Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7-11 July 2008
Session number 26

Effects of coral mortality on the community composition of cryptic metazoans associated with *Pocillopora damicornis*

I.C. Enochs[1], G. Hockensmith[1]

1) University of Miami, RSMAS, 4600 Rickenbacker Cswy., Miami, FL 33149

Abstract. Coral reefs consist of complex three-dimensional habitats occupied by diverse taxa. The term cryptofauna (coelobites) specifically applies to those organisms that live within the interstices of coral reef framework. The remarkably diverse assemblage of cryptic biota in reefs is poorly understood relative to that of the epibenthic and nektonic reef species. It has been postulated that the biomass of this cryptic component of the reef ecosystem is high, possibly exceeding that of the surface biota. Furthermore, coelobites play an important role in reef trophodynamics and bioerosion. In order to evaluate the dependency of the cryptic community on the biotic nature of the substrate it occupies, both living and dead *Pocillopora damicornis* colonies were defaunated and returned to the reef. After six and twelve months *in situ*, associated coelobites were collected, identified, counted, and weighed. Communities associated with live coral colonies had greater biomass and were more similar than those associated with dead corals. These findings have important implications for how reef communities may respond to coral mortality.

Key words: cryptofauna, eastern Pacific, coral mortality.

Introduction

Coral reefs are considered to be the most biologically diverse ecosystems in the marine realm (Paulay 1997; Reaka-Kudla 1997). They maintain high biomass and high abundances of organisms despite their occurrence in what are classically considered to be oligotrophic regions. The majority of this concentrated biodiversity (Reaka-Kudla 1997) and biomass (Gischler and Ginsburg 1996) resides not on the surface of the reef but within the cavities of complex structural taxa and framework. Despite their prevalence, these cryptic species are poorly studied compared with the more accessible and charismatic surface fauna (Reaka-Kudla 1997).

Preliminary single taxon (polychaete) surveys have found coelobite densities to be as high as 127,900 individuals m^{-2} (Brock and Brock 1977). Another study found over 107 species living within a single colony of *Pocillopora damicornis* (Grassle 1973).

Although cryptic organisms spend most of their time hidden in cracks and crevices, they are functionally connected to both nektonic species and benthic epifauna. Coelobites are integral components of reef food webs and nutrient dynamics. They provide an essential energy source to many families of marine fish including Balistidae, Cirrhitidae, Haemulidae, Lutjanidae, Labridae, and Serranidae.

Energy, in turn, is incorporated into the coelobite community through a variety of different pathways. Cryptic suspension feeders capture and recycle particulate organic matter from surrounding reef waters (e.g., sponges, lithophage bivalves, polychaetes, barnacles: Richter and Wunsch 1999; Glynn 2008). Cryptic herbivores (e.g., amphipods, chitons, echinoids, limpits, opisthobranchs; Glynn 2008) feed on abundant supplies of algae which are all too often present on modern reefs. Carnivores (e.g., crustaceans, fishes, flatworms, nemerteans, gastropods, octopuses, polychaetes) are also prevalent in the cryptic environment and may exert a high degree of predatory pressure on the community as a whole (Glynn 2006, 2008). Cryptic coral symbionts have been found to benefit coral health and protect their host colonies from predation (e.g, *Trapezia ferruginea* and *Alpheus lottini*; Glynn 1983). Still other cryptic organisms (e.g., lithophage bivalves, polychaetes, sipunculans), play an active role in bioerosion, the biological destruction of coral skeletons and carbonate frameworks. These taxa effectively alter the reef habitat, providing shelters for other opportunistic cryptic species (Hutchings 1983) and ultimately reducing substrate complexity after coral mortality.

The composition of this important coelobite community is thought to be highly dependent on the surface area, volume, and porosity of the substrate it occupies (Hutchings 1974, 1983). Relatively little is known concerning the relationship of the cryptic community with the type of biological substrate it is associated. Some researchers have suggested that coelobite abundances are higher in areas of high algae cover. This may be due to a greater availability of food (Klumpp et al. 1988) or an absence of predation on settling larvae by the coral animal (Hutchings and Weate 1977). Despite these hypotheses, we are not

aware of any study that has directly compared cryptic community composition on living and dead coral.

A large and growing body of evidence has pointed to a worldwide decline in coral cover (Gardner et al. 2003; Bruno and Selig 2007) and increasing occurrence/magnitude of coral mortality events (Glynn 1993). The effect that coral death has on the diverse community of reef taxa is poorly understood. The few studies that have attempted to investigate the effects of coral mortality events have primarily focused on a single taxon (i.e., fishes). Assemblages of fish species have been found to change dramatically within short time periods after mass coral bleaching (mortality) events. Lindahl and others (2001) observed an increase in herbivore abundance and decrease in coral-associate abundance, resulting in an overall increase in fish species diversity. However, over longer time periods, a subsequent loss in habitat complexity may ultimately lead to lower abundance and diversity of fishes (Sano et al. 1987; Booth and Beretta 2002).

Because coral reefs are highly complex and diverse ecosystems, it is important to evaluate the response to coral mortality on multiple taxa assemblages. This study attempts to quantify the difference in community composition of invertebrates associated with live coral (*P. damicornis*) versus those associated with dead coral skeletons (six and eighteen months after mortality).

Material and Methods

Study Area:

This study was conducted at the Uva Island patch reef (7°48'52"N 81°45'34W), located in the non-upwelling Gulf of Chiriquí on the Pacific coast of Panamá. The reef is 2.5 ha and composed primarily of *P. damicornis*. Uva Island experiences a dry season from mid December through April and a wet season throughout the rest of the year. The wet season is characterized by light variable winds, higher rain fall, and higher cloud cover. During the dry season, thermocline shoaling may result in punctuated periods of lower water temperature and elevated nutrient concentrations (D'Croz and O'Dea 2007). Previous research on the Uva Island reef (Abele 1976; Glynn 1982, 1983) and others in the western Pacific (Grassle 1973; Patton 1974; Austin et al. 1980) has demonstrated the importance and prevalence of various taxa associated with the complex arborescent structure of *P. damicornis*.

The Uva Island reef has been extensively monitored by P. W. Glynn and others for the past four decades. Disturbances associated with the El Niño-Southern Oscillation (ENSO) have significantly impacted the area. Elevated water temperatures associated with the 1982-83 ENSO resulted in widespread coral bleaching and 75% mortality (Glynn 1984). The 1997-98, ENSO resulted in only13% coral mortality despite a similar thermal anomaly to the 1982-83 event (Glynn et al. 2001).

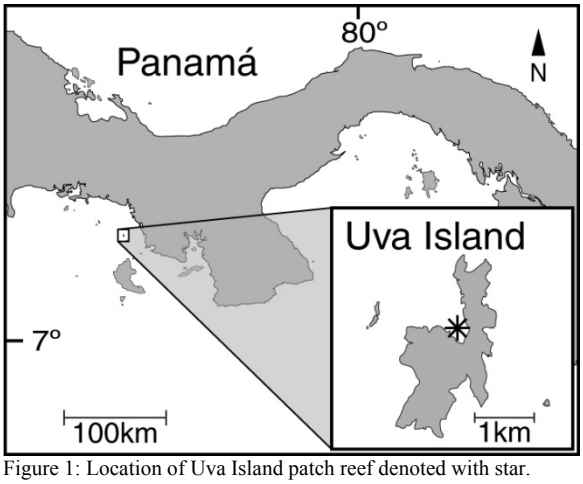

Figure 1: Location of Uva Island patch reef denoted with star.

Field Methods:

In September 2003 sixty colonies of *P. damicornis* were collected from the back reef at the Uva Island site. Maximum and minimum diameter and height were recorded for each colony. All associated metazoans were removed upon collection with aid of forceps and wire probes. Half (30) of the colonies were bleached with fresh water. Necrotic tissue was removed with a high pressure hose, leaving behind bare carbonate skeleton. Crosses were constructed from two pieces of one meter long iron rebar attached at their center. One dead and one living coral colony was affixed to each of two opposite ends of the cross. Live/dead pairs were randomly placed along the fore reef in approximately four to six meters of water.

In March 2004 (six months *in situ*) all experimental units were collected by sealing each colony in a plastic bag underwater. Bags were brought to the surface and each coral colony was defaunated using forceps and wire probes. Seawater from each bag was filtered over a 1mm mesh in order to collect those species that may have come free during collection. Colony dimensions were remeasured and each experimental pair was returned to the forereef. Cryptic metazoans were preserved in 70% ethanol and transported to the University of Miami Rosenstiel School of Marine and Atmospheric Science for further processing.

In March 2005 (12 months since defaunation) 23 of the original 30 experimental units were located and collected. It is likely that after 18 total months *in situ*, significant bioerosion occurred, resulting in the fragmentation and destruction of the missing pairs. Of those that were located, living coral colonies had grown to the point where it was necessary to break them apart in order to collect cryptic fauna. Dead colonies were

also broken apart to eliminate sampling bias. Water from each sampling bag was filtered over 1mm mesh and the dimensions of each colony were recorded. Again, metazoan associates were placed in 70% ethanol and transported to the University of Miami for analysis.

It is important to note that sessile taxa were not cleaned off of dead colonies after the first collection. Therefore, while communities of motile taxa collected in 2005 experienced 12 months *in situ*, the associated encrusting taxa would have developed for 18 months. Additionally, communities of motile fauna collected in 2005 would have experienced both wet and dry seasons during development while those collected in 2004 would have only experienced a single wet season.

Analysis:

Invertebrates were counted and identified to the lowest possible taxonomic level. The bulk wet weight of all individuals of each taxon associated with each colony was recorded. All specimens were deposited in the University of Miami Invertebrate Museum.

The geometric volume of each colony was approximated as a spheroid.

$$V = \frac{4}{3}\pi * \frac{wmax}{2} * \frac{wmin}{2} * \frac{h}{2}$$

Where *wmax* is maximum width, *wmin* is minimum width and *h* is height. Abundances, biomass, and richness were standardized (L^{-1}) by dividing the community parameters for each colony by the theoretical volume of that colony.

Differences in the abundance, biomass, and richness between live and dead colonies were investigated using t-tests and Mann-Whitney rank sum (MWRS) tests when the assumptions of parametric tests were not met. Differences between sampling years were not tested due to the possibility of sampling bias from the use of different methodologies to extract cryptic fauna.

A species by sample abundance (standardized to colony volume) matrix was constructed for each collection year. Abundances were square-root transformed in order to standardize the effects of abundant and rare species on the overall community assemblages. A similarity (Bray-Curtis) matrix was constructed for the transformed abundances using Plymouth Routines in Multivariate Ecological Research (PRIMER 5). The similarity matrix was used to construct an ordination by non-metric multidimensional scaling (nMDS) for each of the two sample years. A cluster analysis (group-average) was also conducted on the same similarity matrix and similarity levels of samples were drawn in the Euclidian space of the nMDS plots.

Results

Abundance:

A total of 1121 individuals were collected from live and dead colonies in 2004 and 4151 individuals were collected in 2005 (Table 1). There was no significant difference in abundance (standardized to volume) between communities associated with live and dead colonies in 2004. In 2005, dead colonies had higher volume-standardized abundances relative to live colonies ($P < 0.01$, MWRS). Proportionally, Crustacea was the most abundant taxon in 2004 (both live and dead) followed in order by Mollusca, Echinodermata, and Polychaeta. In 2005, Crustacea was again the most abundant taxon followed in order by Echinodermata, Mollusca, and Polychaeta. Several common species (mean abundance > 1 L^{-1} in either collection year) were found to be exclusively (e.g., *Alpheus lottini*, *Trapezia* juveniles and *Harpiliopsis spinigera*) or almost exclusively (e.g., *Fennera chacei*, *Pagurus benedicti*, and *Trapezia ferruginea*) associated with live corals. Other abundant species were found to be more closely associated with dead coral (e.g., *Teleophrys cristulipes*, *Palaemonella holmesi*, *Elasmopus* sp., and Gammaridea sp.).

Table 1: The abundance, biomass, and richness of invertebrate communities associated with living and dead *P. damicornis* in 2004 and 2005. Mean values (±SE) have been standardized to one liter by dividing the value for the community associated with each colony by the theoretical volume (approximated as a spheroid) of that colony.

Attribute	2004 (6 months *in situ*, $n = 30$)			2005 (12 months *in situ*, $n = 23$)		
	Live	Dead	Significance	Live	Dead	Significance
Mean Abundance individuals L^{-1}	21.4 (1.6)	22.1 (3.0)	ns MWRS	72.8 (12.2)	135.4 (21.8)	$P < 0.01$ MWRS
Mean Biomass wet weight (g) L^{-1}	3.222 (0.210)	0.820 (0.113)	$P < 0.001$ MWRS	4.224 (0.384)	2.911 (0.584)	$P < 0.01$ MWRS
Mean Richness taxa L^{-1}	8.6 (0.5)	6.3 (0.5)	$P < 0.01$ *t* test	21.3 (1.4)	19.4 (1.2)	ns MWRS

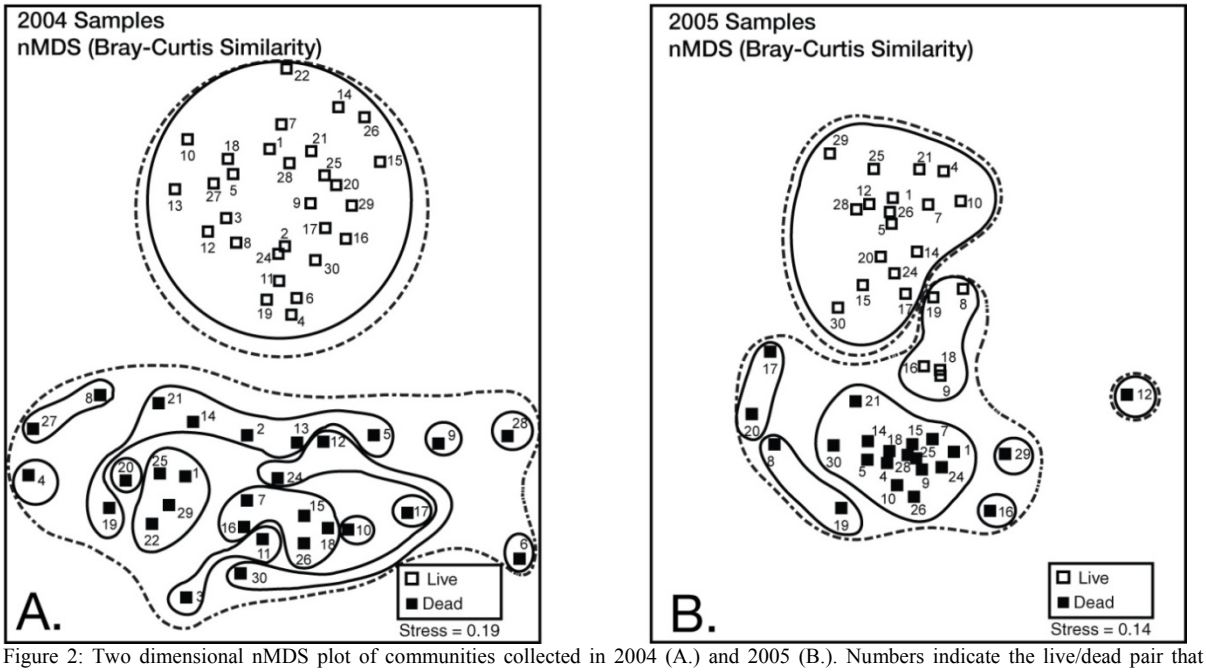

Figure 2: Two dimensional nMDS plot of communities collected in 2004 (A.) and 2005 (B.). Numbers indicate the live/dead pair that each community was associated with. Clusters superimposed at (A.) 22% (dashed line) and 43% similarity (solid line) (B.) 36% (dashed line) and 47% (solid line).

Biomass:

In 2004, 119.3 g of cryptofauna (wet weight) was removed from 30 live/dead pairs. In 2005, a total of 188.1 g of biomass was collected from 23 live/dead pairs. In both 2004 and 2005, the standardized biomass of the community associated with living coral was higher than that associated with dead coral ($P < 0.001$ and 0.01, respectively, Table 1).

Richness:

A total of 117 different taxa were identified (47 to species-level, 43 generic-level, 16 family-level, and 11 higher levels). There was a significantly greater number of taxa associated with living corals in 2004 ($p = 0.002$, *t*-test) but not in 2005 (Table 1).

Ordination:

The nMDS plot of samples collected in 2004 suggests that community composition was more similar between replicates for live coral associated coelobites than dead coral associates (Fig. 2A.). The same pattern was reflected in the ordination of samples collected in 2005. However, a group of five live-associated samples (9, 8, 16, 18, 19) were clustered more closely with dead-associated samples than other live (Fig. 2B.). Communities associated with dead coral in 2005 exhibited a large cluster of greater than 47% similarity which suggests a higher degree of similarity in the 2005 samples than in the 2004.

Discussion

The higher amount of biomass observed in communities associated with living coral colonies suggests a conferred advantage in the form of a greater availability of food and/or protection from predation. Food available to communities associated with a living coral could come from coral fat bodies (Stimson 1990), mucus (Coles and Strathman 1973), or from mucus-trapped plankton (Goldberg 2002). Protection for metazoan associates could be provided from the coral in the form of nematocysts. However, it should be noted that the stinging properties of the corals' nematocysts are ubiquitous and a degree of adaptation would be necessary for a given species to persist in their presence and benefit from their protection.

The qualification that live coral associates must be adapted to cope with the stinging behavior of coral nematocysts may help explain the high degree of similarity observed between live coral communities. Furthermore, several crustacean symbionts (e.g., *Trapezia ferruginea* and *Alpheus lottini*) have been found to be highly territorial and it is likely that they play a role in structuring the community associated with their coral host (Abele and Patton 1976).

The relatively low similarity between many dead coral communities can be explained by higher substrate heterogeneity compared with the live coral habitat. The availability of bare space immediately after coral mortality allowed colonization by a diverse assemblage of fleshy and calcareous algae, sponges, and cyanobacteria. A wider variety of food sources may have led to less specialized, more opportunistic species and consequently greater variability in community assemblages.

This study suggests that coral mortality may directly result in a reduction of cryptic biomass. It is likely that this will lead to a decrease in the biomass of higher trophic groups that directly (invertivore fishes and octopuses) and indirectly (piscivores fishes) utilize the cryptic community as an energy source. The collapse of both predator and prey populations after coral mortality could result in the cessation of important ecosystem functions and ultimately to ecosystem degradation.

It is possible that, given more time, algal growth may be able to support a higher amount of metazoan biomass on dead coral colonies. However, it is more likely that over these longer time scales bioerosion will result in a decrease in habitat complexity and subsequently near to complete cryptic community loss.

Because of the discrepancies in the two sampling years (differences in abundance and richness), it is important to use consistent methodologies to further evaluate seasonal variability and community succession. Furthermore, it is necessary to directly investigate the relationship between encrusting taxa that recruit to dead coral substrate and the motile communities that associate with them. As previously stated, it is likely that post mortality processes (substrate taphonomy, colonization by predator, prey, and territorial species) play in important role in the evolution of cryptic community structure.

Acknowledgement

Assistance with field collection was kindly provided by I Bethancourt, S Colley, P Fong, P Glynn, D Manzello, J Maté, T Smith, and A Simoes Correa. Identification of invertebrate specimens would not have been possible without the expertise of J Garcia-Gomez, P Glynn, A Graefe, L Harris, D Pawson, M Reaka-Kudla, and I Wehrtmann. V Brandtneris and A Costaregni provided valuable help with specimen processing. We would like to thank J Kool and B Riegl for their statistical advice as well as F Forrestal, P Glynn, D Manzello, and L Toth for their advice in writing this manuscript. This research would have not been possible without the support of the Smithsonian Tropical Research Institute, University of Miami Invertebrate Museum and funding from NSF (grant OCE-0526361 and earlier awards) to Peter W. Glynn.

References

Abele LG (1976) Comparative species richness in fluctuating and constant environments: coral-associated decapod crustaceans. Science 192:461-463

Abele LG, Patton WK (1976) The size of coral heads and the community biology of associated decapod crustaceans. J Biogeogr 3:35-47

Austin AD, Austin SA, Sale PF (1980) Community structure of the fauna associated with the coral *Pocillopora damicornis* (L) on the Great Barrier Reef. Aust J Mar Freshwat Res 31:163-174

Booth DJ, Barretta GA (2002) Changes in a fish assemblage after a coral bleaching event. Mar Ecol Prog Ser 245:205-212

Brock RE, Brock JH (1977) A method for quantitatively assessing the faunal community on coral rock. Limnol Oceanogr 22:948-951

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS ONE 2(8):e711. [doi:10.1371/journal.pone.0000711]

Coles S, Strathman R (1973) Observations on coral mucus flocs and their potential trophic significance. Limnol Oceanogr 18:673–678

D'Croz L, O'Dea A (2007) Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. Estuar Coast Shelf Sci 73:325-340

Gardner TA, Cote IM, Gill FA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958-960

Gischler E, Ginsburg RN (1996) Cavity dwellers (coelobites) under coral rubble in southern Belize barrier and atoll reefs. Bull Mar Sci 58:570-589

Glynn PW (1982) *Acanthaster* population regulation by a shrimp and a worm. Proc 4th Int Coral Reef Sym 2:607-612

Glynn PW (1983) Increased survivorship in corals harboring crustacean symbionts. Mar Biol Lett 4:105–11

Glynn PW (1984) Widespread coral mortality and the 1982-83 El Niño warming event. Environ Conserv 11:133-145

Glynn PW (1993) Coral bleaching: ecological perspectives. Coral Reefs 12:1-17

Glynn PW (2006) Fish utilization of simulated coral reef frameworks versus eroded rubble substrates off Panamá, eastern Pacific. Proc 10th Int Coral Reef Sym 1:250-256

Glynn PW (2008) Food web structure and dynamics of eastern tropical Pacific coral reefs: Panamá and Galápagos Islands. In: McClanahan TR, Branch GM (eds) Food webs and the dynamics of marine reefs. Oxford University Press, US, pp 185-208

Glynn PW, Maté JL, Baker AC, Calderón MO (2001) Coral bleaching and mortality in Panama and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982-1983 event. Bull Mar Sci 69:79-109

Goldberg WM (2002) Feeding behavior, epidermal structure and mucus cytochemistry of the scleractinian *Mycetophyllia reesi*, a coral without tentacles. Tissue Cell 34:232–245

Grassle JF (1973) Variety in coral reef communities. In: Jones OA, Edean R (eds) Biology and geology of coral reefs vol. 2, Academic Press, New York, pp 237-270

Hutchings PA (1974) A preliminary report on the density and distribution of invertebrates living in coral reefs. Proc 2nd Int Coral Reef Sym 1:285-296

Hutchings PA (1983). Cryptofaunal communities of coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, Australia, pp 200-208

Hutchings PA, Weate PD (1977) Distribution and abundance of cryptofauna from Lizard Island, Great Barrier Reef. Mar Res Ind 17:99-112

Klumpp DW, McKinnon AD, Mundy CN (1988) Motile cryptofauna of a coral reef: abundance, distribution and trophic potential. Mar Ecol Prog Ser 45:95–108

Lindahl U, Öhman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: effects on fish communities on a Tanzanian coral reef. Mar Poll Bull 42:127-131

Patton WK (1974) Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. In: Vernberg WB (ed) Symbiosis in the sea. University of South Carolina Press, Columbia, pp 219-243.

Reaka-Kudla ML (1997) The global biodiversity of coral reefs: a comparison with rainforests. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, DC, pp 83-108

Richter C, Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs – a new link in reef trophodynamics. Mar Ecol Prog Ser 188:105-116

Sano M, Shimizu M, Nose Y (1987) Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. Mar Ecol Prog Ser 37:191-199

Stimson J (1990) Stimulation of fat-body production in the polyps of the coral *Pocillopora damicornis* by the presence of mutualistic crabs of the genus *Trapezia*. Mar Bio 106:211-218