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The quest for cryptic creatures: Impacts of species-focused recreational diving on corals

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ABSTRACT

Coral reefs are popular with ecotourists, but the impact of divers on reefs is cause for concern. In this study, we assessed the damage to corals caused by divers seeking cryptic but charismatic fish such as seahorses (family Syngnathidae) and frogfishes (Antennariidae), which are found on reefs around the world. These fish are closely associated with the reef substratum, thus bringing divers into close proximity to coral. We found that when in the vicinity of frogfish and seahorses, divers made unintentional contact with corals significantly more often and for longer periods than when these species were absent. This change in diver behaviour resulted in a greater frequency of coral breakage and scarring at seahorse/frogfish sites than at ecologically equivalent control sites. However, the spatial extent of damage appeared limited. Beyond 1–3 m from the seahorse or frogfish, coral breakage and scarring rate decreased to levels similar to those of control sites. None of the coral species, which suffered the most damage, was particularly rare, suggesting that the habitat conservation concern of these marked shifts in diver behaviour is limited. Nevertheless, the use of pre-dive briefings and smaller dive group sizes could minimise the damage caused by divers approaching cryptic species of interest near the reef.

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1. Introduction

The popularity of coral reefs with ecotourists has increased over the last 20 years, concomitantly with the development of a large SCUBA diving industry throughout the tropics (Hawkins and Roberts, 1992; Van Treeck and Schuhmacher, 1998; Inglis et al., 1999). Managing this industry requires balancing tourist use of coral reefs with protection of these habitats (Dixon et al., 1993; Van Treeck and Schuhmacher, 1998; Fernandes et al., 1999; Shafer and Inglis, 2000). However, the high vulnerability of corals to natural and human-caused disturbances (Neil, 1990; Hoegh-Guldberg, 1999; Wielgus et al., 2004), combined with larger number of divers every year,

makes the sustainable management of this diverse ecosystem complicated.

Divers often make contact with coral, which can lead to breakage of branching coral and damage to massive colonies (Van Treeck and Schuhmacher, 1998; Hawkins et al., 1999; Tratalos and Austin, 2001; Zakai and Chadwick-Furman, 2002). The cumulative effects of these disturbances can cause significant localised destruction and ultimately shifts in coral species composition (Hawkins and Roberts, 1994; Roupheal and Inglis, 2001; Tratalos and Austin, 2001). Moreover, it has been suggested that repeated injuries to coral colonies caused by divers can affect the long-term ability of corals to withstand other environmental stressors (Hawkins

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et al., 1999; Oren et al., 2001). Given the degraded state of coral reefs in many parts of the world (Wilkinson, 2004), which is revealed by striking declines in live coral cover (e.g. Gardner et al., 2003), curbing the controllable causes of coral mortality is imperative.

For this reason, there has been great interest in identifying the characteristics of divers and features of dive sites that lead to diver-coral contacts. It is well known that some divers are more likely to damage the coral than others. For example, divers that use photographic equipment, male divers, inexperienced divers and divers who have not received environmental briefings prior to diving are among those who contact the reef substratum most often (Talge, 1990; Medio et al., 1997; Roupheal and Inglis, 2001; Walters and Samways, 2001). However, our understanding of vulnerable dive site features is less complete. Overall reef topography appears to be unimportant in determining impact rates (Roupheal and Inglis, 1997; Zakai and Chadwick-Furman, 2002), but sites dominated by branching coral species experience more contacts by recreational users (Plathong et al., 2000; Roupheal and Inglis, 1997, 2001; Walters and Samways, 2001). It is likely that other biological features of dive sites affect the behaviour of divers underwater but these have not yet been identified.

Although divers are often attracted to sites with large and abundant fish (Rudd and Tupper, 2002), other species can also provide special appeal to a dive site because of their rarity and cryptic nature (Williams and Polunin, 2000). This is the case for seahorses and frogfishes, two families of odd-looking and uncommon species with circumglobal distributions. Divers are willing to pay considerable amounts to be shown such fish in the wild (M.C. Uyerra, personal observation) and are willing to participate in large numbers in unpaid scientific surveys of these species (Goffredo et al., 2004). Seahorses, in particular, have a special significance in many cultures and have been used as flagship species for conservation programmes (e.g. Project Seahorse, www.seahorse.fisheries.ubc.ca). Seahorses and frogfishes have poor swimming ability and are strongly site-attached, which makes them closely associated with a restricted area of substratum for extended periods (Deloach and Humann, 1999; Perante et al., 2002). These features allow dive operators to return repeatedly to known sites, with divers coming into very close proximity to the reef, thereby increasing the potential for collisions and damage to corals.

The aim of this study was to assess the damage to corals caused by divers observing cryptic fish such as seahorses and frogfishes. More specifically, we recorded diver behaviour at seahorse/frogfish sites and control sites, predicting that divers would hover closer to the substratum and make more accidental contacts with the reef when viewing seahorses and frogfish. We also compared coral damage at seahorse/frogfish sites and control sites without such species, predicting that the former would show more coral scars and breakage from diver impacts. Moreover, we quantified the zone of influence of frogfish and seahorses, by recording coral damage at increasing distances from the focal fish. Finally, considering species-specific coral growth and recovery rates, we comment on the longer-term significance of coral damage caused by divers seeking cryptic species.

2. Methods

2.1. Study site

The study was carried out from July to October 2003 on reefs around the Caribbean island of Bonaire (12°10' N, 68°15' W). This small island (180 km²) lies some 80 km north of Venezuela. The waters, and therefore the reefs, surrounding Bonaire and its satellite island, Klein Bonaire, have been protected since 1979 down to a depth of 60 m as part of the Bonaire National Marine Park (van't Hof, 1997). Boat anchoring, spearfishing and collection of any kind are forbidden within the park. Fishing is allowed, although the gear used and the sizes of the catch and species are regulated. Diving is permitted anywhere in the park, except in two small reserves where only scientific diving is allowed. The island is considered to be one of the top 10 diving destinations in the world (Seldon, 2003), having some of the best coral reefs and fish communities remaining in the Caribbean (Hawkins et al., 1999). Bonaire receives an average of 50,000 tourists a year (Tourism Corporation Bonaire (TCB), 2001), of which approximately 50% are divers. Seahorses (*Hippocampus reidi*) and frogfish (*Antennarius multiocellatus*) are regularly seen by divers in Bonaire (Deloach and Humann, 1999). At the time of the study, the locations of 20 seahorses and frogfish were known to divemasters, although only 10 of these were visited by tour operators (M.C. Uyerra, personal observations).

2.2. Diver behaviour

To quantify diver behaviour, we accompanied groups of scuba divers on organised day trips. We carried out 5-min focal observations of individual divers away from seahorse or frogfishes, recording the number and length (in seconds) of intentional and unintentional contacts with the reef and the species of corals touched. We also recorded which body parts (hand, finger, wetsuit) and/or equipment parts (fins, depth gauge, camera) were involved in the contacts, as well as the activity the diver was practising at the time of contact (taking photographs, swimming, peering at the substratum, or adjusting buoyancy) (Roupheal and Inglis, 2001). The same information on the same individual divers was recorded when divers were in the vicinity (<5 m) of a seahorse or frogfish, but observations were then carried out for as long as the diver was near the focal fish. In all cases, observations began once divers had adjusted their buoyancy and started swimming at a constant depth. We also noted diver gender and whether or not the diver was carrying photographic equipment, and from interviews with divers before or after each dive, we obtained information on experience. Because many divers could not recall exactly their total number of dives, we established two categories: little experience (≤20 logged dives) or experienced (>20 logged dives).

Behavioural observations were carried out during 27 dives at 14 different sites. We recorded data on 61 divers, with one to four divers observed per dive. Time and visibility limitations when divers were observing seahorses and frogfish, as well as the frequent failure to find the target species during a dive, meant that repeated observations (i.e. near and away

from seahorses/frogfish) could only be obtained for 28 divers, observed over 10 dives.

Divers were not informed of the purpose of the research prior to the dive so that they would not change their normal underwater behaviour. However, upon returning to the boat, the goals of the study were fully explained and consent to use the data collected was sought. All observed divers gave permission.

2.3. Pattern of coral damage

In addition to the sites used for diver observations, we obtained the location of 10 other popular seahorse and frogfish sites through personal contacts with dive masters. Sites were off Bonaire and Klein Bonaire, at depths ranging from 7 to 15 m. At each site, two 20 m transect lines were placed parallel to the shore at constant depth on either side of the focal fish (or its previous location if the focal fish was no longer present). Using 1-m² quadrats placed along each transect line, we recorded the numbers of broken corals and colony scars and the percentage cover of live coral, dead coral, sponges and rubble (estimated visually). Most corals (32 of 36 taxa) were identified to species; the remaining four taxa (all gorgonians) were identified to genus. A similar pair of 20 m transects were run at each site from a control point lacking seahorse or frogfish and located 25 m beyond the end of one of the first transect lines. Coral damage and percent coral cover were surveyed as described above. On each transect, quadrats were placed 1, 3, 5, 7, 10, 15 and 20 m from the focal fish/control point. We placed an additional pair of quadrats 1 m above and below the focal fish/control point to obtain a more precise assessment of damage in these areas.

2.4. Statistical analysis

Frequencies of intentional and unintentional contacts with the substratum were obtained for each diver and expressed as numbers per 10 min. Average length of contact with the substratum was calculated for each diver and expressed as the proportion of time spent observing each diver. Differences between diver behaviour at seahorses/frogfish sites and control sites were examined using Wilcoxon sign ranks tests, because data did not conform to the assumption of normality or equality of variances. We then calculated the difference for each diver in contact rate and proportion of time in contact with the substratum between observations made at seahorse/frogfish and control sites. These difference variables met the assumption of normality (differences in contact rate: Kolmogorov–Smirnov test, $Z = 1.08$, $p = 0.19$; differences in contact time: $Z = 1.07$, $p = 0.20$), allowing us to use a general linear model (GLM) to examine the effect of gender, use of camera and experience (as fixed factors) on shifts in diver behaviour. We included dive as a random factor to examine the potential non-independence of divers observed on the same dive. We also examined the effect of gender on the absolute rates and lengths of contact with the reef near and away from frogfish and seahorses using Mann–Whitney tests. Finally, to examine whether our sample of divers was representative, we tested for differences in contact rate and contact length between divers we had observed only once

(away from seahorses and frogfish, $n = 33$) and those we had observed both near and away from these fishes ($n = 28$), as well as between all men ($n = 26$) and women ($n = 35$) observed. There were no differences between the samples observed once and twice (Mann–Whitney tests, all $p > 0.30$) and the lack of gender differences obtained with the smaller sample at control sites was also observed with the larger sample (Mann–Whitney tests, all $p > 0.11$).

For each site, the number of scars per m², the number of broken colonies per m² and the percent cover of live coral, dead coral, rubble and sponges were averaged at each distance from the central point of paired transects. Hence, each distance at each site contributed one data point to the analysis. This reduced greatly, although probably did not eliminate completely, the non-independence of data within transect. All data were normally distributed (Kolmogorov–Smirnov tests, $p > 0.05$ in all cases). We examined the effect of the presence of seahorses and frogfish, as well as distance from these fish, on the overall pattern of damage to coral and benthic cover with GLMs, followed by pairwise comparisons and correlations. Presence of seahorses/frogfish and distance from these fish were included as fixed factors. Dive site (i.e. the location of each seahorse/frogfish and associated control sites) was also included as a random factor.

To gain a better understanding of the susceptibility of individual coral species to diver contact, we calculated frequencies of scarring and/or breakage for each hard and soft coral species present at the sites, and correlated these to their relative abundance (% cover). Both frequencies of damage and abundance were obtained by averaging species-specific values obtained in quadrats set 1 m from seahorses/frogfishes across sites. Susceptibility was assessed qualitatively by examining the position of each species on the damage vs. abundance figure, relative to a slope of one.

To investigate the link between diver behaviour and coral damage more directly, we focused on three dive sites (Small Wall, Munk's Heaven, and Andrea I) for which we had both habitat assessment as well as data on diver behaviour. We reduced multiple values of breakage and scarring for same coral species by averaging species-specific recorded values in quadrats within 1-m distance of the seahorse/frogfish across the three sites. These averages were then correlated with the behaviour of divers (expressed as contacts with each species 10 min⁻¹) at those three sites using Pearson's correlations.

3. Results

3.1. Diver behaviour in the presence of seahorses and frogfishes

Data were obtained on the behaviour of 28 divers (19 males, 9 females) near and away from frogfish/seahorse sites, 14 of whom carried photographic equipment. Twenty-five percent of divers touched the reef when away from a frogfish or seahorse, compared with 75% when in the vicinity of these fish ($\chi^2_1 = 14.0$, $p < 0.001$). Divers made significantly more contacts at seahorse/frogfish sites than at control sites (median [interquartile range], seahorse/frogfish: 46.41 contacts 10 min⁻¹ [9.79–126.43], control: 0 contacts 10 min⁻¹ [0–1.07];

Wilcoxon Signed Ranks test, $Z = -3.94$, $n = 28$, $p < 0.001$). Contacts were also longer when near seahorses and frogfish (seahorse/frogfish: 17.1% of time observed [5.5–38.2%], control: 0% [0–0.2%]; $Z = -4.01$, $p < 0.001$).

When away from seahorses and frogfishes, divers made very few contacts with the reefs, and we could not detect a difference in numbers of intentional and unintentional contacts (35.7% intentional vs. 64.3% unintentional, total $n = 14$ contacts; $\chi^2_1 = 1.14$, $p = 0.28$), whereas at frogfish/seahorse sites significantly more contacts were unintentional (86% unintentional vs. 14% intentional, total $n = 200$ contacts; $\chi^2_1 = 5.49$, $p < 0.001$). The highest number of overall contacts were made with fins (56%); however, different body/equipment parts were involved in coral contacts at frogfish/seahorse and control sites ($\chi^2_5 = 21.97$, $p = 0.001$). At control sites cameras were involved in 31% of the contacts, followed by fins (23%) and fingers (15%), whereas at frogfish/seahorses sites fins represented 59% of the contacts, followed by depth gauge (13%) and hands (12%).

The different sources of contact reflected the different activities carried out when near and away from cryptic fishes. At the seahorse/frogfish sites, the activities resulting in coral contact were close observation of the substratum (i.e. observation of frogfishes and seahorses) (42%), photography (26%) and buoyancy control (22%). By contrast, in the absence of frogfish and seahorses, only photography (54%) and swimming (46%) resulted in most contacts with the reef ($\chi^2_4 = 31.07$, $p < 0.001$).

Neither experience, gender nor the use of photographic equipment had an effect on the change in frequency of coral contact of divers (GLM, $F_{1,13} < 2.45$, $p > 0.14$ in all cases). There was no difference among dives in the shift in contact rate ($F_{1,13} = 0.61$, $p = 0.77$). There was also no significant interaction between these variables ($F_{1,13} < 0.28$, $p > 0.61$ in all cases). However, divers with cameras and female divers exhibited greater increases in time spent in contact with the substratum when at seahorse/frogfish sites than divers without cameras or male divers; camera effect: ($F_{1,13} = 8.06$, $p = 0.01$); gender effect: ($F_{1,13} = 5.97$, $p = 0.03$). Experience and the dive on which people were observed had no effect on the shift in contact length, nor were there interactions between these variables ($F_{1,13} < 2.11$, $p > 0.17$ in all cases). In absolute terms, women contacted the reef twice as frequently (mean ± 1 SD, women: 114.4 ± 76.3 times 10 min^{-1} , men: 68.4 ± 100.2 times 10 min^{-1} ; Mann–Whitney test, $U = 45.0$, $p = 0.05$) and for twice as long (women: $47 \pm 41\%$ of time observed, men: $23 \pm 32\%$; Mann–Whitney test, $U = 46.0$, $p = 0.05$) as their male counterparts when near seahorses or frogfish. Female divers were not less experienced in terms of number of dives logged than male divers ($\chi^2_1 = 1.05$, $p = 0.31$), nor were they more likely to be using a camera ($\chi^2_1 = 0.16$, $p = 0.69$).

3.2. Pattern of coral damage

The number of scars on coral differed significantly between frogfish/seahorse sites and control sites (GLM, $F_{1,112} = 14.56$, $p < 0.001$; Fig. 1a) and varied with distance from the central point ($F_{6,112} = 3.18$, $p = 0.006$; Fig. 1a). There was also a significant interaction between distance and site ($F_{6,112} = 2.61$, $p = 0.02$); the number of coral scars tended to decrease with

increasing distance from the central point at frogfish/seahorse sites ($r^2_7 = -0.72$, $p = 0.07$) but not at control sites ($r^2_7 = -0.08$, $p = 0.86$; Fig. 1a). In particular, coral scarring was significantly more frequent at seahorse/frogfish than at control sites, but only 1 m away from the central point (paired $t_9 = 2.91$, $p = 0.017$; all other distances: paired $t_9 < 2.00$, $p > 0.08$; Fig. 1a). The patterns of coral breakage were similar to those of scarring (Fig. 1b). In neither case was the effect of dive site significant (scars: $F_{9,112} = 1.70$, $p = 0.10$; breakage: $F_{9,112} = 0.99$, $p = 0.46$).

Unsurprisingly, the percentage of live coral increased significantly with distance from a seahorse or frogfish ($r^2_7 = 0.83$, $p = 0.02$; Fig. 1c). The percentage cover of dead coral, rubble and sponges did not vary with distance from the central point (distance effect, all $F_{6,112} < 1.54$, $p > 0.17$; Fig. 1d–f). There was more dead coral ($F_{1,112} = 4.55$, $p = 0.04$), fewer sponges ($F_{1,112} = 6.19$, $p = 0.01$), and a tendency for less live coral ($F_{1,112} = 3.05$, $p = 0.08$) at seahorse/frogfish sites. However, these characteristics varied significantly more among dive sites (dive site effect, $F_{9,112} > 7.20$, $p < 0.001$ in all cases) than they did between seahorse/frogfish sites at a dive site.

Seven coral species were damaged more frequently than expected from their abundance (Fig. 2). The three species that were disproportionately scarred were all hard coral species (*Montastraea annularis*, *Siderastrea radians* and *Dichocoenia stokesii*), whereas the four taxa that were disproportionately broken were soft coral (gorgonian) species (*Eunicea* spp., *Plexaura homomalla*, *Pseudoplexaura* spp., and *Plexaura flexuosa*).

3.3. Link between diver behaviour and coral damage

For the three seahorse/frogfish sites for which we had data on both habitat composition and diver behaviour, the species-specific frequency of contacts by divers was significantly correlated with the percentage cover of each coral species ($r = 0.54$, $n = 36$, $p = 0.001$). The frequency of scarring on a coral species was significantly related to the time divers spent in contact with this species ($r = 0.48$, $n = 36$, $p = 0.003$) but not to the number of contacts to which the species was subjected ($r = 0.30$, $n = 36$, $p = 0.08$). By contrast, the rate of breakage of coral species was related to both the frequency of contacts ($r = 0.84$, $n = 36$, $p < 0.001$) and time spent in contact ($r = 0.69$, $n = 36$, $p < 0.001$).

4. Discussion

The presence of cryptic but charismatic fish such as seahorses and frogfishes alters significantly the behaviour of recreational divers. Near these sought-after species, divers contacted coral significantly more often and for longer periods, both accidentally and intentionally. Although in most cases we could not record whether these contacts caused immediate damage to coral, we have circumstantial evidence that they did since the frequency of coral breakage and scarring was significantly higher at seahorse/frogfish sites than at ecologically equivalent control sites. Moreover, the rates of scarring and breakage of different species of corals were directly related to how frequently and how long these species were touched by divers. However, the spatial extent of damage appears limited. At 3 m from the seahorse or frogfish, which is

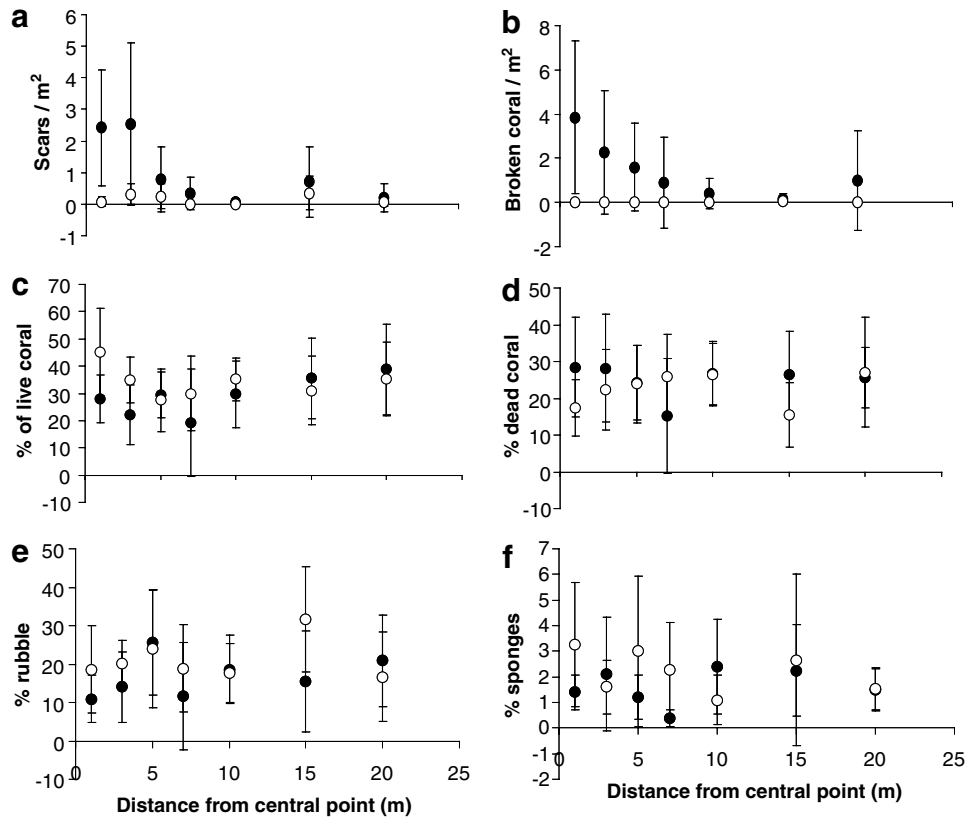


Fig. 1 – Mean number of: (a) scars on coral, (b) coral colonies with evidence of breakage, and percentage of (c) live coral, (d) dead coral, (e) rubble, and (f) sponges, per m² in relation to distance (m) from a frogfish or seahorse site (black circles) or from a control site (open circles). Means are shown $\pm 95\%$ CI, N = 10 for each point.

roughly the length of a diver with fins, coral breakage and scarring rates decreased to levels similar to those of control sites. Such localised damage is explained by the fidelity of these two fish species to their homes, as well as by the generally low contact rates observed away from seahorses and frogfishes.

The increased rate of contact between divers and corals near frogfish and seahorses is clearly related to the cryptic nature and benthic habit of these fishes and the need for divers to come close to the substratum for observation. Away from such points of interest, the rate of diver contact with coral was relatively low, standing at 1.8 contacts 10 min⁻¹. This rate is slightly lower than rates documented elsewhere (e.g. 2.1 contacts 10 min⁻¹, Medio et al., 1997; 2.5–5.5 contacts 10 min⁻¹, Zakai and Chadwick-Furman, 2002), which may stem from the Bonaire Marine Park requirements that all divers submit to a check-out dive to verify buoyancy control (M.C. Uyarra, personal observations). However, when divers hovered close to the reef surface to observe frogfish and seahorses, the contact rate with coral increased 45-fold. A high proportion of these contacts were accidental, as fins and dangling depth gauges scraped coral and divers with poor buoyancy control pushed themselves away from the reef with their hands. These contacts contrast in both appearance and effect with intentional contacts where a diver carefully placed one finger on a small area of coralline rock to maintain his/her position (M.C. Uyarra, personal observations).

Divers with cameras have been reported to cause significantly more damage than their counterparts without cameras (Rouphael and Inglis, 2001). Our results are consistent with this observation, with divers using cameras increasing the time they spent in contact with the substratum significantly more than non-camera users when in the presence of an unusual fish. Recreational specialists, such as underwater photographers, often exhibit specific goal-oriented behaviours which are at odds with other values (Ditton et al., 1992). Thus taking advantage of a unique but time-limited opportunity to photograph frogfish or seahorse may override environmental concerns, and lead diving photographers to underestimate the environmental impact of their actions (Rouphael and Inglis, 2001).

Surprisingly, women showed a larger shift towards damaging behaviour than men when near seahorses and frogfish. Rouphael and Inglis (2001) found that on a normal dive male divers caused more coral damage, which was attributed to their greater willingness to venture close to the substratum. It is therefore possible that the larger increase in time spent in contact with the reef and the larger absolute rate of reef contact by women stems from their relative inexperience at hovering very close to the substratum, despite the fact that they were equally experienced in terms of number of dives.

Although the behaviour of divers was markedly altered by the presence of seahorses and frogfish, the consequences of such change of behaviour were reflected in extremely

restricted areas around the focal fishes. This pattern may be explained by the very limited home ranges of seahorses and frogfishes (Deloach and Humann, 1999). All but one of our focal frogfish and seahorses remained on same site (<1 m² area) for the duration of the study (8 weeks) and there is anecdotal evidence of seahorse residency times on Bonaire extending to more than 18 months (M.C. Uyarra, unpublished data). Moreover, divers almost always quickly resumed proper buoyancy control after moving away from the fish. The damaged areas are therefore restricted, but under chronic pressure from divers.

The significance of diver-induced damage to corals can only be understood in the context of the rarity of the species affected and their scope for recovery. The frequency of damage to each coral species was generally related to its abundance (Fig. 2). However, seven species showed more damage than expected given their abundance. All of these species are relatively common in Bonaire and across the Caribbean (Humann and Deloach, 2002). The species with disproportionate amounts

of scarring were hard coral species whereas breakage mainly affected branching soft coral species. In general, soft coral species are more likely to be contacted by divers because of their arborescent shape (Hall, 2001), but their flexibility and high growth rates (see below), which allow them to recover quickly from extreme events (Sheppard et al., 2002; Fox et al., 2003; Stobart et al., 2005), probably make them relatively resilient to diver damage. By contrast, the hard coral species most contacted by divers had rounded, massive morphologies, which are associated with a low capacity for recovery from damage (Hall, 1997). Hard coral species tend to have slower growth rates than soft corals. For example, the growth rate of *M. annularis*, one of the three species of hard coral with disproportionate signs of scarring at seahorse and frogfish sites, ranges from 0.2 to 0.9 cm a year, depending on depth (Hubbard and Scaturro, 1985). This contrasts with the higher growth rate of the gorgonian *Plexaura* spp., which also showed a high proportion of damage at our seahorse/frogfish sites, which ranges from 2.7 to 4.7 cm a year (Ward-Paige et al., 2005). Diver damage is therefore more likely to have a long-term negative impact on hard coral species. Indeed, shifts in hard coral composition as a result of long-term exposure to divers have been noted (Hawkins et al., 1999), which are likely to be the result of different growth and recovery rates between species.

We have shown that seahorse and frogfish viewing results in diver-induced damage that is heavy but spatially limited to the observation areas. Additional damage is likely to occur in response to observations of other site-attached species, such as various species of morays (Abrams and Schein, 1986), lobsters and turtles hidden in cavities, and other small but attractive invertebrates (e.g. cleaner shrimp) and fish that live on the substratum. This phenomenon is likely to continue since dive masters often profit financially from showing cryptic creatures to tourists. For example, tips by divers having seen a frogfish or seahorse ranged from US\$5–10 on Bonaire (M.C. Uyarra, personal observations). In addition, dive masters offered personal guided evening dives aimed specifically at finding seahorses for a standardised fee of US\$25 (M.C. Uyarra, personal observations). There may therefore be limited incentive to reduce the number of participating tourists, although the damage to coral inflicted by individuals can be managed.

Unlike trampling of vegetation which must occur during wildlife tourism in terrestrial habitats, diver contacts with coral reefs are avoidable. For example, pre-dive environmental briefings by divemasters have been shown to be effective in reducing the number of diver-coral interactions (Medio et al., 1997). In Bonaire, briefings were always given to acquaint divers with Marine Park regulations, but more specific briefings were rarely given prior to dives to view seahorses and frogfishes (M.C. Uyarra, personal observations). These briefings could be used to remind divers to be particularly aware of keeping their fins away from the reef surface and to secure all gauges on clips or pockets, since fins and gauges account for nearly three-quarters of contacts with the reef when divers are in the vicinity of seahorses and frogfish. Barker and Roberts (2004) also found that underwater interventions by divemasters were successful at reducing the number of contacts with corals. A reduction in the number of divers per divemaster (from the maximum of 16:1 observed

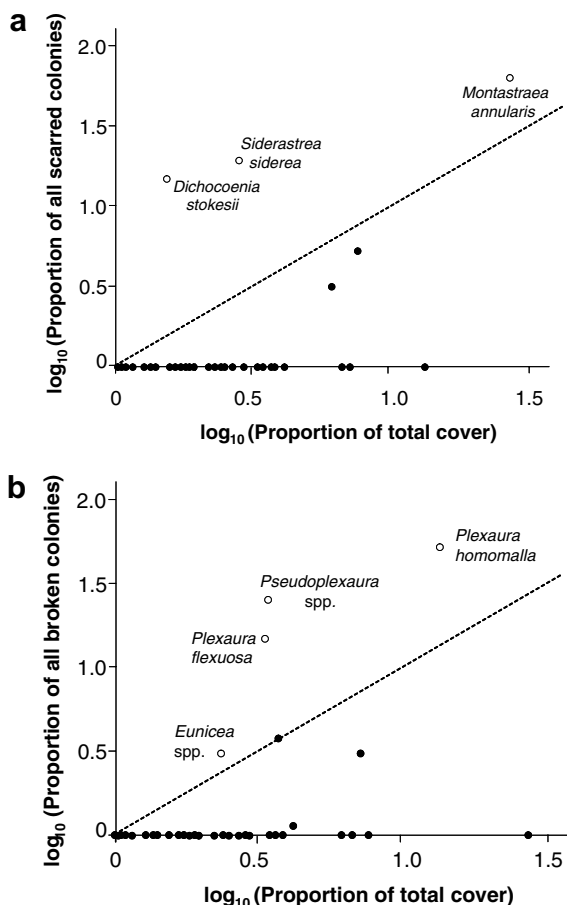


Fig. 2 – Relationships between the proportion of total cover and (a) the proportion of all scarred colonies, and (b) the proportion of all broken colonies accounted for by each coral species encountered. The dashed line represents a slope of 1. Species shown with open circles are those which were damaged more than expected on the basis of their abundance. Both axes have been $\log(x+1)$ -transformed for clarity.

in this study) could allow divemasters to be more vigilant in keeping divers at a distance from the reef when observing the fish or taking photographs. Simple diver management prescriptions could counter the damage-inducing behavioural shifts exhibited by divers near sought-after species.

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REFERENCES

- Abrams, R.W., Schein, M.W., 1986. Individual movements and population density estimates for moray eels on a Caribbean coral reefs. *Coral Reefs* 5, 161–163.
- Barker, N., Roberts, C.M., 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. *Biological Conservation* 120, 481–489.
- Deloach, N., Humann, P., 1999. Reef Fish Behavior: Florida, Caribbean, Bahamas. New World Editions, Jacksonville.
- Ditton, R.B., Loomis, D.K., Choi, S., 1992. Recreation specialization: re-conceptualization from a social world's perspective. *Journal of Leisure Research* 24, 33–51.
- Dixon, J.A., Scura, L.F., van't Hof, T., 1993. Meeting ecological and economic goals – marine parks in the Caribbean. *Ambio* 22, 117–125.
- Fernandes, L., Ridgley, M.A., van't Hof, T., 1999. Multiple criteria analysis integrates economic, ecological and social objectives for coral reef managers. *Coral Reefs* 18, 393–402.
- Fox, H.E., Pet, J.S., Dahuri, R., Caldwell, R.L., 2003. Recovery in rubble fields: long-term blast fishing. *Marine Pollution Bulletin* 46, 1024–1031.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. *Science* 301, 958–960.
- Goffredo, S., Piccinetti, C., Zaccanti, F., 2004. Volunteers in marine conservation monitoring: a study of the distribution of seahorses carried out in collaboration with recreational scuba divers. *Conservation Biology* 18, 1492–1503.
- Hall, V.R., 1997. Interspecific differences in the regeneration of artificial injuries on scleractinian corals. *Journal of Experimental Marine Biology and Ecology* 212, 9–23.
- Hall, V.R., 2001. The response of *Acropora hyacinthus* and *Montipora tuberculosa* to three different types of colony damage: scraping injury, tissue mortality and breakage. *Journal of Experimental Marine Biology and Ecology* 264, 209–223.
- Hawkins, J.P., Roberts, C.M., 1992. Effects of recreational SCUBA diving on fore-reef slope communities of coral reefs. *Biological Conservation* 62, 171–178.
- Hawkins, J.P., Roberts, C.M., 1994. The growth of coastal tourism in the Red Sea: present and possible future effects on coral reefs. *Ambio* 23, 503–508.
- Hawkins, J.P., Roberts, C.M., van't Hof, T., de Meyer, K., Tratalos, J.A., Aldam, C., 1999. Effects of recreational scuba diving on Caribbean coral and fish communities. *Conservation Biology* 13, 888–897.
- Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50, 839–866.
- Hubbard, D.K., Scaturro, D., 1985. Growth rates of seven species of scleractinian corals from Cane Bay and Salt River, St. Croix, USVI. *Bulletin of Marine Science* 36, 325–338.
- Humann, P., Deloach, N., 2002. Reef Coral Identification: Florida, Caribbean, Bahamas. New World Publications, Jacksonville.
- Inglis, G.J., Johnson, V.I., Ponte, F., 1999. Crowding norms in marine settings: a case study of snorkeling on the Great Barrier Reef. *Environmental Management* 24, 369–381.
- Medio, D., Ormond, R.F.G., Pearson, M., 1997. Effect of briefings on rates of damage to corals by scuba divers. *Biological Conservation* 79, 91–95.
- Neil, D., 1990. Potential for coral stress due to sediment resuspension and deposition by reef walkers. *Biological Conservation* 11, 408–412.
- Oren, U., Benayahu, Y., Lubinevsky, H., Loya, Y., 2001. Colony integration during regeneration in the stony coral *Favia fagus*. *Ecology* 82, 802–813.
- Perante, N.C., Pajaro, M.G., Meeuwig, J.J., Vincent, A.C.J., 2002. Biology of a seahorse species, *Hippocampus comes*, in the central Philippines. *Journal of Fish Biology* 60, 821–837.
- Plathong, S., Inglis, G.J., Huber, M.E., 2000. Effects of self-guided snorkelling trails on corals in a tropical marine park. *Conservation Biology* 14, 1821–1830.
- Rouphael, A.B., Inglis, G.J., 1997. Impacts of recreational SCUBA diving at sites with different reef topographies. *Biological Conservation* 105, 179–187.
- Rouphael, A.B., Inglis, G.J., 2001. "Take only photographs and leave only footprints"? An experimental study of the impacts of underwater photographers on coral reef dive sites. *Biological Conservation* 100, 281–287.
- Rudd, M.A., Tupper, M.H., 2002. The impact of Nassau grouper size and abundance on scuba diver site selection and MPA economics. *Coastal Management* 30, 133–151.
- Seldon, L., 2003. World's top ten dive destinations. A guide to the best places to take your next dive trip. WetDawg: Global Headquarters for Adventure Water Sports 6th July. Available from: <www.wetdawg.com/pages/bestdives.html>.
- Shafer, C.S., Inglis, G.J., 2000. Influence of social, biophysical, and managerial conditions on tourism experiences within the Great Barrier Reef World Heritage Area. *Environmental Management* 26, 73–87.
- Sheppard, C.R.C., Spalding, M., Bradshaw, C., Wilson, S., 2002. Erosion vs. recovery of coral reefs after 1998 El Nino: Chagos reef, Indian Ocean. *Ambio* 31, 40–48.
- Stobart, B., Teleki, K., Buckley, R., Downing, N., Callow, M., 2005. Coral recovery at Aldabra Atoll, Seychelles: five years after the 1998 bleaching event. *Philosophical Transactions of the Royal Society, Series B* 363, 251–255.
- Talge, H., 1990. Impact of recreational divers on coral reefs in the Florida keys. In: *Proceedings of the American Academy of Underwater Sciences 10th Annual Scientific Diving Symposium*, October 4–7, pp. 365–374.
- Tourism Corporation Bonaire (TCB), 2001. Bonaire tourism. Annual Report 2001. Tourism Corporation, Kralendijk, Bonaire.
- Tratalos, J.A., Austin, T.J., 2001. Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. *Biological Conservation* 102, 67–75.
- van't Hof, T., 1997. New Guide to the Bonaire Marine Park. Harbour Village Beach Resort Bonaire.

- Van Treeck, P., Schuhmacher, H., 1998. Mass diving tourism – a new dimension calls for new management approaches. *Marine Pollution Bulletin* 37, 499–504.
- Walters, R.D.M., Samways, M.J., 2001. Sustainable dive ecotourism on a South African coral reef. *Biodiversity Conservation* 10, 2167–2179.
- Ward-Paige, C.A., Risk, M.J., Sherwood, O.A., 2005. Reconstruction of nitrogen sources on coral reefs: delta N-15 and delta C-13 in gorgonians from Florida Reef tract. *Marine Ecology Progress Series* 296, 155–163.
- Wielgus, J., Chadwick-Furman, N.E., Dubinsky, Z., 2004. Coral cover partial mortality on anthropogenically impacted coral reefs at Eilat, northern Red Sea. *Marine Pollution Bulletin* 48, 248–253.
- Wilkinson, C., 2004. *Status of Coral Reefs of the World: 2004*. Australian Institute of Marine Sciences, Townsville, Australia.
- Williams, I.D., Polunin, N.V.C., 2000. Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourist. *Environmental Conservation* 27, 382–391.
- Zakai, D., Chadwick-Furman, N.E., 2002. Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. *Biological Conservation* 105, 179–187.