Coral Reefs
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REPORT

Interactive effects of three pervasive marine stressors in a post-disturbance coral reef

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Abstract Ecosystems are commonly affected by natural, episodic disturbances that can abruptly and drastically alter communities. Although it has been shown that resilient ecosystems can eventually recover to pre-disturbed states, the extent to which communities in early stages of recovery could be affected by multiple anthropogenic stressors is poorly understood. Pervasive and rising anthropogenic stressors in coastal marine systems that could interactively affect the recovery of these systems following natural disturbances include high sedimentation, nutrient enrichment, and overfishing. Using a 6-month field experiment, we examined the effects of all combinations of these three stressors on key functional groups in the benthic community growing on simulated, post-disturbance reef patches within a system recovering from large-scale natural disturbances (corallivorous seastar outbreak and cyclone). Our study revealed that sedimentation, nutrient enrichment, and overfishing (simulated using exclusion cages) interactively affected coral survival and algal growth, with taxon-specific effects at multiple scales. First, our treatments affected corals and algae differently, with sedimentation being more detrimental to macroalgal growth but less detrimental to coral (*Porites rus*) survival in caged plots, driving significant interactions between sedimentation and caging for both taxa. We also observed distinct responses between coral species and between algal functional groups, with the most extensive responses from algal turf biomass, for which sedimentation suppressed the synergistic (positive) combined effect of nutrient enrichment and caging. Our findings suggest that different combinations of ubiquitous anthropogenic stressors, related to either sea- or land-based activities, interactively influence community recovery from disturbance and may alter species compositions in the resulting community. Our findings further suggest that anthropogenic stressors could promote further degradation of coral reefs following natural disturbances by inhibiting recovery to coral-dominated states that provide vital ecosystem services to coastal populations worldwide.

Keywords Anthropogenic impacts · Environmental disturbance · Eutrophication · Terrestrial runoff · Ecological resilience · Ecosystem recovery

Introduction

Community structure and diversity can change abruptly and drastically due to natural, episodic disturbances, such as fires, storms, disease outbreaks, or spikes in consumer production (Levin and Paine 1974; Connell 1978). A recent

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synthesis across terrestrial and aquatic systems showed that most systems can fully recover from disturbances on timescales of decades to half centuries (Jones and Schmitz 2009). However, the studies synthesized by Jones and Schmitz (2009) featured systems that were allowed to recover (or even encouraged to do so, via restoration efforts) in the absence of chronic human-induced disturbances.

Human activities can control levels of biological, physical, and chemical properties of natural ecosystems (Foley et al. 2005; Elser et al. 2007), giving rise to 'anthropogenic stressors' that negatively affect organisms or communities. In most systems, multiple stressors co-occur, and recent meta-analyses, based largely on experiments manipulating pairs of stressors, suggest that, more often than not, stressors interact with one another (Crain et al. 2008; Darling and Côté 2008). An interaction between factors causes the effect of one factor to change quantitatively or even qualitatively, depending on the level of a second factor. Thus, combined stressor effects can be synergistic or antagonistic and are frequently unpredictable, even if we understand each stressor effect in isolation. While it is well established that multiple stressors can degrade ecosystems, the extent to which multiple stressors affect recovering systems has rarely been formally explored (Nyström et al. 2000; Hughes et al. 2010). Comparative observational studies in terrestrial and aquatic systems suggest that anthropogenic stressors can inhibit recovery following disturbance (Short and Wyllie-Echeverria 1996; Foster et al. 1999; Chazdon 2003), though field experiments testing these effects are greatly needed.

Coral reefs around the world are affected by regular, often large-scale, natural disturbances including storms and bleaching events, as well as regional outbreaks of the corallivorous crown-of-thorns seastar (COTS), *Acanthaster planci* (Hayne and Chappell 2001; Leray et al. 2012; Lamy et al. 2016). For example, De'ath et al. (2012) estimated that tropical cyclones, COTS, and bleaching were responsible for 24, 21, and 5%, respectively, of coral loss on the Great Barrier Reef over a 27-yr period. However, coral reefs are also threatened by globally pervasive stressors, led by nutrient enrichment and overfishing (Bellwood et al. 2004; Fabricius 2005). Nutrient enrichment stimulates the growth of benthic algae (Littler et al. 2006; Lapointe et al. 2010) that can elicit a suite of harmful effects on corals (McCook et al. 2001; Smith et al. 2006; Rasher and Hay 2010), while overfishing removes consumers that structure the benthic community and, either directly or indirectly (Ruppert et al. 2013), control algal populations (Jackson et al. 2001; Bulleri et al. 2013). A tremendous amount of attention has been paid to testing for interactive effects of nutrient enrichment and overfishing in coral reefs, and a meta-analysis of these works revealed that nutrient enrichment typically leads to much more algae when combined with overfishing effects (simulated with consumer exclusion cages; Burkepile and Hay 2006). This is due to the separate pathways of these stressors; nutrients stimulate algae (bottom-up), which overfishing can release from herbivorous grazing (top-down; Fig. 1). Thus, the combination of nutrient enrichment and overfishing is believed to be a key driver of global declines in coral reefs (McCook 1999; Bellwood et al. 2004; Burkepile and Hay 2006). However, nutrient enrichment is typically driven by terrestrial runoff, which can also deliver sediment loads that attenuate light and smother corals (Rogers 1990; Erftemeijer et al. 2012). Despite frequent co-occurrence and multiple direct and indirect pathways of potential interactions of sedimentation, nutrient enrichment, and overfishing (Fig. 1), strikingly few studies have tested for interactions among these prominent reef stressors.

Ban et al. (2014) revealed that among 176 studies on multiple stressors in coral reefs, only two quantitatively tested for interactive effects of sedimentation and either nutrient enrichment or overfishing on the growth or survival of coral or the growth of benthic algae. These studies consisted of correlative surveys (non-manipulative) that revealed no clear interactive effects on coral cover of either sedimentation and nutrient enrichment (though ranges of stressors were limited; Wielgus et al. 2004), or sedimentation and overfishing (though poaching was likely confounding; Halpern et al. 2012). To date, only a single published study has explored interactions among sedimentation, nutrient enrichment, and overfishing. In this experiment in a Panamanian reef, Muthukrishnan and Fong (2014) showed that on reef patches with near-complete initial coral cover sedimentation reinforced effects of overfishing on algal biomass (positive effects) and the relative cover of large adult coral colonies (negative effects). Similar to the nutrient-overfishing interaction noted above (Burkepile and Hay 2006), this effect was likely driven by separate pathways of sedimentation, which can provide substrate for algae (Nugues and Roberts 2003), and overfishing, which frees algae from herbivory, increasing the competitiveness of algae with coral. Sedimentation also weakened positive effects of nutrient enrichment on filamentous algal turf, potentially due to sediment inhibiting algal uptake of nutrients (Muthukrishnan and Fong 2014). It remains unclear, however, whether similar patterns would hold following a disturbance that leaves in its wake small, newly emerging coral colonies (typically more vulnerable to mortality; Madin et al. 2014) and exposed, dead areas of reef. Consequently, despite their ubiquity in coral reefs prone to natural disturbances, the effects of different combinations of sedimentation, nutrient enrichment, and overfishing on reef communities following disturbance remain untested.

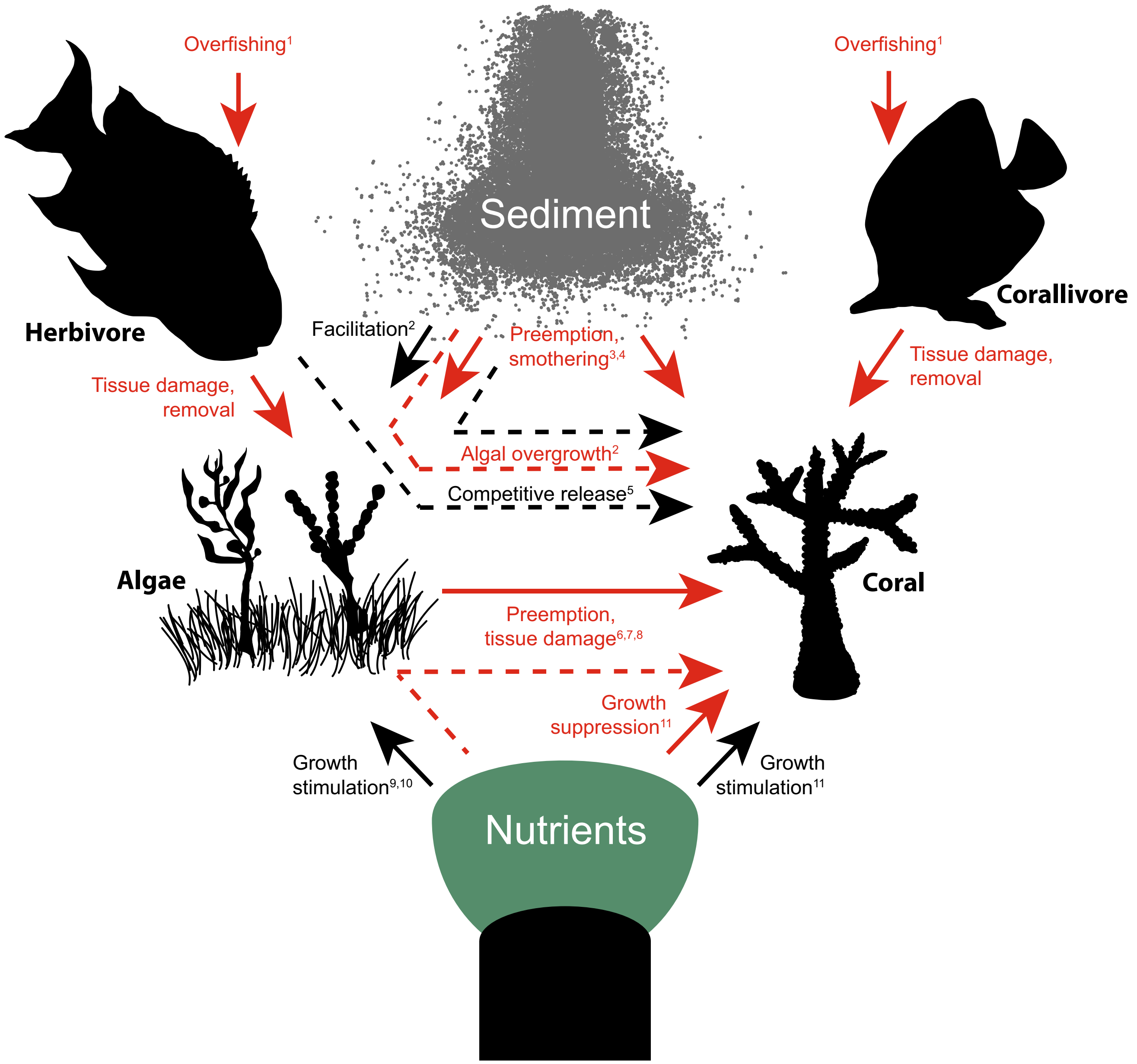


Fig. 1 Conceptual diagram illustrating the nature (*black* positive, *red* negative) of direct effects, represented by *solid arrows* with putative mechanism(s) noted, and indirect effects, represented by *dashed arrows* that manifest through benthic algae (*middle left*), of sedimentation, nutrient enrichment (e.g., from a sewage outfall), and consumers that are removed by overfishing (represented by both the herbivorous fish at the *top left* and the corallivorous fish at the *top right*), on the settlement, growth, and survival of coral. Figure references: [1]Jackson et al. (2001), [2]Nugues and Roberts (2003), [3]Rogers (1990), [4]Birrell et al. (2005), [5]Bulleri et al. (2013), [6]McCook et al. (2001), [7]Rasher and Hay (2010), [8]Smith et al. (2006), [9]Lapointe et al. (2010), [10]Littler et al. (2006), [11]Gil (2013)

Patches of reef substrate cleared by natural disturbances (De'ath et al. 2012) may later be accompanied by small, emergent coral colonies that can establish the next generation of corals to support the ecosystem. Thus, to assess how recovery of coral reefs can be affected by multiple stressors, we simulated post-disturbance reef habitat patches using both open, hard substrate and small coral fragments. We subjected these patches to a fully crossed, three-factor manipulation in situ for 6 months in a recovering reef system. We tested for interactive effects of sedimentation, nutrient enrichment, and the exclusion of large consumers (those targeted by fishing) on key functional groups in the benthic community: two species of corals with distinct morphologies that represent two of four cosmopolitan coral life-history strategies (thin-branching, 'competitive' strategy: *Acropora pulchra*; thick branching and mounding, 'weedy' strategy: *Porites rus*; Darling et al. 2012) and two of three key algal functional groups (filamentous algal turf and macroalgae; Littler and Littler 2007).

We tested a series of hypotheses based on previous findings that sedimentation, nutrient enrichment, and overfishing will generally have positive effects on algae and negative effects on corals (Rogers 1990; Nugues and Roberts 2003; Burkepile and Hay 2006; Fabricius 2011); nutrients and overfishing will interact to reinforce positive effects on algae and negative effects on corals (Burkepile and Hay 2006); sedimentation and nutrient enrichment will either not interact (Wielgus et al. 2004) or interact to limit each other's positive effects on algae and negative effects on corals (Muthukrishnan and Fong 2014); and sedimentation and overfishing will either not interact (Halpern et al. 2012) or will interact to reinforce positive effects on algae and negative effects on corals (Muthukrishnan and Fong 2014). Furthermore, life-history traits, including growth rate and morphology, could influence stressor effects on settlement or early growth (Lenihan et al. 2011; Darling et al. 2012). Thus, we also hypothesized that faster-growing taxa (*A. pulchra* and algal turf) would be more sensitive to our stressor treatments than related, slower-growing taxa (*P. rus* and macroalgae).

Materials and methods

Study site and experimental units

We conducted this study in January–July 2013, at a back-reef/lagoon location off the north shore of Mo'orea, French Polynesia (17°28′59″S, 149°49′55″W). This system is in recovery, following two recent, large-scale natural disturbances: a COTS (*A. planci*) outbreak that lasted several years and dissipated in 2010, and cyclone *Oli*, which hit the north shore in February 2010 (Leray et al. 2012; Lamy et al. 2016). These disturbances directly affected the fore reef more than the back reef, but these fore reef effects likely extend to the back reef, because fore reef populations serve as important sources of corals, fish, and other taxa that recruit to the back reef (Leichter et al. 2013). Furthermore, concentrations of 100 COTS km^{-2} were observed in the back reef of Mo'orea in 2009–2010 (Mills 2012). At our study location and nearby coral collection site, sedimentation rate and the concentration of water-column nutrients (nitrate + nitrite) averaged at just 12.6 mg cm^{-2} d^{-1} and 0.57 µM, but reached maximums of 89.9 mg cm^{-2} d^{-1} and 1.2 µM over 5- and 6-yr periods, respectively (Alldredge 2012, 2013). Thus, corals used in our study were not pre-conditioned to chronic sedimentation or nutrient enrichment, but may have experienced infrequent pulses of these stressors due to pronounced rainfall events.

We selected the thin-branching coral *A. pulchra* (Brook, 1891) and the more bulbous coral *P. rus* (Forsskal, 1775) as study species because of their differing ecological functions (Nyström 2006), morphologies and life-history strategies (Fig. 2; Darling et al. 2012), which may affect their susceptibility to stressors (Bulleri et al. 2013). In addition, the genera of these species are common in Mo'orea and are globally distributed (Veron 1995). In January 2013, we collected eight coral fragments from each of nine *A. pulchra* and nine *P. rus* colonies at ~1.5–2 m depth near our study site (17°29′15″ S, 149°53′18″ W) and immediately transported fragments in coolers to the Richard B. Gump South Pacific Research Station. We mounted each fragment onto hard plastic mesh using epoxy (Splash Zone, Carboline Company, St. Louis, Misouri, USA) and recorded its weight using the buoyant mass technique (Davies 1989).

Two days after collecting corals, we assembled experimental units in situ. Each experimental unit was supported by a concrete block ($l \times w \times h = 25 \times 20 \times 11$ cm), to which we attached one fragment of *A. pulchra* (height = 54 ± 9 mm [mean ± SD]) and one fragment of *P. rus* (height = 30 ± 5 mm), using cable ties woven through plastic bases. We also used pre-cemented set screws and wing nuts to attach to each unit four unglazed terracotta tiles (Fig. 2), which are commonly used as proxies for reef substratum (Adjeroud et al. 2007; Penin et al. 2010). We arranged experimental units in nine randomized, complete blocks, in which blocks accounted for potential spatial patterns in responses as well as effects due to coral colony of origin (i.e., the eight coral fragments from a given colony were assigned to the same block). To minimize nutrient spillover among treatments (see next subsection), we separated the units of each block by at least 2 m (Wartian 2006) and arranged them in a straight line perpendicular to the unidirectional south-southeast current that predominates at the study site (Hench et al. 2008). Further, a natural channel separating our study location from nearshore waters likely minimized the influence of terrestrial runoff on our study (Alldredge 2012, 2013). We placed experimental units among coral habitat patches (within 1 m of hard bottom reef habitat) on sand at 2–3 m depth with the same orientation to the current (Fig. 2).

Anthropogenic stressor manipulations

We simulated sedimentation, nutrient enrichment, and overfishing over a six-month period to investigate potential interactive effects of these stressors on coral reef recovery. First, the 'high sedimentation' treatment was chosen to have a sedimentation rate of 212 mg cm^{-2} d^{-1}: our applied rate (200 mg cm^{-2} d^{-1}) + the ambient rate (12 mg cm^{-2} d^{-1}; Alldredge 2012), because: (1) it greatly exceeds natural (i.e.,

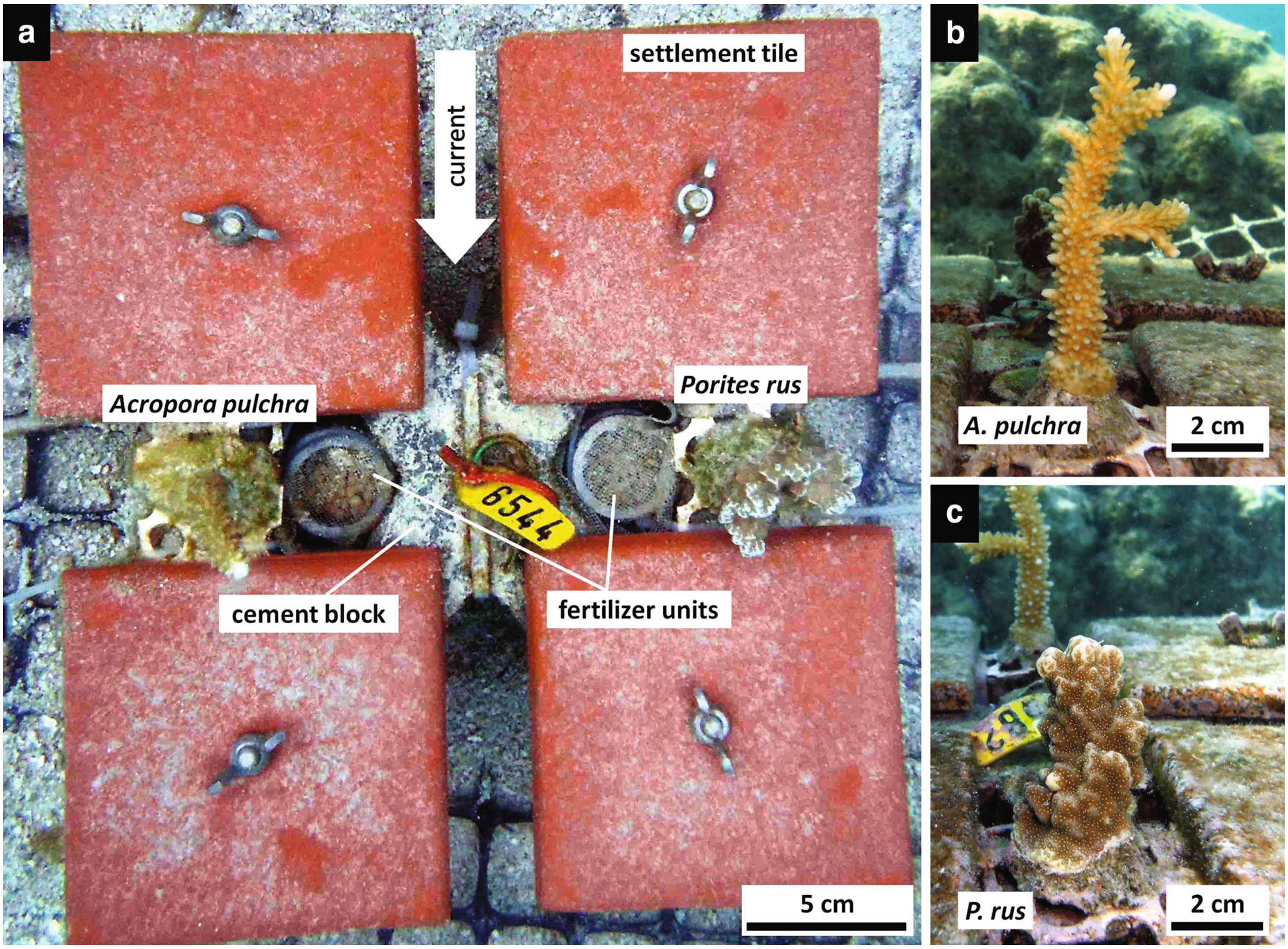


Fig. 2 Experimental unit in the field: **a** *top-view* of a complete unit during the first week of the experiment, and *side-views* of **b** *Acropora pulchra* and **c** *Porites rus* fragments 2 months after the start of the experiment

'pristine') sedimentation rates (Rogers 1990), (2) it falls well within known sedimentation rates affecting various coral reefs (Electronic Supplementary Materials, ESM, Table S1), and (3) similar sedimentation rates have been shown to negatively affect or even kill various coral species (Erftemeijer et al. 2012). The high sedimentation treatment was imposed by applying sediment of terrestrial origin to experimental units in multiple, daily pulses over a course of 2–3 d each week (see ESM Appendix 1 for additional details on sediment collection and application).

Nutrient enrichment was imposed by first placing two PVC tubes, sealed at the bottom and covered by mosquito netting at the top, within the two gaps in the cement block supporting each experimental unit (Fig. 2). We filled each PVC tube in nutrient-enriched units with 50 g of Osmocote (The Scotts Company, Marysville, Ohio, USA) slow-release garden fertilizer (N:P:K-ratio = 19:6:12), and this fertilizer was replaced every 4 weeks (Burkepile and Hay 2009). We filled the PVC tubes in unenriched units with sterilized sediment, to prevent colonization by small fishes or invertebrates. We slowly extracted water samples using a 30-mL syringe (Burkepile and Hay 2009) from the bases of coral fragments from three complete experimental blocks (24 units) at two times points (4 and 23 d after fertilizer replacement). Each water sample was immediately run through a 0.45-µm glass fiber filter and frozen until analysis for nutrient (nitrate + nitrite) concentrations at the University of Florida/IFAS Analytical Services Laboratories (Gainesville, Florida, USA). These water samples revealed that, as intended, our enrichment procedure achieved a significantly elevated availability of nutrients (approximately threefold) in enriched relative to unenriched units (nitrate + nitrite concentration: 0.448 ± 0.116 [mean ± SE] µM for control vs. 1.24 ± 0.323 µM for nutrient-enriched units; ESM Fig. S1). Our control measurements were similar to ambient nitrate + nitrite concentrations measured annually from nearby sites (0.570 ± 0.085 µM; Alldredge 2013).

We mimicked effects of overfishing by excluding large consumers, such as herbivorous and corallivorous fish that can be drastically depleted in overfished reefs (Bellwood et al. 2004; Hughes et al. 2010), using plastic exclusion cages (diameter = 50 cm, height = 32 cm, mesh = 4 cm). This mesh size was chosen to avoid cage artifacts; previous work has shown that mesh sizes of 2.5 cm do not demonstrably affect current flow or the growth of benthic organisms (Burkepile and Hay 2009). Fouling organisms were brushed off the cages weekly. We video-recorded visiting consumers for a subset of our replicates (ESM Fig. S2), indicating that a mixture of herbivorous and corallivorous fish (all >4 cm in size) frequently foraged from our uncaged experimental units.

We fully crossed two levels (ambient and elevated) of each of the three factors (sediments, nutrients, fishing), resulting in eight experimental treatments, with one replicate in each of nine replicated blocks for a total of 72 experimental units. At the conclusion of the experiment, we retrieved the corals, obtained their buoyant weights, and visually estimated using the naked eye the % of the surface area of each coral colony that supported live coral tissue. We also removed and separated filamentous algal turf and macroalgae from all surfaces of two settlement tiles from each unit and dried these samples in an oven at 70 °C until the mass was stable. Lastly, we first removed non-calcified organic matter from the second pair of tiles from each unit by soaking them in a bleach solution. We then used a microscope to count coral polyp skeletons on all surfaces of one of the tiles from each unit; we did not analyze the second tile due to logistical constraints.

We quantified stressor effects and interactions using an ANOVA with seven orthogonal contrasts, comprised of main effects for each of the three factors (sedimentation, nutrient enrichment, and caging), three two-way interactions (i.e., between stressor pairs), and one three-way interaction (i.e., among all three stressors) for each response variable. Interactions among factors were calculated based on an additive null model, because this approach is: (1) simple and straightforward (Brook et al. 2008), (2) generally used in factorial stressor experiments (Crain et al. 2008), and (3) used in multiple stressor applications (Halpern et al. 2008). We also quantified effects of algal biomass (turf and macroalgae) on *P. rus* survival with linear models. We conducted statistical analyses of main effects and interactions of stressor manipulations, as well as algal effects on coral survival using randomization tests (for each response variable) based on 10,000 randomly drawn permutations, in which errors were stratified by block, using the lmPerm package (Wheeler 2010) in the program R (R Core Team 2013). This statistical approach is robust across response variables with differing distributions and for which assumptions about parent distributions used in standard parametric tests cannot be meet (e.g., percent live tissue cover of coral fragments).

Results

Results from all seven planned (orthogonal) comparisons, testing for main effects, two-way interactions (between stressor pairs), and a three-way interaction (among sedimentation [S], nutrient enrichment [N], and caging [C]) for each of six response variables (coral recruitment, turf biomass, macroalgal biomass, *A. pulchra* growth, *P. rus* growth, and *P. rus* survival) are summarized in Table 1.

Settlement to barren substrate

For the biomass of filamentous algal turf that grew on our initially barren settlement tiles (Fig. 2), all three pairwise interactions (S × N, $p = 0.047$; S × C, $p = 0.0015$; N × C, $p = 0.034$) were significant, indicating that sedimentation had a stronger negative effect on turf growth in the presence of nutrient enrichment or caging and that the positive effects of nutrient enrichment on turf growth were greatest in the presence of caging (Fig. 3a). The three-way interaction (S × N × C, $p = 0.022$) was also significant for turf biomass, because algal turf benefited from reduced grazing (due to caging) to a greater degree in the absence of high sedimentation (Fig. 3a). Relative to algal turf, the biomass of macroalgae on settlement tiles was generally lower. For macroalgal biomass, the main effect of caging (positive effect, $p = 0.021$) was significant, while main effects of sedimentation (negative effect, $p = 0.38$) and nutrient enrichment (negative effect, $p = 0.62$) were insignificant, but there was a significant interaction between sedimentation and caging (antagonistic; $p = 0.034$), in which sedimentation had a negative effect in caged units but a positive effect in uncaged units (Fig. 3b; Table 1). All other interactions were insignificant for macroalgal biomass (Table 1). In contrast to benthic algae, we observed very few coral recruits at the end of our six-month experiment (23 total recruits, on 20 of 72 settlement tiles), for which we were unable to detect significant main effects or interactions (Table 1).

Coral fragment survival and growth

We observed responses in survival of coral fragments that differed across treatments and between coral species (Table 1). First, *A. pulchra* was extremely sensitive to our

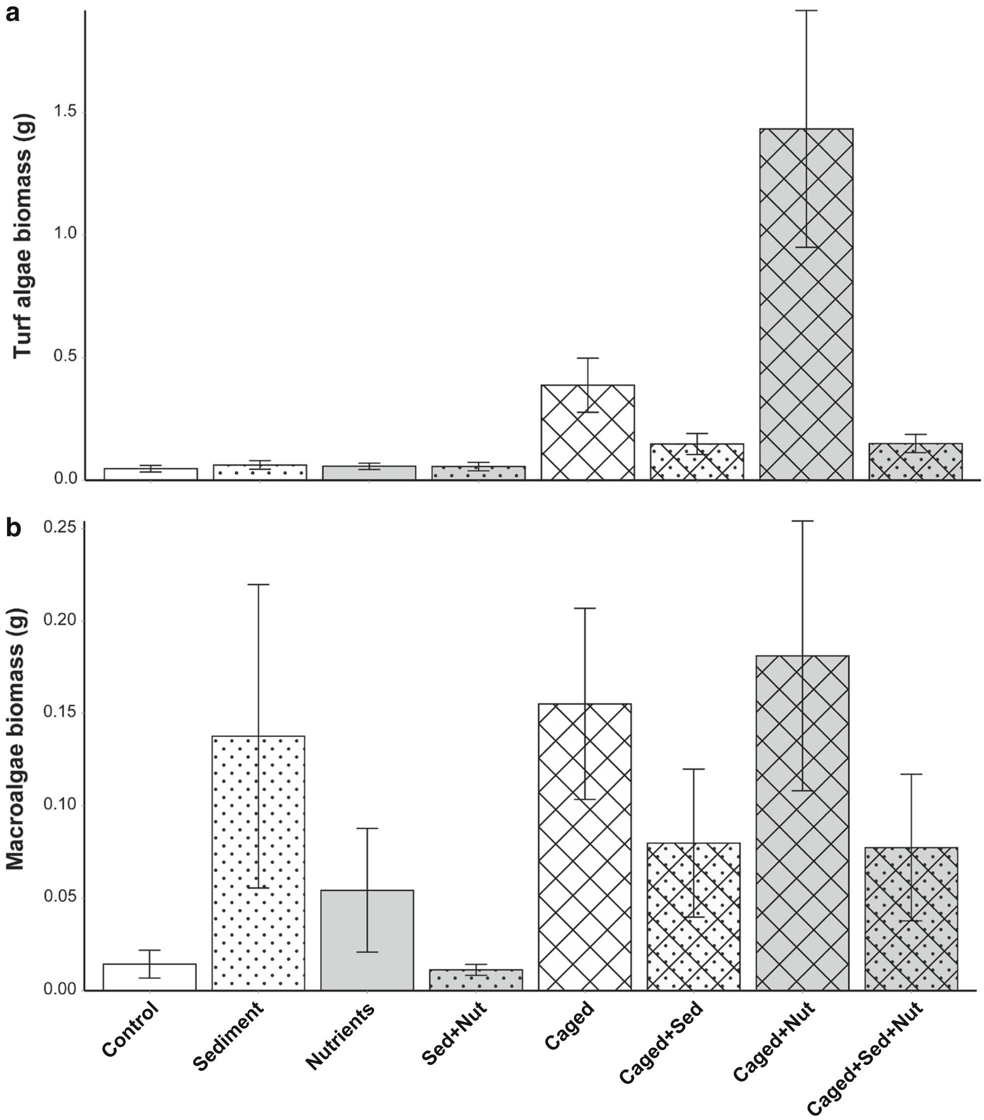
Table 1 Summary of statistical modeling results for main effects and interactions for algal growth and coral growth and survival data (*Porites rus* survival was measured as the % of each colony that survived)

Response	Factor	Coefficient	P	Significance
Algal turf biomass	Sediment	−0.36	0.0066	**
	Nutrients	0.01	0.070	
	Caging	0.32	<0.0001	***
	S × N	−0.53	0.047	*
	S × C	−0.76	0.0015	**
	N × C	0.52	0.034	*
	S × N × C	−1.06	0.022	*
Macroalgal biomass	Sediment	−0.031	0.38	
	Nutrients	−0.018	0.62	
	Caging	0.075	0.021	*
	S × N	−0.098	0.18	
	S × C	−0.15	0.034	*
	N × C	0.055	0.41	
	S × N × C	0.14	0.30	
Coral recruits	Sediment	0.19	0.16	
	Nutrients	−0.083	0.56	
	Caging	0.023	0.82	
	S × N	0.056	0.83	
	S × C	−0.39	0.14	
	N × C	−0.28	0.28	
	S × N × C	−1.00	0.074	
Porites rus % survival	Sediment	−7.19	0.51	
	Nutrients	−10.86	0.31	
	Caging	7.53	0.49	
	S × N	9.94	0.62	
	S × C	45.61	0.024	*
	N × C	−25.06	0.21	
	S × N × C	−57.89	0.19	
	Turf (un-caged)	−247.27	0.132	
	Macroalgae (un-caged)	−111.26	0.041	*
	Turf (caged)	−7.36	0.44	
	Macroalgae (caged)	46.01	0.38	
Acropora pulchra growth	Sediment	−1.67	0.44	
	Nutrients	4.86	0.022	*
	Caging	NA	NA	
	S × N	−1.89	0.65	
	S × C	NA	NA	
	N × C	NA	NA	
	S × N × C	NA	NA	
Standardized *Porites rus* growth	Sediment	−1.26	0.22	
	Nutrients	2.13	0.025	*
	Caging	1.59	0.15	
	S × N	1.33	0.98	
	S × C	3.36	0.12	
	N × C	−0.99	0.66	
	S × N × C	1.86	0.67	

Significance codes for estimated model coefficients: 0 '***' 0.001 '**' 0.01 '*' 0.05

Blocking was significant only for main effects on *P. rus* growth

Fig. 3 Dry biomass (g) of **a** filamentous algal turf, and **b** macroalgae, across all treatment combinations ($n = 9$; mean ± SE). See Table 1 for a summary of statistical comparisons



caging treatment, suffering complete mortality via consumption (i.e., colonies were completely bitten off down to the base by corallivores) in all uncaged units in the first week of the study, while all caged colonies achieved 100% survival (i.e., complete live coral tissue cover on each fragment). Conversely, many *P. rus* fragments suffered at least partial mortality of coral tissue across treatments, with 28 out of 72 colonies suffering complete mortality. For % live tissue cover per colony of *P. rus*, out of all three main effects and four interactions tested, the only significant effect was that of the interaction between sedimentation and caging ($p = 0.024$; Table 1), due to negative effects of high sedimentation on uncaged colonies only (Fig. 4; Table 1). Our data further revealed a significant negative effect of macroalgal biomass ($p = 0.041$) on % live tissue cover of uncaged *P. rus* colonies, while algal effects on caged *P. rus* survival were insignificant (Table 1).

Our sample sizes of coral growth measurements were reduced for both coral species because of colonies that suffered 100% mortality. Thus, coral growth measurements were limited to caged *A. pulchra* ($n = 9$) and subsets of each treatment of *P. rus* ($n = 7$, 3, 6, 5, 5, 8, 5, and 5 for 'no stressors', S, N, S + N, C, C + S, C + N, and C + S + N treatments, respectively; ESM Fig. S3). For *P. rus*, we calculated standardized growth, by taking the change in buoyant mass (g) and multiplying it by the proportion of live tissue cover for each colony. This allowed us to calculate a growth metric not confounded by the partial mortality suffered by many colonies. For growth of both coral species, the main effect of nutrient enrichment had a significant positive effect ($p = 0.022$ and $p = 0.025$, for *A. pulchra* and *P. rus*, respectively), while remaining main effects and all interactions were insignificant (Table 1; ESM Fig. S3).

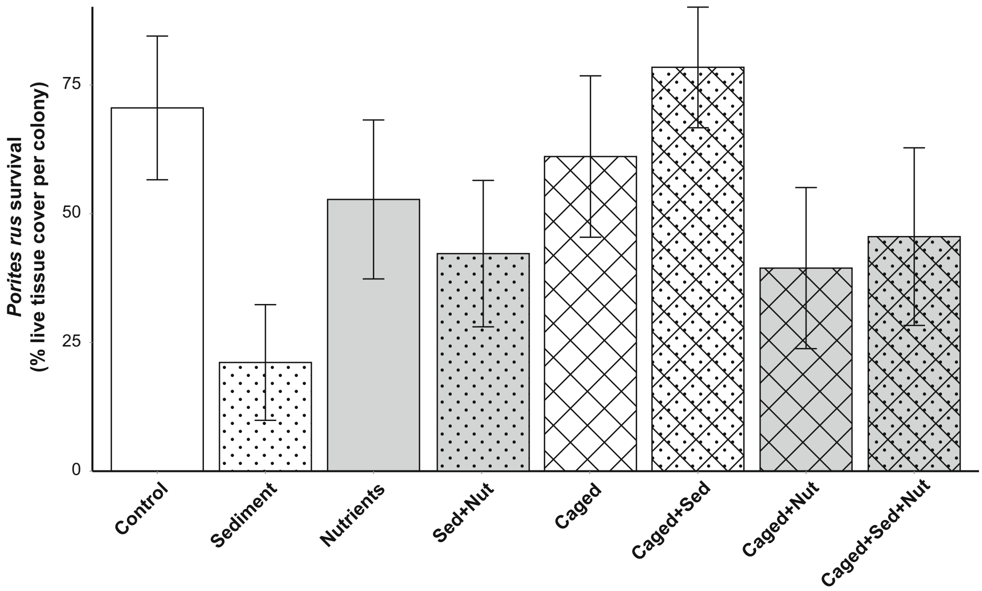


Fig. 4 *Porites rus* survival (% live colony cover) across all treatment combinations ($n = 9$; mean ± SE). There was a significant sediment by caging interaction ($p = 0.038$), in which sediment had a negative effect in uncaged units but a positive effect in caged units (Table 1)

Discussion

Here, we showed that multiple, pervasive anthropogenic stressors, through novel interactions, affect key functional groups of the benthic community in simulated post-disturbance coral reefs. In particular, our results revealed that sedimentation reduced coral survival (*Porites rus*) only in the presence of corallivores; however, in the absence of consumers (caged units), sedimentation allowed for greater coral survival, potentially through suppression of algae (Figs. 3, 4; Table 1). This pattern is distinct among previous findings and our hypotheses that sedimentation would reinforce effects of overfishing on algae (positive effect) and corals (negative effect; Muthukrishnan and Fong 2014) or that these stressors would be non-interactive (Halpern et al. 2012). Furthermore, the novel three-way interaction our study revealed for algal turf biomass (Fig. 3a; Table 1) expands upon previous findings that nutrient enrichment and overfishing can synergistically enhance algal abundance (Burkepile and Hay 2006; Ban et al. 2014), by showing that this effect depends on sedimentation load that can suppress algal growth and mask effects of enrichment (Fig. 3a). In addition to showing contrasting responses between corals and algae, our study revealed taxon-specific responses within corals and algae, further suggesting that the taxonomic and functional composition of recovering coral reef communities will depend on the combination of sediment, nutrient, and fishing pressures on the system.

The two algal functional groups examined, algal turf and macroalgae, responded differently to our stressor manipulations. The range of algal turf biomass observed across treatments greatly exceeded that of macroalgae, while algal turf was quite responsive to different treatment combinations, slower-growing macroalgae were less so. Macroalgae exhibited only a significant positive response to caging and a caging by sedimentation interaction (Fig. 3b), in which sedimentation had a negative effect on macroalgae in the absence of large consumers (caged units) but a positive effect in uncaged units. This positive effect could be the result of sedimentation deterring herbivory, by making sediment-fouled algae less attractive (Bellwood and Fulton 2008). Negative effects of sedimentation on algal growth in our study contrast positive effects shown by Muthukrishnan and Fong (2014) at much lower levels of sedimentation (3.8% of the rate imposed in our experiment). This suggests a potential nonlinear relationship between sedimentation and algal growth (sensu Gil 2013), in which low sedimentation facilitates algal growth (Nugues and Roberts 2003), which is suppressed at high sedimentation. Though algal turf generally predominated over macroalgae in our six-month experiment, studies suggest that this pattern will hold for the long term when both herbivore abundance and the level of sedimentation are low, but that macroalgae will eventually dominate if chronic nutrient enrichment is also present (Littler et al. 2006; Littler and Littler 2007).

While we observed minimal coral settlement across treatments, our study period may not have captured commonly episodic coral settlement events (Adjeroud et al. 2007; Penin et al. 2010). Despite the limited inference provided by our coral settlement data, our algal growth data indicate that barren areas on coral reefs (as simulated by our tiles) can become dominated by algae, depending on levels of sedimentation, nutrient enrichment, and fishing, and these algae could inhibit coral settlement (Birrell et al. 2005; Kuffner et al. 2006; Fig. 3). Furthermore, growth of algae, which are better equipped to settle on soft substrate than corals (Fong and Paul 2011; Harrison 2011), was generally limited by high sedimentation (Fig. 3), which can also greatly limit coral recruitment (Birrell et al. 2005; Jokiel et al. 2014). This suggests that barren areas of reef resulting from natural disturbances may remain largely unsettled by algae or coral if subjected to high sedimentation rates (e.g., on the order of 212 mg cm^{-2} d^{-1} or greater).

Our study is the first to reveal distinct interactive effects of sedimentation, nutrient enrichment, and overfishing on morphologically and functionally disparate coral species. First, the complete and rapid consumption within the first week of all *A. pulchra* colonies, by bioeroding corallivores such as triggerfish or parrotfish (Lenihan et al. 2011, 2015), in uncaged conditions (simulating natural consumer pressure or the absence of overfishing) suggests that overfishing can, in some cases, alleviate corallivory (Fig. 3a). However, it is important to note that our study system is subjected to consistent fishing pressures that target large piscivores (e.g., grouper, snapper; Leenhardt et al. 2016), potentially allowing for predator release of corallivorous fishes (Dulvy et al. 2004). Thus, our observed effects might change quantitatively or qualitatively under different ambient fishing scenarios (e.g., enforcement of species-specific restrictions or a no-take reserve). Conversely, caging and sedimentation had interactive effects on *P. rus* (Fig. 4), suggesting that negative effects of high sedimentation on the survival of coral fragments may be: (1) enhanced by or, at the levels tested, even contingent upon the presence of consumers (i.e., corallivores), (2) driven by indirect negative effects via sedimentation enhancing the growth of algae in the presence of consumers (i.e., suppression of herbivory; Bellwood and Fulton 2008), and/or (3) driven by indirect positive effects via sedimentation inhibiting the settlement and growth of algae in the absence of consumers (i.e., herbivores; Fong and Paul 2011; Fig. 1). Regarding hypothesis (1), sedimentation and corallivory could synergistically reduce coral survival, if corallivore-induced coral tissue damage is less repairable when physically covered by high sedimentation, a mechanism that we are unable to evaluate with our data. On the other hand, our data support hypothesis (2) as a likely contributor to the pattern in *P. rus* survival, which, in uncaged units only, showed a significant negative response to the biomass of macroalgae growing on adjacent settlement tiles (Table 1). Finally, hypothesis (3) could occur if the direct (and putatively negative) effect of sedimentation is weaker than the indirect positive effect of sedimentation as an inhibitor of algae in the absence of consumers (Fig. 1), though the relationship between algal biomass on tiles and *P. rus* survival in caged units was not significant (Table 1).

Despite differences in survival, our two species of coral fragments both showed a significant positive growth response to nutrient enrichment (Fig. 3a). Nutrient enrichment has been shown to have unimodal effects on coral growth (Gil 2013), with positive effects of low-level enrichment attributed to heightened sugar provisions to corals from the stimulation of their nutrient-limited endosymbiotic algae, zooxanthellae (Hoegh-Guldberg and Smith 1989; Dunn et al. 2012). However, nutrient-enhanced coral growth can also result in a reduction in coral skeletal density and thus an increase in susceptibility to breakage (Koop et al. 2001). Sedimentation had insignificant effects on the growth or survival of *A. pulchra*, a result supported by recent coral growth assays across a gradient in sedimentation (Jokiel et al. 2014). This resilience of *A. pulchra* to sedimentation was likely driven by its thin, cylindrical morphology that retains less sediment on coral tissue surfaces than the more domed morphology of *P. rus* (see Fig. 2). However, our sedimentation treatment, directly deposited just above the experimental unit, led to minimal light attenuation, which would likely be much higher in natural sedimentation scenarios. Thus, *A. pulchra* may be more sensitive to chronic sedimentation in nature than our results suggest. It is also important to note that the extreme sensitivity of *A. pulchra* to caging suggests that the strong recovery potential of *Acropora* species (Johns et al. 2014) likely depends strongly on pressure from corallivores (e.g., as determined by the structure of the predator community; Ruppert et al. 2013). Similarly, consumer pressure is likely a fundamental driver of the limited distribution of *A. pulchra*, relative to that of *P. rus*, in Mo‘orean coral reefs.

Our study was modeled after and nested within a system recovering from large-scale natural disturbances (Leray et al. 2012; Leichter et al. 2013; Lamy et al. 2016). Though the spatiotemporal scale of our field experiment was limited by logistical and ethical constraints (associated with large-scale stressor manipulations), our findings may apply more generally to open habitat patches (i.e., those dominated by barren substrate) of various sizes or to corals at early growth stages within coral reefs. For example, large-scale surveys coincide with our findings that anthropogenic stressors affect the recovery of ecosystems from disturbance: recently, researchers showed that recovery from a mass, climate-induced coral bleaching event was compromised in coral reefs low in fish density and high in nutrient load, leading to system-wide regime shifts to algal dominance (Graham et al. 2015). Similarly, the failure of seagrass meadows in the Dutch Wadden Sea to recover from disturbance has been attributed to multiple anthropogenic stressors (Short and Wyllie-Echeverria 1996). Fortunately, effects of massive disturbances on ecosystems can be reversed, even rapidly so, as long as systems are given the chance to repair themselves (Jones and Schmitz 2009; Beldade et al. 2015). For example, recent surveys showed a nearly fivefold increase in coral recruitment 12 years after a mass climactic disturbance event at a highly isolated reef, free of most anthropogenic influences (Gilmour et al. 2013). Similarly, a Hawaiian reef destroyed by a hurricane exhibited substantial recovery, following implementation of an offshore sewage disposal system (Grigg 1995).

Our findings, reinforced by long-term monitoring studies (see previous paragraph), have broad implications for integrated, ecosystem-based management efforts in coastal ecosystems globally threatened by diverse anthropogenic stressors. First, our results point to the need for coastal ecosystem managers to consider stakeholder activities (whether sea- or land-based) that affect levels of sedimentation, nutrient enrichment (e.g., coastal development), or consumer densities (e.g., fishing, consumer habitat loss, or fragmentation) when trying to control the abundance of benthic algae. Benthic algae can harm foundation species, including corals, seagrasses, and kelp, and thus remediation of benthic algal blooms is a leading conservation priority for coastal systems worldwide (McCook et al. 2001; Orth et al. 2006; Smith et al. 2006; Connell et al. 2008; Rasher and Hay 2010). Furthermore, our findings emphasize the importance of monitoring and remediating sedimentation loads, a potent, highly interactive stressor that has received far less attention than nutrient enrichment or overfishing in coastal studies Figs. 3 and 4 (Orth et al. 2006; Ban et al. 2014). More generally, our study reinforces conclusions from recent meta-analyses: ecosystem managers must recognize the potential for co-occurring stressors to yield effects that are difficult to predict without experimentation, due to stressor interactions, indirect effects, and species-specific responses (Crain et al. 2008; Darling and Côté 2008). However, our work extends this recommendation to include the temporal context of stressors, with respect to natural disturbances: ecosystem managers must also consider that interactive effects of stressors can begin molding benthic communities at early, potentially vulnerable (Madin et al. 2014), stages following natural disturbances, the timing, frequency and severity of which should be considered in management plans to mitigate anthropogenic stressors and foster resilience. As climate change increases the rate and magnitude of natural disasters (Dilley et al. 2005), and as human population growth increases the magnitude and diversity of anthropogenic stressors (Crain et al. 2008; Darling and Côté 2008), it is increasingly important that we understand and implement management options that best facilitate ecosystem recovery and, thus, the maintenance of valuable ecosystem services (Worm et al. 2006; Barbier et al. 2011).

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