Effects of Human Activities on the World’s Most Vulnerable Coral Reefs: Comoros Case Study

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Effective management of highly biodiverse and threatened reefs requires the identification of human activities driving declines on the particular reef to be managed. The island nation of the Comoros is a model setting to investigate effects of human activities on diverse and threatened coral reefs, with abundant and diverse marine life, local dependence on reef resources, and a variety of anthropogenic pressures on reefs rendering the nation vulnerable to coral reef degradation. Using data from 21 sites throughout the Comoros, we evaluated the relative influence of human activities and other natural and anthropogenic factors on benthic cover and fish richness, abundance, and biomass with the goal of providing prioritized management targets. Human activities including fishing, beach sand extraction, and beachfront housing and development had the strongest relationship with degraded reefs but with some seasonal fluctuation, while geographic patterns most consistently predicted reef degradation across seasons. Comparing analyses conducted with and without human activities as predictors, the inclusion of human activities greatly improved explanatory power. Baseline data on reef biotic composition and localized anthropogenic impacts, monitoring over time, and controlled experiments can facilitate an adaptive management approach for protecting fragile reef ecosystems in the Comoros and elsewhere.

Keywords anthropogenic impacts, coastal development, coral reef, fisheries, sand mining

Introduction

Drivers of coral reef degradation are context specific, with high local and regional variability in key drivers of reef threats and management efforts (Burke et al. 2011). Studies evaluating effects of human activities at sub-regional scales tend to investigate individual activities (most often fishing; e.g., Jennings and Polunin 1996; McClanahan, Hicks, and Darling 2008) or cumulative impacts in which the effects of particular human activities are indiscernible (e.g., Sala et al. 2012). Human activities other than fishing and their effects on coral reefs have been studied in few locales, including boating (e.g., Burgin and Hardiman 2011), sand extraction (e.g., Huber and Meganck 1990), coastal development (e.g., Wolanski, Martinez, and Richmond 2009), and agriculture (e.g., Fabricius and
De’ath 2004). More recent studies investigating the effects of human activities on coasts (e.g., Halpern et al. 2008; Halpern et al. 2009; Klein et al. 2010) focus on a large regional scale rather than providing detailed information at the smaller scale at which most management regimes operate. From the studies of individual or cumulative impacts at sub-regional scales to the larger scale studies, it remains difficult to translate findings into management action due to incomplete information on human activity effects on coral reefs, scale mismatch, and lack of relevance for poorly studied reef areas with the highest diversity and the greatest need for effective management (Burke et al. 2011; Fisher et al. 2011).

Current research on human activities and their effects on coral reefs not is not only selective in types of activities studied and lacking in use of spatial scales relevant to local management, but is also poorly geographically situated. Research effort has not concentrated on coral reefs under heaviest anthropogenic pressure and the most at risk for coral reef degradation (Fisher et al. 2011). Instead, research effort is highly clustered, positively related to per capita Gross Domestic Product (GDP), and actually declines in relation to coral diversity (Fisher et al. 2011; but see Dorenbosch et al. 2005; Cinner et al. 2006; Graham et al. 2008 as examples of research in locales with low GDP and high coral diversity). The poor allocation of research effort means that the impacts of many heavily practiced activities on reefs in resource dependent (and low GDP) locales are poorly understood and unlikely to be effectively managed.

Vulnerable coral reefs could be more effectively conserved with greater knowledge and understanding of local causes of reef degradation. Although local managers often recognize the presence of various human activities that are likely to affect coral reefs, the activities are rarely studied in a way that informs successful management (e.g., Ohman, Rajasurya, and Linden 1994; Ahamada et al. 2002; Munday 2004). Given the financial, personnel, and time constraints of any management operation, management will most effectively conserve the ecosystem when threats are identified and scientifically studied to inform and prioritize management actions (Klein et al. 2010).

This study evaluates, at a management-relevant scale, the relationship of human activities with the biotic composition of coral reefs in the Comoros islands. The Comoros is listed among nine nations most vulnerable to the effects of coral reef degradation due to high reef dependence, highly threatened reefs, and low adaptive capacity (Burke et al. 2011). Like other understudied reefs, the reefs of the Comoros contain high biodiversity and experience high levels of anthropogenic pressure (e.g., coastal population growth and exploitation of reef resources). The objectives of the study were (1) to identify human activities most influential on coral reef biota and (2) to compare the effects of human activities on coral reef biota to the effects of natural and anthropogenic factors. We expected to find a suite of human activities (most likely including fishing and beach sand extraction) would best explain the variation in biotic composition among the study sites and would enhance explanatory power of analytical models in comparison with models including only more commonly studied natural factors (e.g., wave exposure, sedimentation, and recruitment patterns; Done 1982; habitat and wave exposure; Friedlander et al. 2003; habitat; Pinca et al. 2012) and anthropogenic factors (e.g., population, distance to markets, and socio-economic development; Cinner and McClanahan 2006; Cinner et al. 2009). The results of this investigation inform management efforts at the study sites by revealing the influence of human activities on local coral reef biota. This study also informs coral reef research and management efforts in other locales by providing a method of identifying local threats to coral reefs, identifying human activities likely to affect coral reefs under heavy resource
use, and recommending a management approach that can improve management at reef resource dependent sites throughout the world.

Methods

Study Site and Design

The islands of the Comoros archipelago that make up the Comoros Union include N’gazidja (Grande Comore), Ndzuwani (Anjouan), and Mwali (Mohéli). These volcanic islands were produced from geologic ‘hotspot’ processes less than 10 million years ago (Emerick and Duncan 1982). The coral reefs that surround the islands are seldom subject to catastrophic storms or crown of thorns outbreaks and have proven to be resilient to major coral bleaching events such as the 1998 event (Ahamada et al. 2002). The reefs studied consist mainly of fringing reefs with high hard coral diversity; we identified 23 scleractinian coral genera during the study, most often observing Acropora, Porites, Favites, Echinopora, and Goniastrea.

While national legislation exists to protect biodiversity, coastal habitats, and key species, such laws receive little attention and enforcement; most environmental action is decentralized and occurs through community groups (Ahamada et al. 2002; Bigot et al. 2002). Support from external agents such as international nongovernmental organizations (NGOs) comes in the form of occasional project grants awarded for specific and short-term (usually 2–5 years) actions for environmental protection. Thus, a neo-traditional form of community-based co-management is practiced in most settlements and is the most consistent institution for environmental protection and resource management within the Comoros. Although local pressure on reefs can be high, most resource use is for subsistence with no major commercialization of reef products and virtually all reef-resource trade occurring solely within the country. A wide variety of fish are consumed, with the main target groups including groupers (Cephaplopholis miniata and others), snappers (Lutjanus kasmira and others), tuna (Thunnus obesus and others), and bonito (Euthynnus affinis and others).

We conducted interviews and ecological surveys at 21 sites throughout the Comoros. Each site consisted of a local community with a population between approximately 250–13,000 inhabitants (unpublished 2003 census data from Comoran government) and an adjacent area of reef frequented by the community along 250 m–1,000 m of coastline. Each reef area was identified by members of the local community as the area of reef nearest and/or most frequented by community members. Researchers surveyed the reef area to verify it was predominantly coral reef habitat (rather than seagrass or sand). Sites were distributed geographically along each island to the extent possible and based on reef access via snorkel (SCUBA is unavailable for most of the sites).

We evaluated sites where one or more human activities took place. True “control” sites free of human activities were not available for this study. Accounting for other sources of variation in reef biotic composition, including environmental and geographic factors such as wave exposure and coastline orientation (see supplemental Table 1 for a complete list), we assumed that any discernible relationship between human activities and reef biota would be a conservative estimate of the true effects of human activities that could be more precisely quantified were control data available. The diversity of activity intensity and frequency among sites provided a gradient of human activity and management efforts against which reef biotic composition was compared, a common way to detect correlational patterns of coral reef biotic composition and degradation (e.g., Barott et al. 2012; Weijerman, Fulton, and Parrish 2013).
### Table 1
Fish identified in surveys by targeted and non-targeted taxa and by functional group

| Fished taxa             | Fish-eating predators                                      | Non-fished taxa                          |
|-------------------------|------------------------------------------------------------|------------------------------------------|
| Subfamily Epinephelinae | *Lutjanus kasmira*                                         | *Chaetodon auripes*                      |
|                         | *Cephalopholis miniata*                                    |                                          |
|                         | *Epinephelus merra*                                         |                                          |
|                         | *Lethrinus harak*                                           |                                          |
|                         | *Aethaloperca rogaa*                                        |                                          |
|                         | *Cephalopholis argus*                                       |                                          |
|                         | *Epinephelus fasciatus*                                     |                                          |
|                         | Subfamily Scaridae                                          |                                          |
|                         | *(zooplankton, fish eggs, crustaceans)*                     |                                          |
|                          | *Acanthurus thompsoni*                                       |                                          |
|                          | Family Lutjanidae                                            |                                          |
|                          | Carnivore (filamentous/benthic algae)                       |                                          |
|                          | Herbivores                                                  |                                          |
|                          | *Naso lituratus*                                             |                                          |
|                          | *Naso unicornis*                                             |                                          |
|                          | Leafy brown algae                                            |                                          |
|                          | Herivores                                                    |                                          |
|                          | *Acanthurus gahhm/A. nigricauda*                             |                                          |
|                          | *Ctenochaetus striatus*                                      |                                          |
|                          | *Ctenochaetus strigosus*                                     |                                          |
|                          | *Rhinicanthus aculeatus*                                     |                                          |
|                          | *Balistapus undulates*                                       |                                          |
|                          | Family Balistidae                                            |                                          |
|                          | Omnivores                                                    |                                          |
|                          | *Acanthurus triostegus*                                      |                                          |
|                          | *Acanthurus leucosternon*                                    |                                          |
|                          | *Acanthurus lineata*                                         |                                          |
|                          | *Phytoplanktivores*                                          |                                          |
|                          | Exclusive corallivores                                       |                                          |
|                          | *Chromis viridis*                                            |                                          |
|                          | *Chaetodon trifasciatus*                                     |                                          |
|                          | *Chaetodon meyeri**                                           |                                          |
|                          | *Chaetodon trifascialis**                                    |                                          |
|                          | *Chaetodon auriga*                                           |                                          |
|                          | *Chaetodon lunula*                                            |                                          |
|                          | *Dascyllus aruanus*                                           |                                          |
|                          | *Abudefduf sexfasciatus*                                     |                                          |
|                          | *Plectroglyphidodon dickii*                                  |                                          |
|                          | *Pomacentrus sulfureus*                                      |                                          |

**Notes:** *Acanthurus gahhm and A. nigricauda were recorded together as they are difficult to distinguish. **Included in rainy season surveys only.*

### Reef Biotic Composition

Reef health can be measured in many ways, usually with some measure of biotic composition as a key component. A recent study found total fish biomass, live coral cover, crustose coralline algal cover, and presence of pathogenic bacteria to be effective reef health indicators (Kaufman et al. 2011). In this study we evaluated live hard coral cover, turf algal...
cover, and fish biomass, abundance, and taxonomic richness (a measure of relative rather than absolute richness, as in Garpe et al. 2006).

Ecological surveys were designed to closely match protocols utilized by Wildlife Conservation Society in Kenya (McClanahan 2008) while maintaining consistency with methods used in the Comoros for GCRMN reports (e.g., Ahamada et al. 2002). We conducted ecological surveys on fringing reef at <1–6 m deep at low tide, using line-point-intercept transects (25 m in length, 2–3 per site) for benthic cover, identifying benthic cover at 25 cm intervals along each transect (100 observations per transect). Each benthic cover observation was reported as one of nine categories: live scleractinian coral cover; non-scleractinian coral cover; turf algal cover; macroalgal cover; coralline algal cover; crustose coralline algal cover; dead coral cover; abiotic cover (sand, silt, bare substrate); and other biotic cover (zoanthids and gorgonians). Mean percent cover of each category was determined for each site using the numbers of observations in each category for each transect. We conducted belt transect surveys (25 m in length and 5 m width, 2–3 per site) for fish along the benthic cover transects. Fish surveys were conducted before benthic surveys or after completion of the benthic survey plus a waiting period of approximately 15 minutes without researchers in the transect area to avoid scaring fish and introducing survey bias. A total of 30 reef-associated fish species were included in the surveys, 13 of which were indicator species from Connand et al. (1998). Groupers (subfamily Epinephelinae), parrotfish (subfamily Scaridae), snappers (family Lutjanidae), and triggerfish (family Balistidae) were also included due to local anthropogenic or ecological importance although not all individuals were identified to species (see Table 1 for species and importance).

One observer conducted all fish and benthic surveys to avoid observer bias. We recorded counts of each species (or other taxonomic group) and size of individuals in categories of 3 to 10 cm, >10 to 30 cm, and >30 cm to facilitate biomass estimation. Mean fish abundance was calculated for each site from the number of fish per transect (reported as number of individuals 100 m$^{-2}$). Fish biomass was calculated using species Length-Weight tables (Froese and Pauly 2012) to determine the average weight of fish in each species and size class. The average weight was then multiplied by the number of fish observed in that species-size class for each transect to determine mean biomass per transect (reported as kg 100 m$^{-2}$) for each site. Fish richness was reported as the total number of species and other taxonomic groupings (of 34 possible) observed at each site. We conducted surveys twice at each site to account for seasonal differences, once during the pre-rainy season from September–December 2010 and once during the rainy season from January–March 2011. We did not conduct surveys from April–August due to high winds and wave action and poor visibility during those months.

**Human Activities**

As there is virtually no existing data on local human activities in the Comoros, we selected eight human activities for this study that were identified as contributors to reef degradation and recognized as in urgent need of management in the 2002 GCRMN World Status of Coral Reefs report for the Comoros (Ahamada et al. 2002). These activities are: men’s fishing; women’s fishing; coral extraction; sand extraction; beachfront housing and development; tourism; agriculture; and transport in and around reef areas. The influence of each of these activities on coral reef biota has been studied individually or cumulatively on other reefs (supplemental Table 1).

Due to sparse existing information and the large number of activities to investigate, we gathered data on each activity through interviews with community members knowledgeable
of coastal activities at each site. Although we did not have the time or resources to obtain absolute measures of activity intensity, we used information from the interviews in a scaled comparison of relative intensity of activities and management across sites. Interviewees were selected on the basis of knowledge of the community and local fishing practices. Interview questions focused on the eight human activities and management of the three commonly practiced activities involving use of common-pool resources: men’s fishing, women’s fishing, and sand extraction. The interviews included open-ended questions that allowed us to gather qualitative information and structured questions for which responses were scored (supplemental Table 1). Scored responses were combined into a scaled variable of intensity of activity and management for each activity (Table 2). We conducted interviews and observations from May through August 2009 with additional interviews and observations from September 2010 through March 2011 to update our findings to coincide with collection of ecological data and to determine whether any changes had occurred since our last interviews.

Other Natural and Anthropogenic Variables

We collected information on environmental, geographic, and anthropogenic variables including: island, latitude, longitude, coastline orientation, wave exposure, reef depth, rugosity, habitat types adjacent to the reef, distance to seagrass habitat, distance to mangrove habitat, visibility, season, time (measured by the number of days since first sampling day that a site was surveyed), population of adjacent human settlement, and distance to major markets (Table 1). The number of transects that were repeated in each season at each site was also included as surveys were planned to be conducted along permanent transect lines in each season, but some of the markers were lost between seasons and required us to conduct surveys along new transect lines.

Data Analysis

We employed linear regression and Pearson correlation coefficients to investigate relationships between individual predictors and reef biotic composition variables. Linear regression was used for preliminary data exploration as well as post-multivariate analyses for further explanation of findings.

We used Principal Components Analysis (PCA; MASS package in R) of benthic data from all transects to identify and remove outliers (Jolliffe 1986) and log-transformed fish abundance and biomass to meet assumptions of normality. Of the nine benthic categories surveyed, two (live hard coral cover and turf algal cover) were retained for analysis as all other benthic cover types made up less than one third of total benthic cover at each site and did not meet the requirement of few zero-values in the data for redundancy analysis (Zuur, Ieno, and Smith 2007). Fish biomass and abundance were analyzed using the summed values for all taxa as a high proportion of zero-values made values for individual taxa and functional groups unsuitable for analysis (Zuur, Ieno, and Smith 2007). Analysis was performed on a total of 18 sites each with two samples, one in the pre-rainy season and one in the rainy season (n = 36 for analysis of combined seasons).

We selected a subset of predictors to include in the analysis due to small sample size as well as multi-collinearity among predictors. Selected predictors had few zeros, few missing data, and high variance without gaps in levels of treatment. Preference was given to predictors with Pearson correlation coefficients of 0.50 or greater with multiple other predictors. One to three predictors were retained in each category: geographic (2: island and coastline
Table 2
Activity variables and scoring

| Attribute                  | Score | Description                                                                                           |
|----------------------------|-------|-------------------------------------------------------------------------------------------------------|
| Women’s fishing            | 0 = none | none                                                                                                 |
|                            | 1 = yes with strong management (rules respected by all, community is involved in management)       |
|                            | 2 = yes with moderate management (rules mostly respected or not respected only by outsiders, community may or may not be involved in management) |
|                            | 3 = yes with weak management (rules exist but poorly enforced, community may or may not be involved in management) |
|                            | 4 = yes with no management                                                                       |
| Men’s fishing              | see Women’s fishing (above)                                                                       |
| Coral extraction           | 0 = none | none                                                                                                 |
|                            | 1 = some | some                                                                                                 |
| Sand extraction            | 0 = none since 20 years or more                                                                  |
|                            | 1 = none since 10-19 years ago                                                                    |
|                            | 2 = none since 2-9 years ago                                                                     |
|                            | 3 = none since less than 2 years ago                                                               |
|                            | 4 = yes with strong management (rules respected by all, community is involved in management)       |
|                            | 5 = yes with moderate management (rules mostly respected or not respected only by outsiders, community may or may not be involved in management) |
|                            | 6 = yes with weak management (rules exist but poorly enforced or payment only, community may or may not be involved in management) |
|                            | 7 = yes with no management                                                                       |
| Beachfront housing and development | 0 = no housing                              | no housing                                                                                           |
|                            | 1 = little housing                                                                             |
|                            | 2 = decreasing housing                                                                        |
|                            | 3 = housing present with no change                                                               |
|                            | 4 = increasing; development                                                                    |
| Transport by motorized boat from reef site | 0 = none                                      | none                                                                                                 |
|                            | 1 = little                                                                                      |
|                            | 2 = decreasing                                                                                   |
|                            | 3 = some with no change                                                                          |
|                            | 4 = increasing                                                                                   |
| Tourism                   | See Transport by motorized boat (above)                                                          |
| Agriculture                | See Transport by motorized boat (above)                                                          |

orientation of each site), environmental (3: depth, rugosity, and time), anthropogenic (1: population of the adjacent community from 2003 census, log-transformed), and activities (3: men’s fishing, sand extraction, and beachfront development). Where data were missing for depth at one site, we used the mean depth of all other sites as a place holder to retain the site for analysis.
To assess the relationships between reef biotic composition variables and activities, population, and geographic and environmental variables, we performed redundancy analysis (RDA) and a permutation test of significance of the model. In RDA, ordination axes are constrained to a linear combination of the explanatory variables (Legendre and Legendre 2012; Zuur, Ieno, and Smith 2007). We plotted the RDA results using a distance triplot as a two-dimensional approximation of the correlation between response and predictor variables (Zuur, Ieno, and Smith 2007).

To determine the relative effect of human activities and other predictor variables on reef biotic composition, we partitioned the variance of reef biotic composition variables among human activity, environmental, geographic, and anthropogenic categories using partial redundancy analysis (partial RDA; vegan package in R). In partial RDA, a matrix of species or other response variables is related to a matrix of environmental or other explanatory variables while removing the effects of another explanatory matrix (Zuur, Ieno, and Smith 2007). We also conducted partial RDA analysis on each seasonal data set separately to identify seasonal discrepancies. We plotted seasonal data of individual reef biotic composition variables as a function of individual predictor variables to further enumerate seasonal differences.

Results

Of the predictor variable categories studied, human activities had the strongest relationship with reef biotic composition. Men’s fishing, women’s fishing, and agriculture were the most commonly practiced activities and were present at all sites. Hook and line fishing is the most common method for men’s fishing, with a few fishers at a few sites utilizing nets, cages, and/or harpoon guns. Women’s fishing is practiced from the shore with baskets and small nets as main catch methods for fish and spears for octopus. Poison was also used at a few sites to catch fish, and reports of breaking coral and digging for shellfish were found for one site each. Moderate or better management (in which the community respects management; see Table 2) took place at 11 sites for men’s fishing and 9 sites for women’s fishing. Coastal housing was present at 13 sites with continuing development along the beach taking place at five of those sites. Sand extraction was practiced at 13 sites with moderate or better management of the activity at two sites. Tourism and transport by motorized boat each took place at 13 sites. While interviewees at several sites stated that coral extraction was a common practice over twenty years ago, it is currently the least commonly practiced activity, being occasionally practiced at two sites. The practice ceased mainly with the import of cement which replaced the need for lime produced from harvested coral. Current coral collection is infrequent and in very small quantity for use as a decorative makeup. Most interviewees recognized the detrimental effects of coral removal.

Benthic cover and fish richness, abundance, and biomass varied among sites and seasons. Scleractinian coral cover ranged from 1% to 35% across sites. Turf algal cover was between 42% and 83% across sites. Dead coral and abiotic cover were in low abundance (<10% cover) at most sites. Non-scleractinian coral, macroalgae, coralline algae, and other benthic cover including hydroids and zoanthids were present at few sites and in low abundance. Fish taxonomic richness was between 4 and 14 for each site, mean fish abundance was between 19 and 79 individuals 100 m$^{-2}$ for each site, and mean fish biomass was between 0.88 and 80 kg 100 m$^{-2}$ for each site. Seasonal differences in biotic composition of reefs were observed, with fish abundance, biomass, and richness increasing at many sites during the rainy season (Figure 1). For fish biomass, increases were greatest at sites with fewest numbers of fishing boats (as a proxy for fishing pressure; Pinca et al. 2012),
Figure 1. Seasonal changes in fish abundance, biomass, and richness. Linear regressions of rainy season to pre-rainy season differences in (a) fish abundance ($r^2 = 0.0004, p = .93$), (b) fish biomass ($r^2 = 0.234, p = .04$), and (c) fish richness ($r^2 = 0.0411, p = .42$).

but this pattern was not as apparent for fish abundance and richness. Linear regression revealed that the number of fishing boats at each site had a significant negative correlation with seasonal change in fish biomass ($r^2 = 0.234, p = .04$, Figure 1b), but no significant correlation with fish abundance or richness ($r^2 = 0.0004, p = .93$, Figure 1a; $r^2 = 0.0411, p = .42$, Figure 1c; respectively).

Redundancy analysis (RDA) revealed relatively strong relationships among reef biotic composition variables and the selected human activity, population, geographic, and environmental variables (Figure 2). RDA results indicated that fish richness and biomass were negatively related to population, unmanaged men’s fishing, island, and depth (Figure 2). Fish richness decreased with depth and fish biomass was highest at mid-depths ($>1–2$ m). Turf algal cover was positively related to Eastern coastline orientation (Figure 2). Live hard coral cover and fish abundance were positively related to Western coastline orientation (Figure 2). Approximately 51% of the variation in reef biotic composition variables was explained by human activity, population, geographic, and environmental variables, with the first two axes explaining 29% (RDA1) and 13% (RDA2) of variation ($p \leq .001$ for both
Figure 2. Redundancy analysis plot (distance triplot) of biotic composition variables (plotted as vectors) with respect to predictor variables (plotted as vectors). Predictor variables (in blue) include: time (days); depth; island; log of population from 2003 census (logpop2003); men’s fishing (MF); coastline orientation (ort); rugosity; sand extraction (SAND); beachfront development (TH). 

axes). RDA1 may represent a gradient of reef degradation, from reefs with diverse benthic cover and abundant and diverse fish populations to turf algal dominant reefs with low fish abundance, biomass, and diversity. Turf algal cover increased along RDA1 while live hard coral cover, fish richness, abundance, and biomass decreased. This gradient was associated positively with human population, island, and North-Eastern coastline orientation. RDA2 may represent a gradient of poor to robust fish diversity and size as fish richness and biomass increased along RDA2. Turf algal cover was also positively related to RDA2, while live hard coral cover and fish abundance were negatively related to RDA2. Rugosity and sand extraction were strongly positively correlated with RDA2 while human population, men’s fishing, depth, and island were negatively correlated with RDA2.

Partial RDA revealed that human activities most related to reef biotic composition. Of the 51% of variance explained by the geographic, environmental, anthropogenic, and human activity variables and their interactions, the largest proportion of variance was explained by human activities (15%), followed by geographic variables (13%), environmental variables (11%), population (7%), and interactions among all variables (5%) (Figure 3).

Seasonal RDA and partial RDA results indicated that the effects of human activities were most strongly apparent in the pre-rainy season and much less apparent in the rainy season. Human activities accounted for 24% of variance in the pre-rainy season (the most
Figure 3. Partial RDA results. Variance explained by activities (15%), geography (13%), environment (11%), population (7%), variables and their interactions (5%), and unexplained variance (49%).

of any predictor categories) and for 15% in the rainy season (Figure 4). The proportion of variance explained by environmental variables and population also decreased in the rainy season (from 16% to 15% and from 12% to 9%, respectively), while the interaction term increased (from <1% to 8%; Figure 4). Across both seasons, the percentage of variance explained by geographic variables remained the same (18%; Figure 4).

Figure 4. Partial RDA results by season. Variance explained by activities (pre-rainy: 24%; rainy: 15%), geography (pre-rainy: 18%; rainy: 18%), environment (pre-rainy: 16%; rainy: 15%), population (pre-rainy: 12%; rainy: 9%), variables and their interactions (pre-rainy: <1%; rainy: 8%), and unexplained variance (pre-rainy: 30%; rainy: 35%).
When comparing RDA results with and without human activities as predictor variables, it is clear that human activities greatly enhanced explanatory power, with the full suite of predictors explaining 51% of variance and the suite of predictors without human activities explaining 36% of variance. Geography and population explained less variance in the absence of human activities, most likely due to some co-linearity of these predictors. In partial RDA without human activity predictors, geography explained 5% of variance, environment explained 11%, population explained 7%, interaction terms explained 13%, and 64% of variance remained unexplained.

Discussion

This study identified, for reefs of the Comoros, the human activities most influential on reef biotic composition and most in need of management. Not only did inclusion of men’s fishing, sand extraction, and beachfront development greatly improve explanatory power of predictors in RDA, these human activities were identified as the most influential suite of predictors for reef biotic composition. Other studies that include a single activity or a cumulative assessment of activities as predictors of fish assemblages and other reef biota have similar or lower explanatory power (e.g., Pinca et al. 2012; Sala et al. 2012). This study also identified the relative effects of human activities and natural and anthropogenic factors on reef biotic composition. Geographic factors of island and coastline orientation and environmental factors of depth, rugosity, and time followed human activities as influential predictors of reef biotic composition. Sea temperature, currents, and nutrient flows are likely factors contributing to both geographic and temporal patterns of reef biotic composition (e.g., Andrews and Gentien 1982; Choat, Ayling, and Schiel 1988; West and Salm 2003; Sala et al. 2012). An important conclusion from this study is that human activities are more influential than geographic and environmental factors on reef biotic composition of the study sites.

The findings from this study directly inform management at the study sites. For prevention of further coral reef degradation in the Comoros, we recommend testing the use of fishery closure areas, beach closures and sanctions for sand extraction, and zoning for coastal development. Each of these management practices can be easily tested for effectiveness through an adaptive management approach of monitoring reef biotic composition post-implementation. The adaptive management process allows managers and scientists to test the effectiveness of management practices in prevention of coral reef degradation. We use the term adaptive management to describe the process, defined by Salafsky, Margoulis, and Redford (2001), of incorporating "... research into conservation action. Specifically, it is the integration of design, management, and monitoring to systematically test assumptions in order to adapt and learn.” Fishery closures in the form of no-take areas or periodic harvest areas have been found to be effective for coral reefs in settings similar to the Comoros at increasing fish richness, abundance, and biomass (e.g., McClanahan et al. 2006, 2007). Closing a beach to sand extraction and imposing sanctions to deter sand extraction may reduce or eliminate the erosion and poor water quality caused by sand extraction (e.g., Huber and Meganck 1990). Zoning to control coastal urbanization and housing development may prevent polluted runoff and erosion that can reduce water quality and kill coral (e.g., Wolanski, Martinez, and Richmond 2009). Prioritization of management actions should be selected at each site to address local intensity and frequency of activities and to include local community members and stakeholders in the decision-making and implementation process. With local participation, alternative management practices may also be devised and implemented to suit local social conditions.
and ecological conditions. Continued monitoring as well as scientific, management, and community involvement, along the lines of adaptive co-management described by Armitage et al. (2009), provide the best conditions for successful adaptive management. While the effect of human activities on reefs, the types of activities affecting reefs, and the management solutions are context dependent, the study methods and the adaptive management approach can be applied to inform management of coral reefs under direct human pressure and resource use throughout Western Indian Ocean region and the world.

The findings of this study reveal similarities and a few differences in human activity effects on coral reefs of the Comoros compared to other vulnerable reefs in the region and the world. Men’s fishing and human population were among the predictors most strongly related to poor coral cover and low fish richness, abundance, and biomass. These findings are consistent with other studies (e.g., Russ and Alcala 1989; McClanahan 1994; Williams et al. 2008; Stallings 2009). The predictive power of human population is similar to a study of fishery closures in the Western Indian Ocean that found population (along with level of infringement) to be the strongest predictor of change in fish biomass (Daw et al. 2011). While some studies have found that market distance or socioeconomic development have strong relationships with fish size, biomass, and trophic level (e.g., Cinner and McClanahan 2006; Cinner et al. 2009), human population was a stronger predictor than market distance in our analysis. This difference is likely due to the greater variation among study sites in human population than market distance, thus making human population a more detailed predictor, and the relatively small size of Comoran markets, making market pressure in the Comoros weaker than in areas with larger and more influential markets. Level of socioeconomic development across the study sites was too similar to test its influence on reef biotic composition.

One limitation of this study was poor data availability forcing exclusion of some variables that may affect reef biotic composition. For example, freshwater output and terrestrial runoff deposition on reefs may further explain reef degradation at some sites, but this data was not available for all sites. We suspect that these variables account for some of the unexplained variance in this study. Some might argue that sampling only snorkel-accessible reefs biased the results. Use of SCUBA would have widened the options for potential study sites, but snorkel-accessible reefs are numerous and are most likely the reefs most vulnerable to human activity. Were reefs at greater depths and accessible only by SCUBA included in future studies, we would expect to find reduced influence of human activities relative to the influence of environmental factors (especially depth) on reef biotic composition.

Lack of control sampling may also be considered a limitation of this study, especially since partial RDA results indicate that relationships between human activities and reef biotic composition were partly masked by spatial and temporal variability within and among sites. The primary seasonal differences were fish richness, abundance, and biomass, with a significant negative relationship between number of fishing boats at a site and seasonal change in fish biomass (Figure 1). While explaining seasonal differences was not a main objective of this study, these observations may be attributed in part to decreases in overall fishing effort and switching of fishing effort to pelagic and other non-reef associated species during the rainy season (Coordination des Comores 1996; personal observation), and are worth investigating in future studies. We expect that were control samples available (either as areas free of human activity, or from prior to human activity), the results would have revealed even greater influence of human activities on reef biotic composition. By sampling sites with a gradient of human activity and through consideration of other natural and anthropogenic factors, this study was able to evaluate the relative effects of human activities on reef biotic composition. While this study cannot attribute causality of reef
degradation to the factors studied, the findings do shed light on human activities that may be identified through further study as causes of reef degradation at the study sites. If recommended management actions are implemented at the study sites, the data from this study could serve as control data for future studies post-management implementation.

Further evidence and understanding of the direct effects of human activities at specific study sites can be obtained over time and with additional research. Additional research is also necessary to identify site-level differences in drivers of reef degradation. For example, intensive sand extraction has occurred at a few sites and is likely the key driver of reef degradation at those sites, but is less influential at sites where extraction has ceased or is less intense (personal observation). Study of sedimentation rates at reef sites with known sand extraction levels could also provide further insight into the relationship of sand extraction with reef degradation and may provide evidence of a causal relationship. Causal relationships are commonly studied when examining the relationship of fishing with reef degradation (e.g., Jennings and Polunin 1996; Mumby et al. 2006) and have been applied to investigations of agriculture and reef degradation (Fabricius and De’ath 2004). Detection of human activity effects on reef biotic composition could be improved with modifications to data collection to address spatial and temporal variability, including more concerted sampling effort at sites with high spatial heterogeneity in benthic and fish assemblages and long-term monitoring of temporal patterns.

For the world’s most diverse and vulnerable reefs, studies of effects of human activities on reef biotic composition are sparse and limit our ability to effectively manage vulnerable reefs. This study demonstrated that a local assessment of human activities associated with reef degradation and an evaluation of the relative contributions of human activities and other natural and anthropogenic factors to reef degradation can provide substantial information and direction to management for conservation of vulnerable coral reefs. Local coral reef management efforts that include research-based knowledge of anthropogenic effects on coral reefs and adaptive management approaches will have the best chance of addressing the drivers of reef degradation and thereby maintain coral reefs over time.

Supplemental Material
Supplemental data for this article can be accessed on the publisher’s website.

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