

## INDIRECT IMPACTS OF RECREATIONAL SCUBA DIVING: PATTERNS OF GROWTH AND PREDATION IN BRANCHING STONY CORALS

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### ABSTRACT

The highest recorded rates of recreational SCUBA diving occur on coral reefs at Eilat in the northern Red Sea, where many scleractinian corals are damaged by physical contact with divers. We compared coral skeletal growth and damage at sites that were protected vs unprotected from diving tourism, and identified tissue mortality through monthly monitoring of the branching stony coral *Acropora hemprichii* (Ehrenberg, 1834). We also monitored several genera of branching stony corals at sites that varied in levels of recreational diving. Major causes of tissue mortality in *A. hemprichii* were unknown (possibly bleaching and disease) and predation by the corallivorous snail *Drupella cornus* (Röding, 1798), both of which were much more frequent at heavily-dived than at undived sites. High frequencies of coral damage led to significantly slower coral growth at heavily-dived than undived sites. Annual rates of damage to branching corals were approximately twice as high at a site open to divers than at a closed site, and were intermediate at a site with restricted diving. The proportions of colonies infested by *D. cornus* increased significantly during the study year at sites open to divers but not at closed and restricted sites. We conclude that frequent mechanical injury by divers to coral colonies leads to enhanced susceptibility to predation and possibly to coral disease. Current levels of recreational diving at Eilat severely compromise the growth and survival of major reef-building corals, not only via direct mechanical damage, but also through a positive feedback loop of indirect effects on coral predators.

Tourism associated with coral reefs is on the rise worldwide, as the number of people learning to SCUBA dive increases every year (Davis and Tisdell, 1995; Barker and Roberts, 2004; Davenport and Davenport, 2006). In addition, the price of diving gear is decreasing, reefs are becoming more accessible, and facilities are improving. Consequently, ever-increasing numbers of people are visiting coral reefs (Hawkins and Roberts, 1993). Corals at sites with high diving intensities may become chronically damaged by divers kicking, touching, standing, trampling, and increasing sedimentation on the reef (Hawkins and Roberts, 1993; Barker and Roberts, 2004). Divers can cause breakage, tissue abrasion, and mortality of coral colonies (Zakai and Chadwick-Furman, 2002; Hasler and Ott, 2008).

The city of Eilat, Israel, is a popular tourist destination that attracts more than a million tourists every year, many of whom visit the small (3.5 km long) fringing reef area. Located at the northern tip of the Gulf of Aqaba, Red Sea (29°30'N, 35°00'E), this coral reef experiences the highest recorded rates of recreational diving (Zakai and Chadwick-Furman, 2002). Ten SCUBA shops operate in this small area and there are no limitations on diving at most reef sites. Wielgus et al. (2003) estimated the annual loss in potential tourism income due to the reef degradation at Eilat to be US\$2.86 million.

Riegl and Velmirov (1991) found that 11.2% of all scleractinian corals at Eilat were broken, which was higher than the 4% damage considered to be ecologically sus-

tainable (Hawkins and Roberts, 1997; Hawkins et al., 1999; Jameson et al., 1999). The condition of the Eilat reef has worsened since, and a 1996 survey revealed that 40%–80% of the coral colonies were physically damaged at heavily-dived sites (Zakai and Chadwick-Furman, 2002).

Most studies on effects of recreational diving on coral reefs have compared the condition of the reef among visited and unvisited sites using one-time surveys (Hawkins and Roberts, 1992, 1993; Tratalos and Austin, 2001; Zakai and Chadwick-Furman, 2002; Hasler and Ott, 2008). While this method may provide a snapshot of spatial variation in reef condition among sites, it yields limited information that includes percent live coral cover, numbers of loose fragments, and mean colony sizes (Hawkins and Roberts, 1992, 1993, 1997; Tratalos and Austin, 2001; Zakai and Chadwick-Furman, 2002). In contrast, long-term monitoring of individual coral colonies using time-series photographs can reveal processes of tissue damage, predation, disease, and breakage under various conservation regimes, and predict trends in reef dynamics (Rouphael and Inglis, 2002; Hawkins et al., 2005). While such detailed monitoring studies are laborious, they can serve as essential management tools that provide quantitative long-term data for the assessment of conservation policies.

Regulation of diving tourism is a sensitive economic and political issue, which may affect the livelihoods of many people, thus it is not surprising that reef managers sometimes have to fight an uphill battle for enforcement (Jameson et al., 1999). However, divers are willing to pay more to dive at pristine vs deteriorated reef sites (Wielgus et al., 2003). Thus, accurate evaluation of the ecological condition of diving sites is critical not only for effective management of healthy reef ecosystems, but also for the potential economic revenue they provide.

In the present study, we focused on determination of the effects of diving on branching stony corals, since previous studies indicated that these corals often are the most susceptible to damage by divers (Hawkins and Roberts, 1992, 1993; Rouphael and Inglis, 1997; Zakai and Chadwick-Furman, 2002; Hasler and Ott, 2008). In particular, colonies of the genus *Acropora* often bear the brunt of coral damage from trampling on reefs (Kay and Liddle, 1989). *Acropora hemprichii* (Ehrenberg, 1834) was selected as an indicator species because it is a dominant coral at 5–15 m depth in the Red Sea (Loya, 1972; Sheppard and Sheppard, 1985), and accounts for about 25% of live coral cover and 50% of branching coral cover on the reef slope of the Coral Beach Nature Reserve (CBNR) at Eilat (Guzner et al., 2007). Colonies of this species are delicate in structure and are the most frequently damaged *Acropora* corals at Eilat (Riegl and Velmirov, 1991). Populations of *A. hemprichii* in the Red Sea also are deteriorating due to their susceptibility to white syndrome disease and predation by the corallivorous gastropod *Drupella cornus* (Röding, 1798) (Antonius and Riegl, 1997). The abundance and percent cover of *A. hemprichii* correlate with the percent cover of stony corals at Eilat (Guzner et al., 2007), so this coral species may serve as an indicator of reef condition.

Here we describe major agents of injury and rates of skeletal growth vs loss in colonies of *A. hemprichii* at sites open vs closed to recreational SCUBA diving. We also compare rates of partial and complete tissue mortality, skeletal breakage, and predation on acroporid and pocilloporid branching corals among sites with different diving intensities within the CBNR, and discuss implications for the management of recreational diving on coral reefs.

## METHODS

**STUDY SITES.**—This study was conducted at 5–8 m depth on the coral reef slope of the CBNR at Eilat (Fig. 1), which is dominated by a diverse assemblage of branching acroporid and pocilloporid corals (Loya, 1972). Divers spend most of their time at the above depths due to reef topography within the CBNR (Zakai and Chadwick-Furman, 2002). All sites were within a few hundred meters of each other along a continuous fringing reef, and were about equidistant from major pollution sources near the city of Eilat (Fig. 1). Thus, they varied in human impacts mainly in terms of diving pressure, and were assumed to be free of other differential damages. The Closed site served as a reference, and was the only site fully protected from recreational diving. We selected five study sites: (1) Closed, inaccessible to recreational divers since 1992 (0 dives per year, immediately south of Japanese Gardens site in Zakai and Chadwick-Furman, 2002), (2) Restricted, open to a low frequency of up to 4000 dives per year (= Japanese Gardens site, Zakai and Chadwick-Furman, 2002), (3) Princess, medium frequency of about 6000 dives per year (= Tables site, Zakai and Chadwick-Furman, 2002), (4) Open, high frequency of about 8000 dives per year (= Central Reserve site of Zakai and Chadwick-Furman, 2002), and (5) Caves, very high frequency of about 16,000 dives per year (Zakai and Chadwick-Furman, 2002).

**MONTHLY MONITORING OF COLONIES OF *A. HEMPRICHI*.**—Four of the above sites also were monitored for patterns of coral growth and partial and complete mortality in colonies of the stony coral *A. hemprichii* (Fig. 1): Closed, Princess, Open, and Caves.

During July 2003, 20 undamaged large colonies of *A. hemprichii* (length > 10 cm) were selected haphazardly at each site by swimming in a straight line using a compass along ca. 50 m of the reef slope at 5–8 m depth. Each colony was photographed from above, mapped for further monitoring, and tagged without touching the coral to avoid damage. We carried plastic laminated photographs from the initial census on all subsequent surveys to assure that

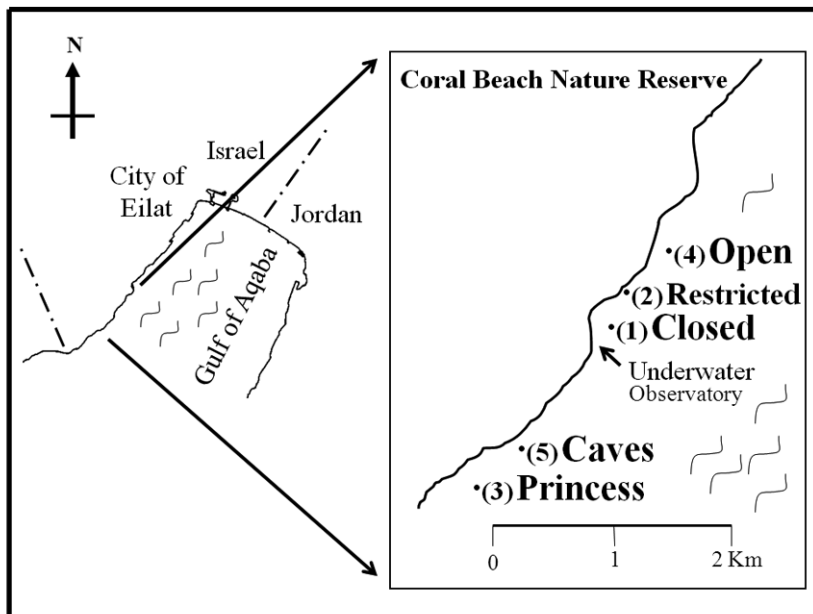


Figure 1. Map of five study sites within the Coral Beach Nature Reserve at Eilat, northern Red Sea. Sites are numbered in order of increasing frequency of recreational SCUBA dives per year: (1) Closed, (2) Restricted, (3) Princess, (4) Open, and (5) Caves. See text for details.

monitoring photographs from different dates were oriented at the same angle. A measuring tape was included in each photograph for scale. The corals were photographed monthly for 1 yr to quantify patterns and mechanisms of damage. Photographs were analyzed using *Image Tool* image analysis software (University of Texas Health Science Center, San Antonio, TX, USA). The width and length of each coral were measured from the photographs of the first and last censuses. Coral height could not be estimated directly from overhead photographs, so it was measured manually in the field at the beginning and end of the study year. Linear coral dimensions were converted to geometric mean radius (GMR, after Loya, 1976) according to the equation:  $GMR = 1/2 (\text{length} \times \text{width} \times \text{height})^{1/3}$ , and used to calculate approximate coral buoyant weight using the relation between GMR and buoyant weight of *A. hemprichii*: buoyant weight =  $1.27 (GMR)^{2.77}$  (Guzner et al., 2007). Colonies of *A. hemprichii* do not form spheres, but we used GMR because it accurately predicts colony buoyant weight (Guzner et al., 2007). Coral growth was calculated by comparing the estimated weight of each coral at the beginning and end of the study. Corals of different sizes may grow similarly in the linear dimension of GMR, but the total weight gain of large corals, which is a three-dimensional measure of growth, is much greater than that of small corals (Guzner et al., 2007). Conversion of coral sizes from GMR to weight allowed accurate estimation of coral calcification rates, which most precisely measure coral growth (Vago et al., 1997). Photographs of damaged colonies were analyzed to quantify the percent skeleton or tissue lost, which then was converted to estimated weight loss.

To determine the extent to which damage affected coral skeletal growth, we compared observed with expected growth for the 20 monitored corals at each site. If no damage was inflicted on the coral, then observed and expected growth were the same. In corals that experienced partial tissue mortality, the total coral skeletal dimensions (including bare dead skeleton) were used for expected growth. These corals grow in a symmetrical colony shape if not damaged. Thus, if skeletal breakage was observed on a coral, we estimated the missing area from the symmetry of the rest of the colony, and used the total coral dimensions if symmetrical, to calculate expected growth. Observed growth was calculated as the coral dimensions not including the areas of skeletal loss or bare skeleton with dead tissue, and thus was less than expected growth in damaged corals. Skeletal regeneration was not observed on colonies with partial tissue mortality, and broken colonies showed only minor regeneration at fractures during the study year. Thus, compensatory growth of regenerating damaged colonies was negligible within the time frame of this study. If the coral died, observed growth was negative initial colony weight, and expected growth was the one-year growth of a same-sized colony based on the known growth rate of *A. hemprichii* at Eilat: annual growth ( $g$ ) =  $0.087 \times \text{initial weight} + 50.615$  (Guzner et al., 2007).

We selected initially undamaged corals so that any damage occurring during the study year, and the causes of damage, could be determined in monthly observations. Damage agents were classified as: (1) predation by the corallivorous snail *D. cornus*, evidenced by scarred coral tissue or bare skeleton adjacent to *D. cornus* individuals (Gur, 1988; Al-Moghrabi, 1997), (2) mechanical breakage, evidenced by skeletal fracture and missing fragments (minor coral breakage < 5% of the colony was not included, and was attributed to natural causes such as fish nibbling, after Hawkins and Roberts, 1992), (3) colony dislodgment, observed as detachment of whole colonies from the substrate, and (4) unknown causes, observed as coral tissue damage, bleaching or lysis with no *D. cornus* present.

ANNUAL MONITORING OF BRANCHING ACROPORID AND POCILLOPORID CORALS.—At three of the above sites (Closed, Restricted, and Open, Fig. 1), we monitored all major genera of branching stony corals on the shallow reef slope: *Acropora* (mainly *A. hemprichii*), *Stylophora* [mainly *Stylophora pistillata* (Esper, 1797)], and *Pocillopora* [mainly *Pocillopora verrucosa* (Ellis and Solander, 1786)] (Loya, 1972). During July 2003, we marked 58–168 of these corals at each site ( $N = 338$  total). The number of corals monitored within each genus depended on their relative abundances. Colonies were selected haphazardly by swimming in a straight line using a compass along ca. 300 m of the reef at 6–8 m depth at each site. All large

(> 10 cm diameter) undamaged colonies belonging to the above genera were tagged. Each colony was photographed from above, mapped for further monitoring, and tagged without physical contact to avoid damage (as for *A. hemprichii* above). In addition, the presence of corallivorous snails (*D. cornus*) was recorded. A plastic ruler was placed adjacent to the coral in each photograph for scale. A second photographic census of the corals was conducted in July 2004. Laminated photographs from the initial survey were used to orient subsequent photographs. In the second census, all colonies were examined for amount of partial or complete tissue mortality, skeletal breakage and/or presence of *D. cornus* snails. Image Tool image analysis software (University of Health Science Center in San-Antonio, TX, USA) was used to quantify percent skeletal breakage and tissue mortality of the corals.

**STATISTICAL ANALYSES.**—Statistical analyses of the data were conducted using Statistica version 6 software (StatSoft Corporation, Tulsa, Oklahoma, USA). To assess whether observed coral growth rates varied significantly among the unprotected sites, we performed a non-parametric Kruskal-Wallis test. Mann-Whitney U-tests were used to examine differences in coral growth between the protected and unprotected sites, and differences in coral size between those damaged by *Drupella* snails and unknown causes. Tests of independence were applied to determine if coral fate (damaged vs undamaged) and the frequency of attack by *Drupella* snails (percent of corals attacked at the start vs the end of the study) depended on site (Closed, Restricted, Open). For statistical analyses, we pooled coral damage categories (breakage, partial and complete mortality) because sample sizes for injured colonies were small in some categories. All data are presented as means  $\pm$  1 standard deviation (SD), unless otherwise indicated.

## RESULTS

**MONTHLY MONITORING OF COLONIES OF *A. HEMPRICHI*.**—The amount of tissue damage on each affected colony varied with the agent of damage. Predation by the corallivorous snail *D. cornus* removed 3.7%–22.3% of the tissue on each affected colony, mechanical breakage 3.2%–14.4%, dislodgment 100%, and unknown causes 1.4%–100%. The total number of corals affected by each damage agent also varied widely. Unknown causes of damage, possibly coral bleaching or disease-mediated tissue lysis, affected the largest number of corals, followed by predation, both of which caused partial and total colony mortality (Fig. 2A). In contrast, predation by *D. cornus* caused greater loss of coral skeletal growth (total = ~900 g annual skeletal growth for the 80 corals examined, or 11.2 g per coral annually) than did unknown agents (loss of ~750 g total, or 9.4 g per coral annually, Fig. 2B). Corals that suffered substantial damage (> 5%) from unknown causes were significantly smaller ( $175 \pm 38$  g,  $N = 6$ ) than those attacked by *D. cornus* snails ( $692 \pm 176$  g,  $N = 5$ , Mann-Whitney U-test:  $P < 0.05$ ; Fig. 2C). Five (6.25%) of the monitored colonies suffered mechanical breakage, and only two (2.5%) colonies became dislodged during the study (Fig. 2A). However, dislodgment was responsible for more loss of coral skeletal growth than was mechanical breakage, because it caused the death of whole colonies (574 g lost to dislodgement vs 205 g to breakage for all 80 corals, or 7.2 vs 2.6 g per coral annually, Fig. 2B).

The total amount of lost coral growth due to all agents of partial mortality was 1251 g for the 80 colonies examined, vs 1594 g from total colony mortality (= 15.6 vs 19.9 g per colony per year). Initiation of damage was highly seasonal, and occurred mostly during the summer months (Fig. 3). During June–August, 15 (18.8%) of the

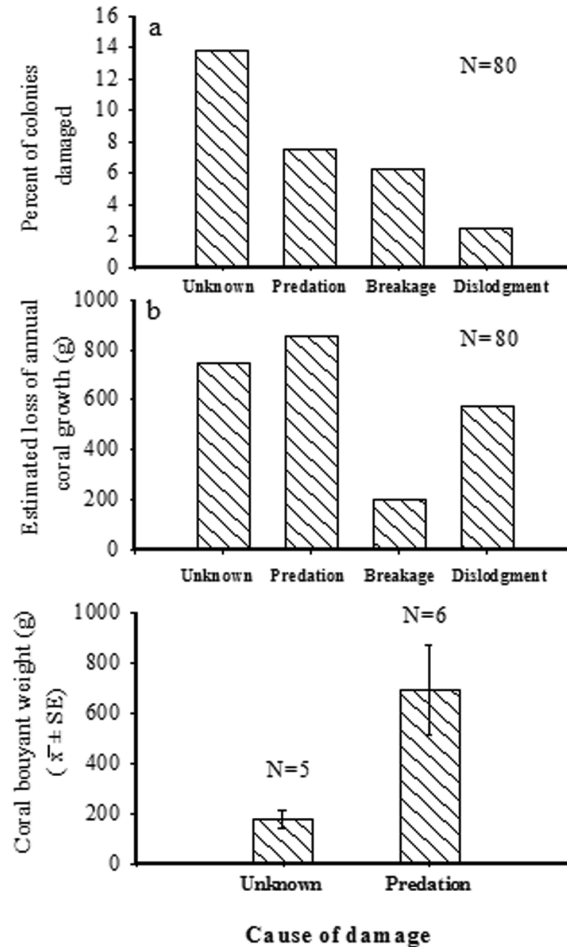


Figure 2. Patterns of damage to monitored colonies of the branching stony coral *Acropora hemprichii* at Eilat, northern Red Sea. (A) Percent of coral colonies damaged by each type of agent. (B) Loss of coral skeletal growth to all 80 monitored colonies caused by each agent. (C) Sizes of coral colonies that suffered damage from unknown causes and from predation by the corallivorous snail *Drupella cornus*.

colonies were damaged compared to only four (5.0%) during December–May, and only one colony (1.3%) in September–November.

In terms of variation in coral damage among sites, seven colonies (35.0%) at each of the three sites that were open to recreational SCUBA diving (Open, Princess, and Caves) were damaged during the year compared to only one colony (5.0%) at the Closed site (Fig. 4). At the Open site, four corals (20.0%) were colonized by predatory *D. cornus* snails (Fig. 4A) and suffered partial tissue mortality during the year (Fig. 4B). At known feeding rates by *D. cornus* snails (Gur, 1988), most of these corals were expected to die within a few months. In contrast to the other two sites, partial mortality was observed on only one coral (5.0%) at the Closed site (Fig. 4B) as a result of predation by a single large individual of *D. cornus* (Fig. 4A).

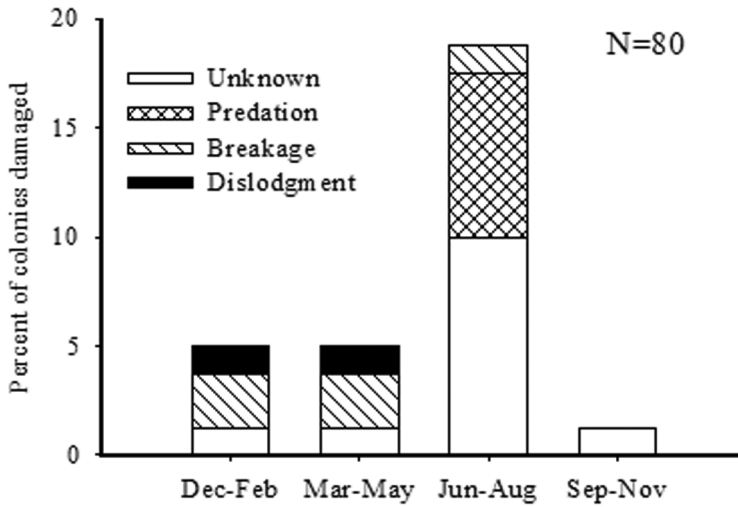


Figure 3. Seasonality of four types of damage to colonies of the branching stony coral *Acropora hemprichii* at Eilat, northern Red Sea. Note that most damage occurred during the summer (June–August).

Observed rates of annual coral growth varied widely among the sites examined. The annual increase in skeletal weight of *A. hemprichii* colonies at the Closed site was 2, 5 and 4× higher than at the Princess, Open, and Caves sites, respectively (Fig. 5A). Data on growth at the three latter sites were pooled because observed coral growth did not differ significantly among them (Kruskal-Wallis test:  $P = 0.65$ ). Observed annual coral growth at the Closed (protected) site was similar to that expected for undamaged colonies (see Methods,  $94.1 \pm 3.9$  g per colony per year vs  $97.1 \pm 3.4$  g, Fig. 5B). However, coral growth at the three unprotected sites was only  $27.7 \pm 7.4$  g per coral colony per year, much lower than the expected rate for colonies of these sizes ( $82.5 \pm 2.7$ , Fig. 5B). Thus, expected coral growth did not differ significantly between protected and unprotected sites (Mann-Whitney U-test:  $U = 448$ ,  $P = 0.09$ ), but observed growth was three times lower at unprotected than protected sites (Mann-Whitney U-test:  $U = 403$ ,  $P < 0.05$ ).

**ANNUAL MONITORING OF BRANCHING ACROPORID AND POCILLOPORID CORALS.**—Damage to genera of branching acroporid and pocilloporid corals varied significantly among the three examined sites (Table 1,  $R \times C$  test of independence:  $df = 2$ ,  $G = 10.63$ ,  $P < 0.01$ ). The lowest levels of coral damage were observed at the Closed site (20.8% of colonies) followed by the Restricted (32.8%) and Open (39.2%) sites. Total coral damage was almost twice as high at the Open vs Closed site (Fig. 6A, Table 1). Of the corals that suffered skeletal fracture, the percent skeleton removed from each colony was significantly higher at the Open site  $22.87 \pm 15.28\%$ , ( $N = 8$  corals fractured) than at the Closed site ( $7.16 \pm 5.98\%$ ,  $N = 6$  corals fractured, Mann-Whitney U-test:  $P < 0.05$ ).

At the beginning of the study in July 2003, 3%–9% of all examined branching stony corals contained individuals of the corallivorous snail *D. cornus* (Fig. 6B). The percent of corals attacked by individuals of *D. cornus* increased significantly during the

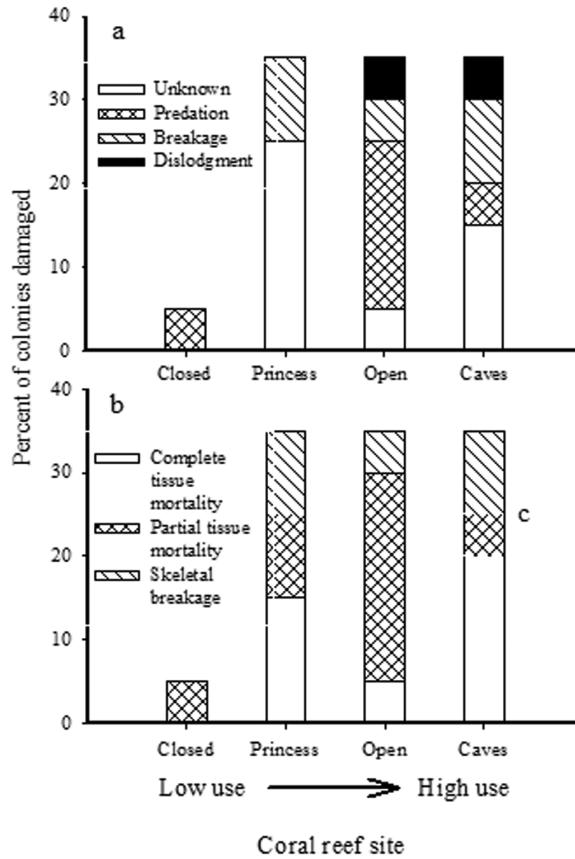


Figure 4. Variation in damage to colonies of the branching stony coral *Acropora hemprichii* among sites with different levels of recreational SCUBA diving. Classification of study sites from low to high use was based on Zakai and Chadwick-Furman (2002). N = 20 colonies examined per site. (A) Causes of damage. (B) Effects of damage.

study year at the Open, but not at the Closed and Restricted sites (G-test of independence:  $\chi^2 = 8.1$ ,  $P < 0.001$ ; Fig. 6B).

DISCUSSION

We reveal here that rates of coral tissue damage by predators and other agents on branching stony corals are much higher at heavily dived sites than at a protected reef site, leading to drastically reduced coral growth. Coral populations at the heavily-dived sites are deteriorating, and current conservation policies for these sites appear to be ecologically unsustainable.

High levels of coral damage caused by unknown agents during the summer may be due in part to seasonally high levels of coral disease and/or bleaching (Douglas, 2003), which are known to be linked to seawater temperature (Ben-Haim et al., 2003). Similarly, we observed that predation by *D. cornus* is also seasonal. The breeding season for these gastropods is May and June (Gur, 1988), and coral infestation



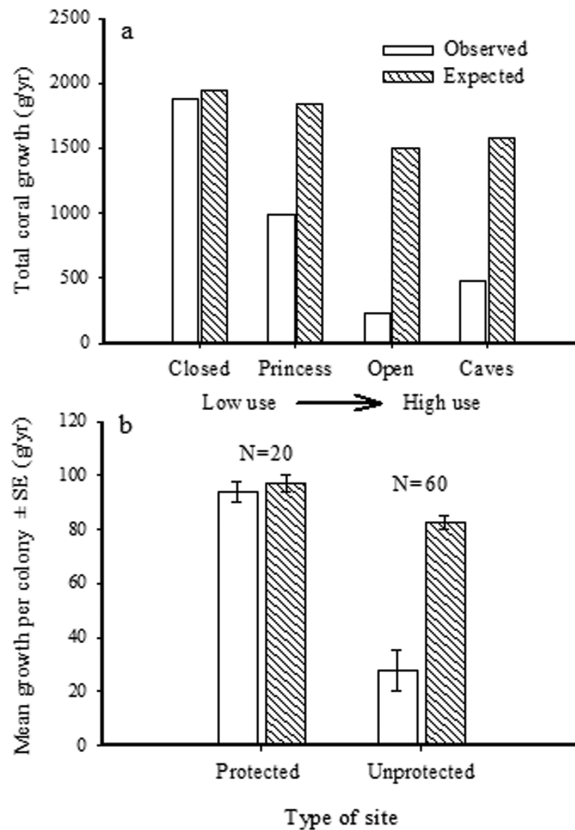


Figure 5. Comparison of expected vs observed growth of colonies of the branching stony coral *Acropora hemprichii* at Protected (Closed) and Unprotected (Open, Caves, and Princess) coral reef sites. Classification of study sites from low to high use in terms of recreational diving was based on Zakai and Chadwick-Furman (2002). (A) Total growth of all 20 colonies examined at each site. (B) Growth per coral colony. See text for details on growth estimates.

occurred during the subsequent summer months. The major role of predation as a damage agent to branching corals at Eilat is similar to the pattern on the Great Barrier Reef of Australia, where > 50% of injuries to acroporid and pocilloporid corals are caused by corallivorous gastropods *Drupella* spp. (Cumming, 2002). In contrast, no seasonal trends were observed in coral breakage except that none occurred in the fall.

Surprisingly, skeletal breakage was not the major cause of damage to branching corals at the heavily dived sites. The effects of divers on this coral assemblage were complex, and lead indirectly to increased predatory attack on the corals due to repeated creation of tissue lesions and possibly compromised physiological condition (Hawkins et al., 1999). These results show that the extent to which coral assemblages are affected by diving tourism may depend in part on the susceptibility of each coral species to pathogens and predators that take advantage of physiological stress. Our results are similar to those of previous studies showing that the effects of recreational diving on coral reefs depend on a variety of interacting factors. Coral assemblages dominated by branching corals are especially susceptible to diver damage due to their delicate and fragile structure (Hawkins and Roberts, 1992; Zakai and

Table 1. Variation in the fate of 338 branching stony coral colonies with site and coral genus in the Coral Beach Nature Reserve at Eilat, northern Red Sea. Undamaged large colonies were tagged in July 2003 and re-examined in July 2004. Damage includes both tissue mortality and skeletal fracture. The number of corals of each genus monitored at each site varied due to differences in their relative abundances.

Coral genus	Fate	Site			All sites
		Closed	Restricted	Open	
<i>Acropora</i>	Damaged	15	14	31	60
	Undamaged	62	30	57	149
	Total	77	44	88	209
<i>Stylophora</i>	Damaged	5	5	23	33
	Undamaged	14	6	26	46
	Total	19	11	49	79
<i>Pocillopora</i>	Damaged	3	0	10	13
	Undamaged	13	3	21	37
	Total	16	3	31	50
All genera	Damaged	23	19	64	106
	Undamaged	89	39	104	232
	Total	112	58	168	338

Chadwick-Furman, 2002; Rodgers and Cox, 2003). Divers can cause tissue lesions in addition to skeletal breakage on branching corals, through physiological stress and tissue dieback after abrasion and fractures from diver contact (Zakai and Chadwick-Furman, 2002). However, the abundance of massive corals also may be reduced at heavily-dived sites due to their relatively slow rates of growth and regeneration following repeated damage, in comparison with branching corals (Hawkins et al., 1999). Thus, some diving-impacted coral reefs may experience a reduction in hard coral cover due to a loss of branching corals, while others may lose massive coral cover. Moreover, some coral assemblages may experience no change or even an increase in coral cover due to the proliferation of weedy opportunistic coral species that take advantage of the reduced abundance of superior competitors (Hawkins et al., 1999; Roupheal and Inglis, 2002). The susceptibility of any given coral community to intensive recreational diving and repeated coral injury thus depends on local environmental conditions, community structure, and the types of coral predators and pathogens.

The relatively high vulnerability of small vs large coral colonies to tissue loss and disease is well-documented (Hughes and Jackson, 1980; Babcock, 1991; Meesters et al., 1996; Cumming, 2002; Nugues, 2002). In contrast, corallivores such as *D. cornus* select relatively large corals for attack, possibly because they provide better nutrition or more effective refuges from predation than do small coral colonies. Upon infection by *Drupella*, coral colonies invariably die within a few months (Gur, 1988). Consequently, although *Drupella* snails may damage fewer corals than do other agents such as coral disease, they attack larger corals and completely kill them, thus causing a larger amount of tissue loss.

The observed variation in infestation rates by *D. cornus* among our study sites may have been due in part to variation in the abundance of their preferred *Acropora* prey (Gur, 1988; Turner, 1994). A relatively high proportion of infested corals occurred at

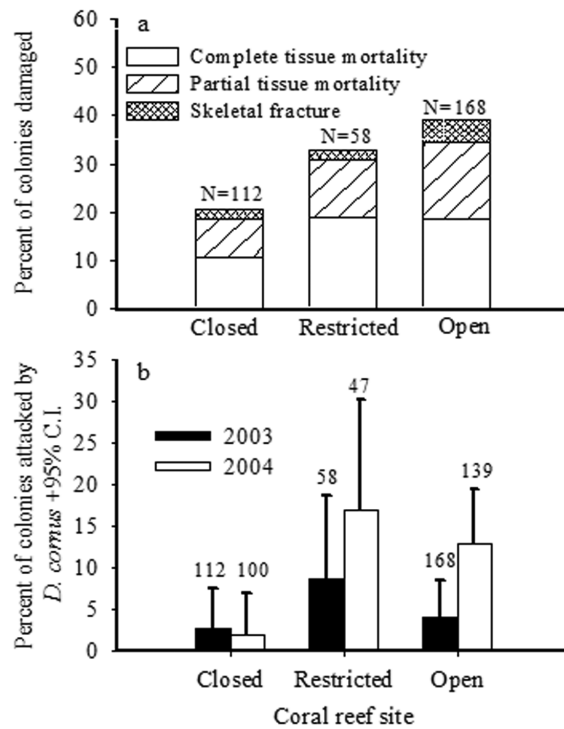


Figure 6. Variation in damage to branching stony coral colonies among sites with different levels of recreational SCUBA diving. (A) Effects of damage. (B) Percent of colonies attacked by the corallivorous snail *Drupella cornus*. Numbers above bars represent sample sizes of number of coral colonies examined.

the Restricted site, which also contained a high abundance of acroporids relative to the other sites examined. The increase in predation that we observed at dived sites during the study year resulted from the synergistic effects of a larger total number of infected corals in the second census, and the death of some corals that led to smaller coral populations. *Drupella* snails prefer to attack corals that are physiologically compromised (Morton et al., 2002), and coral colonies that have been injured previously are especially susceptible to predation (Turner, 1994; Cumming, 2002). The corals at sites open to diving lost almost a quarter of their skeletal mass to breakage during the study year (see Results). Some of these corals thus sustained large fractures, and breakage was not minor or limited to branch tips. Outbreaks of *Drupella* and other corallivorous gastropods tend to occur on coral reefs that are under prolonged stress (Knowlton et al., 1981; Turner, 1994; Antonius and Riegl, 1997; Morton et al., 2002). Predation by corallivores at heavily-dived sites in Eilat thus potentially could become a full-blown outbreak, in which a positive feedback loop between coral tissue damage and levels of predation (Fig. 7) causes *Drupella* to become a major agent of mortality to large acroporid and pocilloporid reef-building corals.

The five times slower observed coral growth at unprotected vs protected sites is alarming, and indicates substantially reduced reef calcification at sites that are heavily visited by recreational divers. This reduced growth occurred in a dominant Red

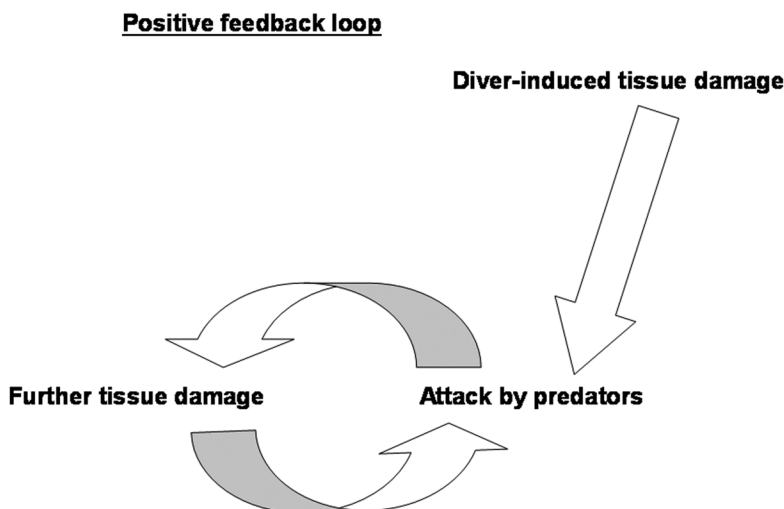


Figure 7. Positive feedback loop of damage to coral colonies at reef sites impacted by recreational diving. Removal of coral tissue by divers through abrasion and skeletal fracture initiates this loop. Then coral predators (especially individuals of the gastropod *Drupella* spp.) and potentially coral diseases and other agents preferentially attack corals that already have lesions of exposed skeleton (tissue loss) due to diver damage. Predators and other consumers of coral tissue increase the size of these lesions, leading to the attraction of more predators and other consumers. Positive feedback between tissue damage (exposed skeleton) and attraction of predators which cause further damage leads to a downward spiral in coral colony condition, ending in whole-colony mortality. Note that this loop is initiated and exacerbated by repeated creation of coral lesions through intensive diving tourism.

Sea reef coral, *A. hemprichii* (Loya, 1972; Sheppard and Sheppard, 1985), and indicates a need for major change in the management of these coral reefs.

In stony corals, energy is allocated first to tissue regeneration and colony maintenance and then to other colony processes such as sexual reproduction and defense against predation (Harrison and Wallace, 1990; Hall, 2001). Repeated injuries to coral colonies at heavily-dived sites thus are expected to reduce their ability to defend against pathogens and predators, and also to reduce their resource allocation toward sexual reproduction, leading to lowered coral fecundity (Zakai et al., 2000). Coral injury ultimately can cause reductions in the recruitment of juvenile corals to sink populations, because coral recruitment is driven by adult fecundity (Hughes et al., 2000). Moreover, small changes in fecundity could result in disproportionately large changes in recruitment, as recruitment correlates exponentially with fecundity (Hughes et al., 2000).

Several problems in our methods potentially limit the interpretation of our results. We did not collect data on the abundance and sizes of all branching corals at each site, and thus did not document potential variation in the vulnerability of each site to diver impacts or injury by *Drupella* snails. However, despite this potential variation in site vulnerability, we were able to document significant variation in coral damage with levels of diving intensity. We also examined only one reference site where recreational diving did not occur, because recreational use was allowed at all other coral reef sites in the Israeli Red Sea. This sampling design was suboptimal, because comparison between a reference location and treatments can be confounded by site-specific effects (Hurlbert, 1984). Variation in the degree of storm-generated wave

exposure, abundance of corallivorous fishes, boat anchoring, and other factors can vary among coral reef sites and impact rates of coral damage (Tilmant and Schmahl, 1981). However, storms are rare in the northern Red Sea and this region does not experience hurricanes as do other coral reef areas (Zakai and Chadwick-Furman, 2002). Boat anchoring is not allowed at any reef site within the CNBR. In addition, bite marks on corals from fishes are distinctive in appearance and were excluded from this study. As reviewed in our previous studies on effects of diving tourism on these coral reefs (Zakai and Chadwick-Furman, 2002; Guzner et al., 2007), no other factors clearly vary among these sites that could cause coral damage. All examined sites occurred along only 3 km of desert coastline in an enclosed sea, and thus all experienced similar environmental conditions. The major environmental difference between these five coral reef sites was the level of recreational diving use, which varied widely from zero to 16,000 dives per year (Zakai and Chadwick-Furman, 2002). Finally, we have quantified patterns of diver behavior, and observed divers to break the skeletons and abrade the tissue of stony corals at rates that can cause the levels of damage recorded here (Zakai and Chadwick-Furman, 2002). Therefore, despite some limitations to our methods, we feel that we have interpreted accurately the most likely factors to cause the coral damage patterns observed here. Further study is needed to explore the mechanisms by which divers may enhance predation on stony corals.

We conclude that a positive feedback loop appears to occur between frequent injury and susceptibility to further damage in stony corals, leading to acceleration of reef decline at heavily dived sites (Fig. 7). As such, the cumulative energetic and reproductive effects of repeated sub-lethal injury to corals by divers ultimately may be as important as whole-colony mortality in affecting coral community structure (Wahle, 1985).

The Restricted site at Eilat is the only local dive site with limited access by tourists. This site has been restricted to 4000 dives per year, which is below the estimated carrying capacity of Eilat reefs for diving tourism of 5000–6000 dives per year (Zakai and Chadwick-Furman, 2002). This study reveals that high rates of damage and predation on corals continue to occur at this site indicating that current limitations on diving activity are insufficient to protect branching coral populations. Thus, the annual carrying capacity for recreational SCUBA diving on coral reefs at Eilat may be considerably below 4000 dives per site, and local management policies need revision.

To ensure that these coral reefs are preserved for future generations, we recommend the following: (1) Reduce recreational SCUBA diving at most sites in the CNBR to allow coral populations to recover. Maintain annual levels of visitation well below 4000 dives per site. (2) Open new dive sites containing artificial reefs and divert as many tourist activities as possible to them. (3) Require pre-dive briefings and underwater supervision (guided dives) throughout the CNBR, both of which are known to reduce damage caused by divers (Barker and Roberts, 2004 and references therein). (4) Establish a program to monitor the population dynamics of key stony coral species, to assess long-term trends and allow early detection of reef decline. (5) Collect fees for diving activity to support the actual costs of maintaining healthy coral reefs (Hawkins et al., 2005), including effective monitoring of coral population dynamics and enforcement of sustainable levels of diving tourism. Recent studies indicate that recreational divers are willing to pay more to access high quality coral reefs, so establishment of a fee system based on dive site quality is likely to be feasible (Wielgus et al., 2003).

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