# Evaluating Artificial Means to Increase Acropora Coral Populations and Increase Associated Fish Communities in Jamaica

NORMAN J. QUINN<sup>1</sup> and BARBARA L. KOJIS<sup>2</sup> <sup>1</sup>Discovery Bay Marine Lab, University of the West Indies Discovery Bay, St. Ann, Jamaica <sup>2</sup>Division of Fish and Wildlife St. Thomas, US Virgin Islands 00802

# ABSTRACT

Shallow water Acropora species were nearly extirpated on Jamaican reefs in the late 1970's and early 1980's. They remain uncommon on Jamaican reefs today. With the loss of acroporids from hurricanes and disease and the reduction of grazers from disease and over fishing, macroalgae have proliferated on Jamaican reefs. Restoration of acroporids has been proposed to increase reef complexity and to assist fishers by increasing fish populations through the improvement of essential fish habitat on the reefs. Comparative fish counts on similar reefs with and without A. cervicornis populations demonstrate higher fish diversity and abundance, on reefs with A. cervicornis populations. Since June 2004, we have been involved with Jamaican fishers, hotel operators and environmental groups to increase the biomass of A. cervicornis and the complexity of reef habitat. With localized protection of these restored reefs we anticipate an increase in fish abundance which should result in greater fish catches for subsistence fishers. However, the potential for Acropora spp. to naturally recover should be examined before efforts to restore them are undertaken. Efforts to transplant or restore acroporids are very expensive and unnecessary if they have the natural capacity to recover. We have observed juvenile colony recruitment of A. palmata and A. prolifera on Jamaican reefs, but recruitment of A. cervicornis was rarely observed. While A. palmata and A. prolifera are showing signs of recovery, it appears that the long-term survival of A. cervicornis is threatened by lack of successful larval recruitment. This study assessed methods of restoring A. cervicornis populations in selected habitats. Experimental transplants using several techniques were attempted to develop a suitable technology for restoring A. cervicor*nis* populations. In one technique the mean survivorship after 55 weeks was > 60% with a high growth rate.

KEY WORDS: Coral restoration, fisheries, tourism

# Evaluando Medios Artificiales Para Aumentar Las Poblaciones de Corales *Acropora* Poblacions y Aumentar Las Commundades de Peces Asociados a Estas Poblacions en Jamaica

A finales de 1970 y principios de 1980, las especies del género Acropora localizadas en las aguas llanas de arrecifes en Jamaica se encontraron al borde de extinción, y hasta el día de hoy es poco común encontrar esta especie en arrecifes de Jamaica. Con la perdida de los corales Acropora sp. a causa de huracanes y enfermedades, y la reducción de hervíboros a causa de enfermedades y sobre- pesca se han proliferado las macro algas en los arrecifes de Jamaica. Se ha propuesto la restauración de los corales Acropora sp. para aumentar el complejo de los arrecifes y a la vez beneficiar a los pescadores aumentando las poblaciones de peces a traves del mejoramiento del hábitat esencial para peces en los arrecifes. Los contajes comparables de peces en arrecifes similares con y sin poblaciones de A. cervicornis demuestran una mayor diversidad de peces y abundancia de arrecifes con poblaciones de A. cervicornis. Los arrecifes que contienen una mayor biomasa de A. cervicornis tienen poblaciones de peces más altas. Desde junio de 2004, hemos unido esfuerzos con pescadores de Jamaica, operadores de hoteles y grupos ambientalistas con el propósito de aumentar la biomasa de A. cervicornis y el complejo de habitat de arrecifes. Anticipamos que la protección de estos arrecifes restaurados tendría como resultado un aumento en la abundancia de peces y mayores capturas para los pescadores. Sin embargo, se debe estudiar el potencial de una recuperación natural de Acropora sp. antes de llevar a cabo esfuerzos para su restauración. Los esfuerzos de transplante y restauración de especies de Acropora sp. son muy costosos y no serían necesarios si éstos tuvieran una capacidad de restauración natural. Hemos observado el reclutamiento de colonias de juveniles de A. palmata y de A. prolifera en arrecifes de Jamaica, pero no de A. cervicornis. Mientras que las poblaciones de A. palmata y de A. prolifera están comenzando a recuperarse, aparentemente la supervivencia a largo plazo de A. cervicornis está siendo amenazada por el poco éxito en el reclutamiento de larvas. En este estudio se avaluan métodos de restauración de poblaciones de A. cervicornis en hábitats seleccionados. Se llevaron a cabo transplantes experimentales utilizando varias técnicas con el propósito de desarrollar la tecnología apropiada para la restauración de poblaciones de A. cervicornis. En una de las técnicas utilizadas la sobrevivencia fue de >60% con un alto radio de crecimiento.

PALABRAS CLAVES: Caribe, restauración de corales, turismo, pesquerías

## INTRODUCTION

Acropora cervicornis was one of the most important reef-building corals on Jamaican reefs three decades ago (Goreau and Wells 1967). However, this species has declined throughout the region, becoming locally extinct on many reefs (Knowlton *et al.* 1990). The Caribbean wide decline of Acropora corals in recent decades has serious consequences, affecting coral reef biodiversity, coastal geology, and the fisheries and tourism economies of the region. The seriousness of the decline is reflected in the recent proposed listing of *A. cervicornis* and *A. palmata* as threatened in the United States (50 CFR Parts 223 and 224). This is a first for reef-building scleractinian corals globally.

Several decades ago, the Acropora cervicornis population at the West Fore reef at Discovery Bay was reduced to a mere 4% of its original cover by Hurricane Allen (Woodley *et al.* 1981). Eight years later when Hurricane Gilbert struck, the few recovering stands of Acropora that had survived Allen were smashed again (Woodley 1981). Subsequent incidents of predation and disease reduced the population to < 1% of its original level (Knowlton *et al.* 1981).

Habitat complexity, defined by various measures of benthic community structure, complexity and reef rugosity, is a predictor of reef fish assemblage structure (Sale 2002). The loss of acroporid communities in the Caribbean has resulted in loss of important fish habitat and changes in fish assemblages (Shulman and Ogden 1987). In the Indian Ocean, transplanted corals have been shown to enhance fish abundance and diversity (Lindal 2003).

Even on reefs where measures to address the root causes of coral decline have been implemented, *A. cervicornis* populations do not appear to be recovering. The causes are many, but one of the most important may be lack of larval recruitment (Quinn and Kojis 2005a, 2005b, In press). There are a number of possible reasons for the lack of larval-based recovery. Among them is that most of the surviving *A. cervicornis* populations are too small to successfully produce sufficient planula to re-colonize reefs (Kojis and Quinn 1985, 1993, 2001, Quinn and Kojis 1999).

Given the lack of observed recovery of *A. cervicornis*, we sought to conduct experiments to determine which coral restoration techniques would be most effective in enhancing the recovery of this species. We also compared fish species diversity and abundance on reefs with a high percent cover of *A. cervicornis* and reefs with no *A. cervicornis*. It was hypothesized that reefs with a high percent cover of *A. cervicornis* would have a greater abundance of larger edible fish species.

# METHODS

# **Coral Restoration**

A large, healthy *Acropora cervicornis* population at Dairy Bull Reef (18°28.24 N; 77°24.08 W) at 9 m was used as a source population for the restoration experiments. On June 2, 2004, 160 fragments 5 - 14 cm in length were collected and transported in shaded buckets filled with sea water to the experimental sites. The transportation process took < 4 hours.

A - Frame Experiment — Five Acropora cervicornis fragments were attached using cable ties to each outer side of 14 wire mesh "A-frames" (0.8 m x 1.2 m bent at 90°) (Figure 1). A total of ten A. cervicornis fragments were attached to each frame. The frames were tagged for identification and weighted with dive weights or cement blocks to increase stability.



**Figure 1.** Coral fragments on cement disks on wire mesh (left) and on A-frames (right) in transit to experiment site.

The frames were deployed within Discovery Bay at Columbus Park Reef ( $18^{\circ}46.448 \text{ N}$ ;  $77^{\circ}41.428 \text{ W}$ ) - depth 6 m; East Back Reef ( $18^{\circ}46.856 \text{ N}$ ;  $77^{\circ}40.454 \text{ W}$ ) - depth 4 m; the Blue Hole ( $18^{\circ}47.252 \text{ N}$ ;  $77^{\circ}41.662 \text{ W}$ ) - depth 2 m, Back Reef Canoe Channel ( $18^{\circ}28.305 \text{ N}$ ;  $77^{\circ}24.950 \text{ W}$ ) - depth 2 m; and outside the bay at West Fore Reef ( $18^{\circ}47.252 \text{ N}$ ;  $77^{\circ}41.662 \text{ W}$ ) - depth 6 m.

Water quality and wave exposure varied among sites. At Columbus Park Reef, the water was turbid with a visibility frequently < 10 m. *A. cervicornis* had dominated Columbus Park Reef for at least 6,000 years b.p., until its demise a couple decades ago (Wapnick *et al.* 2004). The East Back Reef site was an area with clear water but was subjected to breaking waves. The frames at Blue Hole were located in a back reef, lagoon environment with slightly turbid water. The Canoe Channel site was just behind the reef crest at the West Fore Reef in clear ocean water often was subjected to wave action. Black plastic netting shade cloth was suspended over the frames for three months at the shallow, clear Canoe Channel site to reduce sun intensity.

Fragments attached to the A-frames were monitored for survivorship and growth. Percent survivorship was calculated by dividing the total number of live fragments by the total number of original fragments. A fragment was considered live if some living tissue remained. Missing fragments were counted as dead. Growth was measured from the fragment base to the apical polyp of the dominate branch and then from the branching point to the apical polyp of each sub-branch. The lengths were added together and actual linear growth in length and percentage growth calculated.

Cement Base Experiment — A 50/50 cement/sand mixture was pressed and dried into a 5 cm circular disk. A nylon monofilament line was placed through the disks to secure the small (5 - 7 cm) coral fragments. The 211 disks were secured to a wire mesh sheet at the Canoe Channel (Figure 1) and were monitored for survivorship and growth.

Line Experiment — In June 2004, sixteen A. cervicornis fragments were collected and within  $\sim 4$  hours the fragments were attached to monofilament nylon lines 1.5 m above the substrate strung between iron rebars at the Canoe Channel. In September 2004, the experiment was repeated with 40 fragments. This time the fragments were deployed within 30 minutes of collection. The fragments were monitored for growth and survivorship.

# **Fish Census**

The abundance and standard length (SL) of seven families of edible fishes (Groupers - F. Serranidae, Grunts - F. Haemulidae, Parrot fish - F. Scaridae, Snappers - F. Lutjanidae, Squirrelfish - F. Holocentridae, Surgeon fish -F. Acanthuridae, and Triggerfish - F. Balistidae) were surveyed on reefs with Acropora cervicornis % cover >40% and reefs depauperate of A. cervicornis (~ 0% coral cover). The stationary point-count method was used, in which fish families were identified and individuals larger than 10cm were counted for 10 minutes within 10 m diameter cylinders (Polunin and Roberts 2004). Standard lengths of fish within each family were estimated and recorded to the nearest two cm. Ten observations were made at on reefs with > 40% A. cervicornis cover and on reefs with  $\sim 0\%$  cover. A. cervicornis has a patchy distribution. Sites having reefs with high percentage cover of A. cervicornis and also reefs devoid of A. cervicornis were found at Dairy Bull (A. cervicornis coral cover ~ 900  $m^2$ ) and East Rio Bueno (A. cervicornis coral cover ~ 1700  $m^2$ ).

# RESULTS

#### **Coral Restoration**

*A-frame Experiment* — Corals were deployed on A-frames for 55 weeks at four sites. Columbus Park Reef had the highest survivorship - 78%. The lowest survivorship was at the two most exposed sites East Back Reef (7%) and the Canoe Channel (4%). Survivorship at Blue Holes was 32%. Although Hurricane Ivan passed south of Jamaica in September 2004, very large waves crashed over the reef crest and severely damaged the experiment at Canoe Channel. The growth rate of corals on the frames was measured 55 weeks after deployment. The mean linear growth rate was 7.3 cm (S.E. 7.0 cm; n = 63), ranging from a mean of 1.1 cm (S.E. 0.6 cm; n = 16) at Canoe Channel to 15.3 cm (S.E. 4.6 cm; n = 40) at Columbus Park. The mean growth rate was 0.19 cm/week - annualized mean growth rate of 9.7 cm/year.

*Cement Disk Experiment* — During the first months the survival and growth of the colonies on the cement disks was very good. Based on the first eight weeks of growth, the annualized growth rate was 23 cm/year. Colonies quickly grew and established multiple branches with apical polyps. However, after 37 weeks survivorship was only 19%, and only 40 of the original 211 fragments were still alive. Many of the corals were killed or severely damaged by wave action from Hurricane Ivan. After one year (June 2005) few complete colonies were alive. Several colonies had live areas, but no apical polyps.

Line Experiment — Two days after deployment in June 2004, most coral fragments in this experiment bleached. All of the fragments were bleaching after five days and algal growth on the branch skeletons was visibile. None of the colonies recovered. A second deployment of fragments on lines occurred in September 2004. Five days later none of the corals exhibited any bleaching despite water temperatures being at their annual maximum (Quinn and Kojis 2003a). After 26 weeks, fragments from the second attempt had a 32% survival rate. The difference in survivorship between June and September is attributed to the shorter length of time that colonies were held in containers prior to deployment in September compared with June. In June 2005, the remaining colonies were doing extremely well with an annualized percentage growth rate exceeding 400%. Colonies were vigorously growing from both ends and have numerous branches with no sign of Hermodice carunculata predation or Stegastes bites.

90

80

70

#### **Fish Census**

Five of the seven familes of fish (groupers (F. Serranidae), grunts (F. Haemulidae), snappers (F. Lutjanidae), squirrelfish (F Holocentridae) and surgeon fish (F. Acanthuridae)) had a greater abundance on the Acropora reefs (AR) than on the non Acropora reef (NAR). (Figure 2). The mean number of edible fish observed on the Acropora reefs (AR) varied from 3.3 fish per observation period for triggerfish (F. Balistidae) to 73.2 fish per observation period for grunts. Parrot fish - F. Scaridae were significantly more abundant on NAR (*t*-test, p < 0.05; n = 20). Groupers were not significantly (*t*-test, p > 0.05; n = 20) more abundant on NAR by 1.9 fish per obserservation. Parrot fish were more abundant on NAR, but the difference was not significant. Surgeon fish were not significantly more abundant on AR (*t*-test, p < 0.05; n =20). There was no significant difference observed (t-test, p > 0.05; n = 20) in the standard lengths of fish between AR and NAR (Figure 3).

# DISCUSSION

The results suggest that the success of restoration is very site specific. Local variations in abiotic conditions like wave exposure, salinity, depth, and turbidity influence survival and growth rates. As well, biotic influences such as abundance of fire worms and damselfish can influrence growth and survival. Frames on sand did considerably better than frames on rock or rubble. Frames on sand were away from lurking places of predatory Coraliophila snails and Hermodice fire worms, as well as Stegastes damselfish (Family Pomacentridae) territories. Weighing the frames down with cement blocks at some sites resulted in the inadvertent creation of ideal Stegastes habitat, with subsequent negative impacts to the corals. The size of the wire mesh also affected growth and survival. Small mesh frames provided ideal shelter for damselfish and permitted more surface area for the farming algae. In January and March 2005, new wire frames with larger apertures (20 x 20 cm) were placed on sand at least 1 m from a reef. The size of the mesh reduced algal farming by Stegastes and the distance from the reef inhibited predation while still being close enough to the reef for herbivorous fish to visit the frames regularly for cleaning.

## **Management Implications**

Arguments Acropora cervicornis restoration to reefs that are expirated are compelling for many reasons. A. cervicornis is a keystone species of critical importance to biodiversity, fisheries, and tourism interests. It is particularly vital as fisheries habitat due to it being the only large open-branched coral species of reef slope, back reef, and lagoonal environments. Its loss represents a loss to the biodiversity and essential fish habitat of Caribbean reefs.



**Figure 2.** Mean number of edible fishes from selected families on acroporid reefs vs non acroporid reefs.



**Figure 3.** Standard length of edible fish from selected families on acroporid vs non acroporid reefs.

#### ■ Acroporid Reefs □ Non Acroporid Reefs

The *Acropora* reefs had a greater abundance of schooling species. Parrot fish were slightly more common on NAR possibly because their food was more abundant there. Another possibility is that they are avoiding space occupied by other species. There were slight differences between standard lengths between the two reef types, but the difference was not significant. Considering the intense fishing pressure in the area and the relatively small area of healthy reef, it is probable that fishing pressure is too high too observe any statistically significant difference.

A. cervicornis is not returning to reefs where it was formerly common (Wapnick *et al.* 2004), as sexual recruitment of *Acropora* is rare or absent in the Caribbean (Sammarco 1985; Quinn and Kojis 2005a). Given the low levels of sexual recruitment of *A. cervicornis*, its long-term survival is threatened and a proactive approach may be needed to restore healthy populations. *A. cervicornis* provides habitat for many edible fish, serving as a vital nighttime resting place and providing shelter from predation during the day. Reefs with with higher percentage *Acropora* cover have more edible fish.

However, restoring healthy, breeding populations of staghorn coral inexpensively, even in limited areas, is not likely to succeed until the factors that caused the population collapse are better understood and mitigated. Current observations suggest that the long-term survival of A. cervicornis is threatened unless root causes of decline are more effectively addressed throughout the region, and successful sexual reproduction occurs. There are many factors that are considered to have influenced the rapid reduction in populations. Runoff from land contributes to algal overgrowth by increasing nutrients in the water column and contributes to outbreaks of coral disease (Bruckner et al. 1997). Increased sediment is known to reduce coral fecundity (Kojis and Quinn 1984) and may diminish the success of settlement of coral larvae (Quinn and Kojis 2005a). In the Caribbean, chronic over fishing is an ever increasing threat to coral reefs (Hughes 1994). Overfishing combined with the decline in the grazing sea urchin, Diadema antillarum (McClanahan 1994), has resulted in algal overgrowth (Szmant 1997) and reduced space for new coral to settle (Jackson 1997). The decline has also been linked to the lack of predators, especially fish predators, resulting in increases in corallivorous gastropods (McClanahan 1997) and in Acropora harming Stegastes fish (Lewis 1986).

Due to the high costs of restoration, we need innovative, efficient techniques to guide us in restoring damaged habitats. We are working to determine what techniques work best to restore *Acropora cervicornis* on select reefs sites. Restoration may not be necessary in some situations if the populations can naturally recover (Kojis and Quinn 1981) as they do on some Pacific Reefs (Quinn and Kojis 1999, 2003b).

The experimental strategy is to increase habitat and coral diversity by successfully transplantating A. cervicornis branches from populations where it is abundant to habitats where it once thrived but is no longer found. Surviving A. cervicornis populations may be resistant white band disease and tolerant of higher sea water temperatures, some of the causes of the decline of this species. The population would still be prone to predation and hurricane damage and vulnerable to declines in water quality. With the implementation of measures to address the root causes of coral reef decline, including the establishment of no-take marine reserves in several Caribbean countries, transplanted patches of A. cervicornis may survive and flourish. Once the fish, crustaceans, echinoderms and other species that positively influence coral health become more abundant, coral populations could improve without further assistance.

## ACKNOWLEDGEMENTS

We are grateful for the financial assistance provided by USAID through the CWIP2 program and for the use of the facilities of the Discovery Bay Marine Laboratory, University of the West Indies. Additional financial support was provided by Counterpart International, Tropical Discoveries Fund, and the National Institutes of Health through the University of Mississippi under the terms of agreement No. R21 TW006645 funded by the Fogarty International Center and the National Institute for Research Resources for the International Cooperative Biodiversity Groups. The opinions expressed herein are those of the authors and do not necessarily reflect the views of the National Institutes of Health or the University of Mississippi. A Bowden-Kerby and M Stennett deserve particular recognition for their assistance in the initial phase of the coral restoration experiment. This is DBML publication #722.

# LITERATURE CITED

- Bruckner, A.W., R.J. Bruckner, and E.H. Williams Jr. 1997. Spread of black-band disease epizootic through the coral reef system in St. Ann's Bay, Jamaica. *Bulletin of Marine Science* **61**:919-928.
- Goreau, T.F. and J.W. Wells. 1967. The shallow-water Scleractinia of Jamaica: revised list of species and their vertical distribution range. *Bulletin of Marine Science* **17**:442-453.
- Hughes, T.P. 1994. Catastrophes, phase shifts and largescale degradation of a Caribbean coral reef. *Science* **265**:1547-1551.
- Jackson, J.B.C. 1997. Reefs since Columbus. *Proceedings* of the 8<sup>th</sup> International Coral Reef Congress. 97-106 pp.

- Kojis, B.L. and N.J. Quinn. 1981. Factors to consider in transporting coral to accelerate regeneration of damaged coral reefs. Pages 183-1871in: *Proceedings* of the Environmental Engineering Conference, 1981.
  8-10 July, Townsville, Queensland Institute of Engineers Publication 8/81.
- Kojis, B.L. and N.J. Quinn. 1984. Seasonal and depth variation in fecundity of *Acropora palifera* at two reefs in Papua New Guinea. *Coral Reefs* 3:165-172.
- Kojis, B.L. and N.J. Quinn. 1985. Puberty in Goniastrea favulus: age or size limited? Proceedings of the δ<sup>th</sup> International Coral Reef Symposium 4:289-293.
- Kojis, B.L. and N.J. Quinn. 1993. Biological limits to Caribbean reef recovery. Pages 35-41 in: A comparison with western South Pacific reefs. Global Aspects of Coral Reefs, Health, Hazards, and History. Miami, Florida USA.
- Kojis, B.L. and N.J. Quinn. 2001. The importance of regional differences in hard coral recruitment rates for determining the need for coral restoration. *Bulletin of Marine Science* 69(2):967-974.
- Knowlton, N., J.C. Lang, M.C. Rooney, and P. Clifford. 1981. Evidence for delayed mortality in hurricane damaged Jamaican staghorn corals. *Nature* 294:251-252.
- Knowlton, N., J.C. Lang, and B.D. Keller. 1990. Case study of natural population collapse: Post hurricane predation of Jamaican staghorn corals. *Smithson. Contributions in Marine Science* **31**:1-25.
- Lewis, S.M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* **56**:183-200.
- Lindahl, U. 2003. Coral reef rehabilitation through transplantation of staghorn corals: effects of artificial stabilization and mechanical damages. *Coral Reefs* **22**:217-223.
- McClanahan, T.R. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity and sea urchins. *Coral Reefs* **13**:231-241.
- McClanahan, T.R. 1997. Dynamics of *Drupella cornus* populations on Kenyan coral reefs. *Proceedings of the* 8<sup>th</sup> International Coral Reef Symposium 1:633-638.
- Polunin, N.V.C. and C.M. Roberts. 2004. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* **100**:167-176
- Quinn, N.J. and B.L. Kojis. 1999. Case studies of natural variability in coral recruitment from the Caribbean and Pacific. Which reefs need restoration assistance? Page 159. in: Proceedings of the International Conference on Scientific Aspects of Coral Reef Assessment, Monitoring and Restoration, Ft. Lauderdale, Florida USA.

- Quinn, N.J. and B.L. Kojis. 2003a. Variation in subsurface seawater temperature off Discovery Bay, Jamaica and the U.S. Virgin Islands. *Revista de Biologia Tropical* 51(4):181-187.
- Quinn, N.J. and B.L. Kojis. 2003b. The dynamics of coral reef community structure and recruitment patterns around Rota, Saipan, and Tinian, Western Pacific. *Bulletin of Marine Science* **53**:646-661.
- Quinn N.J. and B.L. Kojis. 2005a. Patterns of sexual recruitment of acroporid coral populations on the West Fore Reef at Discovery Bay, Jamaica. *Revista de Biologia Tropical* 53(1):83-90.
- Quinn, N.J. and B.L. Kojis. [2005b]. Natural variability in the recovery of reef ecosystems. In: W.F. Precht (ed.). *Coral Restoration*. CRC Publications, Boca Raton, Florida USA. In press.
- Quinn, N.J. and B.L Kojis. [In press]. Evaluating the potential of natural reproduction and artificial means to increase Acropora cervicornis (Lamark, 1816) populations. Revista de Biologia Tropical.
- Sale, P. 2002. The science needed for effective management. Pages 359-376 in: P. Sale (ed.). Coral Reef Fishes: Dymanics and Diversity in a Complex Ecosystyem. Academic Press, San Diego, California USA.
- Sammarco, P.W. 1985. The Great Barrier Reef vs. the Caribbean: comparisons of grazers, coral recruitment patterns and reef recovery. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4:391-397.
- Shulman, M.J. and J.C. Ogden. 1987. What controls reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon fla*volineatum. Marine Ecology Progress Series **39**:233-242.
- Szmant, A.M. 1997. Nutrient effects on coral reefs: A hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2:1527-1532.
- Wapnick, C., W.F. Precht, and R.B. Aronson. 2004. Millennial-scale dynamics of staghorn coral in Discovery Bay, Jamaica. *Ecology Letters* 7:3564-361.
- Woodley, J.D., E.A. Chornesky, P.A. Clifford, J.B.C. Pearson, J.W. Porter, M.C. Rooney, K.W. Rylaarsdam, V.J. Tunnicliffe, C.M. Wahle, J.L. Wulff, A.S.C. Curtis, M.D. Dallmeyer, B.P. Jupp, M.A.R. Koehle, J. Niegel, and E.M. Sides. 1981. Hurricane Allen's Impact on Jamaican Coral Reefs. *Science* 241 (4522):749-755.
- Woodley, J.D. 1981. The effects of Hurricane Gilbert on Coral reefs At Discovery Bay. Appendix 9 in: UNEP Regional Seas Reports and Studies, No. 110.