

Effects of Mechanical Fracturing and Experimental Trampling on Hawaiian Corals

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ABSTRACT / *In situ* trampling occurred under experimental conditions to quantify the differences in the responses to anthropogenic trampling in four dominant species of Hawaiian corals, *Porites compressa*, *Porites lobata*, *Montipora capitata*, and *Pocillopora meandrina*. Trampling was simulated daily for a period of nine days at which time further breakage was minimal. Forty treatment colonies produced 559 fragments. Trampling was followed by an 11-month recovery period.

Coral colony and fragment mortality was low. All four species were highly tolerant of inflicted damage, suggesting that some

species of corals can withstand limited pulse events that allow time for recovery.

Growth rates following trampling were significantly lower in the treatment groups for three of the four species. This study demonstrated that very few trampling events can produce significant changes in growth even after a long recovery period.

Survivorship of fragments is clearly size- and species-dependent in *M. capitata* and *P. compressa*. Smaller fragments (<5 cm) had higher mortality than larger fragments (>5 cm). High breakage rates for *M. capitata* and *P. compressa* are consistent with the nearshore, low-energy regions they inhabit—the same environment frequented by skin divers and waders.

Mechanical tests were conducted to determine tensile and compressive strengths. *Pocillopora meandrina* exhibited the strongest skeletal strength, followed in decreasing order by *Porites lobata*, *Porites compressa*, and *Montipora capitata*. The skeletal strength obtained from the experiments correlate with the wave energy present in the environments in the regions they inhabit, suggesting that structural strength of corals is an adaptive response to hydraulic stress.

The global increase in coral reef tourism has been accompanied by heightened concern for anthropogenic stresses on nearshore environments. In addition to problems associated with nearshore development, direct contact with corals by waders, skin divers, or scuba divers can result in mortality, fracturing, tissue damage, decrease in reproductive output, or reduced growth (Woodland and Hooper 1977; Liddle and Kay 1987; Brosnan and Crumrine 1994; Brown and Taylor 1999). Environmental managers require quantitative data to formulate policy decisions. The best causal scientific data come from controlled and replicated experiments. Hawaii can serve as a model system for the

investigation of the impacts of trampling because corals have not been subjected to mass mortality events such as disease or bleaching.

In Hawaii, a large percentage of reefs are easily accessible to the human population because they are located near major urban centers and tourist concentrations. By 1997 nearly 7 million tourists were visiting Hawaii annually, with over 1,000 ocean recreation companies doing business in the state (Seji Naya DBEDT personal communication). Mortality and coral fragmentation associated with reef walking and/or diving has been described in Australia (Woodland and Hooper 1977; Liddle and Kay 1987), the Maldives (Allison 1996), Egypt (Hawkins and Roberts 1993), Israel (Epstein and others 1999), and the Caribbean (Michell-Tapping, 1983; Tratalos and Austin 2001). These studies have shown that there is a strong relationship between morphology of coral colonies and resistance to damage from reef walkers or divers. Corals such as acroporids, with fine branching and open skel-

KEY WORDS: Trampling; Mechanical fracturing; Coral skeletal strength; Anthropogenic stress; Fragmentation

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etal structures, are perceived to be the least resistant to breakage (Marshall 2000), while colonies with robust branches or a lobate or encrusting morphology are most resistant to damage. Fragmentation in many coral species also serves as an effective asexual reproductive strategy. These differences in morphology have also been related to the environmental factors impacting corals, with lobate and encrusting colonies found more commonly in exposed areas with high wave activity and finer-branched corals restricted to sheltered areas (Wainwright and others 1976; Vosburg 1977; Chamberlain 1978; Schuhmacher and Plewka 1981).

The most common corals in Hawaii include *Porites lobata*, *Porites compressa*, *Montipora capitata*, (ranked first, second, and third in abundance), and *Pocillopora meandrina* (ranked sixth in abundance) (Coral Reef Assessment and Monitoring Program 2001). Three of these species are branched, *P. compressa*, *P. meandrina*, and *M. capitata*, while *P. lobata* forms massive colonies. *Porites compressa* and *M. capitata* are usually found in sheltered environments, such as shallow bays or deeper water. *Porites lobata* and *P. meandrina* are commonly found on reef slopes exposed to higher wave action. Based on their morphological characteristics and environmental distributions, we hypothesized that *P. compressa* and *M. capitata* would be less resistant to breakage than *P. meandrina* and *P. lobata*. We evaluated this hypothesis using standardized engineering tests for tension and compression strength and by simulated reef trampling. Measuring the differences in the responses to trampling in four commonly occurring species of corals in relation to visitor use patterns provides a quantitative basis for management decisions.

The response of corals to mechanical damage is typically determined by the resistance to stress and the resilience or recovery following damage. Resistance was measured by using standard engineering tests to compute tension and compression strength of dead coral skeletons. In addition, the simulated trampling tests *in situ* directly measured the fragmentation of live colonies subjected to reef walking. Resilience was measured by tracking survivorship of damaged colonies and fragments and growth rates of damaged colonies.

Methods

Collection and Preparation of Specimens

Healthy, undamaged colonies of the four test species were collected from Kaneohe Bay, Oahu, Hawaii, *Porites lobata* and *Pocillopora meandrina* were collected from the barrier reef flat near the margin of Kaneohe Bay and *Porites compressa* and *Montipora capitata* were collected

from a patch reef within the central portion of Kaneohe Bay. Both plate-like and branching morphologies of *M. capitata* were collected.

Colonies were dried for three weeks before preparation for engineering tests. Dried, dead skeletal material has been shown to be representative of living corals in response to fracture stress. Substances lacking substantial amounts of organic material do not alter their mechanical properties significantly when dry (Taylor and Layman 1972; Currey 1975), and Wainwright (1963) found only 0.1% organic matter by weight in *P. damicornis* skeleton. Acroporid skeletons ranged in organic content from 0.24–0.66% (Bucher and others 1998). Chamberlain (1978) determined that strength testing of dry, dead coral material was statistically similar to the strengths of living corals.

Ten live colonies of each species were used for the field trampling experiments. These colonies of similar size were sawed in half to allow for paired comparisons of growth rates from these artificial clones. Colonies were stained with Alizarin red (concentration <15 ppm, Lamberts 1974) in laboratory tanks for eight hours with constant aeration. Colony replicates were attached with plastic coated wire to 20 plastic trays (40 × 40 cm) for field deployment.

Tensile Strength

Prisms (6 × 6 × 25 mm) were obtained by cutting the coral with a band saw and sanding with a belt sander to achieve reasonable (± 1 mm) tolerances. The number of replicates per colony ranged 1–11 and was limited by the dimensions of the colony and/or the number of branches. The number of colonies and replicates per colony is given in Table 1. Depth, width, and length of prisms were measured using a digital caliper. A modulus of rupture apparatus, scaled to approximately 1/24 of an apparatus used for testing concrete according to the American Society for Testing and Materials (ASTM) C 78 (ASTM 1997), was used to apply a transverse load to the prism. A digital camera was used to record the breaking point for each test.

Tensile strength (as modulus of rupture) was computed for each prism using the following equation:

$$R = PL/bd^2$$

where R is the tensile strength (modulus of rupture) in MPa, P is the load applied to the specimen in N , L is length (mm), b is the width of prism (mm), and d is the prism depth (mm).

Compressive Strength

Compressive strength was evaluated using cores cut from colonies. Cylindrical cores were cut with a lathe

Table 1. Tensile strength of coral species. Both mean and standard deviation (s.d.) for replicates from each colony and mean and standard deviation for the species are given in MPa

Species	Colony	# Replicates	Mean in MPa (s.d.)
<i>M. capitata</i> —plate	A	1	1.78
	B	2	2.25 (0.559)
	C	2	2.81 (0.438)
	D	7	3.85 (0.563)
Species (morph) mean			2.67 (0.890)
<i>M. capitata</i> —branching	A	2	3.91 (0.212)
	B	4	2.30 (0.728)
	C	5	4.83 (1.24)
	D	9	2.82 (1.40)
Species (morph) mean			3.47 (1.13)
<i>P. compressa</i>	A	1	7.00
	B	2	5.70 (0.474)
	C	3	6.43 (0.393)
	D	3	3.54 (0.597)
	E	4	5.10 (0.413)
	F	4	4.50 (1.34)
	G	4	4.53 (0.874)
Species mean			4.80 (1.03)
<i>P. lobata</i>	A	9	5.92 (1.07)
	B	11	6.38 (0.782)
Species mean			6.15 (0.330)
<i>P. meandrina</i>	A	1	10.1
	B	2	8.24 (4.21)
	C	2	2.56 (0.035)
Species mean			6.96 (3.93)

equipped with a 19-mm diameter core bit. Therefore, compressive strength could only be estimated for *Porites lobata* and *P. compressa*, species with sufficient volume for extraction of cores. Three colonies of *P. compressa* and six colonies of *P. lobata* were sampled. The number of replicates per colony is shown in Table 2.

Prior to coring, colonies were cast with Fixall brand plaster in a cylindrical steel form. Red food coloring was added to the plaster to distinguish it from the coral skeletal material. A lathe equipped with a 19-mm diameter core bit was used to saw the cores. The cores were then cut to lengths of 25–32 mm. Plaster caps were cast on both ends of each core to ensure that the stress was uniformly distributed over the cross-section during the compression test. An Instron (model 4206) with a 130 KN capacity was used to apply the compressive force at a strain rate of 0.25 mm/min⁻¹.

Compressive strength was calculated from the equation:

$$f = P/A$$

where f is the compressive strength in MPa, P is the load applied to the specimen in N , and A is the cross-sectional area of the core in inches.

Table 2. Compressive strength of *P. lobata* and *P. compressa*. Both mean and standard deviation (s.d.) for replicates from each colony and mean and standard deviation for the species are given in MPa

Species	Colony	# Replicates	Mean in MPa (s.d.)
<i>P. compressa</i>	A	1	8.14
	B	1	6.00
	C	3	4.70 (0.690)
Species mean			6.28 (1.74)
<i>P. lobata</i>	A	1	12.87
	B	1	12.91
	C	1	16.66
	D	3	19.35 (11.31)
	E	3	22.79 (1.06)
	F	6	10.21 (3.32)
Species mean			15.80 (4.70)

Table 3. Fracture strength of *M. capitata*, *P. compressa*, and *P. meandrina*. Species mean and standard deviation (s.d.) are given in MPa

Species	Colony	Fracture load (N)	Fracture strength in MPa
<i>M. capitata</i>	A	294	0.68
	B	96	0.59
	C	124	0.54
	D	454	6.30
Species mean		242	2.03(3.85)
<i>P. compressa</i>	A	178	5.51
	B	232	5.39
	C	76.9	4.86
	D	759	8.37
	E	310	1.99
Species mean		311	5.22(2.27)
<i>P. lobata</i>	A	6726	
<i>P. meandrina</i>	A	2440	25.87
	B	898	26.48
	C	2175	23.84
Species mean		1834	25.4 (1.38)

Colony Fracture Strength Under Simulated Trampling

Colonies of each species were subjected to compressive forces that were intended to simulate trampling forces caused by a human standing or walking on the colony. Samples sizes are given in Table 3. One colony of *P. lobata* was tested, but did not fracture in tension. To prepare colonies for compression tests, each colony base was cast in concrete to assure an upright position during testing. A 200 × 200 × 25 mm neoprene pad was placed between the coral and the load head of the Instron testing machine to simulate a diver's fin or ocean footwear and distribute the load over the colony.

The load was applied by lowering the load head at a rate of 0.25 mm/min⁻¹. This load rate was slow enough for inertial effects to be neglected.

Fracture stresses obtained by subjecting colonies to these simulated trampling tests were calculated with the following equation:

$$\sigma = Mc/I - P/A$$

where σ is the fracture stress given in MPa, P is the load in N , A is the cross-sectional area at the location of the fracture (mm²), M is the bending moment ($N - m$) determined by multiplying the applied load by its moment arm, c is the distance (mm) from the neutral axis to the extreme fiber at the location of the fracture, and I is the moment of inertia (m⁴).

Colonies with branching morphologies tended to fracture in tension caused by bending of the branches. The one colony of *P. lobata* that had a lobate morphology fractured in compression. Calculation of the stress generated for the compression fracture is complex due to the geometry of the coral, and therefore compression fracture strength could not be calculated for this colony.

In Situ Trampling Experiment

Plastic trays containing the clones of the colonies were placed at a depth of 1 m on the windward reef flat of Moku o Loe (site of the Hawaii Institute of Marine Biology). Colonies were not exposed during low tide periods. Experimental and control trays were placed side by side to minimize differences between physical or chemical factors that might affect coral growth.

To simulate impact by skin divers and waders, contact was applied by volunteers wearing dive fins or booties and ranging 27–73 kg in weight. Volunteers walked back and forth along experimental rows of plastic trays during each trampling event for approximately two minutes. Following each event, all fragments were recovered and counted. Trampling events continued until almost no additional breakage was occurring, a total of nine events over a period of 12 days.

Detached fragments were recovered following each trampling event, measured and sorted into two size classes, <5 cm and >5 cm. Fragments were placed loose in plastic trays that simulated falling from a parent colony and returned to the field. All colonies remained in the field for an additional 11-month period to allow for recovery and measurements of growth. At the end of the experiment, linear extension was measured as the distance between the Alizarin mark and new branch tip or outer edge of the lobate form. Extension rates were expressed as mm/yr. Multiple measurements were collected for each clone. Growth be-

tween experimental and control clones for each species was compared using a paired t-test. All fragments were recovered and survivorship by size recorded.

Results

Tensile Strength

Tensile strength could be measured for all four species, including the two morphologies for *M. capitata*. Values reported (Table 1) include the mean strength for each colony tested, with number of replicate tests per colony indicated. Species means were calculated from colony means. The rank order from highest tensile strength to lowest is *P. meandrina* > *P. lobata* > *P. compressa* > *M. capitata*. There was no significant difference between the mean strengths for the plate form and branching form of *M. capitata*.

Compressive Strength

Due to the morphology of the species, compression tests could only be performed on cores taken from colonies of *P. lobata* and *P. compressa* (Table 2). Differences in mean strength between species were significant (Kruskal-Wallis one-way nonparametric ANOVA, $F = 14.51$, $P = 0.0066$). Both species had higher compressive strength than tensile strength. This phenomenon is commonly seen in other materials such as concrete, or bone and other marine organisms such as molluscs, echinoderms, and crustaceans (Chamberlain 1978).

Colony Fracture Strength Under Simulated Trampling

Simulated trampling tests were conducted with all four species, although only the branched morphology of *M. capitata* was tested (Table 3). All colonies except *P. lobata* demonstrated tension failures so that the fracture strength could be calculated. The one colony of *P. lobata* demonstrated compression failure. Calculation of the stress generated for the compression fracture is complex due to the geometry of the coral. However, the fracture load for the one specimen that failed in compression was in excess of 6700 N, much greater than the expected weight of a human (approximately 670 N).

In Situ Trampling

A total of 559 fragments were recovered, with the majority of the breakage (46%) occurring after the first trampling event (Figure 1). Each successive trampling produced fewer new fragments (21%, 13%, 9%, and 2% of the total fragments produced). *Montipora capitata*

Figure 1. Number of fragments produced in *in situ* trampling experiment from 10 colonies each of *Porites compressa*, *Porites lobata*, *Montipora capitata*, and *Pocillopora meandrina*.

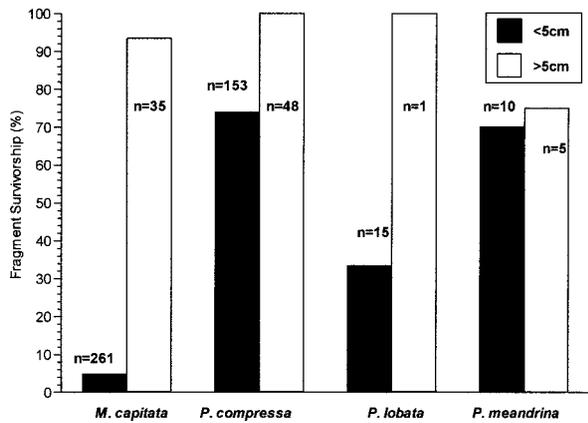
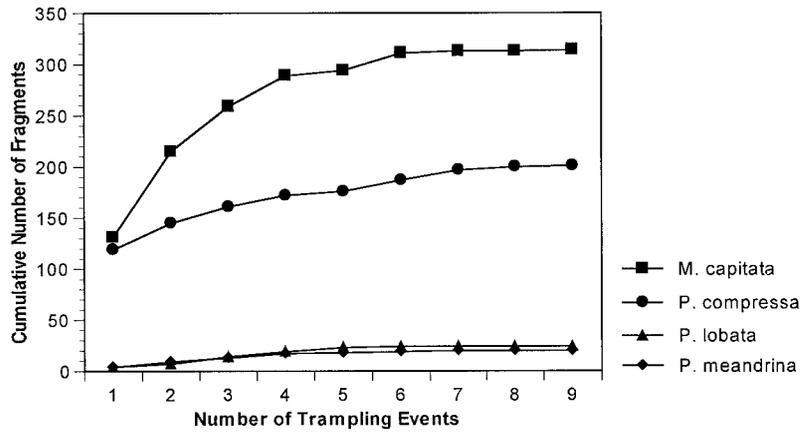


Figure 2. Survivorship of coral fragments in two size classes.

produced the majority of fragments (56%), followed by *P. compressa* (36%). *P. lobata* and *P. meandrina* produced only 8% of the total, approximately equal numbers of fragments. Survivorship of fragments was high, although survivorship was size dependent, particularly for *M. capitata* (Figure 2). Only 5% of the small (<5 cm) *M. capitata* fragments survived, while 77% of the larger fragments were collected following 11 months. Survivorship for large fragments was greater than 70% in all species, while survivorship for small fragments ranged from 5% to 70%.

Fragment survival was also species dependent. *M. capitata* and *P. lobata* had few surviving small fragments. Larger fragments exhibited 15 times higher survival rates than smaller fragments for *M. capitata* and three times higher rates for *P. lobata*. *P. meandrina* and *P. compressa* showed low mortality in both size classes relative to the other two species.

Coral colonies had high survivorship over the 11-month period, with mortality of only three of 40 colonies in the experimental group and two of 40 colonies

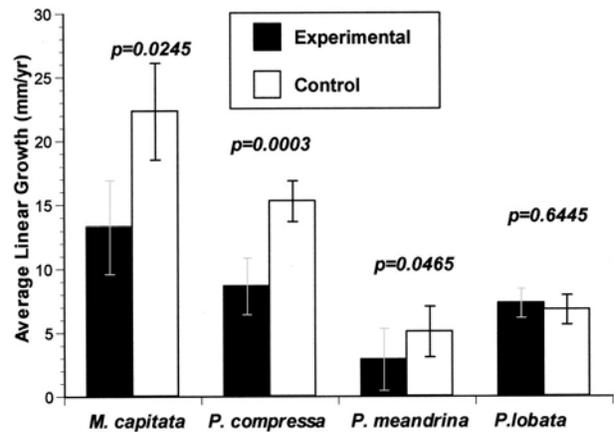


Figure 3. Average linear extension rates (mm/yr) for coral colonies in *in situ* trampling experiments (*p* values from paired comparisons).

in the control group. However, linear extension rates were statistically decreased in the experimentally trampled colonies of *M. capitata*, *P. compressa*, and *P. meandrina* (Figure 3). Extension rates over the 11-month experimental growth period for *M. capitata* were 14.5 mm and 24.3 mm for the experimental and control clones, respectively, 9.4 mm and 16.7 mm for *P. compressa*, and 3.1 mm and 5.5 mm for *P. meandrina*. Growth rates for clones of *P. lobata* showed no difference between control (7.4 mm) and experimental (8.0 mm) clones.

Discussion

The results of this study showed a hierarchy in resistance to damage associated with mechanical trampling, with the two branched species from sheltered environments showing the lowest tension and compression

Table 4. Compressive strengths for biological skeletal and industrial materials. Results for coral tensile and compressive strength from present investigation. Echinoderm data from Curry (1975). Granite data from Wainwright and others (1976). All other data as described in Chamberlain (1978)

Group	Tensile Strength (MN/m ²)	Compressive Strength (MN/m ²)	Organics (%)
Biological Materials			
Corals	3–7	2–25	0.02–0.2
Molluscs	5–121	88–270	5
Echinoderms	27–58	48–96	1
Vertebrates-Human Bone	140–190	210	50
Engineering Materials			
Granite		52	0
Concrete	3–5	20–40	0
Steel	450–800	450–800	0
Aluminum	600	600	0

strength and the highest fragmentation rates under simulated trampling. Marshall (2000) found a similar result for Australian species, where massive *Porites* spp. were more resistant to damage, and thin branched acroporids and pocilloporids were least resistant. In Hawaii, the species with lower skeletal strength, *Montipora capitata* and *Porites compressa*, are found in some of the areas that are most used by tourists, sheltered environments with low wave activity. This increases the likelihood of damage from reef walkers or skin divers. *Porites lobata* and *Pocillopora meandrina* had higher tension and compression strengths and produced fewer fragments under simulated trampling. These two species are more commonly found in wave exposed environments, where tourist use may be reduced during episodes of large waves.

Morphology, geometry, size, porosity, density, and boring organisms are mechanical properties of the coral material that contribute to the resistance of corals to natural and anthropogenic breakage (Liddle and Kay 1987). A comparison with other materials showed that coral skeletal strengths are low (Table 4). Corals rank slightly below concrete and echinoderm spines. The high strength of mollusc shells and compact bone results from a combination of viscoelastic organics and ceramics. Wainwright and others (1976) found the strength of a skeleton can be augmented by particular combinations of viscoelastic materials. Crystalline composites without significant organic components, such as coral skeleton, exhibit very low tensile strengths. Other crystalline composites include industrial materials such as concrete, stone, glass, cast iron, and numerous artificially produced materials (Chamberlain 1978; Massel 1999).

Although the engineering tests suggested that the massive coral *P. lobata* and the heavy branched form *P. meandrina* were least likely to suffer from damage, the *in*

situ trampling experiment demonstrated that even these robust species do fragment when trampled. All coral colonies showed high survivorship following the experimental trampling suggesting that some species of corals can withstand limited pulse events that allow time for recovery. Yet, most accessible near-shore environments throughout Hawaii receive continuous or chronic trampling impacts with little or no time for undisturbed recovery. Although coral mortality was low in these experiments, there were reductions in growth rates for the branched species, demonstrating a sub-lethal stress resulted from trampling. Another potential sub-lethal stress, unmeasured in this study, could be a reduction in reproductive output of these coral colonies (Smith and Hughes 1999)

Fragmentation can be a form of asexual reproduction in corals (Highsmith 1982). Larger fragments created by the *in situ* trampling had high survivorship, but within the controlled environment of this experiment Unrestrained on the reef flat, these fragments may have been rolled and further abraded, or moved out of suitable habitat. Other studies have shown that survivorship of fragments varies among different habitats and species of corals (Highsmith 1982; Smith and Hughes 1999).

Coral skeletal strengths are usually measured in relation to studies of the wave environment in the regions the corals inhabit. Typically these studies have shown that corals with higher skeletal strength are found in areas with greater wave energy (Chamberlain and Graus 1975; Wainwright and others 1976; Schuhmacher and Plewka 1981). In this study, the species with the higher measures of skeletal strength are typically found in areas of greater wave energy.

Analysis of compressive and tensile strengths can also be used to predict the relative ability of coral species to withstand diver and trampling impacts. This

study ranked the common Hawaiian corals in relation to their skeletal strength. The *in situ* trampling experiment demonstrated that the same ranking applied to the degree of fragmentation and sub-lethal stress suffered by the coral species. These rankings can also be useful in community analyses to predict species composition in areas with known physical forces. This study has also demonstrated that even robust species, as determined by responses to mechanical tests, can be impacted by direct and sub-lethal stress from trampling. In this study, both *Porites lobata* and *Pocillopora meandrina*, robust species, produced fragments when trampled, and *P. meandrina* had a reduced growth rate following trampling. Coral species with low skeletal strength, *Montipora capitata* and *Porites compressa*, produced many fragments and had slower growth following trampling. These results suggest that with increasing numbers of tourists visiting shallow coral reef areas, coral reef management must take into account direct and indirect stress due to trampling.

Marine protected areas (MPAs) are designed to protect the environment and conserve the resources. Although removal of marine organisms is usually prohibited, public accessibility is not limited and MPAs are popular destinations for tourists. This study has demonstrated that even low levels of trampling can inflict damage to corals therefore it is critical for managers to consider the effects on trampling to corals in formulating policy.

To reduce damage to corals, we recommend two potential solutions to manage human trampling of corals. One solution is to restrict high use to a limited number of sites. High use is predominately associated with commercial tourist activities. These regions are likely to suffer sustained coral damage, but access to reefs can include visitor education, regarding the impacts of trampling. An example of this is the education program implemented at Hanauma Bay Nature Park on Oahu (Alan Hong personal communication). A second recommendation, which may be logistically difficult to implement, is to open and close areas to allow for coral recovery. As these experiments have demonstrated, acute trampling may not be fatal to impacted corals, but recovery from sub-lethal stress may require additional time. Managers can use these experimental results to promote what may be unpopular policy decisions.

Literature Cited

- Allison, W. R. 1996. Snorkeler damage to coral reefs in the Maldives Islands. *Coral Reefs* 15:215–218.
- ASTM. 1997. *Annual Book of ASTM Standards*. American Society for Testing and Materials, Easton, MD.
- Brosnan, D. M., and L. L. Crumrine. 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology* 177:79–97.
- Brown, P. J., and R. B. Taylor. 1999. Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal. *Journal of Experimental Marine Biology and Ecology* 235:45–53.
- Bucher, D. J., V. J. Harriot, and L. G. Roberts. 1998. Skeletal micro-density, porosity and bulk density of Acroporid corals. *Journal of Experimental Marine Biology and Ecology* 228:117–136.
- Chamberlain, J. A. 1978. Mechanical properties of coral skeleton: compressive strength and its adaptive significance. *Paleobiology* 4:419–435.
- Chamberlain, J. A., and R. Grans. 1975. Water flow and hydromechanical adaptations of branched reef corals. *Bulletin of Marine Science* 25:112–125.
- Jokiel, P. L., E. K. Brown, A. Friedlander, K. Rodgers, and W. R. Smith. 2001. Hawaii coral reef initiative final report 1999–2000. Coral Reef Assessment and Monitoring Program, HI.
- Currey, J. D. 1975. A comparison of the strength of echinoderm spines and mollusc shells. *Journal of Marine Biological Association*. 55:419–424.
- Epstein N., R. P. M. Bak, and B. Rinkevich. 1999. Implementation of a small scale, “no use zone” policy in a reef ecosystem. Eilat’s reef lagoon 6 years later. *Coral Reefs* 18:327–332.
- Hawkins, J. P., and C. M. Roberts. 1993. Effects of recreational scuba diving on coral reefs: trampling on reef flat communities. *Journal of Applied Ecology* 30:25–30.
- Highsmith, R. C. 1982. Reproduction by fragmentation in corals. *Marine Ecological Progress Series* 7:207–226.
- Lamberts, A. E. 1974. Measurements of Alizarin deposited by corals. Pages 241–244 in A. M. Cameron (ed.), *Proceedings of the Second International Coral Reef Symposium*, Brisbane.
- Liddle, M. J., and A. M. Kay. 1987. Resistance, survival and recovery of trampled corals on the Great Barrier Reef. *Biological Conservation* 42:1–18.
- Marshall, P. A. 2000. Skeletal damage in reef corals: related resistance to colony morphology. *Marine Ecological Progress Series* 200:177–189.
- Massel, S. R. 1999. *Fluid mechanics for marine ecologists*. Springer-Verlag, Berlin.
- Michell-Tapping, H. S. 1983. Experimental fracturing of various corals in the reef environment. *Caribbean Journal of Science* 19:49–52.
- Schuhmacher, H., and M. Plewka. 1981. The adaptive significance of mechanical properties versus morphological adjustments in skeletons of *Acropora palmata* and *Acropora cervicornis* (Cnidaria, Scleractinia). Pages 121–128 in *Proceedings of the Fourth International Coral Reef Symposium*, Manila.
- Smith, L., and T. Hughes. 1999. An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology* 236:147–164.

- Taylor, J. D., and M. Layman. 1972. The mechanical properties of bivalve (mollusca) shell structures. *Palaeontology* 15: 73–87.
- Tratalos, J. A., and T. J. Austin. 2001. Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. *Biological Conservation* 102:67–75.
- Vosburgh, F. 1977. The response to drag of the reef coral *Acropora reticulata*. Pages 477–481 in *Proceedings, Third International Coral Reef Symposium*, Miami, FL.
- Wainwright, S. A. 1963. Skeletal organization in the coral, *Pocillopora damicornis*. *The Quarterly Journal of Microscopical Science* 104:169–183.
- Wainwright, S. A., W. D. Biggs, J. D. Currey, and J. M. Gosline. 1976. *Mechanical design in organisms*. Princeton University Press, Princeton.
- Woodland, D. J., and J. N. A. Hooper. 1977. The effects of human trampling on coral reefs. *Biological Conservation* 11: 1–4.