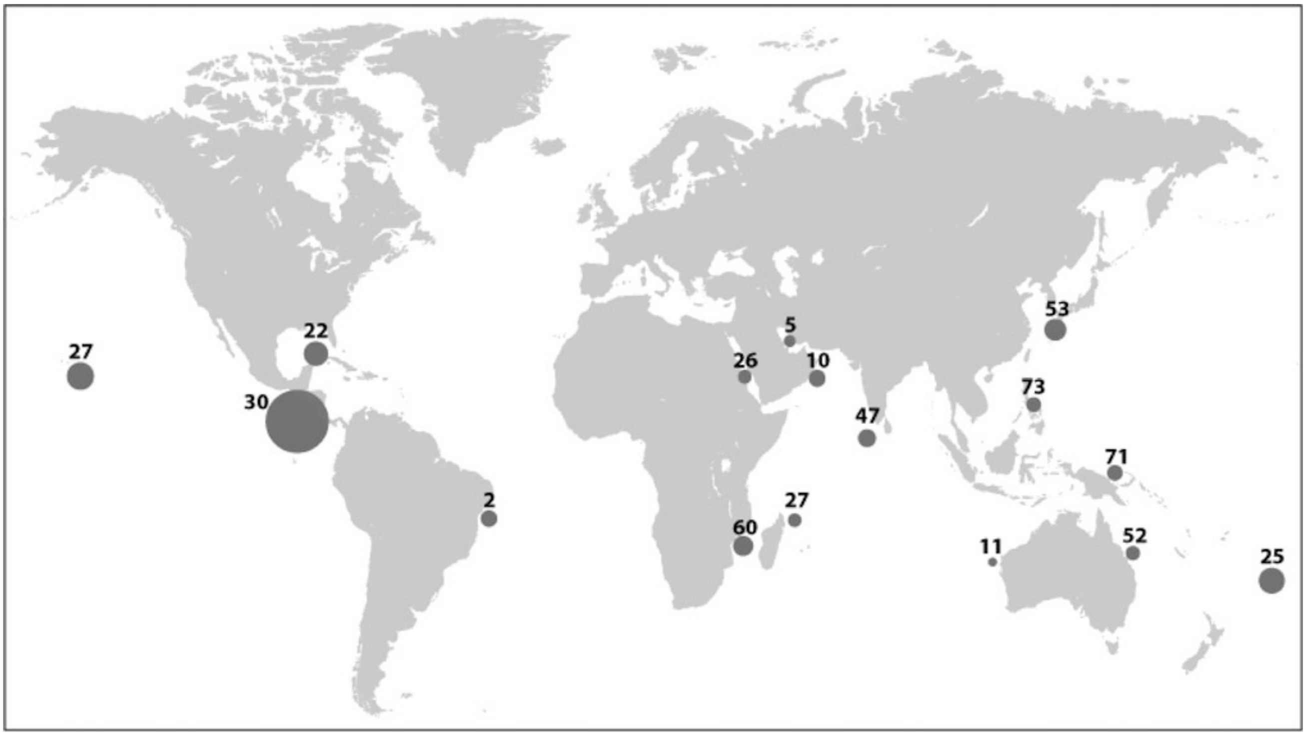

Fig. 10.1 Prominence of corallivore feeding strategy among global coral reef regions. Numbers are known corallivore species from Rotjan and Lewis (2008). Circle areas represent the number of corallivore species divided by the number of coral species in each region (Veron 1995). Note that this review (Table 10.1) includes several corallivore species not included in the analysis of Rotjan and Lewis. These numbers would further inflate this ratio yet are not included here due to the bias of our study towards the eastern Pacific fauna

and the cryptic behaviors of many small inconspicuous corallivorous taxa, it is unsurprising that information as to the diversity and distribution of corallivores within the eastern Pacific are incomplete. Herein an attempt is made to compile the disparate sources containing species distributions throughout the 14 eastern Pacific biogeographic regions recognized by Glynn and Ault (2000), as well as Rapa Nui (Table 10.1). From this compilation, it is apparent that Guatemala, Nicaragua, and Rapa Nui are in need of further study, while the Gulf of California, Panama, and the Galápagos Islands have received a greater amount of attention in the literature. Fishes account for 25 of the 47 corallivorous species presently known from the eastern Pacific, with the remaining invertebrate species divided among Arthropoda, Echinodermata, and Mollusca. The known distribution of fishes throughout the eastern Pacific is therefore likely more complete than for the invertebrates. In contrast to other reef regions, currently no corallivorous annelids are known to exist in the eastern Pacific.

Study of corallivores in the eastern Pacific likely began with the conspicuous and often destructive crown-of-thorns sea star (*Acanthaster planci*). A reference and photograph of this sea star exists in the popular American author John Steinbeck's "Sea of Cortez: A Leisurely Journal of Travel and Research" published with Edward Ricketts in 1941. The genus was subsequently reviewed by Madsen (1955) and Caso (1962), who focussed on specimens from the eastern Pacific (Mexico). These papers were followed by Chesher's (1969) review of the corallivorous, and potentially destructive nature of *Acanthaster* in Guam and Palau. Following this seminal work, the 1970s saw an explosion of interest into the ecology and corallivorous nature of *Acanthaster*, with many notable papers focusing on populations within the eastern Pacific (Dana and Wolfson 1970; Glynn et al. 1972; Porter 1972; Glynn 1973, 1974). Investigation of *Acanthaster* has steadily continued since and is discussed in more detail below. Since the 1970s, reef ecologists have expanded their scope to include numerous other invertebrate and fish corallivores and much of this work has been conducted on eastern Pacific reef systems (e.g., Robertson 1970; Glynn et al. 1972; Glynn 1983a; Gilchrist 1985; Reyes-Bonilla and Calderon-Aguilera 1999).

In this chapter we first begin with a review of the biology and ecology of the more conspicuous and well-studied corallivorous species, including numerous families of fishes as well as the invertebrates *Acanthaster planci* and *Eucidaris galapagensis*. We follow with a review of cryptic and lesser known corallivores, including species within the phyla Mollusca and Arthropoda. Finally, we address the various ecological roles of corallivores, highlighting the numerous positive influences that corallivory can have on corals and coral reef ecosystems in the eastern Pacific.

10.2 Conspicuous Corallivores

10.2.1 *Acanthaster planci*

Acanthaster planci is remarkably well adapted to feed on the tissues of all growth forms of virtually all zooxanthellate coral species (Moran 1986; Birkeland and Lucas 1990). Although *Acanthaster* was collected in the eastern Pacific as early as the Nineteenth Century (Caso 1962), its ecological importance did not become realized until the early 1970s, following Chesher's (1969) alarming report of coral devastation in the western Pacific. The sea star's feeding behavior and effects on corals in the Gulf of California (Mexico) were first reported by Dana and Wolfson (1970), and Barham et al. (1973), and in Panama by Glynn (1972) and Porter (1972).

In early systematic studies, two taxa of *Acanthaster* were recognized in the eastern Pacific, *Acanthaster ellisii* (Gray) and the subspecies *Acanthaster ellisii pseudoplanci* (Caso). On the basis of gross morphology and meristic data, Glynn (1974) concluded that eastern Pacific populations of *Acanthaster* should be assigned to the species *planci*, contrary to the studies of Madsen (1955), Caso (1962) and Barham et al. (1973). Recent molecular evidence supports the occurrence of *A. planci* in the eastern tropical Pacific, and demonstrates significant genetic divergence of *Acanthaster* within the Indo-Pacific region. Eastern Pacific *A. planci* has been shown to belong to one of four clades broadly distributed across the central and western Pacific Ocean (Vogler et al. 2008). *Acanthaster* in the three remaining clades demonstrates distinct distributions in the Indian Ocean and Red Sea.

Relatively high numbers of *Acanthaster* have been observed in the lower half of the Gulf of California, in the Gulf of Chiriquí in western Panama, at Costa Rican mainland sites, and also at Mexico's Revillagigedo Islands. *Acanthaster* has been reported to be rare at the offshore island sites of Clipperton (Glynn et al. 1996), Malpelo Island (Narváez and Zapata 2010), and the Galápagos Islands (Hickman 1998) with only one or a few individuals reported. A new distributional record was made recently of two individuals on coral reefs at Gorgona Island, southern Colombia (M.M. Palacios, pers. comm.). This extends the southern occurrence of *Acanthaster* on the eastern Pacific continental shelf by five degrees latitude, from 8°N in Panama to 3°N in Colombia (Glynn 1974). The absence of *Acanthaster* from eastern Pacific upwelling centers (Glynn 1974) is likely due to low sea temperatures that inhibit larval development (Henderson and Lucas 1971; Yamaguchi 1973). Larval developmental stages are also sensitive to small changes in salinity (Henderson and Lucas 1971; Lucas 1973) and this may limit the sea star's presence in other

Table 10.1 Recorded distribution of corallivores in the eastern tropical Pacific

	GOC	MXM	REV	CLP	GUA	ELS	NIC	CRC	COC	PAN	COL	MAL	ECD	GAL	RPN	Sources
Arthropoda																
Alpheus lottini	1	1	1	1				1		1	1	1		1	1	1,2,3,4,5,6,7
Aniculus elegans	1	1				1		1		1			1	1		1,3,5,6,7,8,9,10,11
Calcinus obscurus						1	1	1		1	1		1	1		1,4,8,10
Trapezia corralina	1			1						1				1		1,3,4,7,12
T. cymodoce	1		1							1	1				1	1,4
T. digitalis	1	1	1	1						1	1	1	1	1		1,2,3,4,5,7,12
T. ferruginea	1	1	1	1					1	1		1	1	1	1	1,2,3,4,5,7,12
Trizopagurus magnificus	1	1				1		1		1			1	1		1,3,4,5,7,8,9,10,13
Echinodermata																
Acanthaster planci	1		1	1				1	1	1	1	1		1		1,2,3,4,7,8,9,11,14,15,16,17,18,19
Diadema mexicanum	1	1		1		1	1	1	1	1	1	1		1		1,2,4,8,9,14,15,18,19,20,21
Eucidaris galapagensis	1	1	1	1		1		1	1	1	1	1		1		1,2,3,4,7,8,9,11,15,16,18,19,20
Nidorellia armata	1	1				1	1	1		1	1	1	1	1		1,2,3,4,7,11,18,19,20
Pentaceraster cumingi	1	1						1		1			1	1		1,2,4,8,18,19,20
Pharia pyramidata	1	1	1			1		1		1	1	1	1	1		1,2,3,4,7,11,18,19,20
Mollusca																
Calliostoma mcleani	1							1		1	1					2,4,11,22
Coralliophila monodonta	1	1		1			1	1		1	1			1		2,4,9,13,14,23,24
C. violacea			1	1					1					1	1	1,14,22,23,25
Jenneria pustulata	1	1		1		1		1		1	1		1	1		1,2,3,4,7,8,9,11,13,14,22,23,24
Latiaxis hindsii	1									1		1	1	1		2,3,4,13,22
Muricopsis zeteki	1	1						1	1	1	1		1	1		1,2,3,4,13,22,24
Phestilla spp.[a]	1			1				1	1	1						2,4,8,9,11
Reliquiaecava robillardi				1												14

(continued)

Table 10.1 (continued)

	GOC	MXM	REV	CLP	GUA	ELS	NIC	CRC	COC	PAN	COL	MAL	ECD	GAL	RPN	Sources
Chordata																
Balistidae																
Balistes polylepis	1	1	1	1	1	1	1	1	1	1	1	1	1	1		2,4,26,27,28,29
Melichthys niger	1		1	1	1	1	1	1	1	1	1	1		1		2,4,14,26,27,28,29
Sufflamen verres	1	1	1	1	1	1	1	1	1	1	1	1	1	1		2,3,4,8,9,26,27,28,29
Chaetodontidae																
Chaetodon humeralis	1	1	1		1	1	1	1	1	1	1	1	1	1		2,4,8,26,27,28,29
Forcipiger flavissimus	1		1	1					1			1	1	1	1	2,4,26,27,28,29
Johnrandallia nigrirostris	1	1	1	1	1	1	1	1	1	1	1	1	1	1		2,4,8,26,27,28,29
Prognathodes falcifer	1		1											1		2,4,28,29
Monacanthidae																
Aluterus scriptus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2,4,8,26,27,28,29
Cantherhines dumerilii	1	1	1	1					1	1	1	1		1	1	2,4,8,25,26,27,28,29
Pomacanthidae																
Holacanthus passer	1	1	1		1	1	1	1	1	1	1	1	1	1		2,4,8,26,27,28,29
Pomacanthus zonipectus	1	1	1	1	1	1	1	1	1	1	1	1	1	1		2,4,8,26,27,28,29
Pomacentridae																
Microspathodon dorsalis	1	1	1		1	1	1	1	1	1	1	1	1	1		2,4,9,26,27,28,29
Stegastes acapulcoensis	1	1	1		1	1	1	1	1	1	1	1	1	1		2,4,8,9,26,27,28,29
S. arcifrons								1	1		1	1	1	1		2,4,26,28,29
Scaridae																
Calotomus carolinus	1		1						1					1		2,4,27,28,29
Scarus ghobban	1	1			1	1	1	1	1	1	1	1	1	1		2,3,4,8,11,26,27,28,29
S. perrico	1	1	1		1	1	1	1	1	1	1	1	1	1		2,3,4,11,26,27,28,29
S. rubroviolaceus	1	1	1	1				1	1	1	1	1	1	1		2,3,4,8,26,27,28,29
Tetraodontidae																

(continued)

Table 10.1 (continued)

	GOC	MXM	REV	CLP	GUA	ELS	NIC	CRC	COC	PAN	COL	MAL	ECD	GAL	RPN	Sources
Arothron hispidus	1	1	1	1	1	1	1	1	1	1	1	1	1	1		2,3,4,7,8,9,11,26,27,28,29
A. meleagris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2,3,4,7,8,9,11,14,16,25,26,27,28,29
Canthigaster amboinensis									1	1				1		2,11,28,29
C. janthinoptera										1	1			1		2,4,28,29
C. punctatissima	1	1	1	1		1	1	1	1	1	1	1	1	1		2,4,26,27,28,29
C. valentini									1					1		2,28,29
Zanclidae																
Zanclus cornutus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2,4, 26,27,28,29
Total	40	30	28	25	15	24	20	33	30	40	33	29	29	43	9	

[a] Two species are known to graze on corals in the eastern Pacific—*Phestilla lugubris* and *Phestilla melanobrachia*

Reef Regions: GOC—Gulf of California, including all islands, MXM—Mexican mainland south of Mazatlán, REV—Revillagigedo Islands, CLP—Clipperton Atoll, GUA—Guatemala, ELS—El Salvador, NIC—Nicaragua, CRC—Costa Rican mainland, COC—Cocos Island, PAN—Panamanian mainland, COL—Colombian mainland, MAL—Malpelo Island, ECD—Ecuadorian mainland, GAL—Galápagos Islands, RPN—Rapa Nui

Sources (1) NMNH Invertebrate Collections http://collections.nmnh.si.edu/search/iz/; (2) OBIS http://www.iobis.org; (3) Glynn (1983a); (4) GBIF http://data.gbif.org/occurrences/; (5) Hickman and Zimmerman (2000); (6) Wicksten and Hendrickx (2003); (7) Glynn (1983b); (8) Glynn (2008); (9) Guzmán (1988a); (10) Moran (1984); (11) Glynn (1982); (12) Garth (1974); (13) Guzmán (1988b); (14) Glynn et al. (1996); (15) Lessios (2005); (16) Reyes-Bonilla and Calderón-Aguilera (1999); (17) Narváez and Zapata (2010); (18) Alvarado et al. (2010a); (19) Hickman (1998); (20) Alvarado and Fernández (2005); (21) Alvarado et al. (2010b); (22) Hickman and Finet (1999); (23) Robertson (1970); (24) Zamorano et al. (2008); (25) Glynn et al. (2003); (26) NMNH Vertebrate Collections Fishes http://collections.mnh.si.edu/search/fishes/; (27) Allen and Robertson (1994); (28) Froese and Pauly (2011) http://www.fishbase.org; (29) Robertson (2009)

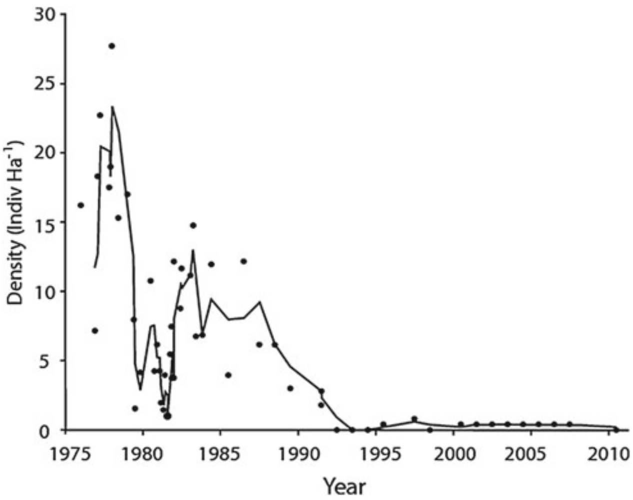

Fig. 10.2 Population density of *Acanthaster planci* at Uva Island coral reef, 1976–2010. Moving average curve is based on two census points

eastern Pacific areas. High abundances of 27 individuals (1 ind per 117 m^2) were reported for one site in the Gulf of California (Dana and Wolfson 1970) and 36 individuals (1 ind per 143 m^2) at the Uva Island reef in Panama. Comparing feeding rates and coral growth at sea star population densities of 26–65 ind ha^{-1}, Glynn (1973) concluded that the Uva reef in Panama could still exhibit positive growth. At a simulated outbreak density of 260 ind ha^{-1}, however, the Uva coral reef would cease to grow. The maximum numbers of *Acanthaster* observed at the ~2.5 ha Uva reef, 36 individuals in September 1972, has demonstrated an irregular decline to only 1–2 individuals over a 22 year period (Fong and Glynn 1998). Updated censuses (n = 12) at the Uva reef from 1995 to 2010 revealed a mean abundance of 0.9 individuals ha^{-1}(Fig. 10.2).

Observations on the feeding behavior of *Acanthaster* have demonstrated distinct prey preferences. Since *Acanthaster* was often found feeding on *Pocillopora* spp., fast-growing and competitively dominant eastern Pacific taxa, Porter (1972, 1974) proposed that the selective removal of these species would increase coral community diversity. Glynn's (1974, 1976) observations and field experiments showed that *Acanthaster* preyed predominantly on small pocilloporid colonies and the dislocated broken branches of larger colonies. These small and fragmented coral prey were defended from *Acanthaster* attacks less intensely by symbiotic crustacean guards than were large intact colonies. When *Acanthaster* was offered a choice between pocilloporid and certain non-pocilloporid species the latter were preferred, especially if the former were well defended by their crustacean guards. Examples of species with a high electivity index were *Gardineroseris planulata* and *Pavona* spp. (Glynn 1974). In the eastern Pacific these guards are trapeziid crabs, four species in the genus *Trapezia* (Castro 1982, 1996), and the alpheid shrimp *Alpheus lottini* (Kim and Abele 1988). Thus, Glynn (1974, 1976) argued that the selective removal of relatively rare coral species and their replacement by *Pocillopora* spp. would tend to depress coral community diversity.

Other effects observed in Panama in areas with and without *Acanthaster* were colony size differences and the abundances of preferred prey (Glynn 1987). Six coral species demonstrated significantly smaller colony sizes where *Acanthaster* was present than in habitats without the corallivore. Fong and Glynn (1998) also demonstrated shrinkage of the size classes of *Gardineroseris planulata*, a preferred prey species, at increasing numbers of *Acanthaster*. Additionally, in four of five species the frequency of dead colonies in habitats exposed to *Acanthaster* predation was significantly higher than at sites without the corallivore. A final example of how pocilloporid crustacean guards can affect coral longevity was observed during the 1982–83 El Niño disturbance at the Uva Island reef in Panama. Elevated sea temperatures caused the bleaching and mortality of continuous stands of crustacean guard-defended *Pocillopora* surrounding massive colonies of *Gardineroseris*. Before the bleaching and death of *Pocillopora* spp. these corals formed a protective barrier around *Gardineroseris*, preventing *Acanthaster* from feeding on this species. With the elimination of the protective barrier, *Acanthaster* then gained access to the refuge and began preying on *Gardineroseris*.

Because of concerns over the relatively recent *Acanthaster* outbreaks in the Indo-Pacific region, particularly beginning in the 1960s, some workers have searched for evidence of earlier sea star abundances and have proposed that such outbreaks are not unprecedented. Sediment coring studies have found *Acanthaster* skeletal remains concentrated at particular depth levels in reef sediments of 3000 (Frankel 1977, 1978) to 7000 year BP (Walbran et al. 1989a, b), suggesting cyclic abundances and probable past sea star outbreaks similar to those of today. The evidence supporting this work has been criticized, however, with potential difficulties arising from bioturbation and size-dependent preservation that could distort the sedimentary record (Moran et al. 1986). In spite of this criticism, Birkeland and Lucas (1990) concluded that the occurrence of skeletal elements in sediments probably at least indicates the presence of *Acanthaster* in the past.

To investigate the possibility of the occurrence of *Acanthaster* in the eastern Pacific in the recent past, sediment samples at Uva Island were cored and analyzed quantitatively. These samples were collected from fore reef habitats where *Acanthaster* was foraging. Approximately 1 kg samples of sediment were collected and analyzed at ~30 cm depth intervals from four sites. Each sample was examined microscopically with reference to a known collection of *Acanthaster* skeletal elements. Push-core samples revealed the presence of skeletal elements throughout the sediment pile to a maximum depth of 260–270 cm. Carbon-14 dating of coral and crustose

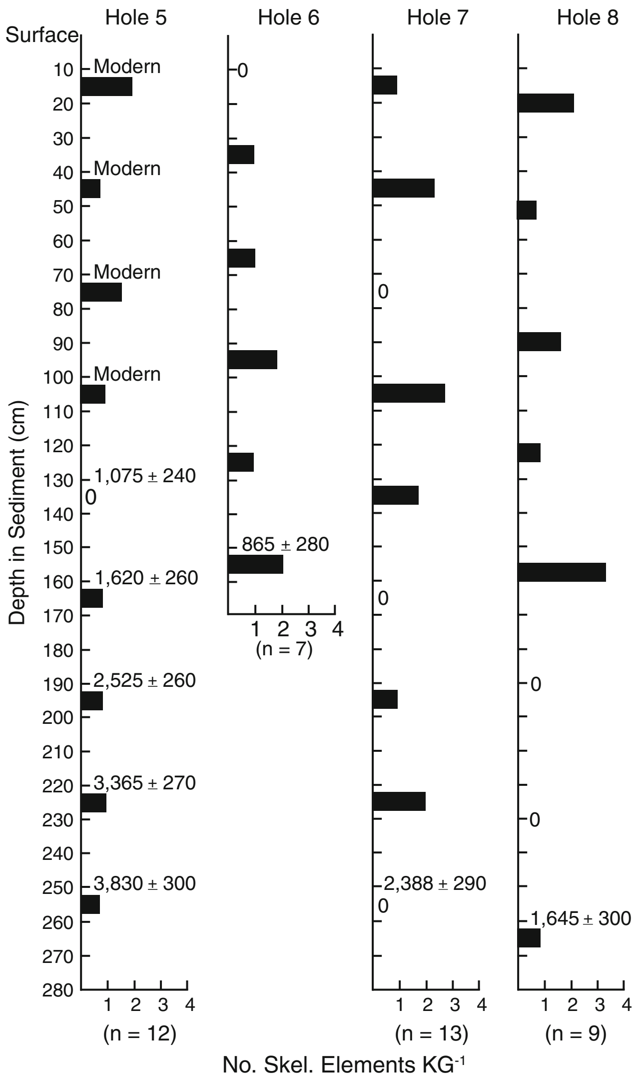

Fig. 10.3 Recovery of *Acanthaster planci* skeletal elements from push core samples collected in seaward reef-front zone sediments, 3 m isobath, Uva Island reef, 8 August 1985. Maximum penetration was 260–270 cm with samples collected at approximately 30 cm intervals. Approximately 1 kg samples, passed through 0.461 mm mesh sieve were sorted under 5 X magnification and compared with a reference set of known *A. planci* skeletal elements. Radiocarbon dating performed at the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS), Woods Hole Oceanographic Institution (Druffel 1995). Radiocarbon dates were calibrated using Calib 6.0 software (Stuiver and Reimer 1993; Stuiver et al. 2005)

coralline algae at the same sediment horizons with *Acanthaster* skeletal ossicles suggests a long-term occurrence of the sea star on the Uva reef of nearly 4000 year BP (Fig. 10.3).

Table 10.2 *Acanthaster planci* skeletal elements recovered from ~1 kg surface samples collected at Uva Island coral reef, Gulf of Chiriquí, Panama, and Gulf of Oman, Sultanate of Oman

Reef site	Dates collected	Number of samples	Samples without elements	Average elements per sample
Panama				
Uva Island	Jul'84; Feb, Aug '85	40	23 (57.5 %)	0.65 ± 0.14
Oman				
Daymaniyat Iss	Oct '85	4	1 (25.0 %)	11.5
Banda Jissah	Oct '85	5	0 (0 %)	2.8
		9	1 (11.1 %)	6.7 ± 2.9

A comparison of the numerical densities of skeletal elements in surface sediment samples from Panama, with relatively low population densities of *Acanthaster*, and from Oman where sea star outbreaks occurred in 1978–80 (Glynn 1987, 1993) revealed notable differences. Skeletal elements were absent from over one-half of samples (~58 %) from Panama whereas only a single sample from Oman (~11 %, 1 of 9 total) did not contain *Acanthaster* skeletal remains (Table 10.2). In addition, the mean number of skeletal elements per sample in Panama was only about one-tenth of that in Oman. The high skeletal densities in Oman are in line with those reported by Walbran et al. (1989a, b) for the John Brewer reef in Australia, which experienced two major episodes of *Acanthaster* predation since 1962. These results provide indirect evidence supporting low, but sustained population densities of *Acanthaster* on the Uva Island reef.

10.2.2 *Eucidaris galapagensis*

The first eastern Pacific record of the sea urchin *Eucidaris* feeding on live coral tissues was made in 1975 in the Galápagos Islands by Glynn et al. (1979). *Eucidaris galapagensis* is a facultative corallivore, and was observed grazing on live *Pocillopora* spp. and massive species of *Porites* and *Pavona*. Most of its feeding activities, however, involve the grazing of micro-filamentous algae, both epibenthic and endolithic, on dead coral skeletons and basalt rock. It is an effective grazer, capable of rapid bioerosion when present in large numbers (Glynn et al. 1979; Glynn 1994; Reaka-Kudla et al. 1996; Glynn et al. 2015). *Eucidaris* efficiently abrades coral and rock substrates employing Aristotle's lantern, a complex feeding apparatus of plates, muscles and ligaments that support five sharp calcareous teeth.

Recognizing the correct identity of *Eucidaris* in the eastern Pacific has created some confusion. For many years, the Galápagos species of *Eucidaris* was assigned to *thouarsii*, which occurs commonly along mainland shores from the Gulf of California to southern Ecuador. *Eucidaris thouarsii*, unlike *E. galapagensis*, is relatively small, a herbivore/omnivore in feeding habit, and seldom attains high abundances. In a phylogeographic study, Lessios et al. (1999) found that populations of *Eucidaris* inhabiting offshore islands (Galápagos Islands, Isla del Coco and

Clipperton Atoll) comprised a clade sufficiently distinct from mainland populations to justify separation and assignment to *E. galapagensis*, a resurrected species from the older taxonomic literature. Although Kroh (2010) has reduced *E. galapagensis* to subspecies rank, namely *E. thouarsii galapagensis*, we prefer to retain the full species binomen.

Eucidaris galapagensis can reach high abundances in Galápagos coral communities with population densities of 20–30 ind m^{-2} not uncommon, and maximum densities as high as 50–90 ind m^{-2} reported (Glynn et al. 1979; Glynn and Wellington 1983; Glynn 1988). High densities were observed at the Devil's Crown patch reef (Floreana Island) in areas of moderate to high coral cover, whether the coral was alive or dead. *Eucidaris* is a large species, with test diameters of 5 to 6 cm in adults. At the Devil's Crown study reef, about 36 % of *Eucidaris* were feeding on live corals on the reef crest and 52 % at the reef edge. Pocilloporid skeletal grains made up 30–40 % and coralline algae 40–50 % by weight of the gut contents of sea urchins feeding on the reef.

Recent studies in the Galápagos Islands suggest possible negative interactions between El Niño disturbances and anthropogenic activities that affect sea urchin abundances. A strong relationship between *E. galapagensis* abundances (and at least two other sea urchin species) and fishing pressure has been observed in the southern archipelago. Sea urchin numbers are generally higher where their natural predators (e.g., spiny and slipper lobsters, and hogfish) have been over-harvested (Sonnenholzner et al. 2009; Edgar et al. 2010) or in rubble refugia (Dee et al. 2012). This has resulted in intense sea urchin grazing and a shift from macroalgal and coral communities to "urchin barrens" dominated by crustose coralline algae. This phase shift has been implicated in causing declines and local extinctions of species associated with the more biologically-structured habitats (Edgar et al. 2010). If sea urchin overgrazing continues it is likely that coral recruitment would be severely limited, resulting in a prolonged delay of coral community recovery.

10.2.3 Other Echinoderms

Three additional species of echinoderms, all asteroids, are known to prey on corals in the eastern Pacific. *Pharia pyramidata* everts its stomach to feed on pocilloporid corals, in a manner similar to *Acanthaster* (Dana and Wolfson 1970). This feeding behavior has been observed in the Gulf of California and mainland Ecuador, but not in the Galápagos Islands (Dana and Wolfson 1970; Glynn 1983a). By contrast, *Nidorellia armata* is known to feed on corals in the Galápagos, but not in Panama where it instead subsists on a diet of sponges and sometimes algae (Chesher 1972; Glynn 1983a). In the Galápagos, *N. armata* consumes the tissues of *Pavona clavus* (0.5–1 m diam.), on which it leaves small (2–5 cm) feeding scars (Glynn 1983a). Experiments on the exclusion of the above species from damselfish territories in the Galápagos suggest that the order in which they are preferentially ejected by damselfish correlates with their corallivory potential. The corallivorous sea urchin *Eucidaris galapagensis* was removed most actively, followed by *N. armata*, and finally *P. pyramidata*, which is not known to exhibit corallivorous tendencies in the Galápagos (Glynn 1983a). A third species of asteroid, *Pentaceraster cumingi*, has been recorded in large groups among fungiid coral communities in the Galápagos (Glynn 2003). While these sea stars feed on fungiids such as *Diaseris distorta*, they more frequently consume algae, sponges, sea urchins, and even colonies of *Psammocora stellata* (Glynn 2003). It should be noted that none of the aforementioned asteroid species, with the exception of *Acanthaster*, is considered to be an obligate corallivore. This dietary diversity, in conjunction with relatively low population densities, usually limits the destructive potential of these sea stars on eastern Pacific coral reefs.

10.2.4 Fishes

No fewer than 25 fish species have been observed to prey consistently, or at least incidentally, on live corals in the eastern Pacific (Table 10.1). Only a few of these species are obligate corallivores with corals making up the bulk of their food intake. Most are facultative corallivores, feeding predominantly on algae, other non-scleractinian invertebrates, and only incidentally on corals. Some species appear to concentrate more on coral grazing as juveniles than as adults. Feeding behavior varies greatly among fish taxa, from browsers that consume live coral tissue only, to scrapers that remove live tissues and some skeletal carbonate, and excavators that remove live tissues as well as a major portion of the skeleton (Rotjan and Lewis 2008). Remarkably, as early as the 1920s William Beebe, an intrepid pioneering naturalist *cum* marine biologist, performed observations on the feeding behavior of eastern Pacific reef fishes. This was accomplished by hardhat diving in Darwin Bay at Tower Island, Galápagos Islands (Beebe 1924, 1926). Beebe coined the term "coral grazers" in an early attempt to relate mouth structure and dentition to coral feeding, herbivory and invertivory in several fish families.

10.2.4.1 Tetraodontidae

Several species of puffers (Tetraodontidae) and butterflyfishes (Chaetodontidae) are often the most conspicuous corallivores in eastern Pacific coral communities. One of the most important corallivores in terms of biomass consumed is the guineafowl puffer, *Arothron meleagris* (Fig. 10.4). This species often concentrates its feeding activities on the

Fig. 10.4 *Arothron meleagris* feeding on *Pocillopora damicornis* at Uva Island reef, Panamá (1 m depth, March 2004, photo by T.B. Smith)

branch-tips of *Pocillopora* spp. and *Psammocora* spp., biting off 1 to 2 cm-long fragments with its sharp beak-like teeth. Analysis of the stomach contents of 14 individuals of *A. meleagris* in Panama revealed that the branch tips of *Pocillopora* spp. made up 91.3 % of the dry mass (Glynn et al. 1972). It also feeds on small nodular species such as *Porites panamensis*, and massive corals in the genera *Porites*, *Pavona*, and *Gardineroseris*. Grazing is usually concentrated along the margins, on nodules or ridges of large massive species where sufficient leverage can be achieved. Population densities are reviewed in Palacios et al. (2014) and can range from 0 to 320 ind ha^{-1} in Costa Rica, Panama, Colombia and the Galápagos Islands (Guzmán and Robertson 1989; Guzmán and López 1991).

Recent work by Palacios et al. (2014) at Gorgona Island, Colombia has shown that the feeding activities of *Arothron meleagris* can result in the removal of nearly 16 % of the annual calcium carbonate production of pocilloporid coral prey. These authors observed that the majority of predation events were sublethal and that colonies that were preyed upon had calcification rates comparable to those that were shielded from predators. Exposure of *Pocillopora* spp. to *A. meleagris* bites, however, significantly reduced linear extension and over time resulted in a change in colony morphology that favored a more robust and "stubby" form (see Chap. 12, Alvarado et al.).

Although *Arothron meleagris* consumes large amounts of coral, it may not contribute directly to higher trophic level predators because of its toxicity and apparent avoidance by piscivores. It is possible that its distinctive color phases have an aposomatic function, deterring potential predators. Nuñez-Vázquez et al. (2000) have found relatively high concentrations of tetrodotoxin in the tissues of *A. meleagris* in the Gulf of California. The pufferfish deposits large accumulations of skeletal fragments in its feces, and this likely attracts micro-scavengers that would play a role in nutrient recycling. Another potentially important ecological role could be served in the dispersal of zooxanthellae. Parker (1984) found that the zooxanthellae of *Aiptasia* ingested by *A. meleagris* in Hawaii remained viable after defecation, and could infect aposymbiotic *Aiptasia*. Whether this type of transmittal can occur in eastern Pacific puffers feeding on zooxanthellate scleractinian corals needs to be investigated.

Arothron hispidus is a facultative corallivore, feeding commonly on other non-scleractinian taxa such as sponges, hydroids, polychaete worms, bryozoans, crustaceans and molluscs (Glynn et al. 1972). When feeding on corals it often concentrates on *Pocillopora* spp., but also has been observed feeding on *Porites lobata* in the Galápagos Islands (Isabela Island, F. Rivera, pers. comm.). Its abundance at Caño Island (Costa Rica), ~8 ind ha^{-1}, is similar to *A. meleagris* at that site, however, it varies greatly in numbers in other eastern Pacific areas (Guzmán 1988b).

At least three species of small monogeneric pufferfishes have been observed in eastern Pacific coral communities, however, they all have varied diets including, in addition to coral polyps, filamentous algae, sponges, polychaete worms, and crustaceans. *Canthigaster punctatissima* is endemic to the eastern Pacific, occurring in coral communities from the Gulf of California to the Galápagos Islands. Two additional species, *Canthigaster amboinensis* and *Canthigaster janthinoptera*, occur sporadically in the eastern Pacific, perhaps a result of dispersal from the central Pacific region during ENSO events.

10.2.4.2 Chaetodontidae

Of 128 fish corallivores listed by Cole et al. (2008), no fewer than 54 % belong to the family Chaetodontidae, commonly known as butterflyfishes. Butterflyfishes have small protractile mouths with bristle-like dentition, which are well suited for grazing on corals (Motta 1988), but only 52 % of butterflyfish species do actually feed on corals (Cole and Pratchett 2014). In all, there are 24 species of butterflyfishes that are obligate hard coral-feeders (Pratchett 2014), which feed almost exclusively (>80 %) on scleractinian corals, and a further 65 species that only occasionally graze on corals. Obligate coral feeding butterflyfishes are numerically dominant on many Indo-Pacific reefs (Cole and Pratchett 2014), but are often under-represented at marginal reef locations (Pratchett et al. 2013). Similarly, there are no obligate corallivores in the eastern Pacific, and even facultative coral-feeding species are scarce; only three species of butterflyfishes are routinely found in the eastern Pacific (*Chaetodon humeralis*, *Johnrandallia nigrirostris*, and *Forcipiger flavissimus*) feed on corals, but all these species feed predominantly on non-coral prey including algae and mobile benthic invertebrates. In Panama, *C. humeralis* and *J. nigrirostris* are often observed nipping on *Pocillopora* spp. (Glynn 2008). *Johnrandallia nigrirostris* also occupies 'cleaning stations' where it visits large fish clients to feed on ectoparasites, tissues and mucus. At least six other facultative coral-feeding butterflyfishes (*Chaetodon auriga*, *Chaetodon kleini*, *Chaetodon lunula*) occur sporadically in the eastern Pacific, usually during or shortly following El Niño events (Allen and Robertson 1994).

While there are marked interspecific differences in dietary preferences, most coral-feeding butterflyfishes feed preferentially on *Acropora* and/or *Pocillopora* corals (Pratchett 2014). In locations where butterflyfishes are abundant, strong selective feeding may exert a strong influence on the abundance and fitness of preferred corals (Cox 1986; Cole et al. 2012). In the eastern Pacific, however, coral-feeding butterflyfishes are relatively rare, and also feed on a diversity of different prey. In the Gulf of Chiriquí (Panama) two chaetodontid species are ranked among the top 20 in abundance, but at densities much lower than in the western Pacific; *Chaetodon humeralis* and *Johnrandallia nigrirostris* occur at densities of only 0.4 and 0.9 ind per 1000 m^2 respectively (Dominici-Arosemena and Wolff 2006; Glynn et al. 2014). Considering the broad diets (i.e. extending well beyond corals) and low abundances of eastern Pacific butterflyfishes, their impacts on coral communities are expected to be negligible. There is, however, a need for explicit research on the diet composition, and especially relative consumption of different coral species, for coral-feeding butterflyfishes in the eastern Pacific.

10.2.4.3 Scaridae

Four species of parrotfishes have been implicated in excavating corals, namely *Scarus ghobban*, *Scarus perrico*, *Scarus rubroviolaceous* and *Calotomus carolinus*. These parrotfishes feed on various species of *Pocillopora*, *Pavona* and *Porites* (Table 10.1). Particularly conspicuous are the bite marks on massive corals after a feeding bout (Fig. 10.5). The bite marks are typically 1–2 cm in length and a few mm deep. They are most often scattered over the surface of massive corals, a condition known as 'spot biting' (Bruckner et al. 2000) but may also target particular skeletal features (Fig. 10.6). On the Uva Island reef in Panama, schools of *S. rubroviolaceus* have been observed spot biting *Gardineroseris planulata*; this is a new corallivore/coral feeding record.

Fig. 10.5 Probable parrotfish bite marks on *Porites lobata*, Darwin Island reef, Galápagos Islands (13 m depth, 4 June 2012, photo by J.S. Feingold)

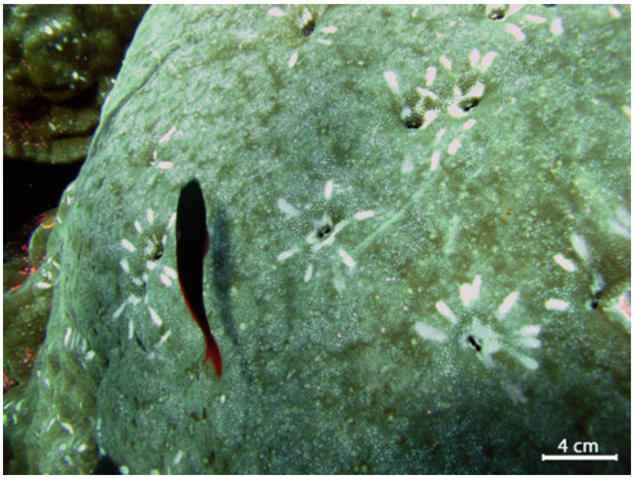

Fig. 10.6 Bite marks on *Porites lobata*, Darwin Island reef, Galápagos Islands (12 m depth, 3 June 2012, photo by V.W. Brandtneris). Star-shaped pattern is likely due to parrotfish targeting raised surfaces surrounding lithophagine bivalve bore holes

Rotjan and Lewis (2008) have argued that the negative effects of parrotfishes grazing on live corals have been underestimated, especially in recent decades with rapidly declining coral populations. This view was challenged by Mumby (2009) who concluded that parrotfishes on Caribbean coral reefs have a net positive effect by limiting algal growth that would interfere competitively with coral recruits. These ecological interactions are in need of further study in the eastern Pacific.

10.2.4.4 Balistidae

Four triggerfish species have been implicated in feeding on corals in the eastern Pacific (Glynn et al. 1972; Guzmán and Cortés 1989b). This number can be reduced to three triggerfish species since Glynn et al. (1972) mistakenly identified *Balistes polylepis* for *Pseudobalistes naufragium*; the latter was observed massively excavating *Pavona varians*. Actually, *P. naufragium* was breaking apart the coral to expose endolithic bivalves, the prey objects of this destructive behavior. *Porites* spp. and other massive corals with bivalves also are subject to significant breakage by *P. naufragium*, but without ingestion of live coral tissues (Guzmán and Cortés 1989b).

Branching and massive coral fragments contribute importantly to the gut contents of some individuals of *Sufflamen verres*, suggesting a concerted targeting of corals

(Glynn et al. 1972). The gut contents of other triggerfishes, however, reveal few coral fragments, perhaps a result of incidental ingestion while extracting coral-associated invertebrates. *Melichthys niger*, a tropical cosmopolite triggerfish, has been classified as a facultative corallivore on the basis of small coral fragments (mean < 1 % by volume) present in the guts of 17 individuals examined (Randall 1967). While this species has been observed feeding in small groups on large colonies of *Pavona gigantea* (>1.5 m high) at Gorgona Island, Colombia (M. Palacios pers. comm.), we are unaware of any other records of this feeding interaction from other regions in the eastern Pacific.

10.2.4.5 Monacanthidae

Two species of filefishes occasionally observed on eastern Pacific reefs are facultative corallivores: *Aluterus scriptus* and *Cantherhines dumerilii*. Randall (2005) noted that *A. scriptus* feeds on *Millepora*, and *C. dumerilii* on *Acropora, Pocillopora, Montipora* and *Leptoseris* in the South Pacific. Both species prey on a variety of taxa in addition to corals. Glynn (2008) indicated that *Pocillopora* spp. are consumed by these fishes in the eastern Pacific.

10.2.4.6 Pomacentridae

The high percentage of acroporid corals in the guts of some Indo-Pacific damselfishes, up to 96 %, suggests a dominantly corallivorous feeding mode (Rotjan and Lewis 2008). Three species that bite and kill corals, not listed by Rotjan and Lewis (2008), are *Stegastes acapulcoensis*, *Stegastes arcifrons*, and *Microspathodon dorsalis*. All are widely distributed across the eastern tropical Pacific (Wellington 1982; Guzmán 1988a; Guzmán and Cortés 1989b; Dominici-Arosemena and Wolf 2006; Glynn 2008; Table 10.1). In the Pearl Islands, Panama, Wellington (1982) observed persistent biting of *Pavona gigantea* by *S. acapulcoensis* at shallow depths, which resulted in extensive mortality and an influential factor in controlling coral zonation. It is not known if the damselfish gains a nutritional benefit from this behavior. Numerous circular bite marks on *P. lobata* (Fig. 10.7), adjacent to an algal lawn defended by *S. acapulcoensis*, are an example of the lesions caused by a browser and suggest directed coral feeding and a nutritional benefit. The damselfish is the suspected predator, but it was not observed biting the coral.

10.2.4.7 Zanclidae, Pomacanthidae

Three species occasionally observed grazing on corals are the Moorish Idol *Zanclus cornutus* (Zanclidae) and two angelfishes, *Holacanthus passer* and *Pomacanthus zonipectus* (Pomacanthidae). *Zanclus cornutus* was recently observed browsing on *P. lobata* polyps at Darwin Island, Galápagos Islands (J.S. Feingold, pers. comm.). The fish left circular, 3–5 mm diameter lesions with no apparent damage to the underlying skeleton. McClanahan et al. (2005) observed *Zanclus canescens* and other fishes (Chaetodontidae, Tetraodontidae, Scaridae) preying on corals in the Indian Ocean after bleaching, concluding this would interefere with recovery. Coral browsing by angelfishes may be more common in juvenile than adult life history stages.

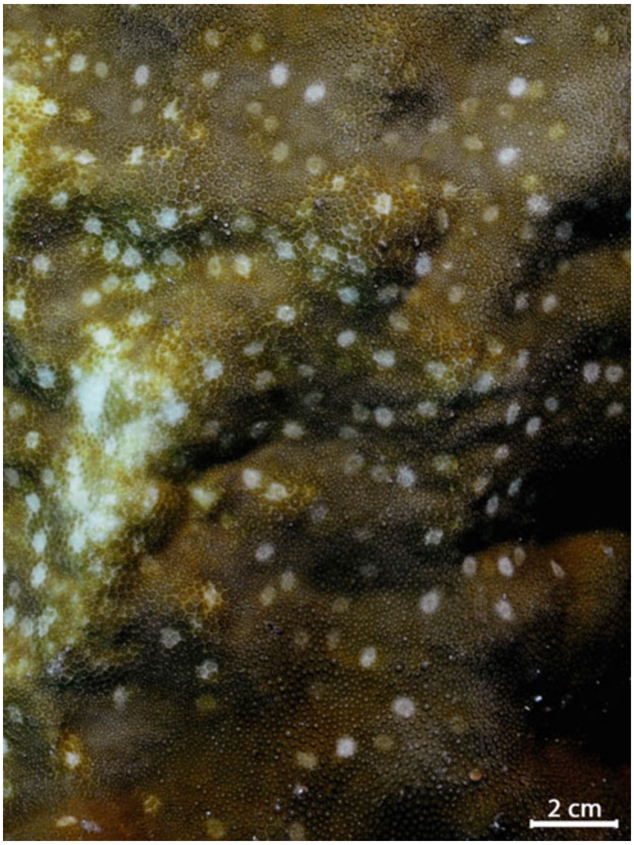

Fig. 10.7 Possible *Stegastes arcifrons* bite marks on *Porites lobata*, Darwin Island reef, Galápagos Islands (13 m depth, 3 June 2012, photo by J.S. Feingold). Circular marks 0.5–1.0 cm in diameter

10.3 Cryptic Corallivores

Many of the species known to exhibit corallivorous feeding behaviors in the eastern Pacific have cryptic tendencies. The prevalence of this behavior is especially telling considering that these species remain hidden from easy observation and study, and are poorly known relative to epibenthic and nektonic species. The potential that numerous additional cryptic corallivores exist is therefore high; presently unknown due to minute, obscured, and often brief feeding interactions. Those eastern Pacific cryptic corallivores that are known are diverse, both taxonomically (Table 10.1) and in their feeding behaviors. Literature concerning these species is sparse, yet perhaps less so in the eastern Pacific relative to other reef regions. Below we discuss many of the more inconspicuous taxa belonging to the phyla Mollusca and Arthropoda.

10.3.1 *Coralliophila monodonta*

Several studies refer to the corallivorous activity of both *Quoyula madreporarum* (Glynn et al. 1972; Glynn 2004) and *Quoyula monodonta* (e.g., Guzmán 1988b) in the eastern Pacific. Robertson (1970), however, referenced the host-dependent morphological plasticity demonstrated by Maes (1967) and concluded that *Q. madreporarum* is synonymous with the earlier named taxon *Q. monodonta*. More recently, the genus *Quoyula* has been considered a junior synonym of *Coralliophila* and the correct name is therefore *Coralliophila monodonta* (Oliverio 2008).

Coralliophila monodonta is known from reefs throughout the Pacific and almost exclusively associates with corals in the family Pocilloporidae (e.g., Robertson 1970; Coles 1980; Black and Prince 1983). Demond (1957), however, reports several instances of these gastropods associating with both acroporid and poritid corals in Micronesia; this family-specific affinity, therefore, cannot be considered obligate.

In the eastern Pacific, *Coralliophila monodonta* generally occupies the sheltered bases of *Pocillopora* colonies (Guzmán 1988b), perhaps to escape from predatory hermit crabs, octopuses, and various invertivore fishes (Glynn 2004). These gastropods create small feeding scars on the coral surface immediately under their shells and remain relatively sedentary at these sites (Robertson 1970; Glynn et al. 1972). Activity, however, increases during the night and many individuals have been collected that were not associated with scars (Guzmán 1988b).

Densities of *C. monodonta* have been recorded as high as 29 individuals in a 1/8 m^2 quadrat on a *Pocillopora* reef at Chapera Island, Pearl Islands, Panama (Glynn et al. 1972). Guzmán (1986) reported a mean density of 10.6 *C. monodonta* per m^2 on a Caño Island reef, Costa Rica, however these measurements were made shortly after the 1982–83 El Niño-related and 1985 red tide-coincident coral die-offs. Later, at the same locality, Guzmán (1988a) recorded *C. monodonta* on 72 % of 245 *Pocillopora* colonies and a single 27 cm diameter colony was found to host 17 snails. Guzmán (1988a) recorded a mean feeding rate of 0.64 cm^2 coral tissue ind^{-1} d^{-1} on a Costa Rican reef which, given observed densities of *C. monodonta*, could result in the complete elimination of coral tissue from the base of a 10 cm diameter *Pocillopora* colony within 30 days. Guzmán concluded that this corallivorous activity could have widespread ramifications for the reproduction and erosion of pocilloporid corals as well as the distribution and community structure of coral communities on eastern Pacific reefs.

10.3.2 *Jenneria pustulata*

The pustulate egg shell, *Jenneria pustulata*, is well documented throughout the eastern Pacific (Table 10.1), in part due to its conspicuous and uniquely orange-spotted shell (Bertsch 1984). It is the sole species within the genus *Jenneria* and it occurs in eastern Pacific and Hawaiian waters (Robertson 1970). While present in the Galápagos (Glynn 1983a), it was absent during early surveys of Clipperton (Glynn et al. 1996). This gastropod is primarily found associated with pocilloporid corals across all reef zones (Glynn et al. 1982). It remains cryptic within coral colonies during the day and moves outward to feed at night (Glynn et al. 1972). High risk from predation may be responsible for this behavior as indicated by an abundance of broken *J. pustulata* shells within reef sediments (Glynn et al. 1972). Indeed, in a laboratory setting, Oramas (1979) observed that the feeding of *Jenneria* was restricted to the basal branches of pocilloporid corals in the presence of a potential porcupine fish predator (*Diodon holocanthus*).

Jenneria feeds primarily on pocilloporid corals (Glynn et al. 1982; Navas-Camacho et al. 2010), though it has also been observed to consume several other eastern Pacific coral species (e.g., *Pavona* spp., *Porites lobata*, *Porites panamensis* and *Psammocora* sp., Achurra-Cárdenas and Valdés-Araúz 1980; Paz-García et al. 2012). Under laboratory conditions, *J. pustulata* has been noted to feed on other non-eastern Pacific coral species including *Porites* sp., *Phyllangia americana*, *Siderastrea siderea*, and *Madracis mirabilis* (D'Asaro 1969; Glynn 1985). *Jenneria* feeds on all surfaces of its pocilloporid hosts, removing 0.80 g skeleton and tissue a day on average (Glynn et al. 1972). Feeding scars appear similar to white band disease and consist of areas of white, denuded coral skeleton (Navas-Camacho et al. 2010; Paz-García et al. 2012).

Jenneria is often found in clusters as high as 50–100 individuals per colony of *Pocillopora* (Panama, Glynn 2004), 15–40 per colony of *Porites* (Gulf of California, Paz-García et al. 2012), and 24 ind m^{-2} on reefs around Gorgona Island, Colombia (Glynn et al. 1982). Mean densities, however, were much lower in the Panamanian Pearl Islands at 1.8 ind m^{-2} (Glynn et al. 1972). At this last density, and at the aforementioned feeding rate reported by Glynn et al. (1972), *Jenneria* was responsible for an estimated 5.31 metric tons of coral mortality ha^{-1} $year^{-1}$ (skeleton and tissue), accounting for 79 % of the total coral mass removal considered by Glynn et al. (1972) in a corallivore-coral model.

Densities of *Jenneria pustulata* have been shown to be significantly affected by bleaching events associated with El Niño thermal anomalies. Glynn (1985) observed that after the 1983 El Niño-associated bleaching event, *J. pustulata* population densities dropped from 23.7 to 1.7 ind m^{-2} and dead, intact shells were found in 15 % of quadrats at the Panamanian study sites. *Jenneria* is known to starve within weeks if it has limited or no access to coral food, and it is likely that coral mortality played a part in its rapid die-off (Glynn 1985). Laboratory experiments, however, indicate that elevated water temperatures may also have direct detrimental impacts, as *J. pustulata* held in aquaria at 31.8 °C died even when food was present (Glynn 1985).

10.3.3 Other Molluscan Corallivores

Latiaxis hindsii and *Muricopsis* (*Babelomurex*) *zeteki* are not as well-known as the aforementioned molluscan corallivore species, and are muricid gastropods that have been observed to consume coral tissues in the Galápagos Islands (Glynn and Wellington 1983). While documented as present at numerous additional localities (Table 10.1), observations on the corallivorous activities of these species are limited. In the Galápagos, both *L. hindsii* and *M. zeteki* have been observed feeding on pocilloporid corals in groups of two to five individuals (Glynn and Wellington 1983). In each instance where a colony was observed to be infested by these gastropods, tissue damage was not severe, accounting for less than 10 % of the total colony surface area.

An aeolid nudibranch in the genus *Phestilla* was first reported feeding on coral in the eastern Pacific by Highsmith (pers. comm.) who observed it grazing at night on *Porites lobata* in Panama (Glynn 1982). This species was described as *Phestilla panamica* (Rudman 1982) and more recently has been considered as *Phestilla lugubris* (Behrens and Hermosillo 2005; Camacho-Garcia et al. 2005). More recently an additional species—*Phestilla melanobrachia*—was reported to feed on *Tubastrea*. Terrence Gosliner (pers. comm.) observed *P. lugubris* feeding on *Porites* sp. (probably *Porites lobata*) in the Gulf of Chiriquí, Panama, and at Caño Island, Costa Rica. *Phestilla lugubris* also was observed laying eggs on *Porites* in Panama (T. Gosliner, pers. comm.). *Phestilla lugubris* is wide ranging throughout the eastern tropical Pacific and Indo-Pacific regions while *P. melanobrachia* is widespread throughout the Indo-Pacific (Gosliner et al. 2008). Within the genus *Phestilla*, strong species-specific feeding preferences have been reported with a single nudibranch species only consuming coral prey in a particular family or genus (e.g., *Phestilla sibogae* consumes *Porites* spp.; Harris 1975; Gosliner et al. 2008). Whether *Phestilla* consumes other coral taxa in the eastern Pacific is in need of study. *Phestilla* spp. are better known throughout the western Pacific and have been the focus of a study in Hawaii (Rotjan and Lewis 2008). In experimental tanks in Hawaii, *Phestilla* has been observed to infest and ultimately kill *Porites compressa*. Evidence of infestations of this magnitude are lacking from the wild, leading some to conclude that naturally occurring populations are controlled by fish and crustacean predators (Gochfeld and Aeby 1997). Regardless, single individuals may consume an average of 3.1 cm^2 of tissue per day (Haramaty 1991). The nudibranch utilizes small radular teeth to remove both polyps and coenosarc, indiscriminately scraping the soft tissues into its mouth (Rudman 1981). There is, however, some evidence that food selection occurs within the guts of the nudibranchs, with different species deriving nutriment from different parts of their coral prey (Rudman 1981). Live zooxanthellae have been observed within *Phestilla* species, and measurements of O_2 consumption by animals held in illuminated and dark aquaria revealed a reduction in net oxygen consumption in the light, thereby suggesting that the zooxanthellae were photosynthetically active and capable of conferring energetic benefits to their corallivore hosts. Finally, it should be noted that while *Phestilla* spp. are likely not capable of significant damage to eastern Pacific corals and reefs through their corallivorous activities, recent evidence suggests that they are a potential vector for transmitting coral disease (Dalton and Godwin 2006). These small, cryptic, and poorly known corallivores should therefore not be dismissed as unimportant to reef ecosystem health, and further investigation is necessary.

10.3.4 Hermit Crabs

Three species of diogeniid hermit crabs (*Trizopagurus magnificus*, *Calcinus obscurus*, and *Aniculus elegans*) have been observed to exhibit corallivorous feeding behaviors in the eastern Pacific. All are known from coral and rocky habitats at shallow depths (<40 m), however *A. elegans* has also been found to occupy sand and gravel habitats, and *C. obscurus* algal substrates (Ayón-Parente and Hendrickx 2010). *Trizopagurus magnificus* and *A. elegans* occur in the Sea of Cortez, Mexican, and Panamic provinces as well as the offshore Malpelo and Galápagos islands. *Calcinus obscurus*, however, is known solely from Panamic waters (Ayón-Parente and Hendrickx 2010).

Both *Trizopagurus magnificus* and *Aniculus elegans* are known to feed primarily at night; scraping the branch tips of pocilloporid corals, removing both skeletal material and tissues, and producing sediments (Glynn et al. 1972). Gilchrist (1985) described the feeding behaviors of *T. magnificus* and *Calcinus obscurus* in detail, noting size-dependent feeding behavior in *T. magnificus*. Larger individuals of this species scraped the surface of coral tissues with their major chelae, transferring organic matter to their maxillipeds and then to their mouths. Smaller individuals, however, picked at the surface of the coral with their maxillipeds. *Aniculus elegans* exhibited a scraping behavior similar to larger *T. magnificus*, though this feeding method was used regardless of size-class and was displayed subsequent to the snipping of the coral's surface tissues with their chelae.

In addition to damage inflicted by the feeding behavior of these species, both were observed to abrade coral tissues as they moved their shell across the live colony surfaces. In cases where this behavior was especially concentrated, such as when a crab tried to free itself when wedged among branches, colonies exhibited pronounced stress responses such as mucus production. Gilchrist (1985) also noted the sheltering behavior of hermit crab corallivores, which take refuge among the branches and dead bases of *Pocillopora* colonies, exhibiting limited mobility. Larger *Trizopagurus magnificus*, however, were observed to move between individual colonies more frequently, perhaps due to a reduced susceptibility to invertivore fishes.

At Isla del Caño, Costa Rica, densities of *Trizopagurus magnificus* and *Aniculus elegans* ranged from 0–24 and 0–28 ind m^{-2}, respectively (Guzmán 1988a). Glynn et al. (1972) recorded mean densities of *T. magnificus* in the Pearl Islands as high as 27.5 ind m^{-2}, and densities of *A. elegans* at 0.02 ind m^{-2}. In this same study, *T. magnificus* was found to consume 10.3 mg mean coral mass (tissue and skeleton) per day while large individuals of *A. elegans* removed a mean of 1.24 g of coral per day. At these rates and densities, hermit crabs were estimated to remove 1.12 metric tons of coral material per hectare of reef per year (Glynn 1974).

10.3.5 *Trapezia* spp.

The coral guard crabs *Trapezia* spp. as well as the alpheid shrimp *Alpheus lottini* are among the few corallivorous species that have not received the, albeit anthropocentric and over-simplified, distinction of harmful to corals and coral reefs. These obligate coral associates are known to reduce mortality and predation pressure (see below), yet still utilize their coral hosts as a food source.

Trapeziid crabs are primarily found associated with corals in the family Pocilloporidae and are widely distributed across the Indian and Pacific Oceans. Adults generally live in male-female pairs and occupy the living inter-branch spaces of their coral hosts, while juveniles are known to have an intra-colony distribution confined to the more-protected dead base of the coral. Numerous studies have investigated various aspects of the ecology of these crab associates, including resource partitioning and competition (Preston 1973; Huber and Coles 1986), seasonal reproduction patterns (Gotelli et al. 1985), inter-colony movements (Castro 1978) as well as their responses to coral bleaching and host death (Glynn et al. 1985; Caley et al. 2001; Stella et al. 2011).

Patton (1974) reviewed early studies discussing the diet of *Trapezia* spp. and lists invertebrates, detritus, and sediments, as well as coral mucus and tissues as food sources. Knudsen (1967) presented detailed descriptions of the feeding behaviors of *Trapezia ferruginea* and *Trapezia areolata* collected from Enewetok Atoll. Crabs were observed to introduce the tips of their walking legs into living polyps and rapidly scrape away surface materials. Substances adhering to the brush-like setae of their legs, including mucus, were removed by the mouthparts and consumed. Additionally, Knudsen (1967) described scraping of polyps and inter-polyp tissues (coenosarc), and noted food transfer from the crab's chelae.

Experimental evidence for the metabolic reliance of *Trapezia* on host corals can be found in Glynn et al. (1985). Heterosexual pairs of *Trapezia* were maintained on healthy, bleached, and dead coral colonies. Significant decreases in crab lipid content were observed on metabolically impaired (bleached and dead) corals versus those associated with healthy live coral colonies. Furthermore, emigration of crabs from their hosts and crab mortality were observed. Later studies by Stimson (1990) revealed that trapeziid crabs feed upon lipid-rich fat bodies produced by host *Pocillopora damicornis* colonies. This food source is available in abundance only when the crabs are present, suggesting that the crabs directly stimulate their hosts to produce it.

The most conclusive evidence for *Trapezia* corallivory is that of Rinkevich et al. (1991), who incubated *Stylophora pistillata* colonies with radioactive ^{14}C and then transplanted *Trapezia cymodoce* to each coral colony. These workers observed that compounds made by the photosynthetic activity of zooxanthellae were transferred to their coral hosts and finally into the tissues of *T. cymodoce*. The translocation of radioactive carbon from coral to crab associate was accomplished primarily through tissue consumption rather than mucus. Rates of ^{14}C accumulation corresponded to roughly 140 cm^2 of coral tissue surface area per month, roughly the amount of tissue on coral branches 40–45 cm in length.

10.3.6 *Alpheus lottini* and Other Caridean Shrimps

Alpheus lottini is well known throughout the eastern Pacific where it is found in heterosexual pairs, exclusively associated with pocilloporid corals. In other Indo-Pacific localities, however, it is also known to inhabit coral colonies within the genera *Seriatopora* and *Stylophora* (Castro 1971). The shrimp is omnivorous and has been observed to consume eggs (Coutière 1899), small invertebrates, algae, coral tissues (Barry 1965 in Castro 1971), and coral mucus (Barry 1965 in Castro 1971; Patton 1974). The diverse food sources of *A. lottini* may be explained by its seemingly indiscriminate feeding behavior, which involves brushing setose appendages across the surface of its coral host and removing the collected scrapings with its mouthparts (Patton 1974).

There are several other species of caridean shrimps known to associate with *Pocillopora* spp. in the eastern Pacific and it is likely that many of these rely, at least in part, on the metabolic byproducts of their hosts for nutriment. For example, *Thor amboinensis* is a small hyppolitid shrimp known to associate with a variety of invertebrate hosts across the Pacific, including in Panamanian waters (Patton 1974; Abele and Patton 1976). Gut content analysis of those collected from coral colonies has indicated coral mucus as a probable food source though individuals collected from sea anemones have been observed to utilize suspension feeding (Patton 1974). Similarly, shrimps belonging to the genus *Harpiliopsis* are known to associate with a diverse array of coral genera, including *Pocillopora* in the eastern Pacific (Castro 1971; Abele and Patton 1976). Knowledge of their feeding habits is limited to the gut contents of four individuals of *Harpiliopsis depressus* examined in the 1960s, which revealed a diet of coral mucus, zooxanthellae, and algal spores (Barry 1965 in Castro 1971). While the feeding habits of the aforementioned caridean shrimps have not been observed in as great of detail as *A. lottini*, since they consume coral products they may therefore be considered corallivorous.

10.4 Ecological Role of Corallivores

The positive impacts of corallivores on reef ecosystem health and function are often overlooked and underappreciated. While it is true that population explosions or "outbreaks" of corallivorous species such as the crown-of-thorns sea star can have devastating consequences for corals and reef communities (e.g., Chesher 1969; Birkeland and Lucas 1990), corallivory in the eastern Pacific is integral to ecosystem function. Corallivores are known to ameliorate the deleterious consequences of bleaching, they deter more efficient predators, aid in coral asexual reproduction, and finally they form a trophic pathway that supports diverse and abundant invertivorous and piscivorous species (see Chap. 9, Enochs and Glynn). Several of these positive impacts are noted by Rotjan and Lewis (2008), Glynn (2013), and Castro (2015).

The prevalence of these positive impacts within eastern Pacific reefs, and the importance of coral food sources in reef ecosystem trophodynamics, is likely related to the unique biology and ecology of pocilloporid corals. Species within this genus form many of the reef frameworks within the region. They are fast growing and branching, providing an abundant and accessible food source that regenerates relatively rapidly. Furthermore, their morphology provides an ideal shelter for cryptic associates, and their tissues and metabolic by products are an especially nutritious food source for their occupants (Stimson 1990). Together, these characteristics contribute to not just the enhancement of corallivorous populations, but to the corals' persistence despite the abundant and diverse species that feed on them.

10.4.1 Keystone Predators

Do any eastern Pacific corallivores exhibit keystone species characteristics, i.e. relative to a low or moderate abundance can they exert disproportionately strong effects on coral community structure? Among invertebrate corallivores, *Acanthaster planci* is a likely candidate, but perhaps only locally because this sea star is generally in low abundance except at some sites in the Gulf of California, the Revillagigedo Islands, and the Gulf of Chiriquí, Panama. Where *A. planci* is abundant in some areas (Panama), preferred prey species are small and exhibit high proportions of pre-existing dead skeleton (Glynn 1987). One could argue that the crustacean symbionts of pocilloporid corals, *Trapezia* spp. and *Alpheus lottini* would qualify as keystone corallivores because they enhance the survival of their hosts by warding off potential predators, prevent the settlement of alien taxa, and enhance boundary layer circulation and gas exchange. The facultative corallivore *Eucidaris galapagensis* plays a keystone role in the Galápagos Islands because of its pronounced excavating feeding behavior, which affects mature live corals, coral recruits, and the integrity of coral skeletons and carbonate framework structures. The degradation and loss of habitat structure is critical for a multitude of cryptic organisms (Glynn 2011; Enochs 2012; Enochs and Manzello 2012).

Among the facultative fish corallivores, the ubiquitous territorial damselfishes have been suggested to play keystone roles on coral reefs (Williams 1980; Hixon and Brostoff 1983). Gochfeld (2010) has offered data to support the role of damselfishes in affecting the relative abundances of corals. She found that *Pocillopora damicornis* colonies inside damselfish territories were protected from butterflyfish predation, and persisted for several years. Colonies experimentally removed and placed outside of territories were attacked and heavily grazed by butterflyfishes. Other studies in the central and western Pacific have demonstrated that several territorial damselfish species also protect acroporid corals, resulting in a local diversifying effect (e.g., Glynn and Colgan 1988; Done et al. 1991; Jones et al. 2006). Wellington's (1982) demonstration of *Stegastes acapulcoensis* controlling the zonation of branching and massive corals in the Pearl Islands (Panama) is a compelling example of the functional role of damselfish in shaping coral community structure and regulating the depth distribution of community types.

It is highly likely that the feeding behavior of the guineafowl puffer, *Arothron meleagris*, which characteristically nips the branch-tips of *Pocillopora* spp., can promote the lateral expansion of these coral communities by asexual propagation. Some coral branch segments that are broken but not ingested may survive and continue to grow if deposited on suitable substrates, e.g. course sediments at reef margins with ample sunlight. Several eastern Pacific localities in Mexico, Panama, and the Galápagos Islands have exhibited high abundances of pocilloporid asexual recruits, and a high proportion of these have probably been generated by pufferfish feeding (see Tables 15.12 and 15.13 in Chap. 15, Glynn et al.). One of the highest population densities of *A. meleagris* reported in the eastern Pacific, 171 ind ha^{-1} on a reef at Gorgona Island (Colombia), has not depressed coral colony mass, calcification or reef persistence and growth at this site (Palacios et al. 2014).

10.4.2 Cleaning

In a three month study conducted by Glynn (1983b) on the Pacific coast of Panama, corallivorous crab and shrimp symbionts (see Sects. 10.3.5 and 10.3.6), were found to increase mucus production, skeletal extension, and ultimately the survivorship of their pocilloporid coral hosts. Glynn postulated that these positive effects were conferred to the host due to the symbionts directly removing harmful substances settling on the coral's surface (e.g., sediment and colonizing organisms such as algae and invertebrates) as well as their stimulation of the coral's natural mucosal cleansing. Stewart et al. (2006) observed a similar phenomenon in Moorea. When *Trapezia* crabs were experimentally removed from *Acropora* and *Pocillopora* colonies in the field, the corals accumulated sediments, bleached, and ultimately died.

10.4.3 Defense from Harmful Species

Symbiotic crustaceans (trapeziid crabs and alpheid shrimps) are known to defend their coral hosts from *A. planci*, emerging from the protective interstices of the coral's branches and aggressively snipping with their chelae the tube feet and spines of the attacking asteroid (e.g., Weber and Woodhead 1970; Glynn 1976, 1983c). This defensive behavior is triggered, in large part, by chemicals naturally produced by *Acanthaster* that are detected at close range by the crustacean guards (Glynn 1980). In the western Pacific, Pratchett (2001) observed that the defensive behavior of trapeziid crabs is of sufficient magnitude to influence the hierarchical feeding preferences of *Acanthaster*, with the sea star preferentially preying upon less protected corals harboring weaker symbionts.

The strong defensive behavior of these symbiotic crabs and shrimps presents an apparent paradox in that they are able to coexist despite strongly territorial tendencies. It has been shown that the competitively inferior shrimp mimics the mannerisms of the trapeziid crabs, communicating with behaviors that are not used with conspecific shrimp (Vannini 1985). This display can result in the appeasement of the crabs' aggressive tendencies and facilitate the coexistence of the different species.

The positive nature of these corallivorous symbionts in ameliorating the deleterious effects of interspecific interactions is not limited to the exclusion of predatory *Acanthaster*. In Moorea, and throughout much of the Indo-Pacific, the sessile vermetid gastropod *Dendropoma maximum* is known to inhabit live coral colonies. While *Dendropoma* is not a corallivore, it extends mucus nets during feeding and is known to negatively influence coral growth and colony morphology (e.g., Shima et al. 2010). When present, trapeziid crabs were found to reduce the negative effects that *Dendropoma* had on coral growth rate (Stier et al. 2010). The authors of the latter study hypothesized that this was due to mucus removal by the crab, either inadvertently or through feeding and coral cleansing activities. It is likely that similar interactions occur in the eastern Pacific but remain unstudied.

10.4.4 Asexual Coral Reproduction

Many fast growing branching coral species fragment naturally due to physical and biological disturbances (e.g., Tunnicliffe 1979; Highsmith 1982). If tissue mortality is not severe following fragmentation, the resulting pieces may grow into new colonies. This form of asexual reproduction results in localized scattering, but when combined with long-distance dispersal of sexually produced offspring, it can be a highly effective life-history strategy in marginal reef environments with patchy habitable substrates (Bothwell 1981). While clonal reproduction is of limited importance to populations of *Pocillopora damicornis* in some localities (e.g., Miller and Ayre 2004), in many areas throughout its geographical range it remains one of the dominant forms of reproduction (Stoddart 1984; Adjeroud and Tsuchiya 1999; Whitaker 2006). This is true in the eastern Pacific, where *Pocillopora* forms large contiguous stands and reef structures (Richmond 1987).

The pufferfish *Arothron meleagris* is known to break off and ingest the tips of *Pocillopora damicornis* branches up to

3 cm in length (Guzmán 1988a). In some situations, where the resulting fragments are not consumed, these branch tips may grow into new coral colonies. This process, combined with physical disturbance by wave action, occurs on the reef slopes of eastern Pacific pocilloporid reefs. The resulting loose coral fragments spread out into adjacent rubble plains, where they eventually take hold and extend the consolidated reef framework seaward (Highsmith 1982). The extent that this process functions in the asexual propagation of *Pocillopora* remains unquantified, and investigation into the number of fragments created and their subsequent mortality rate is needed. However, given that *A. meleagris* can exist in high abundances (up to 171 ind ha^{-1}, Palacios et al. 2014) and consume less than 50 % of the live coral they remove (Glynn et al. 1972), the potential exists for this to be an ecologically important means of reproduction.

10.4.5 Trophic Contribution

In addition to the aforementioned positive influences on their coral food sources, corallivores in turn provide an important food source for the taxa that consume them, transferring energy from coral suspension feeding and zooxanthellae primary production to higher trophic level predators. In the eastern Pacific, this may occur when various piscivorous (e.g., Sphyraenidae, Scombridae, Carcharhinidae) or fish invertivores (e.g., Balistidae, Tetraodontidae) consume corallivore prey. Additionally, small cryptic invertebrates such as octopuses consume corallivorous gastropods and the caridean shrimp and polychaete worms (*Hymenocera picta*, *Pherecardia striata*, respectively) that feed on *Acanthaster planci* (Glynn 1981, 2004). Finally, it is likely that feces produced by corallivorous taxa may be consumed by detritivorous fauna, creating a pathway through which biological materials are recycled on a reef (e.g., Rothans and Miller 1991).

Enochs (2012) sampled motile cryptofauna associated with live and dead coral substrates from a pocilloporid reef on the Pacific coast of Panama. Live coral substrates were found to support significantly more cryptofauna biomass per unit volume than dead coral, suggesting that the trophic benefits of coral may extend to entire communities, beyond those species that directly consume them. In actuality, the number of feeding trophic interactions involving corals and corallivores is high, even in depauperate eastern Pacific systems (Glynn 2004). Quantitative analyses of complex coral reef food webs are rare (e.g., Opitz 1996; Reyes-Bonilla et al. 2014), especially for the multispecies assemblages and corallivore sub-webs found on eastern Pacific reefs.

10.5 Synthesis and Conclusions

In light of recent reviews (Cole et al. 2008; Rotjan and Lewis 2008) and the elevated levels of corallivory summarized here for the eastern Pacific, the pivotal role of coral consumption and the influence of the coral feeding guild to reef trophodynamics and community structure are further reinforced. In spite of a diverse and abundant guild of eastern Pacific corallivores and their prominence relative to the diversity of coral species prey, no records exist of local or large-scale outbreaks that have resulted in massive coral mortality as commonly observed in the Indo-Pacific region. This apparent exception to the rule may provide insight into natural ecological control of predator populations. It may signify that eastern Pacific reef ecosystems have uniquely evolved to support balanced but thriving corallivore populations or it may simply suggest that we have just not yet observed a predator outbreak event.

Regardless of the reasoning, we know that populations of corallivores are inexorably linked to the availability of their prey. Widespread coral mortality that resulted from the 1982–83 El Niño-related thermal anomalies and recovery in the years following have been shown to be strongly correlated with the abundance of corallivorous fishes (Glynn et al. 2014). Similar patterns have also been observed with coral cover and invertivore fishes, many of which feed on cryptic corallivore prey sheltering within the branches of pocilloporid corals (Enochs 2012; Glynn et al. 2014). These correlations point to the importance of the relationships between corals, corallivores, and higher level predators in the eastern Pacific. They indicate strong interconnectivity, a dependence on coral production and ultimately the consumption thereof. These trophic interactions provide a mechanism whereby climate-related coral mortality can have far reaching ramifications for numerous dependent taxa. These relationships/mechanisms are doubtlessly applicable to numerous other reef systems but are more difficult to discern due to higher species and habitat diversity. In their relative simplicity, eastern Pacific reefs and coral/corallivore interactions can therefore serve as informative systems with implications for ecosystem persistence, meriting further investigation.

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