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# Effects of Recreational Scuba Diving on Caribbean Coral and Fish Communities

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**Abstract:** *Scuba diving on coral reefs is an increasingly lucrative element of tourism in the tropics, but divers can damage the reefs on which tourism depends. By studying the effects of diving we can determine what level of use is justifiable in balancing objectives of economic gain and conservation. Off the Caribbean island of Bonaire we compared coral and fish communities between undived reserves and environmentally similar dive sites where maximum use reached 6000 dives per site per year. At these levels of diving, direct physical damage to reefs was relatively minor. There were more loose fragments of living coral in dive sites than reserves and more abraded coral in high- than low-use areas. Diving had no significant effect on reef fish communities. Between 1991 and 1994, diving intensity increased 70% and coral cover declined in two of three dive sites and in all three reserves, suggesting a background stress unrelated to tourism. There was a significant decline in the proportion of old colonies of massive coral species within dive sites (19.2% loss), compared to a smaller loss in reserves (6.7%). Branching corals increased by 8.2% in dive sites, compared with 2.2% in reserves. Despite close management of reefs, diving is changing the character of Bonaire's reefs by allowing branching corals to increase at the expense of large, massive colonies. The impact of background stresses on massive corals seems to have been greater in the presence of diving. Other studies have linked disease infection to coral tissue damage, and the higher rates of abrasion we recorded in dived sites could have rendered corals there more susceptible to disease, thus mediating the decline of massive corals. Our study shows that even relatively low levels of diving can have pronounced effects manifested in shifts in dominance patterns rather than loss of overall coral cover. Bonaire's reefs have among the highest coral cover and greatest representation of ancient coral colonies of reefs anywhere in the Caribbean. Conserving the character of these reefs may require tighter controls on diving intensity.*

Efectos del Buceo Recreacional en Comunidades de Coral y Peces del Caribe

**Resumen:** *El buceo con tanques en arrecifes de coral es un elemento crecientemente lucrativo del turismo en los trópicos; sin embargo, los buzos pueden dañar los arrecifes de los cuales el turismo depende. Al estudiar los efectos del buceo podemos determinar que nivel de uso es justificable al balancear objetivos económicos y de conservación. En las afueras de la isla Caribeña de Bonaire comparamos comunidades de corales y peces entre reservas sin buceo y sitios ambientalmente similares con buceo y en los cuales el uso máximo alcanza los 6,000 buceadas por sitio por año. A estos niveles de buceo, el daño físico a los arrecifes fué relativamente bajo. Existieron más fragmentos sueltos de coral vivo en sitios de buceo que en las reservas y más coral lesionado en áreas de mucho uso que en las de poco uso. El buceo no tuvo un efecto significativo en las comunidades de peces de arrecife. Entre 1991 y 1994 la intensidad del buceo se incrementó un 70% y la cobertura de coral disminuyó en dos de los tres sitios de buceo así como en las tres reservas, sugiriendo un estrés de fondo no relacionado con el turismo. Existió un declive significativo en la proporción de colonias viejas de especies masivas de coral dentro de los sitios de buceo (pérdida de 19.2%) comparado con una pérdida menor en las reservas (6.7%). Los corales de ramas se incrementaron en un 8.2% en sitios de buceo comparado con*

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un 2.2% en las reservas. A pesar del manejo estricto de los arrecifes, el buceo está cambiando el carácter de los arrecifes de Bonaire al permitir el incremento de los corales de ramas a expensas de las colonias masivas. El impacto del estrés de fondo en los corales masivos aparentemente ha sido mayor en presencia del buceo. Otros estudios han relacionado enfermedades infecciosas al daño del tejido del coral y las tasas de abrasión altas que estimamos en los sitios de buceo podrían ocasionar que los corales sean más susceptibles a enfermedades y por lo tanto mediando la disminución de corales masivos. Nuestro estudio muestra que aún los niveles bajos de buceo pueden tener efectos pronunciados, manifestados en forma de sesgo en los patrones de dominancia en lugar de una pérdida general de la cobertura del coral. Los arrecifes de Bonaire tienen las coberturas más altas de coral y la mayor representación de colonias ancestrales de arrecifes que en cualquier lugar del Caribe. La conservación de las características de estos arrecifes requerirá de controles aún más estrictos sobre la intensidad del buceo.

## Introduction

Coral reefs are among the most diverse and spectacular of marine ecosystems. They occur predominantly in the waters of tropical, developing countries and provide a vital source of food and income for millions of people (Munro 1996). Although the gross primary production by reefs is enormous, net fishable productivity is limited, and there is now widespread evidence of adverse ecosystem-level consequences of intensive overfishing (Roberts 1995; Polunin & Roberts 1996).

There is an urgent need to find income-generating alternatives to extractive use of coral reef resources (Birkeland 1997). Tourism is perceived as the alternative with potential to provide the greatest revenues (Cesar 1996; Vogt 1996; Hodgson 1997). It brings economic benefits to local communities and may help protect reefs by providing an incentive to conserve them. Many studies have shown, however, that tourism causes significant damage to reefs (Salvat 1987; Roberts & Harriott 1994; Prior et al. 1995; Roupheal & Inglis 1995; Allison 1996; Harriott et al. 1997; Medio et al. 1997; N. Chadwick-Furman, unpublished data). To ensure long-term viability, it is important that tourist use is kept below damaging levels, but few studies have provided guidance on sustainable reef capacity (but see Hawkins & Roberts 1992a, 1994, 1997; Dixon et al. 1993). We examined how one of the most popular manifestations of coral reef tourism, scuba diving, has affected reefs of the Caribbean island of Bonaire. Our findings shed new light on the question of how to balance conservation and economic development of reef resources.

In terms of coral cover, biodiversity, and fish communities, Bonaire has some of the best coral reefs remaining in the Caribbean (Ginsburg 1994). With tourism a mainstay of the island's economy, recreational divers form a majority of the visitors and contributed approximately \$32 million in revenues in 1991 (Dixon et al. 1993). The people of Bonaire are aware of the value of their reefs and, recognizing potential threats from tourism and development, established the Bonaire Marine

Park in the early 1980s (Fallon Scura & van't Hof 1993). Management of the park is achieved through a combination of user regulations, such as a prohibition on spearfishing, and zoning of activities. Damage caused by boat anchors was identified as a key threat, so mooring buoys were established at all dive sites when the park was established (van't Hof 1983). The park is supported by user fees levied on recreational divers (Dixon et al. 1994), and wardens patrol daily to ensure compliance with regulations.

In 1991, when the reef was faced with a rapidly increasing number of divers, the World Bank commissioned a study to examine how diving was affecting the island's reefs (Dixon et al. 1993; Fallon Scura & van't Hof 1993). The study concluded that sites had a carrying capacity of between 4000 and 6000 dives per year and that increases in diving intensity above this level could result in unacceptable damage to reefs. By 1994 diving intensity had increased to the point where some areas were being dived close to 6000 times per year.

Effects on fish communities are especially interesting given that, under the supervision of dive guides, divers are allowed to feed fish in Bonaire. There has been much controversy over but little study of whether or not this activity is harmful. In some marine parks it has already been banned (e.g., Saba Marine Park in Netherlands Antilles and Ras Mohammed Marine Park in Egypt). Feeding fish might alter the natural composition of the reef community, adversely affecting certain fish populations while favoring others, notably predatory species such as snappers and moray eels (Sweetman 1996). Indirectly, it might even affect corals and other invertebrate communities, but Sweetman's (1996) study of the effects of tourist pontoons on Great Barrier Reef fish and coral communities suggested that this was not the case. Feeding may also make fish behave aggressively toward divers, attacking them in anticipation of food. People in favor of feeding fish argue that it is a popular attraction that can be used to concentrate diver activity away from more vulnerable areas of reef. At the time of the study, fish in Bonaire were regularly fed by dive guides, and or-

ganized tours were available specifically for the purpose of feeding and touching fish.

To determine the effects of diving on coral and fish communities, we compared heavily used areas of dive sites with less-well-used areas close by. We compared dive sites and environmentally similar nondived reserves. In addition, we repeated the 1991 survey of Dixon et al. (1993) to evaluate changes in reef communities attributable to diving.

## Methods

### Site Descriptions

We used the same sites used by Dixon et al. (1993): three popular diving sites located off Klein Bonaire and three reserve sites (Fig. 1). The dive sites were well offshore, and reserve sites were located off the island's little-developed north shore. Hence, none of the study sites were subject to direct impacts from pollution or land-based development (although an oil transshipment facility lies close to one of the reserves). The dive sites included two of the most heavily used in Bonaire, Jerry's Jam and Carl's Hill, and a third moderately used site, Forest. Jerry's Jam and Carl's Hill received 5101 and 5074 dives respectively in 1993, whereas Forest was dived 3850 times. The reserve sites were Slagbaai, Boca Cañon, and Karpata, which apart from a few violations prior to 1992 have been closed to diving since the park was established. They were originally selected so that each reserve site corresponded to a particular dive site in terms of similar location, exposure to waves, and reef structure (Fig. 1), and these paired comparisons with dive sites were intended to be used in monitoring studies (Fallon Scura & van't Hof 1993). Artisanal fishing is permitted in both dive sites and reserves, but levels are low, particularly in the dive sites.

All sites share a similar topography. The shallow zone slopes gently to a reef edge, approximately 10 m deep, after which the reef slopes more steeply, merging into a sandy seabed at approximately 40–45 m. At dive sites, mooring buoys are set at a depth between 5 and 8 m.

### Effects of Diving on Coral Communities

Comparisons were made between areas of high versus low diver use at each of the three dive sites. Divers tend to follow the reef in either direction from the mooring buoy, typically swimming out more deeply and returning in shallower water. In general, a greater proportion of their dive is spent in the vicinity of the mooring buoy because divers descend and ascend there. Hence, measures of diving intensity were based on distance from the mooring buoy, with high-use areas designated 5–25 m away and low-use areas 80–100 m away. For high-use

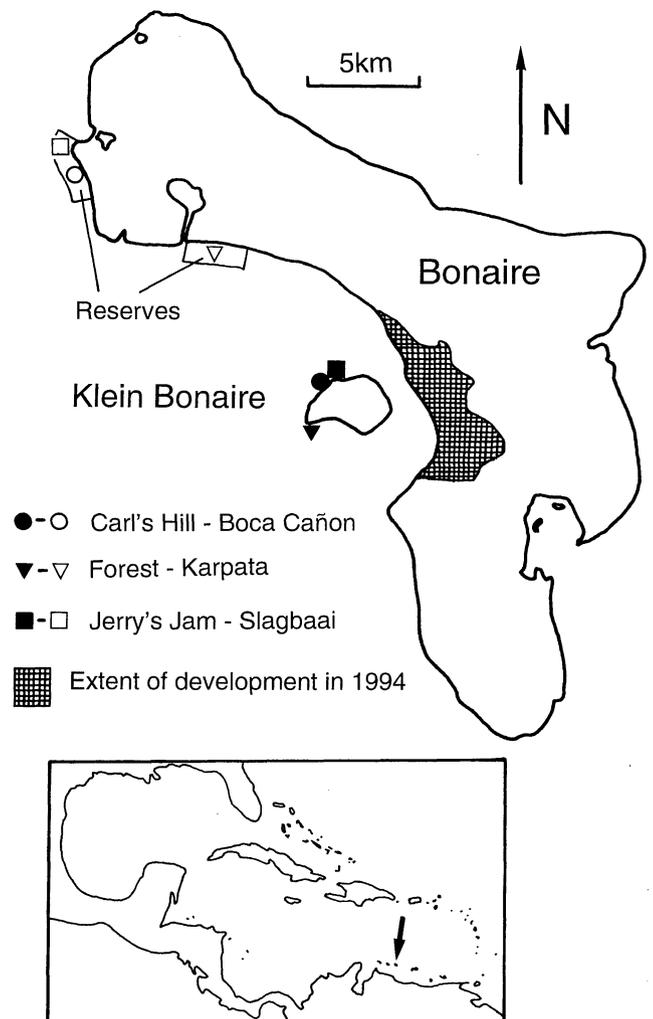


Figure 1. Map of Bonaire showing position of dive sites studied (filled symbols) and ecologically similar paired reserve sites (open symbols). The arrow on the inset map indicates the location of Bonaire in the Caribbean.

areas, sampling began 5 m from the mooring to avoid areas of localized damage caused by dragging moorings. Coral communities were sampled along a tape measure laid along the top of the reef slope at a depth of 10 m. Within each level of diving intensity, 30, 1-m<sup>2</sup> quadrats were sampled randomly from within a 20 × 10 m block centered around the tape measure.

For the reserve sites, locations sampled corresponded exactly to those described by Dixon et al. (1993). At the point of entry, the tape measure was attached to the reef edge at a depth of approximately 10 m and unwound for 20 m following this depth contour. Only one area was sampled in each of the reserve sites, and a total of 30 quadrats was sampled at each.

The following variables relating to hard (scleractinian) corals and *Millepora* species (a stony hydrozoan coral)

were then recorded: numbers of (1) exposed colonies (i.e., those not concealed in crevices or under overhangs), (2) species, (3) broken colonies, (4) abraded colonies, (5) loose fragments of living coral, (6) living fragments reattached to the substratum, and (7) partially dead colonies. The total percent cover of hard corals and branching corals was also estimated.

To repeat Dixon et al.'s study, we took photographs of 1-m<sup>2</sup> quadrats at 3-m intervals along the 10-m depth contour, for a distance of 110 m at all study sites. We extended Dixon et al.'s survey by taking a further series of photographs between 200 m and 300 m from each diving buoy. To analyze the effect of usage (dived areas versus reserves), we compared the first 15 photographs taken at each of the reserve sites and dive sites (corresponding to high-use areas at dive sites). To assess the effects of diving within sites, we used distance as a proxy for diving pressure and compared the first 15 photographs (5–47 m away from the dive buoy), corresponding to the highest levels of diver pressure, with a series of 15 photographs at middle (80–122 m) and far (225–267 m) distances from the mooring buoy to assess the effects of medium and low levels of diving intensity.

Photographic slides were later projected onto sheets of paper, and different scleractinian corals plus *Millepora* visible were identified to species and traced onto the paper to delineate colony areas. From these paper sketches, Sigma-Scan® software was used with a Summasketch II digitizing tablet to obtain the percentage of live coral cover and the percent cover of branching and massive corals. From the photographs, we noted species richness (number of species) for each quadrat and species and calculated diversity using the Shannon-Weiner index,  $H'$ .

The effects of diving activity (high versus low use) and site on the variables measured underwater and from the photographs were analyzed by two-way analysis of variance (ANOVA) and analysis of covariance (ANCOVA). A three-way ANOVA was performed on data derived from our photographs and those taken by Dixon et al. in 1991 to assess changes over time. Because among-site differences in coral communities could affect levels of damage independently of diving pressure (sites differ in susceptibility to damage), ANCOVAs were performed to isolate diver effects from such site effects. For numbers of species, abraded coral colonies, and partially dead coral colonies, the total number of colonies present was used as the covariate. For numbers of broken corals, loose fragments of live coral, and fragments reattached to the substratum, percent cover of branching coral was the covariate. We did this because previous studies have shown that branching corals are the most vulnerable to breakage and generate many fragments capable of reattaching to the reef (Highsmith 1982; Liddle & Kay 1987; Hawkins & Roberts 1993).

All variables were tested for normality and equality of

variance prior to analyses. Percentage values for coral-cover data were arcsine-square-root-transformed, and numbers of broken coral colonies, loose fragments of live coral, and colonies reattached to the substratum were square-root-transformed before analyses.

### Effects of Diving on Fish Communities

Fish communities were sampled at the same sites as coral populations but at two depths, 5 m and 15 m. Within the three dived sites, three counts were made at each depth at high- and low-use areas, that is at distances of 5–25 m and 80–100 m from the mooring buoy, respectively. Within each of the three reserves, six counts were made at each depth.

Fish communities were sampled by the stationary point-count method developed by Bohnsack and Bannerot (1986). At each point sampled, a 10-m-long tape measure was placed onto the reef to delineate an imaginary cylinder with a 5-m radius, extending upward above the reef for a distance of 5 m. All fishes observed within or passing through this cylinder were counted for 15 minutes. The lengths of all individuals of commercially important species were estimated visually to the nearest centimeter. This enabled later calculation of the weight (biomass) of fishes present in the counted area by means of length-weight relationships for the species observed (Bohnsack & Harper 1988). Previous studies have shown that this method provides accurate estimates of numbers and biomass of fishes present (Polunin & Roberts 1993).

To characterize the habitat at each point sampled (an area of 78 m<sup>2</sup>), we visually estimated percent cover of the dominant components of reef substrata, including hard corals, gorgonians, sponges, turf algae, and so forth. In addition, we estimated the structural complexity of the substratum, which is known to have an important influence on fish community structure (e.g., Roberts & Ormond 1987), on a six-point scale: 0, no vertical relief; 1, low and sparse relief; 2, low but widespread relief; 3, moderately complex; 4, very complex with numerous caves and fissures, and 5, exceptionally complex with high coral cover and numerous caves and overhangs. Structural complexity was used as a covariate in ANCOVAs of fish numbers and biomass.

Comparisons of the effects of diving on fish communities were made by ANOVA. Three-factor ANOVAs were used to compare populations at diving sites (factors were site, depth, and use) and between diving sites and reserve areas. For coral community analyses, sites were divided into three groups, each containing a dive site and a paired control reserve site. Factors included in the ANOVA were group, depth, and diving level (dived versus reserve). Substratum composition at the different sites was analyzed by the same method.

## Results

### Effects of Diving on Coral Communities

Within dive sites there was very little difference in levels of damage to corals between high- and low-use areas. The only significant differences were in numbers of abraded and partially dead coral colonies (two-way ANOVA,  $p < 0.01$  and  $p < 0.05$ , respectively). There were more abraded corals in high-use than in low-use areas, consistent with abrasion being caused by divers. By contrast, there were more partially dead corals in low-use than in high-use areas, although differences were small. There were also significantly more partially dead colonies at the two more heavily used diving sites than at the moderately used Forest. Overall, levels of damage to corals were very low, with only around 1 colony in 40 (2.5%) broken. Combining broken and abraded colonies, only 2.7% of colonies had been damaged. Coral communities near the moorings did not differ significantly from those far from the moorings in terms of cover, numbers of species, colonies per square meter, or percentage branching cover.

Results from the photo analyses, where the lowest-use areas sampled were even further from mooring buoys, showed no significant effect of diver use on species diversity either within or between sites. There was, however, one-fifth less coral cover (two-way ANOVA,  $p < 0.05$ ) in areas most heavily used by divers (5–47 m from mooring buoys) than at areas further from the mooring (80–122 m and 226–267 m).

The only significant difference in damage between high-use areas of dive sites and undived reserves was more loose fragments of living coral at dived sites (Table

1), due primarily to the much higher levels at Jerry's Jam than at Slagbaai. For the other two groups of sites, there was virtually no difference. By contrast, there were several notable differences among coral communities. Reserves had significantly higher coral cover (Fig. 2), whereas dive sites had a greater proportion of branching corals and tended to have a greater number of species per square meter than reserves, although the number of colonies per square meter did not differ significantly (Table 1).

Coral cover changed at both dive sites and reserves between 1991 and 1994 (Table 2; Fig. 3). At the five sites where coral cover was high in 1991 (two dive sites and all three reserves), there were marked reductions in overall cover (Fig. 3). At Carl's Hill, however, where cover had been anomalously low in 1991, it had almost doubled by 1994. Averaged across all three dive sites, net change in cover was 0% between 1991 and 1994. Averaged across the three reserves, there was a 12.6% net loss of coral cover (one-fifth of the cover present in 1991). Despite a 70% increase in diving intensity over this period (63,621 dives in 1991 compared to 108,274 in 1994), there was no evidence of diving effects on total coral cover.

There was a subtle but important effect of diving on coral community composition (Table 2; Fig. 4). The proportion of massive corals that made up cover fell at both dive sites and reserves (Fig. 4a), but the fall was much greater at dive sites (19.2% loss vs. 6.7% loss). Concurrently, the proportion of branching coral that made up cover in diving sites increased much more than it did in reserves (8.2% increase vs. 2.2% increase; Fig. 4b). Coral diversity ( $H'$ ) and species richness showed a similar pattern, both increasing by a much greater margin in dive

**Table 1.** Significance ( $p$  values) of two-factor ANOVA showing differences in damage measures and community structure between high-use areas of dive sites and undived reserves in the coral study.

Variable (covariate)	Group <sup>a,b</sup>	Use <sup>a,c</sup>	Direction of effect <sup>c</sup>	Covariate	Interactions <sup>d</sup>
	p	p		p	p
Broken coral	ns	ns		none	ns
Loose fragments of living coral (percent branching coral cover) <sup>d</sup>	<0.005	< 0.005	dived > reserve	<0.001	use × group < 0.001
Reattached coral colonies (percent branching coral cover) <sup>d</sup>	<0.05	ns		<0.001	use × group < 0.02
Number of coral colonies	<0.001	ns		none	use × group < 0.001
Abraded coral (number of colonies)	ns	ns		<0.05	ns
Part dead coral (number of colonies)	<0.01	ns		<0.001	ns
Percent coral cover <sup>d</sup>	ns	<0.001	dived < reserve	none	ns
Percent branching coral cover <sup>d</sup>	<0.01	<0.005	dived > reserve	none	ns
Number of species	ns	<0.001	dived > reserve	none	use × group < 0.001

<sup>a</sup> ns, not significant.

<sup>b</sup> Differences among the three paired dive-site and undived-reserve groups. Paired dive-site and reserve groups consisted of Jerry's Jam-Slagbaai, Carl's Hill-Boca Cañon, and Forest-Karpatha.

<sup>c</sup> Differences in damage measures and community structure between high use dive areas and reserves. The direction of "Use" effect shown in "direction of effect" column where the difference was significant.

<sup>d</sup> Arcsine-square-root-transformed prior to analysis.

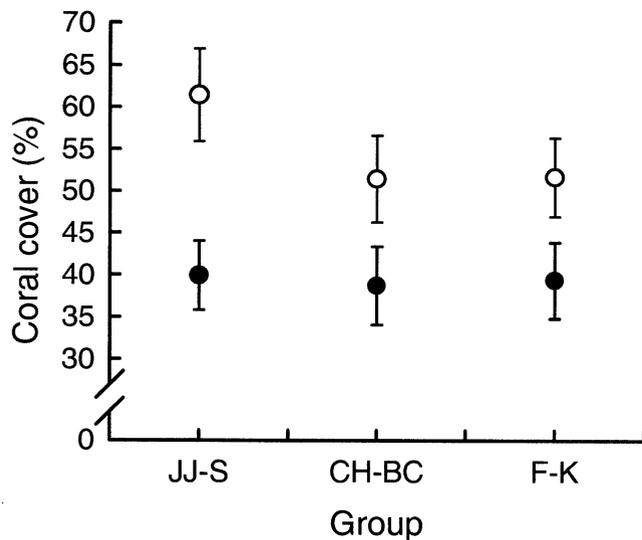


Figure 2. Comparison of total percent coral cover between high-use areas of dive sites (filled circles) and reserves (open circles) (JJ-S, Jerry's Jam-Slagbaai; CH-BC, Carl's Hill-Boca Cañon; and F-K, Forest-Karpata). Figures show means  $\pm$  standard error.

sites than in reserves (Fig. 5c & d). These trends all point toward increased disturbance of Bonaire's reefs from 1991 to 1994, but with greater disturbance in dive sites than in reserves (Table 2, significant use  $\times$  time interactions).

### Effects of Diving on Fish Communities

The larger-scale sampling of coral communities conducted in association with fish counts confirmed the findings of the quadrat-based studies of coral community composition. Reef habitat in areas heavily used by divers was more disturbed than that in areas less well used, with significantly lower hard coral cover (three-factor ANOVA,  $p < 0.03$ ), more gorgonians ( $p < 0.05$ ), and more sand ( $p < 0.01$ ) in high use areas.

Notwithstanding these differences in habitat, compari-

sons of fish abundance in high- versus low-use areas showed a significant difference only for groupers (three-factor ANOVA,  $p < 0.04$ ). The difference was small, however, with an average of  $2.8 \pm 0.4$  (SE) individuals per count in high-use and  $4.2 \pm 0.5$  in low-use areas. When fish sizes were converted to biomass, there were no significant differences between areas of different diving intensity for any of the families examined (Fig. 5). Nor was there any significant difference in total number of species (all diurnal noncryptic species present) observed per count at either depth between high- and low-use areas. On average there were  $33.4 \pm 0.9$  per count in high-use areas and  $34.4 \pm 1.1$  in low-use areas.

Once again the fish study confirmed at a larger scale the differences in habitat detected between dive sites and reserves in the quadrat-based study. Reserves had significantly "higher quality" habitat than dived sites, particularly higher coral cover (three-factor ANOVA,  $p < 0.004$ ), greater structural complexity ( $p < 0.001$ ), and less sand ( $p < 0.001$ ) and bare rock ( $p < 0.001$ ).

Given these habitat differences, it would be surprising not to find some differences in fish communities between dive sites and reserves. There were significantly more snappers (three-way ANOVA,  $p < 0.003$ ), surgeonfishes ( $p < 0.003$ ), and fish overall ( $p < 0.001$ ) in reserves than in dive sites. Contrary to the expectation that dive sites would have more predatory fishes (due to fish feeding), the biomass of predators was greatest in reserves (although not significantly so; Fig. 6). This was due almost entirely to higher abundance of yellowtail snapper (*Ocyurus chrysurus*) in reserves, an average of  $2.5 \pm 0.7$  kg of snappers per count compared with  $1.1 \pm 0.2$  kg per count in dive sites. The biomass of groupers was almost identical between reserves and dived sites, averaging 1.3 kg per count in both.

Most of the difference between dived sites and reserves for surgeonfishes, and herbivores overall, arose from their much greater abundance at Boca Cañon reserve than anywhere else (Fig. 6). Large amounts of algal-covered rubble, originating from a die-off of stagshorn coral (*Acropora cervicornis*) in the mid-1980s, provided abundant food for grazing herbivores at this site. Hence,

Table 2. Significance ( $p$  values) of three-factor ANOVA showing differences in five attributes of coral communities in relation to use, group, and time.

Variable	Use <sup>a</sup> (p)	Direction of effect	Time <sup>b</sup> (p)	Direction of effect	Group <sup>c,d</sup> (p)	Interactions <sup>d</sup> (p)
Coral diversity	<0.01	dived > reserve	<0.01	1991 < 1994	ns	ns
Number of coral species	<0.01	dived > reserve	<0.01	1991 < 1994	<0.01	use $\times$ time < 0.01
Percent coral cover <sup>e</sup>	<0.01	dived < reserve	<0.01	1991 > 1994	<0.01	use $\times$ time < 0.01
Percent massive coral cover <sup>e</sup>	<0.01	dived < reserve	<0.05	1991 > 1994	<0.01	use $\times$ time < 0.05
Percent branching coral cover <sup>e</sup>	<0.01	dived > reserve	<0.01	1991 < 1994	<0.01	use $\times$ time < 0.01

<sup>a</sup>Dive site versus reserve site.

<sup>b</sup>1991 versus 1994.

<sup>c</sup>Paired dive-site and reserve groups consisted of Jerry's Jam-Slagbaai, Carl's Hill-Boca Cañon, and Forest-Karpata.

<sup>d</sup>ns, not significant.

<sup>e</sup>Figures for percent cover were arcsine-square-root-transformed prior to analysis.

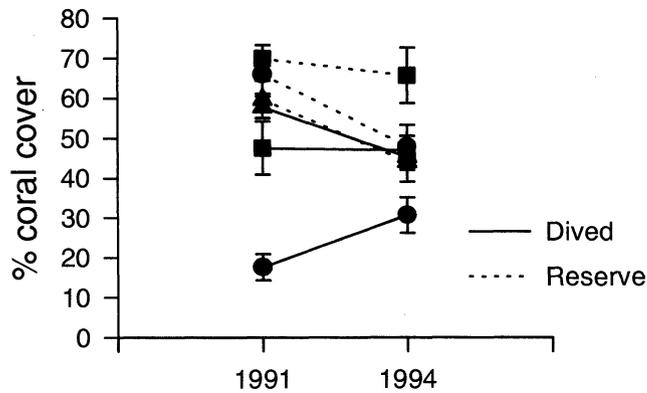


Figure 3. Changes in total coral cover between 1991 and 1994 in high-use areas of dive sites (5–47 m from mooring buoy) and paired reserve sites: square, Jerry's Jam-Slagbaai; circle, Carl's Hill-Boca Cañon; and triangle, Forest-Karpata. Figures show means  $\pm$  standard error.

the difference in surgeonfish and herbivore numbers overall between reserve and dived sites is unlikely to have anything to do with diving or protection from it.

There was a slight but significant difference in the total number of fish species per count between dived and reserve sites, with an overall average of  $33.9 \pm 0.7$  in dive sites and  $34.9 \pm 0.9$  in reserves. There was also a significant difference among groups, the Forest-Karpata group having higher species richness than the other two (Forest-Karpata,  $36.7 \pm 0.8$ ; Carl's Hill-Boca Cañon,  $33.8 \pm 1.1$ ; Jerry's Jam-Slagbaai,  $32.7 \pm 0.8$ ).

## Discussion

Our study provided a unique opportunity to examine the effects of scuba diving on coral reefs. We were able to compare dived and undived reefs that had been matched for similarity of ecological conditions prior to large-scale expansion of recreational diving. Several key points emerge. First, levels of damage to coral colonies were similar between high-use and low-use areas within dive sites and also between dive sites and undived reserves. This suggests that diving at present intensities does little obvious physical damage to corals or that reserves are subject to other sources of damage not occurring at dive sites. An element of both explanations seems likely. Absolute levels of damage were much lower than on the more heavily dived reefs of Egypt and Israel, where around 10% of colonies were broken (Riegl & Velimirov 1991; Hawkins & Roberts 1992b), and were similar to those of the less heavily dived Saba, where an average of 2.8% of colonies were damaged (Hawkins et al. 1993; Hawkins & Roberts 1997). This suggests that, based on measures of recent physical breakage, the Bo-

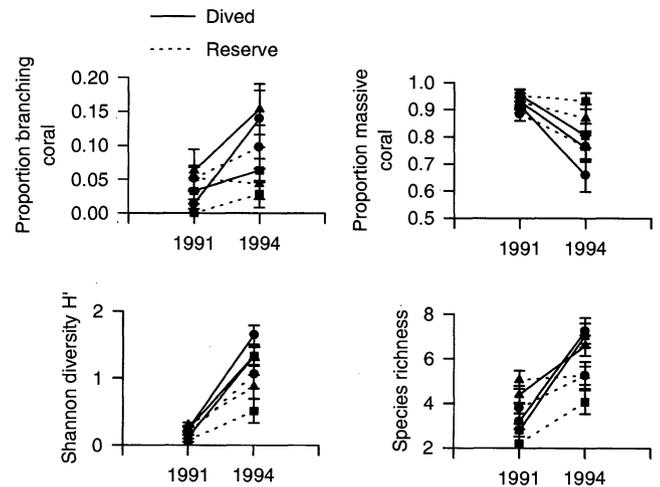


Figure 4. Changes in coral communities between 1991 and 1994 in high-use areas of dive sites (5–47 m from mooring buoy) and paired undived reserves: square, Jerry's Jam-Slagbaai; circle, Carl's Hill-Boca Cañon; and triangle, Forest-Karpata. Figures show means  $\pm$  standard error. Scales differ among graphs.

naire reefs are in good condition. The lower coral cover and higher diversity close to moorings on the photo-quadrat study support the conclusion that high-use areas were subject to greater disturbance. Damage in reserve sites cannot be attributable to diving and is most likely caused by fishermen dropping their small, stone anchors in reserves when fishing some distance away in open water (park regulations allow boats <3.6 m to drop a small, stone anchor). Fishermen do not tend to fish around dive sites, and dive boats are not allowed to drop anchors, so anchoring is a minor source of damage in dive sites. These small, stone anchors, although capable of breaking corals, cause nothing like the damage created by large, steel ones dropped by yachts and diving boats in the past.

Second, we found marked differences in coral community structure between dive sites and reserves, showing that divers can have effects other than breaking corals. Dixon et al. (1993) attributed lower coral cover at dive sites to anchoring prior to installation of mooring buoys in the early 1980s. They suggested that higher diversity, lower coral cover, and a greater proportion of branching corals in dive sites were a consequence of past anchor damage opening up space by destroying some of the massive coral colonies that normally dominate Bonaire's reefs. These areas were in the process of being recolonized by new coral growth, especially the rapidly growing branching species such as *Millepora* spp. and *Madracis mirabilis*. The greater amount of space available promoted species diversity as new colonies from a wide range of species settled and became established.

The changes we detected between 1991 and 1994

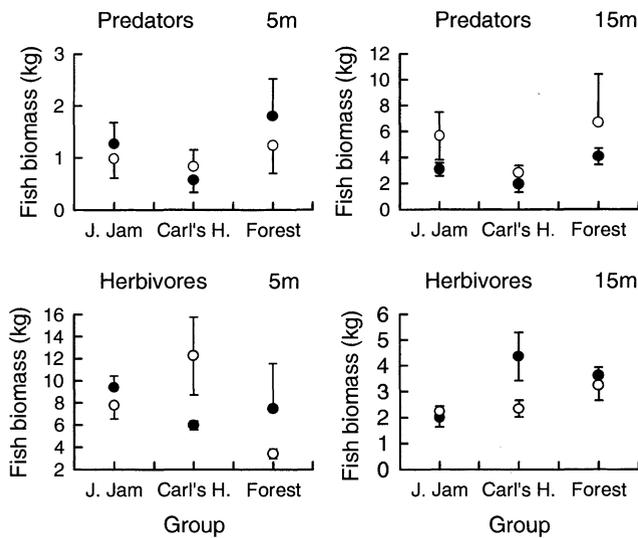


Figure 5. Comparison of fish biomass between high-use (filled circles) and low-use (open circles) areas of dive sites. Figures show means  $\pm$  standard error. Predators include all species of the families of groupers, snappers, and grunts. Herbivores include parrotfishes and surgeonfishes. Scales differ among graphs.

show that over this period dive sites suffered no greater loss of coral cover than reserves and in fact fared rather better. A study by Bak and Nieuwland (1994) at a different reserve in Bonaire found a 44% loss of coral cover at 10 m over the period 1973 to 1992, confirming the background of stress detected by our study. Caribbean reefs have undergone several large-scale disturbances in recent years. A mass die-off of *Diadema* sea urchins occurred in 1983 (Lessios 1988), which greatly increased reef algal biomass, inhibited new coral recruitment, and caused partial mortality of corals by overgrowth at the colony edges (Birkeland 1977; Steneck 1993; Stimson et al. 1996). There has also been growing problems with coral disease outbreaks and coral bleaching episodes, several of which have affected the principal massive coral species, *Montastraea annularis* (Woodley et al. 1997). These agents may well have contributed to the loss of cover we detected.

Decline in the proportion of old, massive corals, equivalent to climax vegetation in a forest, coupled with increases in the proportion of branching corals, equivalent to weedy, opportunistic species, at both dive sites and reserves indicate that Bonaire's reefs are subject to continuing disturbance. Changes in coral communities were much greater at dive sites, suggesting that diving exacerbates the effect of background stress and is causing a change in the character of Bonaire's reefs. One possible mechanism for the greater loss of massive colonies at dive sites may be linked to the higher frequencies of tissue damage (abrasion) due to divers. Coral diseases

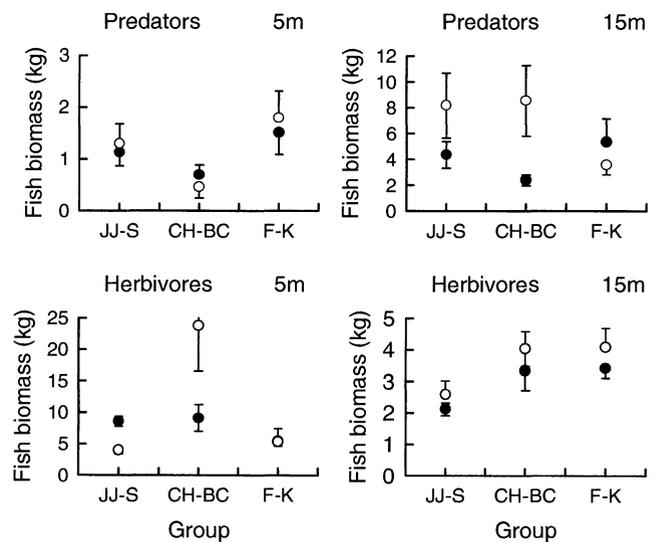


Figure 6. Comparison of fish biomass between dive sites (filled circles) and reserves (open circles) (JJ-S, Jerry's Jam-Slagbaai; CH-BC, Carl's Hill-Boca Cañon; and F-K, Forest - Karpata). Figures show means  $\pm$  standard error. Predators include all species of the families of groupers, snappers, and grunts. Herbivores include parrotfishes and surgeonfishes. Scales differ among graphs.

affecting Bonaire's reefs at the time of the study were mainly infections of massive colonies, including white-band disease, yellow-band disease, and white plague (K.D.M., personal observations). Several studies have linked disease infection to tissue lesions in corals (reviewed in Peters 1997), and diver damage could have increased the susceptibility of colonies in dive sites to infection. In this way, seemingly insignificant, sublethal damage from divers bumping into corals could lead to the eventual death of large, physically robust colonies hundreds of years old. It has often been suggested that different stresses act synergistically to cause greater damage to reefs. Connell (1997) recently showed that recovery from storm damage was much slower for reefs subjected to other stresses than for unaffected reefs. We have shown that reefs subject to diving stress have shifted to a more disturbance-tolerant coral community than those subject only to the background stresses of sea urchin die-off and coral disease.

The fact that diving is indirectly causing a serious loss of large, long-lived colonies is reason for concern. One reason these reefs may be particularly vulnerable to damage from diving is that Bonaire isn't in a hurricane belt. Lack of periodic disturbance by storms has enabled the massive corals to dominate the reefs, forming what might be considered a climax community. In places subject to higher levels of environmental disturbance, such as the Florida Keys, which are regularly affected by hur-

ricanes (Shinn 1976), coral communities may have a higher proportion of disturbance-tolerant species, and ecological changes due to diving disturbance may be less marked. What is a concern about the loss of massive coral cover revealed by our study is the finding that divers affect the coral without physically breaking them. It was previously thought that reefs dominated by massive corals were the most resistant to the effects of diving and so could be targeted as high-intensity dive sites (Hawkins & Roberts 1992b). This management recommendation must be reconsidered.

Based on our findings, how should reef management change? With regard to fish communities our findings suggest that, at these intensities, diving has no adverse effects. There was no evidence that populations of predatory fishes had increased disproportionately at dived sites compared to reserves. The differences detected among dived and reserve sites are attributable mainly to habitat differences, such as the generally higher coral cover and greater structural complexity in reserves than in dived sites. Despite the habitat differences, both dived and reserve sites supported thriving fish communities with similar numbers of species. This suggests that fish feeding need be regulated only if divers are attacked, which was beginning to happen before fish feeding was limited to dive guides only, or if the water becomes polluted by food (as in the enclosed Hanauma Bay, Hawaii, where hundreds of tourists were daily feeding bags of peas to fish (Wells & Hanna 1992). Sweatman (1996) suggests that if feeding is allowed divers should be permitted to offer only proper fish food rather than human food.

With regard to coral communities, previous studies have shown significant loss of coral cover and high frequencies of colony damage at diving intensities greater than approximately 5000–6000 dives per site per year (Riegl & Velimirov 1991; Prior et al. 1995; Hawkins & Roberts 1997). If maintenance of coral cover alone is the objective of management, then diving at intensities below 6000 dives per site per year should not be considered harmful (although the negative impacts of land-based tourist developments may be; Hawkins & Roberts 1997; Price et al. 1998). Scuba diving at these intensities may even increase coral diversity, as in this study. If maintaining the character of reefs is the goal, however, then allowable diving pressure may be considerably less, especially in places subject to additional stresses or where low levels of natural disturbance have allowed the development of coral communities dominated by old, massive corals. In Bonaire the higher coral diversity in dived sites can hardly be considered a beneficial effect of diving, given that the ancient corals are being replaced by short-lived, weedy species. It is important that such considerations be taken into account in projects aiming to develop tourism as an alternative to other economic uses of coral reefs.

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