

**Tools to assess recovery status and convergence rates between restored and
undisturbed coral reef habitats**

RICHARD:

FYI, SUBMITTED
TO RESTORATION ECOLOGY

Diego Lirman ¹

Margaret W. Miller ²

REGARDS



1. Corresponding Author

Rosenstiel School of Marine and Atmospheric Science

University of Miami

4600 Rickenbacker Cswy.

Miami, FL 33149

Tel: 305-361-4168 Fax: 305-361-4600

Email: dlirman@rsmas.miami.edu

2.

NOAA-Fisheries, SEFSC

75 Virginia Beach Dr.

Miami, FL 33149

Email: margaret.w.miller@noaa.gov

Abstract

Boating activities are an increasing source of physical damage to coral reefs worldwide. The damage caused by ship groundings can be significant and may result in a shift in reef structure and function. In this study, we evaluate the status of two restoration projects established in 1995, six years after two freighters, the M/V Maitland and the M/V Elpis, run aground on reefs of the Florida Keys National Marine Sanctuary. Our approach includes field monitoring in support of simulation model development to assess the effectiveness of the restoration efforts. A population model was developed for the coral *Porites astreoides* to predict the convergence rates of coral abundance and population size structure between the restored and surrounding reference habitats.

The coral communities on the restoration structures are rapidly approaching the structure of reference habitats. Species richness and abundance of the dominant coral, *Porites astreoides*, were nearly indistinguishable between the restoration structures and reference habitats after only six years. However, while abundance and size structure of *P. astreoides* populations are rapidly approaching those of the reference habitats (a convergence in size structure within 10 years was predicted), maximum coral size will take twice as long to converge for this species. The sensitivity of the model to maximum recruitment rates highlights the importance of recruitment on the recovery rates of restored habitats, suggesting that special attention should be afforded to provide coral recruits with appropriate recruitment substrate at the time of restoration.

Lastly, the rates of convergence and, hence, the level of success of a restoration effort, were shown to be determined not only by the recruitment and survivorship rates of corals on the restoration structures, but by the characteristics of the reference population as well. Accordingly, reference populations ought to be considered as a "moving target" against which restoration success has to be measured dynamically. The simple, cost-effective monitoring-modeling approach presented here can provide the necessary tools to assess the current status of a restoration effort as well as to predict the time required for coral populations to resemble those found on undamaged reference habitats.

Keywords: Coral restoration, population modeling, monitoring, assessment, convergence rates, *Porites astreoides*

Introduction

Coral reefs worldwide have experienced a drastic decline over the recent past, and a recent study estimated that 58% of the world's reefs are presently threatened by human activities like coastal development, overexploitation, eutrophication, pollution, physical damage, and sedimentation (Bryant et al. 1998). These anthropogenic threats are combined with increasing pressure from natural stressors, such as increased temperature and storm events, and have prompted a myriad of global and local efforts to preserve and restore damaged coral reef communities. The Florida Reef Tract is the only tropical coral reef system on the continental shelf of North America and the biological diversity of Florida reefs makes this ecosystem ecologically, economically, aesthetically, and biogeographically unique. In an effort to protect these unique resources, the Florida Keys National Marine Sanctuary (FKNMS) was established in 1990. Although concern about general decline in reef health along the Florida Reef Tract was the main reason behind the establishment of the FKNMS, the unprecedented succession of three ship groundings over an 18-day period in the fall of 1989 prompted the US Congress to designate the 9500 km² area for special protection and management (FKNMS Draft management Plan 1995).

Boating and harvesting activities have been an increasing source of physical damage to reefs that are exploited extensively by recreational and commercial industries, especially near major population centers (Tilmant & Schmahl 1981; Hudson & Diaz 1988; Gittings et al.

1988; Lutz 1998). Physical damage caused by ship groundings to reefs can be significant and, in the absence of active restoration efforts, may ultimately result in a complete shift in reef structure and function (Precht 1998). The practice of coral reef restoration by the US government often involves expensive construction projects to repair reef framework damaged by acute impacts such as ship groundings (see <http://www.darp.noaa.gov/seregio/elpis.htm> for one example). The stated goals of such projects are often described as providing structural stability to reduce future incidental damage from loose material, and to increase the structural complexity of the site to enhance the recovery of benthic and fish assemblages. In addition, artificial reef structures are often used as a tool to mitigate marine resource damage with the goal of compensating for lost function and productivity, and accelerating the rehabilitation process (Pickering et al. 1998; Yap 2000; Baine 2001). Despite the abundant resources spent on such projects, rigorous quantitative evaluation of either their ecological goals or economic cost-effectiveness have rarely been undertaken (Seaman 2000). Notable exceptions include evaluative work by Edwards and Clark (1998) and Clark and Edwards (1999) on cost-benefit of structural restoration options in mined reefs of the Maldives and on coral transplantation.

The lack of clear scientific goals, a need for hypothesis-driven monitoring efforts, and a general lack of tools to assess restoration success have historically hindered progress in the reef restoration field (e.g., Precht 1998; Milon & Dodge 2001; Precht et al. 2001). In this study, we address some of these concerns by implementing an approach that uses field

monitoring in support of simulation model development. While repeated monitoring can provide instantaneous status reports on both the recovering and the undisturbed coral communities, predictions made by simulation models can project observed trends beyond the few years commonly afforded to monitoring studies. This modeling effort, when supplemented by more classical measurements of coral community condition (e.g., coral diversity, density, size structure) provides a set of endpoints that can be used to assess the effectiveness of the restoration efforts, as well as estimate convergence rates towards the undisturbed reef community structure and function.

The capability to predict the recovery rates of a damaged natural resource is important for comprehensive damage assessment and the collection of damage penalties from responsible parties. Effective tools for predicting recovery of selected coastal communities, such as seagrass beds damaged by boating activities, have been recently developed (Fonseca et al. 2000). However, similar tools are not available yet for damaged coral reefs, highlighting the need for quantitative methods that can be developed with reasonable levels of field effort to improve our current practice of reef restoration. Some of the characteristics of corals that make the translation of existing recovery models difficult include: 1) corals, especially reef-building species that reach large colony size, grow very slow (generally $< 1 \text{ cm yr}^{-1}$), 2) recruitment of corals onto newly created substrate is highly unpredictable and variable in time and space (Kojis & Quinn 2001; Tougas & Porter 2001) and, 3) the clonal characteristics of corals require that unique life history attributes like partial mortality and

fragmentation be quantified (e.g., Hughes 1984; Fong & Glynn 1998; Lirman 2002). In this study we develop a transition-matrix population model for the coral *Porites astreoides* that accounts for these characteristics and predicts the convergence rates of coral population abundance and size structure between the restored and surrounding habitats.

Methods

Coral Surveys

Coral populations at the Maitland (25° 11.983' N, 80° 13.567' W, depth = 2.5 m) and Elpis (25° 8.917' N, 80° 15.150' W, 9-11 m) reef restoration sites were surveyed in August 1998 and 2001 (Figure 1). These sites, previously described in detail by Miller & Barimo (2001), differ in the design and materials used in structural restoration. The dates of the vessel groundings were 25 October 1989 for the M/V Alec Owen Maitland, and 11 November 1989 for the M/V Elpis. The restoration structures were deployed during the summer of 1995 at both locations. While joined concrete armor units were used at the Maitland, limerock boulders were used at the Elpis site (Figure 1). Nearly continuous, low topography habitat is provided by the concrete slabs at the Maitland site, while discrete, high-topography habitats are provided by the boulders placed at the Elpis site.

The boulders at the Elpis site and the concrete armor units at the Maitland site were surveyed for colonies of *Porites astreoides*. This species was chosen for its numerical dominance both within the restoration structures and the surrounding reference habitats at both locations (Miller & Barimo 2001). Coral populations on the undamaged, reference habitats surrounding the restoration structures were surveyed using haphazardly located belt transects (10 x 1 m). At the Elpis site, the reference area was surveyed at a minimum distance of 25 m from the restored area, while at the Maitland site, the reference habitat was surveyed adjacent to the structure (0-10 m from the base of the concrete slabs) and at a minimum distance of 25 m from the structure.

During each survey, all of the *Porites astreoides* colonies found were identified and maximum diameter was measured for each colony to the nearest mm. In addition, the location of colonies was mapped within each boulder surveyed at the Elpis site. Repeated sampling of these boulders provided growth, mortality, and recruitment rates used to parameterize the models developed in this study. Colonies identified for the first time in 1998 and 2001 were assumed to have recruited since the establishment of the restoration structures and between surveys respectively. A list of all hard coral species observed was compiled for each site.

Coral Population Model

A size-structured transition matrix model for *Porites astreoides* was developed following methods outlined by Hughes (1984), Done (1987), Fong & Glynn (1998), and Hughes and Tanner (2000). This model was developed to predict the relative abundance of each size class at time $t + 1$ from the population structure at time t and calculated size-based transitions. The general form of this model is:

$$\mathbf{x}_{(t+1)} = \mathbf{A} \mathbf{x}_{(t)} + \mathbf{r},$$

where $\mathbf{x}$ is a column vector with the population size structure at time t and $\mathbf{A}$ is a matrix of transition probabilities calculated from field observations. Due to the lack of an existing coral population on the newly established restoration structures, recruitment was added each year through a recruitment vector ($\mathbf{r}$). This approach was previously used by Hughes and Tanner (2000) to simulate the dynamics of open coral populations where fecundities are not included in the transition matrix. During each time step ($t = \text{one year}$), colonies can remain within the same category, die, or move into another category through growth, fragmentation, fusion, and fission. The population growth rate (given by the dominant eigenvalue), stable size distribution (provided by the right eigenvector), and the relative contribution of each transition probability to the dominant eigenvalue (estimated through elasticity analysis) were determined following the methods described by Caswell (2001).

The *P. astreoides* populations surveyed were divided into five size classes encompassing the range of colony sizes encountered on the restoration structures: I) 0-10 mm in diameter, II) 11-20 mm, III) 21-30 mm, IV) 31-40 mm, and V) > 41 mm. To simulate the variable nature of coral recruitment, recruitment into the model was simulated stochastically by sampling at random from a uniform distribution ranging from 0 to 0.35 recruits m⁻² following the methods outlined by Fong & Glynn (1998). The output from the model is reported as the average of 25 runs, the variability being created solely by the recruitment function.

Simulation Scenarios

Convergence Rates

The simulation model was used to evaluate the convergence rates of coral population structure and abundance between the restoration blocks and reference habitats. The structure of the reference population was allowed to fluctuate according to our model, thus providing a “moving target” that was compared to the population developing on the restoration structure. Initial conditions were bare substrate (no corals) for the population growing on the restoration boulders, and the abundance and size-frequency distribution documented in 2001 for the reference population. Output from the model runs (mean values for 25 runs) representing the population size structure in restoration and reference habitats were compared each year using goodness-of-fit G-tests, with the proportions of the size categories from the

reference habitat used as expected frequencies (Sokal & Rohlf 1981). Mean abundance of the reference population and the restoration structure were compared each year with a t test.

Recruitment Limitation

To evaluate the role of recruitment onto the restoration structures on the projected dynamics of the *P. astreoides* populations, recruitment rates were modified by adjusting the maximum value of the recruitment function to 0.15, 0.30 and 0.45 recruits m^{-2} . Although maximum rates were increased, recruitment into the model was still simulated stochastically by sampling at random from a uniform distribution ranging from 0 to the maximum level set for each scenario. In these scenarios, recruitment rates were modified only for the populations growing on the restoration structure. To simulate recruitment failure, recruitment was eliminated completely after the population reached stable size distribution.

Results

Coral Surveys

A total of 17 coral taxa (species or genera for those groups not identifiable to species) were observed at the Elpis site compared to only 10 species at the Maitland. Species richness at the restoration structures and the reference habitats converged rapidly at both sites (Table

1). By 2001, only six years after the placement of the restoration structures, 70 % of the taxa were found at both the natural and man-made habitats at the Elpis, while the overlap was even larger at the Maitland (80% of taxa shared).

Within six years of deployment, the restoration units at the Elpis and Maitland sites exhibited abundant populations of *Porites astreoides* (Figure 2). Mean density (± 1 SEM) of *P. astreoides* was unchanged between 1998 (1.4 colonies m^{-2} (0.5)) and 2001 (1.4 (0.2)) at the Elpis site ($n = 16$ boulders), while mean density more than doubled at the Maitland site from 2.1 (0.3) in 1998 to 4.5 (0.4) in 2001 ($n = 12$ units). The mean density of *P. astreoides* colonies was not significantly different between the restoration structure and the reference habitats at either site in 2001 (Mann Whitney U test, $p > 0.1$).

When the size-frequency distribution of *P. astreoides* populations are displayed in 1-cm size classes (roughly representing maximum yearly growth at the Elpis), the progression of cohorts from 1998 to 2001 can be seen at both sites. As additional colonies recruit and existing colonies grow, the population size-range is expanded and the relative contribution of the smallest size classes diminishes (Figure 3). This is also evident when colonies are grouped into the five size classes used in our *P. astreoides* population model (Figure 4). The size-frequency distributions of the *P. astreoides* populations on the restoration structures at the two sites were similar in 1998 (Goodness-of-fit G-test, $p < 0.1$), but differed significantly in 2001 ($p < 0.01$) when a larger percentage of colonies (38%) had progressed into the two largest size categories (IV-V, > 3 cm) at the Maitland compared to only 17% at the Elpis.

Average colony size showed an increasing trend between 1998 and 2001 at both locations. Mean colony diameter was 1.4 cm (0.1) in 1998 compared to 2.2 cm (0.2) in 2001 at the Elpis site, and 1.8 cm (0.1) in 1998 compared to 2.3 cm (0.2) in 2001 at the Maitland site. As expected considering the recent establishment of the restoration structures, mean colony diameter was significantly smaller on the structures compared to the reference habitats at both sites (Figure 2). No significant differences in mean diameter were found in 2001 between *P. astreoides* colonies growing on the Elpis (2.2 cm) and the Maitland (2.3 cm). Furthermore, the maximum size of *P. astreoides* on the restoration structures at both locations was similar in 2001; maximum colony diameter was 10.1 cm at the Maitland and 9.6 cm at the Elpis.

The population structure of the reference habitats differed between the two sites (Figures 3, 4). While no differences in mean colony size were found between colonies of *P. astreoides* growing on the restoration structures in 2001, the reference habitats at the Maitland (4.5 cm adjacent and 8.4 cm away from the structure) had colonies significantly larger than those found at the Elpis (3.3 cm). Maximum colony size also differed between reference sites; maximum colony diameter was 24 cm at the Maitland site compared to 16 cm at the Elpis site. Maximum colony size adjacent to the restoration structure at the Maitland site was 10 cm. The *P. astreoides* population at the Elpis reference site is characterized by smaller mean and maximum colony size, a narrow size spread, and 76% of colonies within size classes I-IV (0-4 cm). In contrast, the population at the Maitland reference site has a

larger mean and maximum size, a wide size range, and a large proportion (58%) of colonies in size class V (> 4 cm).

Based on the maps drawn for the corals found on the Elpis restoration boulders, the percentage of *Porites astreoides* colonies that died between 1998 and 2001 was 45% (15% colonies yr^{-1} assuming constant mortality rates). Average growth rate was 3.6 mm yr^{-1} (1.2 (range = 1-11 mm) and the growth of colonies was related to initial colony size (linear regression, $r^2 = 0.61$, $p < 0.05$, $n = 15$). The mean recruitment rate was $0.3 \text{ recruits m}^{-2} \text{ yr}^{-1}$ (0.2) ($n = 8$ boulders). Recruitment, growth, and mortality rates of *P. astreoides* between 1998 and 2001 were not related to the surface area of the boulders or the coral density documented in 1998 (linear regression, $p > 0.1$). Although colony-specific rates were not calculated for the Maitland site where maps of colonies were not drawn in 1998, the mean net recruitment rate (i.e., colonies that settled – colonies that died) onto the concrete units that were surveyed in 1998 and 2001 was $0.5 \text{ recruits m}^{-2} \text{ yr}^{-1}$ (0.1) ($n = 11$ units). At the maximum growth rate measured and assuming constant growth, it would take *P. astreoides* colonies on the restoration structures 15 years to reach the maximum colony size recorded within the reference habitat at the Elpis site (16 cm), compared to 22 years at the Maitland (24 cm).

Population Model

Table 2 shows the transition probabilities among size classes measured in the field. Retention rates within the same size class were influenced by colony size; colonies within the smallest size categories have the lowest retention rates due to high growth and mortality rates. In contrast, colonies in the largest size category had the highest retention rates. Rates of partial mortality were low overall; only 9% of colonies in size class V shrank in size to the smallest size classes (< 20 mm) through partial mortality. The dominant eigenvalue (λ) was 0.89, indicating that the rates of partial colony mortality were not sufficient to offset the lack of fecundity values in the transition matrix. The right eigenvector, which represents the stable size-distribution suggests that if the conditions where these transitions were calculated persist, *P. astreoides* populations would be dominated by large colonies (39%) (Table 2). The elasticity matrix indicates that the retention of colonies within the largest size class was the most influential transition followed by the growth from size class IV to V (Table 3).

Our simulations indicate that it would take at least 10 years for the size structure of the *P. astreoides* population developing on newly established restoration structures to be statistically indistinguishable from that of the reference population at the Elpis site (goodness-of-fit G-test; $p > 0.05$; Fig. 5). The convergence rates of population abundance between restoration structures and reference habitats are clearly influenced by recruitment rates (Figure 6). When maximum recruitment rates onto the restoration structures were increased from 0.3 to 0.45 recruits m^{-2} , convergence took only 8 years compared to 16 years

(Figure 6). If the increased recruitment rates are maintained, the simulated population abundance would exceed that of the reference habitat by almost 40% after 30 years. In contrast, when maximum recruitment rates are decreased to 0.15 recruits m^{-2} , the populations growing on the restoration and reference habitats do not converge, and mean population abundance on the structures is almost 60% lower than on the reference habitat after 30 years. Finally, when recruitment is turned off, population structure becomes highly skewed to the left (Figure 7).

Discussion

The coral surveys, performed three and six years after the deployment of the reef restoration structures, revealed that abundant coral populations and communities are rapidly developing on the two dissimilar structures surveyed. The implementation of a coral population model developed with field parameters, together with estimates of coral abundance, density, growth, and species richness, suggest that the coral communities recruiting onto the restoration structures are rapidly approaching the structure of reference habitats. Species richness, as well as mean abundance of the dominant coral species, *Porites astreoides*, were nearly indistinguishable between the restoration structures and the surrounding reference habitats at each site after only 6 years.

However, we show here that the assessment of restoration success as well as estimates of convergence rates with respect to undisturbed reference habitats are greatly dependent on the endpoints being measured. While population abundance and size structure of the numerically dominant coral *Porites astreoides* are rapidly approaching that of the reference habitats (model predictions suggested a convergence in size-structure within the first 10 years if recruitment rates are maintained), maximum coral size will take almost twice as long to converge for this species. Similarly, Gittings et al. (1993) documented how coral abundance recovered rapidly within the area damaged by the M/V Wellwood in the Florida Keys compared with coral cover, which would take significantly longer to recover after disturbance.

The rates of convergence to the reference population and, hence, the level of success of a restoration effort, are determined not only by the recruitment and survivorship rates of corals on the restoration structures, but by the characteristics of the reference population as well. In effect, reference populations provide a “moving target” against which restoration success has to be measured dynamically. Accordingly, it must be stressed that the rapid convergence rates observed and simulated in this study for the dominant species, *Porites astreoides*, can not be assumed to be applicable or expected at other grounding sites even within the same region. *P. astreoides* is an opportunistic coral with a relatively small adult colony size, and recruitment and survivorship rates among the highest in the region (Miller et al. 2000; Kojis & Quinn 2001; Tougas & Porter 2001). The fact that the reference communities are

dominated by a coral species with these characteristics clearly improves the chances of convergence.

In contrast, where reference communities are dominated by corals like *Montastraea* spp. and *Acropora* spp. that are broadcast spawners with limited sexual recruitment and very large adult colony size (Szmant 1986), convergence rates can be expected to be significantly slower. This lack of convergence was documented by Aronson & Swanson (1997) at the grounding site of the M/V Wellwood where after more than 10 years, damaged areas had not developed either the coral community structure or the topography of the reference habitat. The documented limited recruitment of large, reef-building species like *Montastraea* spp. and *Diploria* spp. within damaged areas of the Wellwood grounding site, can ultimately delay or even preclude the complete recovery of the original coral community (Gittings et al. 1990). In this case, coral transplantation was proposed as an alternative to restore community composition and habitat complexity (Gittings et al. 1993).

The implementation of predictive models would be even more important in those cases where recovery rates are slow and exceed the duration of the proposed monitoring projects. In such cases, only the application of a simulation model would enable resource managers and scientists to estimate the time required for coral population structure to converge to that found on undisturbed reference habitats.

The development of coral communities on newly established reef restoration structures is completely dependent, at least initially, on the recruitment of propagules from outside

sources. This requirement is also true for the recovery of natural reef areas where coral cover is severely depleted following a major disturbance such as a hurricane or elevated temperature (Pearson 1981; Connell & Keough 1985). The sensitivity of the model to maximum recruitment rates highlights the importance of recruitment on the recovery rates of restored habitats. Accordingly, special attention should be afforded in the design of the restoration structures so that a variety and abundance of recruitment habitats are provided. The influence of settlement substrate on recruitment rates was evidenced at the Maitland site where Miller & Barimo (2001) showed that coral recruitment occurred preferentially onto limerock boulders embedded onto the concrete matrix.

By following coral population development from bare substratum on the restoration structures, we should also be able to elucidate some of the factors that determine coral population structure on natural reef habitats. Reference *P. astreoides* populations at the Maitland site are dominated by larger colonies and have a larger mean and maximum size compared to reference populations at the Elpis site. However, *P. astreoides* populations on the two restoration structures were similar initially. Assuming that the physical and biological factors that determine coral population structure are site-specific and that coral populations on the restoration structures will resemble the outside populations with time, it will be important to determine how the *P. astreoides* populations on the Maitland and Elpis structures diverge to resemble their respective reference populations. Although maximum colony size may be restricted by depth and light availability at the Elpis site, initial growth

rates were similar between the two sites (also shown by Miller & Barimo 2001), suggesting that size-related growth may slow down to a greater extent at the Elpis. Similarly, survivorship rates of larger colonies may be lower at the Elpis, resulting ultimately in a smaller maximum size. An alternative mechanism was derived from our simulations of different recruitment rates. When recruitment rates were significantly reduced and finally turned off completely to resemble recruitment failure, the resulting population structure of *P. astreoides* was similar to that found at reference habitats at the Maitland. These simulations suggest that the *P. astreoides* population at the reference Maitland site may have experienced a series of poor-recruitment years that resulted in the observed skewed distribution. Variable recruitment is a common characteristic of coral populations and may be, at last in part, responsible for the observed distribution. Only the continued monitoring of coral populations on the restoration structures and reference habitats will provide the information required to evaluate this hypothesis.

The methods outlined in this study, which include repeated sampling of marked coral colonies in support of model development, have been used to describe damage and recovery patterns of natural coral populations in the past, and are well-suited for the assessment and prediction of reef restoration success (e.g., Done 1987; Fong & Glynn 1998; Hughes & Tanner 2000). This information, combined with classical measurements of coral diversity, topographical complexity, and the abundance and diversity of associated reef fauna, can be collected easily in the field with limited cost and can provide valuable assessment tools that

should be incorporated into reef restoration projects (Gittings et al. 1993; Precht et al. 2001). To provide the needed scientific basis for improving ecological restoration success, monitoring and evaluation efforts should be commensurate with the resources afforded to the active restoration efforts undertaken at each site, and assessment must be implemented simultaneously to the restoration activities. This is the only way to undertake rigorous cost/benefit evaluation for reef restoration projects; evaluation that has been sorely lacking in the past and is crucial to provide for public support of future ecological restoration efforts. The tractable, quantitative approach presented here can be easily applied to begin to fill this void.

Acknowledgements

Funding and logistical support were provided by the National Undersea Research Center at the University of North Carolina at Wilmington (award # SEGM-2001-07 to D. Lirman), NOAA/NMFS/Restoration Center, and NOAA/NOS/Marine Sanctuaries Division. Field support by John Barimo, Charles Fasano, Robert Carter, Captain Mike Birns, and Otto Rutten is greatly appreciated.

References

- Aronson, R.B., and D.W. Swanson. 1997. Video surveys of coral reefs: uni- and multivariate applications. Proceedings 8th International Coral Reef Symposium, Panama 2:1441-1446.
- Baine, M. 2001. Artificial reef: a review of their design, application, management and performance. *Ocean & Coastal Management* 44:241-259.
- Bryant, D., L. Burke, J. McManus, and M. Spalding. 1998. *Reefs at Risk*. World resources Institute, New York, NY.
- Caswell, H. 2001. *Matrix Population Models. Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA.

- Clark, S., and A.J. Edwards. 1999. An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9:5-21.
- Connell, J.H., and M.J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. Pages 125-151 in S.T.A. Pickett and P. S. White, editors. *The Ecology of Natural Disturbances and Patch Dynamics*, Academic Press, New York, NY.
- Done, T.J. 1987. Simulation of the effects of *Acanthaster planci* on the structure of massive coral in the genus *Porites*: evidence of population resilience? *Coral Reefs* 6: 75-91.
- Edwards, A.J., and S. Clark. 1998. Coral Transplantation: A Useful Management Tool or Misguided Meddling? *Marine Pollution Bulletin* 37:474-487.
- FKNMS Draft Management Plan. 1995. NOAA.
- Fong, P., and P.W. Glynn. 1998. A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the Eastern Pacific? *Marine Biology* 130:663-674.
- Fonseca, M.S., B. Julius, and W.J. Kenworthy. 2000. Integrating biology and economics in seagrass restoration: How much is enough and why? *Ecological Engineering* 15:227-237.
- Gittings, S.R., T.J. Bright, and B.S. Holland. 1990. Five years of coral recovery following a

freighter grounding in the Florida Keys. Pages 89-105 in *Diving for Science: Proceedings*

AAUS 10th Annual Scientific Diving Symposium. USF, St. Petersburg, FL.

Gittings, S.R., T.J. Bright, and D.K. Hagman. 1993. The M/V Wellwood and other large vessel groundings: coral reef damage and recovery. Pages 174-180 in R.N. Ginsburg, editor. *Global Aspects of Corals Reefs. Health, Hazards, and History*. University of Miami, Miami, FL.

Gittings, S.R., T.J. Bright, A. Choi, and R.R. Barnett. 1988. The recovery process in a mechanically damaged coral reef community: recruitment and growth. *Proceedings 6th International Coral Reef Symposium, Australia* 2:225-229.

Hudson, J.H., and R. Diaz. 1988. Damage survey and restoration of the M/V Wellwood grounding site, Molasses Reef, Key Largo National Marine Sanctuary, Florida. *Proceedings 6th International Coral Reef Symposium, Australia* 2:231-236.

Hughes, T.P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *American Naturalist* 123:778-795.

Hughes, T.P., and J.E. Tanner. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81, 2250-2263.

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* 69:967-974.

- Lirman, D. 2002. A simulation model of the population dynamics of the branching coral *Acropora palmata*. effects of storm intensity and frequency. Ecological Modelling (In press).
- Lutz, S.J. 1998. An assessment of unreported boat grounding damage to shallow-water corals in the Florida Keys. Masters Thesis. University of Miami, Miami, FL.
- Miller, M.W., and J. Barimo. 2001. Assessment of juvenile coral populations at two reef restoration sites in the Florida Keys National Marine Sanctuary: indicators of success? Bulletin of Marine Science 69:395-405.
- Miller, M.W., E. Weil, and A.M. Szmant. 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. Coral Reefs 19:115-123.
- Milon, J.W., and R.E. Dodge. 2001. Applying habitat equivalency analysis for coral reef damage assessment and restoration. Bulletin of Marine Science 69:975-988.
- Pearson, R.G. 1981. Recovery and recolonization of coral reefs. Marine Ecology Progress Series 4:105-122.
- Pickering, H., D. Whitmarsh, and A. Jensen. 1998. Artificial reefs as a tool to aid rehabilitation of coastal ecosystems: investigating the potential. Marine Pollution Bulletin 37:505-514.
- Precht, W.F. 1998. The art and science of reef restoration. Geotimes 43:16-20.

- Precht, W.F., R.B. Aronson, and D.W. Swanson. 2001. Improving scientific decision-making in the restoration of ship-grounding sites on coral reefs. *Bulletin of Marine Science* 69:1001-1012.
- Seaman, W., 2000. Artificial reef evaluation with application to natural marine habitats, CRC Press, Boca Raton, FL.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry*. W.H. Freeman & Co., New York.
- Szmant, A. M. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs* 5:43-53.
- Tilmant, J.T., and G.P. Schmahl. 1981. A comparative analysis of coral damage on recreationally used reefs within Biscayne National Park, Florida. *Proceedings 4th International Coral Reef Symposium, Manila* 1:187-192.
- Tougas, J.I., and J.W. Porter, 2001. Differential coral recruitment patterns in the Florida Keys. Pages 789-811 in J.W. Porter and K.G. Porter, editors. *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. An Ecosystem Sourcebook*. CRC Press, Boca Raton, FL.
- Yap, H.T. 2000. The case for restoration of tropical coastal ecosystems. *Ocean & Coastal Management* 43:841-851.

Figure Legends

Figure 1. Photographs of the two grounding and restoration sites surveyed in 1998 and 2001 showing the restoration structures deployed at the Maitland (depth = 2.5 m) and Elpis (9-11 m) sites.

Figure 2. Mean density and colony diameter (± 1 S.E.M.) of *Porites astreoides* at the Maitland and Elpis restoration sites in 2001.

Figure 3. Size structure of the *Porites astreoides* population found at the Maitland and Elpis restoration sites using 1-cm size intervals.

Figure 4. Size structure of the *Porites astreoides* population found at the Maitland and Elpis restoration sites using the size categories used in the population model.

Figure 5. Size structure of the *Porites astreoides* population simulated for the restoration and reference habitats at the Elpis site 10 years after deployment. The output represents the mean (± 1 S.E.M.) of 25 runs. Initial conditions were clean substrate for the restoration structures and the size structure documented for the reference habitat during our 2001 surveys.

Figure 6. Simulated abundance patterns for *Porites astreoides* on the restoration structure and the reference habitat at the Elpis using different maximum recruitment rate scenarios for the restoration structures. The output represents the mean (± 1 S.E.M.) of 25 runs.

Figure 7. Size structure of the *Porites astreoides* population simulated for the Elpis restoration site after 25 years under a recruitment failure scenario (no new recruitment). Initial conditions were those documented on the restoration structure in 2001.

Table 1. Species richness observed during visual surveys performed at two grounding sites within the Florida Keys National Marine Sanctuary in 1998 and 2001.

HARD CORAL SPECIES	MAITLAND		ELPIS	
	STRUCTURE	OUTSIDE	STRUCTURE	OUTSIDE
<i>Agaricia</i> spp.	•	•	•	•
<i>Diploria strigosa</i>	•			•
<i>Diploria labyrinthiformis</i>			•	•
<i>Diplora clivosa</i>	•	•	•	•
<i>Favia fragum</i>	•	•	•	•
<i>Dichocoenia stokesii</i>	•	•	•	•
<i>Manicinia areolata</i>			•	
<i>Montastraea cavernosa</i>			•	•
<i>Montastraea faveolata</i>			•	•
<i>Porites astreoides</i>	•	•	•	•
<i>Porites porites</i>	•	•	•	•
<i>Eusmilia fastigata</i>			•	•
<i>Scolymia</i> spp.			•	
<i>Siderastrea radians</i>	•	•	•	•
<i>Siderastrea siderea</i>	•	•	•	•
<i>Stephanocoenia michilini</i>			•	
<i>Meandrina meandrites</i>		•		•
Total	9	9	15	14

Table 2. Transition matrix for *Porites astreoides* colonies on the Elpis

restoration boulders in 1998 and 2001 expressed as proportions. Size classes:

I = 0-10 mm in diameter, II = 11-20 mm, III = 21-30 mm, IV = 31-40 mm, V = > 41 mm.

$\lambda = 0.89$	Size Classes (1998-2001)					Stable Population Structure (%)
	I	II	III	IV	V	
I	0.1	0.05	0.05	0.02	0.05	5.1
II	0.55	0.35	0.1	0.05	0.04	13.8
III	0.15	0.35	0.3	0.1	0.07	18.3
IV	0	0.1	0.35	0.32	0.15	24.1
V	0	0	0.1	0.38	0.6	38.6

Table 3. Elasticity matrix for *Porites astreoides* on the Elpis restoration

boulders in 1998 and 2001.

	Size Classes (1998-2001)				
	I	II	III	IV	V
I	0.005	0.007	0.009	0.005	0.018
II	0.03	0.051	0.019	0.012	0.016
III	0.009	0.056	0.062	0.027	0.031
IV	0	0.016	0.073	0.087	0.065
V	0	0	0.022	0.108	0.275

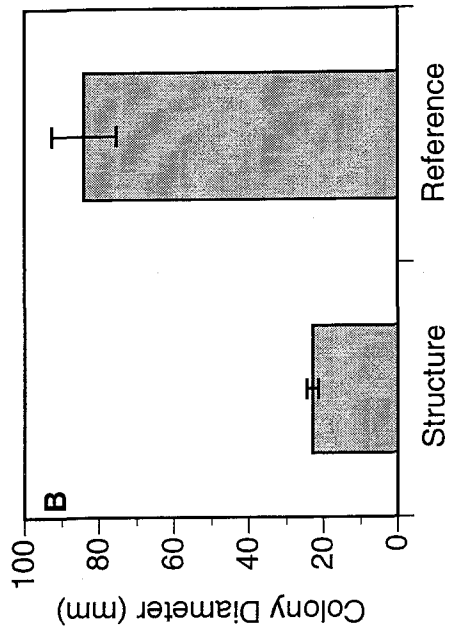
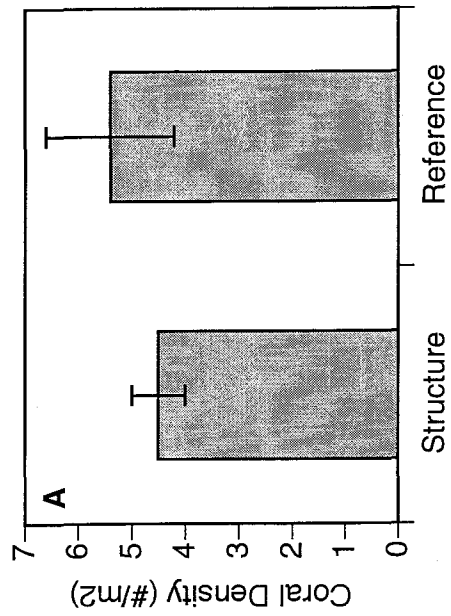
MAITLAND



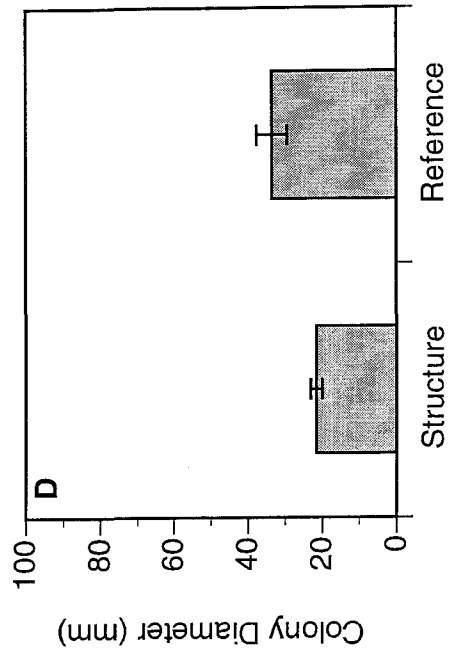
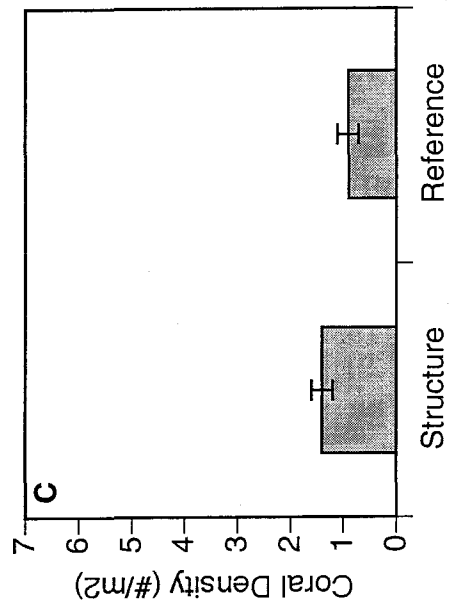
ELPIS



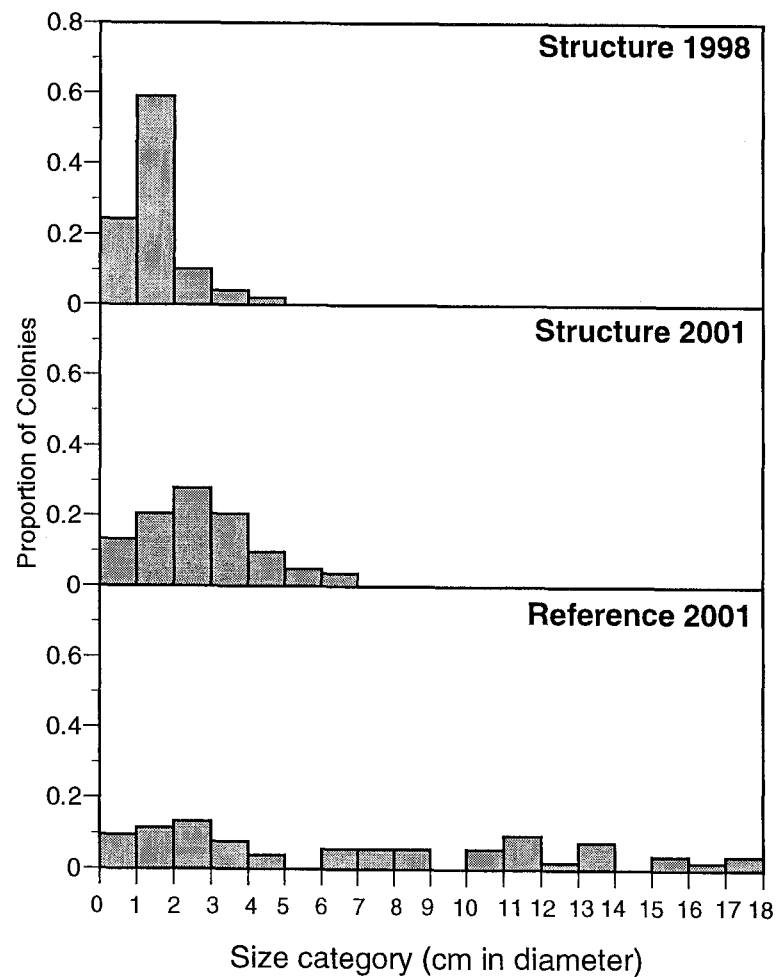
MAITLAND



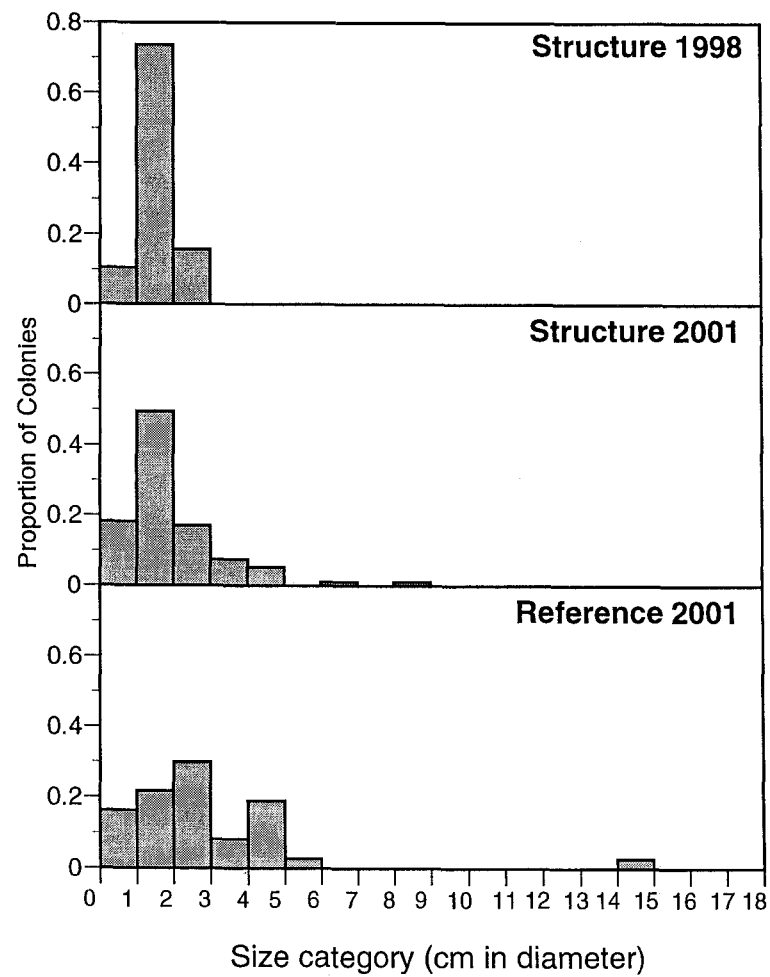
ELPIS



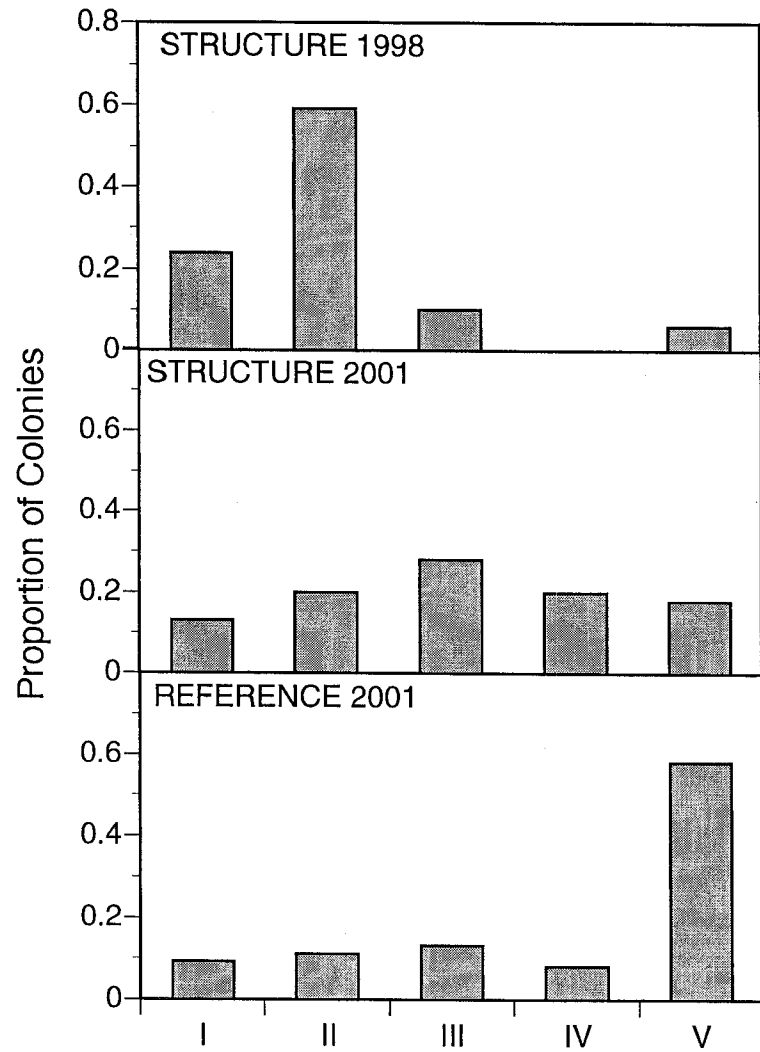
MAITLAND



ELPIS



MAITLAND



Size Categories

ELPIS

