

LIPID DECLINE IN STRESSED CORALS AND THEIR CRUSTACEAN SYMBIONTS

PETER W. GLYNN^{1*}, MIGUEL PEREZ^{2*}, AND SANDRA L. GILCHRIST³

¹Smithsonian Tropical Research Institute, P. O. Box 2072, Balboa, Panamá, ²Escuela de Biología, Universidad de Panamá, República de Panamá, and ³Division of Natural Sciences, University of South Florida, New College of USF, 5700 N. Tamiami Trail, Sarasota, Florida 33580

ABSTRACT

Total lipid levels, determined by the phosphosulphovanillin colorimetric method, declined significantly in ramose scleractinian corals and their xanthid crab symbionts during the 1983 El Niño warming event on the Pacific coast of Panamá. This decline was observed in a controlled laboratory experiment, employing host corals (*Pocillopora damicornis*) and obligate crab symbionts (*Trapezia corallina* and *Trapezia ferruginea*), concurrently with morbidity and mortality observed on coral reefs in the field. Lipid levels decreased from 0.59% (dry weight) to 0.34% in normal *versus* affected and dead corals, and from 4.54% (dry weight) to 1.20% in normal *versus* affected and dead crabs in a two-week period. Lipid depletion in corals accompanied the loss of zooxanthellae and increased morbidity and death; in crabs, a decrease in the number of egg-carrying females, a high emigration rate, a slight increase in mortality, and a decline in defensive behavior occurred. These findings suggest that symbiotic crabs were deprived of food from their coral hosts who initially lost zooxanthellae, an event correlated with the prolonged El Niño sea warming.

INTRODUCTION

Studies on the feeding biology of obligate crustacean symbionts (crabs and shrimp) inhabiting corals have indicated a strong trophic dependency, with crustaceans using coral host mucus and entrapped organic matter (Knudsen, 1967; Patton, 1974, 1976; Castro, 1976). The high lipid content of mucus, an important energy source for the crustaceans (Benson and Muscatine, 1974), is believed to be derived from the symbiotic zooxanthellae present in coral tissue (Crossland *et al.*, 1980; Davies, 1984). Reef-building corals harboring crustacean symbionts were stressed—presumably due to a prolonged El Niño warming spell—and experienced massive zooxanthellae loss (bleaching) and widespread mortality in tropical eastern Pacific waters in 1983 (Glynn, 1983a, 1984). Observations in Panamá demonstrated that mucus release declined significantly in affected (bleached) corals and that the number of crustacean symbionts per colony and agonistic (defensive) behavior of the crabs also declined during this period (Glynn, in prep.).

Advantage was taken of this large-scale warming disturbance to determine the concentrations of lipid stores in the affected corals and in their crustacean symbionts. If the lipid reserves of affected crustacean symbionts could be shown to decline simultaneously with the deterioration of their principal food source, then this would suggest the influence of food deprivation in disrupting the coral-crustacean symbiotic

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* Present address: Division of Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy, Miami, Florida 33149.

bond during the 1983 EL Niño event. It is also possible that the symbiotic crustaceans were adversely affected by temperature alone, but no other reef organisms, including numerous crustacean species, were apparently stressed during the warming period.

In this study we examine lipid levels in coral hosts and crab symbionts affected by the 1983 El Niño sea warming episode in Panamá. Major emphasis is given to the coral-crab mutualism in outdoor aquaria in the upwelling environment of the Gulf of Panamá. These observations are supplemented with data obtained from field populations in the non-upwelling waters of the Gulf of Chiriquí.

MATERIALS AND METHODS

The scleractinian coral host *Pocillopora damicornis* (Linnaeus), and its xanthid crab symbionts, *Trapezia corallina* Gerstaecker and *Trapezia ferruginea* Latreille, were examined. All animals were collected at 3–8 meters depth on a small, pocilloporid patch reef at Urabá Island (8°47'03"N; 79°32'22"W), Taboga Islands, Gulf of Panamá. Three collections were made over the period 1 June to 25 July 1983 to carry out observations during the unusual warming event experienced in 1983 in the Gulf of Panamá. Coral populations in the Gulf of Chiriquí (northwestern Pacific coast of Panamá) were affected in February–March, and corals in the Gulf of Panamá were affected later, beginning in June 1983, after the upwelling season (Glynn, 1983a, 1984). Nearly all corals in the first two collections lost their zooxanthellae and died within a week of collection. By the third collection (25 July), the disturbance had stabilized somewhat, *i.e.*, normal and affected corals remained visibly the same, retaining zooxanthellae and bleached tissues respectively, for 3–4 weeks. This last collection provided the main material for the laboratory observations in this study.

Eight coral colonies of each of four conditions—*normal* (N), usual brown color uniformly present; *partially bleached* (PB), loss of some color, especially on upper branches; *bleached* (B), colony nearly uniformly white; *dead* (D), live coral tissues absent, colony covered with thin growth of pioneering filamentous algae—were selected and assigned to each treatment. These corals were 10–14 cm in maximum colony diameter and contained all live branches, or recently dead branches in the case of the dead group. Crab symbionts were also collected from normal *Pocillopora damicornis* corals obtained on 25 July 1983 at Urabá Island, and one naturally paired male and female was added to each colony in the four treatments. Twenty-one pairs of *Trapezia corallina* and 11 pairs of *Trapezia ferruginea* were introduced onto the experimental corals. Crab carapace widths ranged from 8 to 14 mm (\bar{x} = 10.9, S.D. = 1.73) and dry weights from 137.9 to 758.5 mg (\bar{x} = 326.8, S.D. = 183.4).

Each coral colony with its pair of crab symbionts was maintained in a 2.6 l glass bowl. Plastic netting was attached to the rim of each bowl to prevent the escape of crabs in the overflow. Continuously flowing sea water, filtered through medium coarse #20 silica sand, was supplied at a rate of about 1 l/min. Colonies were placed on partially shaded, outdoor tables receiving 50–70% natural lighting. Colony locations were determined by strict random assignment and they were not moved during the experiment (28 July–11 August, 1983).

At the end of the experiment, branch tips (2–3 cm long) of corals and whole crabs were rinsed gently with distilled water to remove salts and dried to constant weight *in vacuo* over silica gel for seven days. Gravid female crabs with eggs were analyzed *in toto*. After drying, the samples, including tissues and skeleton, were reduced to a fine powder by grinding with a mortar and pestle. Total lipid contents

were determined by the phosphosulphovanillin, colorimetric method of Barnes and Blackstock (1973).

Field observations on the condition of host corals and crab symbionts were also made during the warm water periods March to June, 1983, at Uva Island (7°48'46"N; 81°45'35"W), Gulf of Chiriquí, and during June to October, 1983, at Urabá Island, and the northern Pearl Islands (Saboga Island, 8°37'29"N; 79°03'23"W), Gulf of Panamá.

RESULTS

Median lipid levels (% dry weight) in the host coral *Pocillopora damicornis* differed significantly among the four conditions examined ($P \ll 0.001$, Kruskal-Wallis test). The highest levels found in normal corals (median = 0.59%) were significantly higher than those of the affected (medians = 0.28–0.37%) and dead corals which had statistically similar levels (Kruskal-Wallis multiple comparison procedure, Daniel, 1978, Table I). The lipids found in dead corals (median = 0.36%) were probably present in the algae and other organisms colonizing the skeletal surface.

Trapezia spp. crabs inhabiting normal coral hosts had significantly higher lipid levels, with median = 4.5% lipid, than crabs present in affected and dead corals, with median lipid levels that ranged from 0.80 (in dead coral) to 1.48% (in partially bleached coral) ($P \ll 0.001$, Kruskal-Wallis test). *A posteriori* multiple comparison testing (Daniel, 1978) indicated that the low lipid levels of crabs present in partially bleached and bleached corals were similar, as were the low lipid levels detected in crabs from bleached and dead corals (Table II). A comparison of lipid levels between the two crab species (*Trapezia corallina* and *Trapezia ferruginea*) within each of the four coral conditions failed to reveal any significant differences between species (Table III).

No significant differences in lipid levels between crab sexes were evident (Table III). This result for crabs present in normal corals was unexpected because 50% of the females were carrying large numbers of eggs. Body lipid levels generally increase in female crustaceans in preparation for and during breeding periods (Du Preez and McLachlan, 1983; Tessier *et al.*, 1983). Only one female in eight (12.5%) was gravid in each of the affected and dead groups of coral. The frequency of gravid female

TABLE I

Total lipid levels (% dry weight) in normal (N), affected (PB, B), and dead (D) branch tips of *Pocillopora damicornis*

	Condition of coral host			
	N	PB	B	D
Median	0.59	0.37	0.28	0.36
MCP ¹				
Range	0.24–0.85	0.11–0.45	0.09–0.48	0.14–0.64
0.95 conf. lim. ²	0.44–0.66	0.25–0.41	0.14–0.45	0.24–0.51
Number	8	8	8	8

¹ *A posteriori* multiple comparison procedure (Kruskal-Wallis test, Daniel, 1978), $\alpha = 0.20$, line joins statistically equal median values.

² Confidence limits of median calculated as $K = 0.5(n + 1) - (n)^{1/2}$ of the range, where K is the number of units from each end of the distribution toward the median.

TABLE II

Total lipid levels (% dry weight) of *Trapezia* spp. crabs inhabiting normal (N), affected (PB, B), and dead (D) pocilloporid corals

	Condition of coral host			
	N	PB	B	D
Median MCP ¹	4.54	1.48	1.32	0.80
Range	2.47–12.15	0.95–4.74	0.85–3.05	0.57–1.70
0.95 conf. lim. ²	3.76–5.25	1.24–1.85	1.04–1.61	0.66–1.05
Number ³	12(4)	10(6)	10(6)	10(6)

¹ *A posteriori* multiple comparison procedure (Kruskal-Wallis test, Daniel, 1978), $\alpha = 0.20$, lines join statistically equal median values.

² Confidence limits of median calculated as $K = 0.5(n + 1) - (n)^{1/2}$ of the range, where K is the number of units from each end of the distribution toward the median.

³ First entry denotes number of *Trapezia corallina*, entry in parentheses denotes number of *Trapezia ferruginea*. Results from the two crab species were pooled because no species differences were evident (see Table III).

crabs was significantly higher ($P = 0.042$, Fisher exact test) in normal than in affected and dead coral hosts combined. Since the reproductive condition of crabs was noted only at the end of the experiment, it is not known if the frequency of

TABLE III

Comparisons of total lipid levels (% dry weight) in two crab species (*T. corallina* and *T. ferruginea*) and in female and male crabs

	Condition of coral host							
	Normal		Partially bleached		Bleached		Dead	
	<i>Trapezia corallina</i>	<i>Trapezia ferruginea</i>	<i>Trapezia corallina</i>	<i>Trapezia ferruginea</i>	<i>Trapezia corallina</i>	<i>Trapezia ferruginea</i>	<i>Trapezia corallina</i>	<i>Trapezia ferruginea</i>
Crab species differences								
Median	4.04	6.66	1.56	1.33	1.40	1.28	0.80	0.89
Probability ¹	>0.05		>0.05		>0.05		>0.05	
Range	2.47–12.15	4.55–12.02	1.01–4.74	0.95–2.15	0.85–3.05	1.04–1.61	0.57–1.57	0.62–1.70
0.95 c.l. ²	3.76–4.85	4.55–12.02	1.36–1.85	1.16–1.78	0.95–1.69	1.17–1.39	0.67–0.96	0.66–1.06
Number	12	4	10	6	10	6	10	6
Crab sex differences								
	♀	♂	♀	♂	♀	♂	♀	♂
Median ³	4.70	4.04	1.40	1.56	1.46	1.30	0.80	0.85
Probability ¹	~0.29		>0.36		~0.25		>0.48	
Range	3.50–12.02	2.47–12.15	0.95–4.74	1.01–3.53	0.90–3.05	0.85–1.69	0.57–1.06	0.61–1.70
0.95 c.l. ²	3.76–5.25	3.75–8.62	1.24–1.85	1.16–2.15	1.04–2.60	0.95–1.45	0.67–1.05	0.62–1.57
Number ⁴	8(4)	8	8(1)	8	8(1)	8	8(1)	8

¹ Associated with Mann-Whitney U test.

² Confidence limits of median calculated as $K = 0.5(n + 1) - (n)^{1/2}$ of the range, where K is the number of units from each end of the distribution toward the median.

³ Crabs of each sex were pooled since no significant species differences were evident.

⁴ Number of gravid crabs in parentheses; eggs included in analysis.

gravid females declined in the stressed coral groups, if more crabs released eggs in the normal group, or if their numbers remained unchanged over the two-week period (see field results below).

Trapezia spp. showed a higher rate of emigration from bleached and dead coral hosts than from normal corals (Table IV). The data demonstrating this trend are from two experiments initiated in July and discontinued because of high coral mortality and unrestricted movements or loss of some crabs. In these first experiments the bowls were not rimmed with netting to confine the crabs to their respective coral hosts. Median emigration rates were significantly different among the coral hosts of varying condition in both the 5 July and 20 July experiments ($0.01 > P > 0.001$ in both cases, Kruskal-Wallis test). From 5 to 6 July, 2 crabs/colony/day emigrated from bleached and dead corals, whereas normal and partially bleached colonies lost only 1 crab/day each (Table IV). From 20 to 21 July, no crabs left their normal hosts, but median emigration rates of 0.5 to 1 crab/colony/day were observed in partially bleached, bleached, and dead corals.

All crabs that died in laboratory experiments were associated with either partially bleached, bleached, or dead corals (Table V). Overall crab death in the two experiments ranged from 4.0% in dead corals to 15.4% in bleached corals. Although these results suggest that crab mortality was highest in affected (partially bleached and bleached) and dead corals, statistical testing of the pooled data—normal ($n = 32$) versus affected ($n = 81$)—indicate a nonsignificant difference ($X^2_3 = 6.46$, $0.10 > P > 0.05$).

Although no attempt was made to quantify the defensive behavior of the crabs—which typically involves threat displays and attacks directed toward intruding competitors and predators (Glynn, 1983b; Abele, 1984)—it was clear that by the end of the 28 July experiment the crabs associated with normal corals were more alert and forceful in their movements than those on bleached and dead corals.

TABLE IV

Number of Trapezia spp. crab symbionts emigrating per day from individual coral colonies of varying condition in the laboratory, July 1983

	Condition of coral host			
	N	PB	B	D
5–6 July				
Median ¹	1	1	2	2
MCP ²				
Range	0–2	0–2	1–2	2–2
0.95 conf. lim. ³	0–2	0–1	1–2	2–2
20–21 July				
Median ¹	0	0.5	1	1
MCP ²				
Range	0–0	0–2	0–2	0–2
0.95 conf. lim. ³	0–0	0–1	0–2	1–1

¹ Based on eight coral colonies, each with one pair of crabs.

² *A posteriori* multiple comparison procedure (Kruskal-Wallis test, Daniel, 1978), $\alpha = 0.20$, lines join statistically equal median values.

³ Confidence limits of median calculated at $K = 0.5(n + 1) - (n)^{1/2}$ of the range, where K is the number of units from each end of the distribution toward the median.

TABLE V

Number of Trapezia spp. crab symbionts that died in coral colonies of varying condition in the laboratory, July–August 1983

	Condition of coral host			
	N	PB	B	D
<i>5–20 July</i>				
Number dead	0	3	2	1
Percent dead ¹	0	21.4	20.0	11.1
Total number crabs	16	14	10	9
<i>28 July–11 August</i>				
Number dead	0	1	2	0
Percent dead	0	6.2	12.5	0
Total number crabs	16	16	16	16
Overall percent dead	0	13.3	15.4	4.0

¹ Crabs lost from bowls are omitted from calculations of percent dead.

Threat displays could be easily elicited from crabs in normal corals by probing with forceps, whereas crabs in bleached and dead corals moved away from the probe, remained motionless, or responded only weakly. The median defensive behavior of *Trapezia* spp. in normal coral hosts in the field (Uva Island reef, Gulf of Chiriquí, 27–28 April 1983) was 10 responses per colony per 3 min; this declined to 3 responses in partially bleached corals and the crustacean guards in fully bleached and dead colonies were virtually unresponsive, each exhibiting median responses of 0 (Glynn, in prep.).

As in the laboratory results, a higher proportion of female *Trapezia* spp. were gravid in normal than in affected or dead corals in the field (Table VI). In two collections, the overall frequency of gravid crabs in normal corals was 43.9%, whereas this ranged from 17.9% (partially bleached) to 26.7% (bleached) in affected corals. However, this difference is not statistically significant ($X_3^2 = 5.71$, $0.20 > P > 0.10$). The frequency of gravid crabs also declined in each of the four host coral conditions from April to June (Table VI). This decrease in egg-carrying crabs was

TABLE VI

Number of gravid Trapezia spp. in normal, affected, and dead colonies of Pocillopora damicornis at Uva Island reef in April and June, 1983

	Condition of coral host			
	N	PB	B	D
<i>28 April</i>				
Number gravid	9	2	2	2
Percent	75.0	50.0	33.3	40.0
Number ♀♀ sampled	12	4	6	5
<i>24 June</i>				
Number gravid	9	3	2	0
Percent	31.0	12.5	22.2	0
Number ♀♀ sampled	29	24	9	4
Overall percent gravid	43.9	17.9	26.7	22.2

statistically significant in normal corals ($P = 0.011$, Fisher exact test), but not so in partially bleached ($P = 0.124$), bleached ($P = 0.396$), or dead corals ($P = 0.277$).

DISCUSSION

Large amounts of lipid are often found in the mucus of healthy corals and commonly range from about 20 to 90% dry weight (Benson and Muscatine, 1974; Ducklow and Mitchel, 1979; Daumas *et al.*, 1982). These high lipid levels seem to be derived from zooxanthellar lipogenesis and translocation to coral tissues (Crossland *et al.*, 1980; Davies, 1984). Even if the pure mucus of some coral species contains little lipid (3–4% reported by Krupp, 1982), contamination by nematocysts, bacteria, organic debris, and especially zooxanthellae will usually increase lipid levels considerably. Such high lipid levels probably represent an important energy source for the crustacean symbionts that feed on coral mucus. This nutrient-rich pathway may have served as a basis for selection favoring the formation of coral-crustacean mutualisms, as suggested by Thompson (1982) in the evolution of the mutualistic symbiosis of coral and zooxanthellae. The coral-crustacean energy shunt is one step removed from the usual host-symbiont interactions in nutrient-poor environments, *e.g.*, lichens (algae and fungi) and ant-plant mutualisms. In these mutualisms the algae and ants supply low nutritional inputs to their hosts. In the coral-crustacean partnership the trophic input is opposite in direction with the coral host providing nutrition to the crustacean symbionts via its plant symbionts. While it is possible that the waste products of crustacean symbionts provide nutrients (*e.g.*, nitrogen) for host zooxanthellae, this kind of interaction has not yet been demonstrated (Patton, 1976).

With the approximately 50% decline in lipids in coral branches and 40% decline in mucus release among stressed corals (unpub. data), it is highly likely that crustacean symbionts were deprived of a significant proportion of their food resource. Only symbiotic crustaceans on stressed corals showed a debilitated state (increased emigration, apparent decline in reproductive activity, and reduced defensive behavior), and had a marked reduction in lipid content, to about 30% of values observed in healthy coral hosts. Castro (1978) observed movement in *Trapezia* spp. and concluded that one of the reasons for increased emigration was an insufficient supply of coral mucus. Thus, it appears that the decline in energy-rich mucus of host corals was the main factor leading to the disturbances observed in the symbiotic crabs.

This study provides evidence that lipid reserves can be drawn down rapidly in both corals and crustacean symbionts during periods of stress. In just 14 days lipid levels were reduced by 50% in corals and by 78% in crabs. A rapid decline in lipids, 60% loss in 15 days, has also been found in *Pocillopora damicornis* subjected to reduced light levels in Hawaii (Stimpson, pers. comm.; see Clayton and Lasker, 1982, and Szmant-Froelich and Pilson, 1980 for additional examples of rapid weight loss and lipid decline in corals).

The principal organisms affected during the 1982–83 El Niño warming period were coelenterates containing endosymbiotic zooxanthellae (Glynn, 1984; Suharsono and Kiswara, 1984; Lasker *et al.*, in press). This severe and prolonged sea warming event probably disrupted the coral-dinoflagellate mutualism, resulting in the expulsion or emigration of zooxanthellae. Numerous bleached corals, especially ramose species with high growth rates, died in 2–5 weeks following the loss of zooxanthellae. Repeated observations and quantitative sampling of reef organisms other than reef-building corals (polychaete worms, gastropods, crustaceans, echinoderms, and fishes),

during and after the warming episode in both upwelling and non-upwelling environments, failed to reveal evidence of stress or mortality in non-zooxanthellate bearing species. Even the ahermatypic (non-zooxanthellate) coral *Tubastraea coccinea* Lesson was unaffected by this disturbance. Thus, it seems unlikely that whatever conditions (probably prolonged high temperatures) stressed and killed hermatypic corals also independently affected only the coral crustacean symbionts.

Some evidence suggests that the crustacean symbionts of *Pocillopora* are generally more sensitive to environmental extremes than are their coral hosts. Upwelling and attendant extreme conditions (Abele, 1976, 1979), as well as oxygen depletion (Glynn, unpub. obs. in Panamá and Guam) can differentially kill crab and shrimp symbionts. Such stressful conditions sometimes cause partial coral mortality, but usually the crustacean symbionts are more sensitive and succumb to these disturbances, thus leaving only the surviving coral hosts. It should be noted, however, that extreme low tidal exposures occasionally kill shallow, reef flat corals and allow a high initial survival of crustacean symbionts because of their ability to emigrate to slightly deeper reef habitats (Glynn, 1976). In this study the mass mortality of normally hardy coral hosts caused a secondary and severe mortality of the more sensitive obligate crustacean symbionts. This mortality event is similar to Futuyma's (1973) prediction that the elimination of inflexible or hardy species among groups of species in usually constant environments may lead to the elimination of a suite of interdependent species.

Abele (1976) has demonstrated that crustaceans associated with pocilloporid corals in Panamá show a higher species richness in fluctuating (upwelling) than in constant (non-upwelling) environments. He hypothesized that the periodic disturbances caused by upwelling prevent specialist species from monopolizing the limiting resources of host corals. Since coral host and crustacean symbiont mortalities were similar in the upwelling and more constant non-upwelling environments, it is not likely that this disturbance had a selective and diversifying effect on coral-associated crustaceans in the seasonally fluctuating upwelling environment.

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