

1-1-2011

From microbes to people: tractable benefits of no-take areas for coral reefs

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Recommended Citation

Graham, Nicholas A.J; Ainsworth, Tracy D.; Baird, Andrew H.; Ban, Natalie C.; Bay, Line K.; Cinner, Joshua E.; De Freitas, Debora M.; Dia-Pulido, Guillermo; Dornelas, Maria; Dunn, Simon R.; Fidelman, Pedro I.J; Foret, Sylvain; Good, Tatjana C.; Kool, Johnathan; Mallela, Jennie; Penin, Lucie; Pratchett, Morgan S.; and Williamson, David H.: From microbes to people: tractable benefits of no-take areas for coral reefs 2011, 117-148.

<https://ro.uow.edu.au/lawpapers/149>

From microbes to people: tractable benefits of no-take areas for coral reefs

Abstract

The number of no-take marine protected areas (here referred to as no-take areas, NTAs) on coral reefs has increased considerably in recent decades. Coincident with accelerating degradation of coral reefs, expectations of the benefits that NTAs can provide for coastal societies and sustainability of marine ecosystems has grown. These include increasing abundance of reef organisms both inside and outside NTAs, protecting key ecosystem functions, and providing social and economic benefits through improved fisheries and tourism. However, there is a lack of convincing evidence for many of these expectations. This is the first attempt to synthesize all potential costs and benefits of coral reef NTAs and critically examine evidence of their impacts on both ecosystems and societies. NTAs with high compliance consistently increase the diversity, density and biomass of exploited reef fishes and certain groups of motile invertebrates within their boundaries and have benefits for reef-associated tourism. Some NTAs provide small increases in the abundance of corals and decreases in macroalgal cover. The effects of NTAs on genetic diversity and connectivity among meta-populations are variable or as yet unquantified. There is limited evidence of NTAs providing social benefits through increased fishery yields and tourism revenue. There are examples of both positive and negative effects on social well-being. Finally, sharks, marine megafauna and microbial communities showed few tangible benefits from NTAs. Substantial gaps in the science of coral reef NTAs remain, especially in their capacity to provide socioeconomic benefits. A crucial research priority is understanding how the cumulative effects of climate change will influence the various benefits that NTAs provide. To be effective, NTAs must be used in conjunction with a range of other management tools and applied according to local environmental and societal contexts.

Keywords

people, areas, tractable, take, coral, benefits, reefs, no, microbes

Disciplines

Law

Publication Details

Graham, N. A.J., Ainsworth, T. D., Baird, A. H., Ban, N. C., Bay, L. K., Cinner, J. E., De Freitas, D. M., Dia-Pulido, G., Dornelas, M., Dunn, S. R., Fidelman, P. I.J., Foret, S., Good, T. C., Kool, J., Mallela, J., Penin, L., Pratchett, M. S. & Williamson, D. H. (2011). From microbes to people: tractable benefits of no-take areas for coral reefs. In R. N. Gibson, R. J. A. Atkinson & J. D. M. Gordon (Eds.), *Oceanography and Marine Biology, An Annual Review*, Volume 49 (pp. 117-148). Boca Raton, FL: CRC Press. Original publisher information available [here](#)

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FROM MICROBES TO PEOPLE—TRACTABLE BENEFITS OF NO-TAKE AREAS FOR CORAL REEFS

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Abstract The number of no-take marine protected areas (here referred to as no-take areas, NTAs) on coral reefs has increased considerably in recent decades. Coincident with accelerating degradation of coral reefs, expectations of the benefits that NTAs can provide for coastal societies and sustainability of marine ecosystems has grown. These include increasing abundance of reef organisms both inside and outside NTAs, protecting key ecosystem functions, and providing social and economic benefits through improved fisheries and tourism. However, there is a lack of convincing evidence for many of these expectations. This is the first attempt to synthesize all potential costs and benefits of coral reef NTAs and critically examine evidence of their impacts on both ecosystems and societies. NTAs with high compliance consistently increase the diversity, density and biomass of exploited reef fishes and certain groups of motile invertebrates within their boundaries and have benefits for reef-associated tourism. Some NTAs provide small increases in the abundance of corals and decreases in macroalgal cover. The effects of NTAs on genetic diversity and connectivity among meta-populations are variable or as yet unquantified. There is limited evidence of NTAs providing social benefits through increased fishery yields and tourism revenue. There are examples of both positive and negative effects on social well-being. Finally, sharks, marine megafauna and microbial communities showed few tangible benefits from NTAs. Substantial gaps in the science of coral reef NTAs remain, especially in their capacity to provide socioeconomic benefits. A crucial

research priority is understanding how the cumulative effects of climate change will influence the various benefits that NTAs provide. To be effective, NTAs must be used in conjunction with a range of other management tools and applied according to local environmental and societal contexts.

Introduction

Some of the earliest no-take marine protected areas (here referred to as no-take areas, NTAs) were established on tropical and temperate reefs in the 1960s and 1970s, often with the goal of enhancing biodiversity, tourism (Polunin 2002) or fisheries (Russ 2002). Extraction of any kind is prohibited within the boundaries of NTAs. With numerous accounts of success of these early NTAs, including increased fish and invertebrate biomass (e.g., Roberts & Polunin 1991, Bohnsack 1993), their popularity as a management tool increased. Consequently, the rate at which new coral reef NTAs are established has increased substantially (Mora et al. 2006, Wood et al. 2008). Notable recent additions to the global network of coral reef NTAs include the three largest NTA networks in the world: the 2004 rezoning of the Great Barrier Reef (GBR) Marine Park, the Papahānaumokuākea Marine National Monument in Hawaii (Wood et al. 2008) and the recently announced Chagos Archipelago (British Indian Ocean Territory) protected area. Associated with this proliferation of NTAs, there has been a steadily increasing number of peer-reviewed articles on various aspects of the science of NTAs (Figure 1).

Coral reefs have experienced increasing disturbances and degradation over recent decades, precipitated by a range of anthropogenic stressors and the overarching impact of climate change (Gardner et al. 2003, Hughes et al. 2003, Wilson et al. 2006, Bruno & Selig 2007, Hoegh-Guldberg et al. 2007). Two of the most pervasive threats are overexploitation (i.e., greater-than-maximum

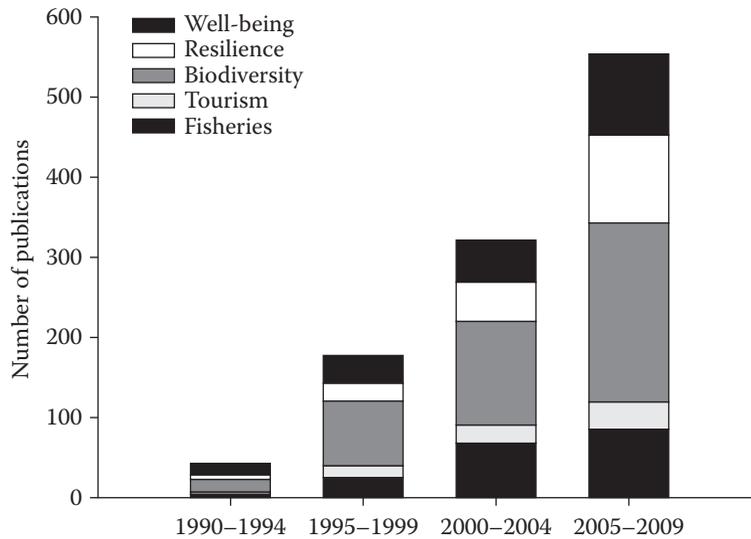


Figure 1 Number of publications by no-take area expectation through time selected from the ISI Web of Science database in 5-year periods. Note that there may be some overlap between categories with articles dealing with more than one category. Publications were selected based on the following keywords: MPA, marine reserves, marine protected area, no-take, in conjunction with ‘coral reefs’. Then for fisheries the additional keywords were selected: fisheries, CPUE (catch per unit effort), profit; for tourism: tourism, tourist, willingness-to-pay, diving, travel cost; for biodiversity: biodiversity, hotspots, species richness, evenness, diversity, endemism, community structure; for resilience: resilience, recovery; for well-being: human health, well-being, poverty, welfare, empowerment, income.

sustainable yield) and habitat degradation. High levels of exploitation have devastating effects not only on the species exploited but also on the reef ecosystem as a whole (McClanahan & Shafir 1990, Hughes 1994). Habitat loss following storms, crown-of-thorns starfish outbreaks, or coral bleaching can lead to reduced topographic complexity of the reef structure and widespread changes to the rest of the ecosystem, such as reduced abundance of fish (Woodley et al. 1981, Sano et al. 1987, Pratchett et al. 2008, Wilson et al. 2008). In conjunction with increasing threats and degradation of reef systems, there has been an increasing realization that managing coral reefs involves managing human activities. Consequently, social science and linked social-ecological systems research has become much more prominent (Pollnac et al. 2001, Hughes et al. 2005, Christie & White 2007, Cinner et al. 2009a, Pollnac et al. 2010).

With increasing threats to coral reefs and emphasis on incorporation of social science into management, the expectations of what NTAs can and should achieve has also grown (Roberts & Hawkins 2000, Game et al. 2009). In particular, the potential for NTAs to bolster resilience of coral reefs to disturbances has gained increasing attention (e.g., Hughes et al. 2003, West & Salm 2003, Game et al. 2008). Likewise, the potential of NTAs to provide social and economic benefits to coastal societies has also been emphasized (Pollnac et al. 2001, Mascia et al. 2010). Indeed, the main expectations of coral reef NTAs can now be divided into five broad categories: (1) tourism, (2) fisheries, (3) biodiversity, (4) ecological resilience, and (5) human well-being. The literature on each of these topics has increased rapidly over the last 20 years (Figure 1). However, the empirical evidence for whether or how coral reef NTAs can meet expectations across all of these categories has yet to be synthesized.

This material reviews the empirical literature to test whether coral reef NTAs have demonstrable impacts on a range of ecological and social measures, from microbial communities to coastal societies. To ascertain impacts of coral reef NTAs, the review focuses on studies that adopt inside-outside or before-after designs. Because limited information is available for certain topics, the Intergovernmental Panel on Climate Change approach has been adopted, in which a level of certainty is assigned for each expectation to be realized, based on the scientific evidence. For clarity, documented effects of NTAs are considered in four broad categories: sessile benthic organisms, motile organisms, other ecological effects and societal effects. How these categories relate to the expectations of NTAs is shown in Table 1. Finally, the implications of climate change on the effectiveness of coral reef NTAs are discussed.

Sessile benthic organisms

Macroalgae

Algal cover and assemblage structure

Establishment of NTAs may have an important but indirect effect on the abundance of benthic algae (i.e., algal turfs, fleshy macroalgae and crustose coralline algae). Increases in the density and biomass of herbivorous fishes may provide sufficient grazing pressure to prevent proliferation of fleshy macroalgae (Mumby & Steneck 2008). This is desirable because predominance of fleshy macroalgae can inhibit coral recruitment (Hughes et al. 2007, Diaz-Pulido et al. 2010) and directly kill live corals (Smith et al. 2006, Rasher & Hay 2010), potentially leading to ‘phase shifts’ to undesirable system states, such as macroalgal domination, providing reduced goods and services to human societies (Hughes 1994, Nyström et al. 2000). There are only a few clear examples supporting these ecological responses. In a 23-year-old Bahaman NTA and a 12-year-old Philippines NTA, increased abundances of herbivorous fishes reduced the abundance of fleshy macroalgae compared to unprotected reefs 4-fold and 13-fold, respectively (Mumby et al. 2006, Stockwell et al. 2009). Similar effects were found in two old NTAs (established in 1979 and 1987) in Guadeloupe (Kopp et al. 2010). At a larger spatial scale, increased abundance of herbivores was associated with reduced

Table 1 Magnitude, mechanism, certainty and benefit of potential effects of coral reef NTAs

Effect	Magnitude	Proposed mechanism	Certainty	Benefit
Benthos				
Coral abundance/cover	Positive, moderate	Reduced damages/trophic cascade	Medium	Fisheries, tourism, biodiversity
Coral recruitment	Positive/neutral, moderate	Trophic cascade	Low	Fisheries, tourism, biodiversity
Coral recovery	Low	Herbivory/predation	Low	Fisheries, tourism, biodiversity
Macroalgal cover	Positive, moderate	Herbivory	Medium	Tourism, biodiversity
Fish				
Abundance	Positive, large	Reduced extraction	High	Fisheries, tourism, biodiversity
Biomass	Positive, very large	Reduced extraction	High	Fisheries, tourism, biodiversity
Diversity	Positive, moderate ^a	Reduced extraction	Medium	Tourism, biodiversity
Piscivores	Positive, very large	Reduced extraction	High	Fisheries, tourism, biodiversity
Invertebrate feeders	Positive, large	Reduced extraction	High	Fisheries, tourism, biodiversity
Herbivores	Positive, large ^a	Reduced extraction	High	Fisheries, tourism, biodiversity, resilience
Planktivores	Positive, moderate ^a	Reduced extraction	Medium	Fisheries, tourism, biodiversity
Corallivores	Positive, small ^a	Reduced extraction and higher coral cover	Medium	Tourism, biodiversity
Sharks	Positive, small ^b	Reduced extraction	Low	Fisheries, biodiversity
Adult spillover	Positive, small	Density-dependent spillover	Medium	Fisheries
Larval recruit export	Not known, but likely	Increased fecundity within NTAs	Medium	Fisheries
Motile invertebrates				
Holothurians	Positive, very large	Reduced extraction	High	Fisheries, biodiversity
Trochus	Positive, large	Reduced extraction	High	Fisheries, biodiversity
Queen conch	Positive, large	Reduced extraction	High	Fisheries, biodiversity
Giant clams	Positive, large	Reduced extraction	High	Fisheries, biodiversity
Spiny lobster	Positive, large	Reduced extraction	High	Fisheries, biodiversity
Urchins: <i>Diadema</i> and <i>Echinometra</i>	Negative, moderate	Trophic cascade	Low	Biodiversity
Crown-of-thorns	Negative, moderate	Trophic cascade	Low	Biodiversity
Megafauna				
Cetaceans	Neutral			
Manta rays	Positive, small ^b	Reduced extraction at critical aggregation sites	Low	Tourism, conservation
Turtles	Positive, small ^b	Reduced extraction at critical aggregation sites	Low	Tourism, conservation
Whale sharks	Positive, moderate ^b	Reduced extraction at critical aggregation sites	Low	Tourism, conservation

Table 1 (continued) Magnitude, mechanism, certainty and benefit of potential effects of coral reef NTAs

Effect	Magnitude	Proposed mechanism	Certainty	Benefit
Dugong	Positive, small ^b	Reduced extraction at critical aggregation sites	Low	Tourism, conservation
Cross-cutting ecological effects				
Microbes	Positive, small	Reduced human pollution and higher fish diversity	Medium	Biodiversity, tourism
Connectivity and genetic diversity	Positive, small	Connectivity; maintaining vulnerable species	Medium	Biodiversity
Social				
Tourism	Positive, large ^c	Increased revenue generation	Medium	Tourism, human well-being
Fisheries	Positive, small	Spillover	Medium	Fisheries, human well-being
Values	Variable	Increased recreation, decreased community values	Medium	Human well-being
Human health	Variable	Improved nutrition, lost fishing grounds	Low	Human well-being
Empowerment	Variable	Increased participatory decision making but may increase conflict	Medium	Human well-being

^a Effects seen when fishing pressure outside reserves is high and non-selective; that is, these groups of fish are targeted.

^b These effects are thought to be small as only a small proportion of the population is protected, and most species are still in decline across their range.

^c Although there may be economic benefits of tourism, there may also be negative ecological and social effects.

macroalgal abundance in NTAs across the entire Caribbean basin (Newman et al. 2006). However, herbivory may be insufficient to control macroalgal increases following large-scale disturbances that make extensive areas of substratum available, particularly if unpalatable brown algae become dominant (Ledlie et al. 2007). In addition, there was a stronger relationship between macroalgal abundance and proximity to cultivated land than NTA placement in a spatial Caribbean study (Mora 2008). NTAs may also cause shifts in the community structure of benthic algae. For example, NTAs in Kenya have a higher abundance of calcareous erect macroalgae and lower abundance of fleshy seaweeds compared to unprotected areas (McClanahan et al. 2001, McClanahan & Graham 2005, McClanahan 2008). The abundance of algal turfs increased in a Philippines NTA probably as a consequence of decreased fleshy macroalgal abundance, but there were no changes in crustose coralline algae (Stockwell et al. 2009).

Competition between corals and algae

Although evidence is increasing that herbivores can enhance recruitment, survival and growth of corals (Hughes & Tanner 2000, Hughes et al. 2007, McClanahan 2008, Mumby 2009, Mumby & Harborne 2010), there is limited descriptive and experimental evidence of the effects of NTAs on coral-algal competition and dynamics (Table 1). A spatial study in the Bahamas demonstrated lower abundance of fleshy macroalgae within a large NTA compared to fished reefs, which was associated with an increase in coral recruits in the NTA (Mumby et al. 2007). However, there was no clear effect on the abundance of juvenile or adult corals. Similarly, no increase in coral cover or change in the coral assemblage structure was evident in Philippines NTAs (Stockwell et al. 2009).

Complexities of reef dynamics and variability associated with the process of competition between corals and algae may explain the lack of clear competitive outcomes between corals and

algae after NTA establishment, although a lack of effect cannot be ruled out. Competitive processes depend not only on algal abundance but also on the nature of the algal community, coral species, habitat, non-fish herbivores as well as ecological and environmental conditions, such as nutrient concentrations and algal seasonality (McCook et al. 2001, Diaz-Pulido et al. 2009). For example, removal of fleshy seaweeds and increases in crustose coralline algae may enhance settlement and recruitment of corals, although the extent of enhancement is dependent on the species of coralline algae and corals present (Harrington et al. 2004). Most fleshy macroalgae inhibit settlement and recruitment of corals and can directly kill them, but the extent of inhibition will depend on properties of the macroalgae (e.g., chemical defences and morphology) (Tanner 1995, McCook et al. 2001, Jompa & McCook 2002, Hughes et al. 2007, Birrell et al. 2008, Diaz-Pulido et al. 2010, Rasher & Hay 2010). The evidence for NTAs reducing macroalgal cover and mediating the interactions among corals and algae is currently weak and from a small number of locations. A great deal more research comparing NTAs of differing size and age to fished areas is necessary to ascertain any generic benefits, and research documenting null effects also needs to be published.

Coral

Coral cover

Cover or abundance of corals can vary between fished and non-fished areas because of reduced direct damage and control of competing algae by herbivores (Table 1). Fishing gear such as explosives and seine nets are destructive to corals and other sessile marine invertebrates. Therefore, the abundance of coral species susceptible to damage from gear, such as branching corals of the genus *Acropora*, should be higher in areas where destructive fishing is excluded. For example, in Aceh, Indonesia, coral cover was on average three times higher in sites where destructive gear was excluded compared to other exploited areas (Baird et al. 2005). In addition, if rates of herbivory are higher in NTAs (e.g., Mumby et al. 2006), coral competition with macroalgae may be reduced (see discussion in preceding section). In contrast, NTAs may also increase the abundance of coral predators such as chaetodontids and some scarids (Harborne et al. 2008), which can slow coral growth rates, increase mortality of juvenile corals (McClanahan et al. 2005, Rotjan et al. 2006, Penin et al. 2010) and potentially cause increases in transmission of coral disease (Raymundo et al. 2009, but see Cole et al. 2009).

A meta-analysis of coral cover inside and outside NTAs through time has shown that in general there is an increase in coral cover with increasing years of protection; however, the changes are extremely small, with an annual difference of 0.05% (Selig & Bruno 2010). On the GBR, hard coral cover was significantly higher on protected reefs at 9 of 12 paired sites, but this pattern was only apparent for reefs that had not been disturbed by crown-of-thorns starfish, *Acanthaster planci*, bleaching, cyclones, or a combination of these factors (Myers & Ambrose 2009), suggesting that NTAs do not bolster coral communities in the face of such disturbances. NTAs in the western Indian Ocean (Kenya, Tanzania, Seychelles) had higher coral cover than adjacent fished areas in the mid-1990s prior to the 1998 bleaching event (Graham et al. 2008). This was attributed to a combination of protection from destructive fishing gear and the NTAs being placed in areas of high coral cover (particularly *Acropora* spp.) to attract tourists (Graham et al. 2008). Conversely, a number of comparative and time series studies have found no significant differences in coral cover between protected and unprotected reefs. For example, no significant differences in live coral cover were found between three 14-year-old NTAs and adjacent fished areas on the central GBR (Graham et al. 2003), 11 areas protected for up to 60 years in Papua New Guinea and Indonesia (McClanahan et al. 2006a), and 15 NTAs and adjacent fished areas in the Philippines with between 0.5 and 11 years of protection (Stockwell et al. 2009). The consensus seems to be that coral cover can increase by small amounts within

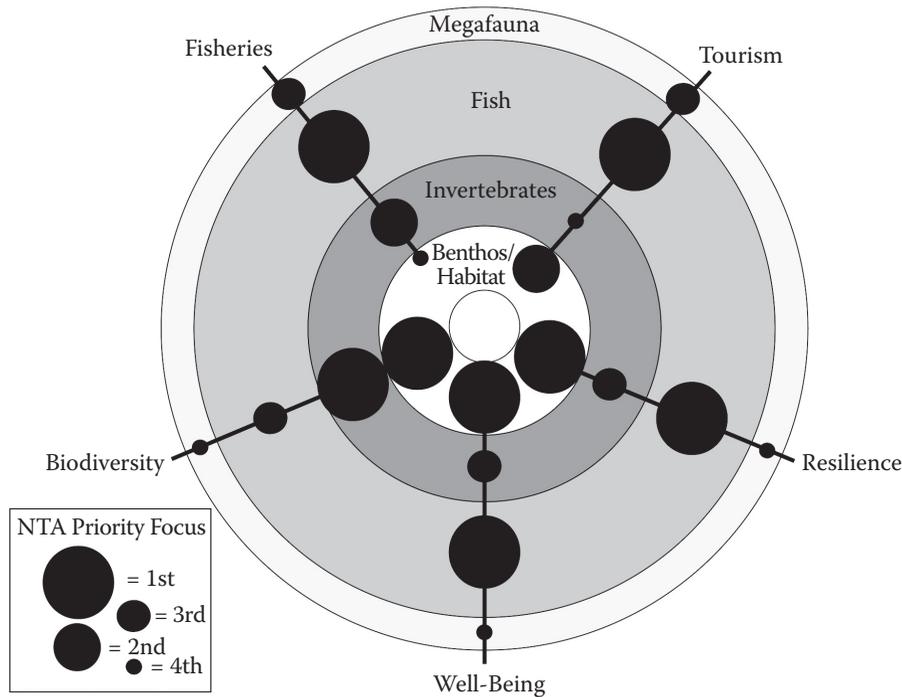


Figure 2 Schematic representation of NTA outcome success (width of concentric circle; wider circles, such as for fish, indicate a larger effect) compared with level of prioritization (1–4: dark circle size = priority) of the five main expectations of NTAs: tourism, fisheries, biodiversity, resilience and human well-being.

protected areas, especially where surrounding areas are subject to destructive fishing methods or intensive fishing of herbivores (Table 1, Figure 2), but this also depends on spatial patterns in occurrence of episodic disturbances (e.g., cyclones) that equally affect both NTAs and adjacent fished areas.

Fecundity and export of propagules

The effect of reduced fishing on the size or age structure of non-target species such as corals is unknown. However, in principle, increased herbivory should result in higher coral fecundity due to a reduction of competitive interactions with macroalgae (Tanner, 1997). Furthermore, if densities of reproductive individuals are higher within NTAs, a greater number of gametes should be spawned, and rates of fertilization should be higher (Oliver & Babcock 1992). However, to date, no published studies have tested these effects on coral reproductive success within NTAs.

Local increases in larval recruitment may be expected in areas where high rates of herbivory increase free space and shift benthic assemblages towards organisms that facilitate coral recruitment, such as crustose coralline algae (Harrington et al. 2004, Harborne et al. 2008). However, spatial differences in rates of larval supply may not necessarily align with NTA placement. Sixfold differences in settlement were apparent among regions on the GBR, where recruitment was consistently higher on reefs in the central GBR when compared to reefs to the north and south (Hughes et al. 1999). The strongest predictor of larval supply was assemblage-level fecundity, which is not necessarily related to adult abundance as not all corals will be gravid (Hughes et al. 2000). Therefore, even if NTAs are effective at promoting high coral cover, this would not necessarily translate into higher fecundity or local recruitment. It is therefore hard to say at present if NTAs have any effects on coral fecundity or recruitment, and this is an area in need of further research.

Motile organisms

Non-coral invertebrates

Abundance of target and non-target invertebrates

Densities of target invertebrates (such as holothurians, trochus, conch, and octopus) may be several orders of magnitude higher inside NTAs than in comparable fished areas (Stoner & Ray 1996, Ashworth et al. 2004, Price et al. 2009) (Table 1, Figure 2). These differences are apparent for harvested species but not for closely related unharvested species (e.g., *Trochus niloticus* versus *T. pyramis*; Lincoln-Smith et al. 2006), demonstrating that differences are attributable to fishing. Benefits of NTAs on local densities of target invertebrates may be apparent within as little as 2 years and within relatively small reserves (Lincoln-Smith et al. 2006). Indeed, the magnitude of differences in abundance of target invertebrates between fished and unfished areas is not necessarily related to the size or longevity of NTAs but largely depends on localized fishing pressure (e.g., Lipcius et al. 2001).

The role of NTAs in providing protection for smaller and less-conspicuous species (e.g., small gastropods) is more controversial. For example, McClanahan (1989) failed to find significant differences in densities of commercially harvested gastropods inside versus outside NTAs in Kenya, but there was some variability associated with predator densities and protection status, particularly in lagoon sites (McClanahan 2002). For these species, which naturally occur at low densities and are lightly exploited, detecting any significant effects of NTAs is likely to be difficult (McClanahan 1989, 2002).

Trophic cascades and ecological release of invertebrate species

Indirect effects of fisheries depletion outside or recovery within NTAs on non-coral invertebrates are potentially important for coral reef ecosystems, but these links are poorly understood. Intuitively, fishing of major predators is likely to result in increases in the abundance of prey species, but trophic interactions among coral reef organisms are highly complex and often involve numerous different species (Jennings & Polunin 1997). Several echinoderms (*Diadema* and *Echinometra* urchins and *Acanthaster planci*) can have higher abundance in fished areas versus NTAs, associated with higher rates of predation within NTAs (e.g., McClanahan & Shafir 1990, Sweatman 2008, Harborne et al. 2009). In Kenya, the abundance of both *Diadema* and *Echinometra* urchins was much (>100 times) higher in fished areas compared to NTAs (McClanahan & Shafir 1990). These differences were attributed to fisheries depletion of potential predators that caused an ecological release of urchin species, which is undesirable because it leads to increased reef erosion (McClanahan & Shafir 1990, McClanahan 2000).

During population outbreaks of *Acanthaster planci*, abundances were higher in fished compared to unfished reefs on the GBR (Sweatman 2008) and in areas with localized depletion of large carnivorous fishes in Fiji (Dulvy et al. 2004). However, both studies showed weak relationships, and the mechanism(s) underlying these findings remain unknown since there is no direct evidence that exploited fishes are significant predators of *A. planci* (Sweatman 2008). If NTAs can prevent atypical increases in the abundance of *Echinometra* spp. and *A. planci*, this would provide a strong basis for the implementation of NTAs on coral reefs because of the detrimental effect of these species on corals and reef growth. Improved understanding of mechanistic links between fished species and habitat-altering invertebrates should therefore be a key research priority.

Reef fishes

Overall abundance, biomass and diversity

Where protection is effective, reduced fishing mortality in NTAs generally leads to increased abundance, biomass, and diversity of reef fishes. Meta-analyses found that density and biomass of reef

fishes were higher in NTAs compared to fished areas (Halpern 2003, Lester et al. 2009), particularly species targeted by fishing (Mosquera et al. 2000, Côté et al. 2001, Molloy et al. 2009). However, there is debate regarding the magnitude of difference and the effects of NTA size and age (Halpern & Warner 2002, Micheli et al. 2004). Such differences may often be a result of meta-analyses combining data from different biogeographic, ecological and social environments (McClanahan et al. 2009), and the ‘file drawer syndrome’, whereby null results are rarely published and are therefore unavailable to meta-analyses (Arnqvist & Wooster 1995). Thus, it is also important to supplement the findings from meta-analyses with robust studies with a large spatial scale that assess multiple NTAs within the same ecosystem.

A number of empirical studies have found higher density and biomass of reef fish assemblages inside NTAs (e.g., Alcala 1988, Polunin & Roberts 1993, Russ & Alcala 1996, Wantiez et al. 1997, McClanahan & Arthur 2001, Friedlander et al. 2003, Harborne et al. 2008, Table 1, Figure 2). However, such studies are often inside-outside comparisons and rarely account for the possibility that the NTAs were initially sited in areas of high fish abundance and biomass. Maliao et al. (2009b) demonstrated just such an effect across 19 reserves in the Philippines, where inside-outside comparisons indicated NTA success; however, temporal analysis highlighted that the differences were apparent in the reserve locations prior to establishment, and the magnitude of the inside-outside differences had not increased subsequently.

To assess NTA effectiveness comprehensively it is clearly important to have temporal studies, with before-after, control-impact designs (Russ 2002). Some such studies are available from Kenya and the Philippines that indicate that a significant build up of reef fish abundance and biomass can be detected within 3–4 years of NTA establishment (McClanahan & Graham 2005, Russ et al. 2005, McClanahan et al. 2007, Russ et al. 2008). However, it takes decades for NTAs to reach full potential in terms of maximum fish abundance and biomass buildup (Russ & Alcala 2004, McClanahan & Graham 2005, Russ et al. 2005, Babcock et al. 2010). The role of NTA size is the effect least well understood on the buildup of reef fish abundance and biomass, with evidence of little effect in the Florida Keys (Bartholomew et al. 2008), or substantial benefits of increasing size on fish biomass up to a size of approximately 5 km² in the western Indian Ocean (McClanahan et al. 2009). In addition, compliance with management rules is a critical issue in the success of NTAs (Russ & Alcala 1989, Pollnac et al. 2010), and NTA benefits in terms of reef fish density and biomass may only be apparent where compliance is high (Jennings et al. 1996, Kritzer 2004, McClanahan et al. 2009).

A number of studies have found that fish species diversity, most commonly represented as species richness, is higher in NTAs, although the magnitude of this effect is smaller than for density and biomass (e.g., Jennings et al. 1996, Wantiez et al. 1997, McClanahan & Arthur 2001, Friedlander et al. 2003, McClanahan et al. 2006b, Harborne et al. 2008). The buildup of species richness appears to be greatest in NTAs in locations where fishing pressure is high: rapid increases from about 18 species in an area of 2000 m² to an asymptote of around 60 species occurred over a 5-year period in Kenyan NTAs (McClanahan et al. 2007).

Specific fish family and functional group responses to protection

Large-bodied, piscivorous fishes (e.g., Serranidae) generally show the greatest response to NTA protection (Russ & Alcala, 1996, Mosquera et al. 2000, Halpern 2003, Evans & Russ 2004, Williamson et al. 2004, Graham et al. 2007, Harborne et al. 2008, Russ et al. 2008, Table 1). Increases in these families may result in the reduction of some small species of reef fish through predation (Graham et al. 2003, Micheli et al. 2004). Planktivores and invertebrate-feeding species are often the groups that benefit the most after piscivores (Russ & Alcala 1998, Halpern, 2003, Graham et al. 2007), generally followed by herbivores (Mumby et al. 2006, Graham et al. 2007, McClanahan et al. 2007, Stockwell et al. 2009). NTAs can also increase the abundance and diversity of corallivores, such as butterflyfishes (Chaetodontidae), most likely through a combination of reduced catch in fish traps

and higher coral cover inside protected areas (Wantiez et al. 1997, Russ & Alcala 1998, Graham et al. 2007, McClanahan et al. 2007, Harborne et al. 2008, Cinner et al. 2009b).

Assessments of changes in abundance, biomass and diversity of functional and family groups of fishes over time have indicated different trajectories of recovery for different fish functional groups. A logistic buildup appears to occur for predatory fish biomass, whereby a slow initial response becomes rapid until an asymptote occurs at full potential (Russ & Alcala 2004). The invertebrate-feeding groups, such as the balistids, labrids and mullids, tend to show different trajectories of recovery to each other, attributed to competition for dietary resources (McClanahan et al. 2007). Interestingly, a similar effect is apparent for the two main herbivorous fish groups, acanthurids and scarids. In both Kenya and the Philippines, scarids recovered rapidly, while acanthurids tended to take longer, likely related to different growth and population turnover rates, competition for resources and potentially increased predation pressure (McClanahan et al. 2007, Stockwell et al. 2009). There is strong evidence that NTAs on coral reefs support a buildup of reef fish abundance, biomass and, to a lesser extent, diversity.

Fecundity and export to fished areas

Buildup of fish abundance, biomass and size is expected to lead to increases in fish abundance and biomass in adjacent fished areas through both spillover of adult fish from NTAs into fished areas and a net export of eggs, larvae, or both from the NTAs (Bohnsack 1993, Roberts 1997, Bohnsack 1998, Russ 2002). Although both expectations are logical, the evidence in support of export is limited (Russ 2002, Sale et al. 2005, Table 1).

Several different methodological approaches have revealed movement of adult reef fish across NTA boundaries (Halpern et al. 2009). Underwater visual censuses have determined that patterns of biomass across NTA boundaries are consistent with spillover of fish biomass (Russ et al. 2003, Ashworth & Ormond 2005). For example, gradients of target reef fish abundance spanned the boundary of Apo Island NTA in the Philippines, with greatest abundances inside, intermediate abundance generally within 50 m of the NTA boundary and abundances consistent with fished areas within 100 m of the NTA boundary (Abesamis et al. 2006). Tagging studies have shown fish moving across NTA boundaries into fished areas, with either one-way movements (Kaunda-Arara & Rose 2004a) or repeated, often seasonal, crossings associated with movement among feeding and spawning grounds (Meyer & Holland 2005). Perhaps the best assessment of spillover is whether fish catch is enhanced adjacent to NTAs and whether this compensates for the area of fishing ground lost to the fishers. This topic is covered in the societal effects section.

The relationship between body size and fecundity is exponential in fishes (Thresher 1984). Thus, a buildup of large individuals (and associated biomass) in NTAs should result in a significant increase in production of larval fish (Roberts & Polunin 1991) and possibly larval export. For example, the fecundity of *Lutjanus carponotatus* increases non-linearly with increasing body size, such that the potential batch fecundity per unit area (the estimated egg production from a single spawning of all mature fish in a given area) of NTAs on the GBR was up to 4.2 times higher than in fished areas (Evans et al. 2008). Furthermore, mean egg size was greater in larger individuals, which may result in higher survival of larvae spawned by the larger fish in NTAs (Evans et al. 2008).

Identifying where fish larvae go and come from is critical to determining the impacts of NTAs, but current scientific knowledge is sparse. Tagging studies suggest that levels of self-recruitment are higher than anticipated (Jones et al. 1999, Swearer et al. 1999, Almany et al. 2007). As average dispersal distance is greater than the typical size of an NTA, net larval export is highly likely. Hydrodynamic dispersal models are being used to predict the dispersal of larvae and connectivity between populations (Paris et al. 2007, Kool et al. 2009). However these models still require validation, and simulating nearshore, shallow-water environments (where NTAs are commonly found) requires fine-scale oceanographic data that is often unavailable.

Sharks

In many coral reef ecosystems, persistent fishery exploitation over a number of decades has led to significant reductions in reef shark abundance and resultant shifts in fish assemblage structure (Friedlander & DeMartini 2002, Sandin et al. 2008, Graham et al. 2010). The effects of fishing and effective NTA protection on reef shark populations has received limited attention (Table 1). In both Hawaii and the Northern Line Islands group, remote atolls had much higher abundances of sharks than more heavily fished areas (Friedlander & DeMartini 2002, Sandin et al. 2008). Within the GBR Marine Park, mean population densities of whitetip (*Triaenodon obesus*) and grey reef sharks (*Carcharhinus amblyrhynchos*) are 80–97% higher around no-entry zone reefs (where humans are not even permitted to snorkel or drive boats through) than around either open reefs or reefs declared as no-take areas (Robbins et al. 2006). The NTA zones were likely exposed to a sufficient level of poaching to cause significant declines in reef shark populations, as confirmed by experimental fishing (Heupel et al. 2009). Even remote, no-go areas, such as the Chagos Archipelago in the central Indian Ocean, have experienced substantial reef shark declines through poaching (Graham et al. 2010), suggesting that NTAs are not sufficient and should be complemented by a suite of conservation tools, from trade regulations to consumer education (Clarke et al. 2007).

Marine megafauna

Most groups of marine megafauna have large home ranges and migrate across wide geographical distributions. NTAs typically provide little protection for species that migrate over large distances because they spend a considerable amount of time outside reserves where they are vulnerable to exploitation (Roberts & Hawkins 2000). Some NTAs have been located in areas where marine megafaunal species aggregate at predictable locations at certain times of the year for feeding, mating or nesting. Examples include whale shark (*Rhincodon typus*) feeding sites in Belize and Australia (Heyman et al. 2001, Wilson et al. 2001); manta ray feeding sites in Komodo Marine Park, Indonesia (Dewar et al. 2008); dugong feeding areas in the GBR (Dobbs et al. 2008) and turtle nesting sites around Australia (Environment Australia 2003). Establishment of these targeted NTAs has resulted in increased abundances at localized spatial scales; however, this has not arrested population declines across the geographic range of most marine megafaunal species (Hooker & Gerber 2004, Hoyt 2005, Bradshaw et al. 2008), again indicating that alternative management approaches are necessary.

Other ecological effects

Microbes

Coral reef microbial assemblages play an integral role in both the physiological processes of individuals and ecosystem function. The microbial members of coral reefs, including those associated in symbiosis with corals and other marine organisms, include bacteria, viruses, fungi, microalgae, and archaea. Microbial communities may influence reef resilience to disturbance (Ainsworth et al. 2010). However, little direct evidence is available on how fishing practices have an impact on microbial communities, or on the role that microbes will play within the ecosystem responses to fishing pressure. In one of the first studies of its kind, Coelho & Manfrino (2007) found no relationship between NTAs and coral disease in Little Cayman Island. In the Philippines, coral disease prevalence (as a measure of an altered microbial community) was negatively correlated with fish taxonomic diversity, suggesting that NTAs with higher fish diversity have significantly less disease than unprotected areas (Raymundo et al. 2009). One interpretation of this result is that the presence of NTAs promotes coral health through minimizing disease occurrence and that top-down

impacts of fishing result in significant changes to host and reservoir species (Raymundo et al. 2009). However, it cannot be ruled out that the NTAs were established in particularly healthy areas. Coral disease outbreaks on Palauan reefs were in fact more severe in NTAs than at unprotected sites, but there was also a strong negative relationship between a measure of disease prevalence and the species richness of fishes targeted by fishers, suggesting that fish diversity may be a key modulator of the spread of disease (Page et al. 2009).

Sedimentation, pollution, thermal stress, water flow, salinity and the proximity to human settlement can have large impacts on microbial communities associated with coral reefs. Increased nutrient enrichment promotes pathogen-associated coral disease, which can lead to or contribute to phase shifts (Voss & Richardson 2006). For example, pollution, sedimentation and nutrient enrichment have been linked to outbreaks of coral black-band disease (Kuta & Richardson 2002, Kaczmarek et al. 2005, Voss & Richardson 2006), *Aspergillus* sp. and other fungal infections (Kim & Harvell 2002), and microbial infection in the sea fan *Gorgonia ventalina*, and *Montastrea* corals in the Caribbean (Bruno et al. 2003). Kline et al. (2006) linked declines in reef ecosystems to increased bacterial populations and dissolved organic carbon, due to pollution, and overfishing. Similarly, Williams et al. (2010) found a close association between coral disease prevalence and localized environmental stressors in Hawaii. In the Northern Line Islands, seawater surrounding more heavily populated islands had up to 10 times more bacterial cells, viral particles, and potential pathogens than seawater more distant from human habitation (Dinsdale et al. 2008). These studies suggest that factors such as water quality and input of human wastes to waters surrounding coral reefs will be more important than fishery regulation if the impacts of harmful, or altered, microbial communities are to be minimized.

Connectivity and genetic variation

Larval dispersal is essential to maintain marine populations and promote recovery from disturbance. Population genetic tools can be used to explore the patterns of connectivity in marine populations where a predominance of larval dispersal makes direct estimates difficult (Ayre & Hughes 2004, Jones et al. 2009). Large variation is evident in levels of connectivity among populations of corals and fishes (summarized in Jones et al. 2009). Therefore, the efficacy of NTAs in maintaining connectivity among populations will greatly depend on the dispersal potential of focal species and the geographic isolation of their populations (Jones et al. 2009). For certain species, NTAs may be useful in maintaining connectivity among protected areas and between non-protected and protected areas. For example, a study in Papua New Guinea found that up to 10% of recruits in NTAs originated from other NTAs located up to 35 km away (Planes et al. 2009). Levels of gene flow were high between protected and exploited Mediterranean subpopulations of white sea bream (*Diplodus sargus*) separated by 5 km (Lenfant 2003). In other instances, the geographical distances from NTAs to fished areas, or to other NTAs, may exceed the dispersive capacity of species. For example, gene flow between populations of limpets in Hawaii was so low that NTAs were ineffective in maintaining connectivity between protected and fished areas (Bird et al. 2007).

Genetic variation is affected by the size of a population and patterns of connectivity among subpopulations. Maintaining genetic diversity is important because it determines, in part, the ability of a population to adapt to environmental perturbations (Frankham 2005). As such, a population with high genetic variation is more likely to contain alleles that will allow it to survive environmental changes resulting from increasing human impacts on ecosystems. Furthermore, high genetic variation in NTAs can offset the loss of economically desirable attributes in exploited populations, such as a reduction in size at maturity caused by fishing pressure (Trexler & Travis 2000). Depletion of genetic diversity can lead to inbreeding depression in which deleterious alleles are exposed, resulting in the rapid decline of populations or local extinction of species (e.g., Newman & Pilson

1997, Briskie & Mackintosh 2004, Frankham 2005). There is considerable variation in genetic diversity among populations in many marine species, including fishes (Bay et al. 2008), corals (van Oppen et al. 2008) and symbiotic dinoflagellates (Howells et al. 2009). Under the assumption that well-designed NTAs sustain large and stable populations with high levels of connectivity among subpopulations, they should consequently be repositories of high genetic variation. However, the effect of NTAs on levels of genetic variation has rarely been tested (García-Charton et al. 2008).

Allozyme heterozygosity in the white-sea bream, *D. sargus*, did not differ between populations inside and outside Mediterranean NTAs separated by 5 km (Lenfant 2003). At a larger spatial scale, populations of *D. sargus* displayed higher allelic richness in protected areas compared to exploited areas (Pérez-Ruzafa et al. 2006). Genetic variation and levels of connectivity varied between two coral species in high-latitude NTAs (Miller & Ayre 2008), but the effect of NTAs compared to fished areas was not explicitly examined. Based on the current literature it is therefore unclear to what extent NTAs are successful in conserving genetic variation (Table 1). Given that processes that affect genetic variation, such as patterns of dispersal and levels of connectivity, vary greatly among species, the efficacy of NTAs in conserving genetic variation is also likely to differ among species.

Societal effects

Coral reef NTAs are hypothesized to benefit people by increasing flows of ecosystem goods and services both inside and outside NTAs. Ecosystem goods and services are benefits people derive from nature (Costanza et al. 1997). Possible ecosystem services provided by coral reef NTAs can be categorized as provisioning services (e.g., increased fisheries yields), cultural services (e.g., tourism), regulating services (e.g., shoreline protection), and human health and well-being.

Fisheries

Coral reef fisheries support the livelihoods of millions of people (Donner & Potere 2007). The vast majority are artisanal (i.e., small-scale and often low-technology subsistence or commercial operations) fisheries in developing countries. However, there are also substantial recreational and commercial reef fisheries, particularly in wealthier countries such as the United States and Australia.

Artisanal fisheries

Several studies, mostly in Kenya and the Philippines, have examined whether total catch or catch per unit effort (CPUE) for coral reef fishes is higher in areas adjacent to NTAs compared with areas further away (McClanahan & Kaunda-Arara 1996, McClanahan & Mangi 2000, Russ et al. 2003, Kaunda-Arara & Rose 2004b, McClanahan et al. 2008b). Catches or CPUE are generally higher in boundary areas compared with more distant areas, but results vary by species and habitat (e.g., Galal et al. 2002, Kaunda-Arara & Rose 2004b, Russ et al. 2004, Table 1, Figure 3). For example, in an experimental study by trap fishing within two Kenyan NTAs and along a transect across their boundaries, there was evidence of spillover effects, but it varied by reef type and was only significant for the most important commercial species (Kaunda-Arara & Rose 2004b). Also in Kenya, CPUE near (1.5 km) and far (6 km) from the Mombasa Marine Park increased by 110% two years after park establishment, but total catch was still 35% lower than before the park was established (McClanahan & Kaunda-Arara 1996). Increases in catch were not enough to compensate for the loss in total yield associated with the establishment of the park (McClanahan & Kaunda-Arara 1996, McClanahan & Mangi 2000).

At Apo Island in the Philippines, hook-and-line catches of surgeonfish (Acanthuridae) and jacks (Carangidae) were 50% higher in late stages of protection (1998–2001, 16–19 years) than before the NTA was established or in early stages (1981–1986) (Russ et al. 2004). Specifically, hook-and-line

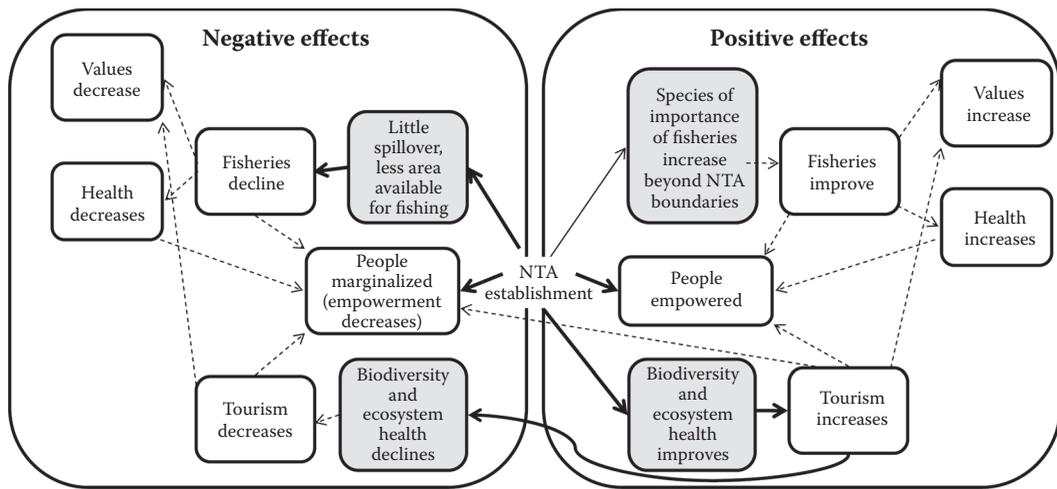


Figure 3 Positive and negative societal interactions with NTA establishment. Boxes with a grey background indicate ecosystem effects; those with a white background show societal effects. Bold solid arrows have the most documented evidence, thin solid arrows have some documented evidence, and dashed arrows have the least documented evidence. The existence and strength of interactions is context dependent.

CPUE of acanthurids was significantly higher near the NTA boundary than further away from it. Conversely, CPUE of carangids was significantly higher further from the NTA compared to closer. CPUE for the acanthurid *Naso vlamingii* in the NTA boundary area was similar to that in an adjacent fishing ground (Katipanan) but 45 times higher in the boundary area than in the wider Apo Island fishing grounds (Russ et al. 2003). Another study of the same NTA found that catch was higher near the reserve, but fishing effort adjacent to the reserve was lower (Abesamis et al. 2006).

Despite the apparent economic benefits from NTAs, two issues in particular were not addressed by most previous studies. First, NTAs are often coupled with other fisheries management measures outside the NTA, which can potentially confound the effects of NTAs. For example, establishment of Apo Island NTA in the Philippines was accompanied by banning fishers from other areas from fishing at the island, the use of explosives, poisons, muro ami (a destructive form of net fishing where corals are broken with rocks to scare fish into the net), small mesh nets, and spearing on scuba (Russ et al. 2004). Catches in the trap fishery were higher close to the Mombasa NTA in Kenya where beach seine netting was excluded, but this relationship was truncated on the side of the park where there was seine netting (although habitat differences may have been a factor) (McClanahan & Mangi 2000). Secondly, from a fisheries perspective, net economic profit rather than gross yield is a more appropriate indicator for measuring the economic welfare of a fishery (White et al. 2008). The mean trophic level of fish catch (species with a higher trophic level are often of higher value) within 5 km of the Mombasa Marine Park was higher than areas far from parks (McClanahan et al. 2008b). Reef fishes of higher trophic level (such as Serranidae and Lutjanidae) can fetch a higher price than lower-trophic-level fishes (such as Acanthuridae). As a result of the higher-value catch and increased fish size in the catch, the income of fishers adjacent to the NTAs in Kenya increased by 135% compared to fishing sites with no NTA management (McClanahan 2010).

Commercial and recreational fisheries

In a developed country context, coral reef fisheries are often recreational or commercial rather than for subsistence. Hypothesized examples of the benefits of NTAs to these fisheries may include increases in catch rates, reduced variation in catch, and improved catch quality (Sanchirico et al.

2002). Conversely, costs include decreases in total catch, displacement of fishing effort, congestion on the fishing grounds, increased user conflicts, higher costs associated with fishing, and reduced safety due to fishing further from shore (Sanchirico et al. 2002, Schroeder & Love 2002, Westera et al. 2003, McCook et al. 2010).

There have been few studies of spatial redistribution of effort by recreational or commercial fishers in response to the establishment of NTAs around coral reefs. The 2004 rezoning of the GBR Marine Park, which increased the area of the park being designated as NTAs from 5% to 33%, resulted in increased crowding in popular fishing areas, increased fishing pressure in the remaining areas, and a spatial displacement of recreational fishing effort by approximately 27% towards remaining open inshore areas within the park (Sutton 2008, McCook et al. 2010). NTAs can protect key values that people have for their fishing experience (including a healthy environment and being able to see wildlife), positively influencing their satisfaction with fishing (Sutton & Tobin 2010). Therefore, high levels of protection may indirectly contribute to improved satisfaction among some recreational fishers. However, there are no empirical studies of recreational fishers' satisfaction before and after the establishment of a coral-reef NTA.

Tourism

Enhancement of tourism is commonly highlighted as a benefit of NTAs (e.g., Gerber et al. 2003, Russ et al. 2004). Tourists seeking high environmental quality are attracted to marine reserves and are often willing to contribute to the costs of reef management (White et al. 2000, Bhat 2003, Peters & Hawkins 2009, Wielgus et al. 2009). This can support tourism-related employment, such as providing services for recreational snorkelling and diving, and the sale of local handicrafts (Russ & Alcala 1999). For example, Belizean NTAs generated revenue of more than US\$17 million in 2007 (Cooper et al. 2008). Sixty per cent of visitors to Tobago visit the only NTA on the island (Burke et al. 2008), and in St. Lucia the Soufriere Marine Management Area generated a net income of US\$48,700 yr⁻¹ from visitor fees (Burke et al. 2008).

Not all tourism is ecologically or socially beneficial (Figure 3). Divers, especially those with little experience, often cause breakage of corals (Epstein et al. 1999, Zakai & Chadwick-Furman 2002, Dung 2009). Increased tourism may alter power dynamics in nearby human communities, often in favour of the elite (Stonich 1998, Christie 2004). Tourism may also lead to increased waste and pollution problems, detrimental impacts on local cultures and increases in prostitution (Brown et al. 1997, 2001).

While there are many studies on tourism in NTAs, few provide comparisons with fished areas or provide before-after information. It is therefore difficult to ascertain whether tourism benefits are because of NTAs or whether the reefs would have attracted tourists regardless of protection. Five of the six studies on NTAs and tourism that did use inside-outside or before-after methodologies suggested that tourism generally has positive impacts on local economies, ecology, and user perceptions (Table 1). Examples include tourists' willingness to pay entrance fees totalling US\$300,000 yr⁻¹ in a Philippines NTA; willingness to pay for a trip to an NTA in the Florida Keys in the United States; and perceptions among Filipino fishers that the local economy has benefited considerably from the tourism generated by the NTA at Apo Island (Russ & Alcala 1999, White et al. 2000, Bhat 2003). Hawkins et al. (2005) found that, across sites, damage to corals was not significantly related to diving intensity and did not accumulate over time; however, in an Israeli NTA, coral breakage was significantly higher in areas used by tourists compared to non-use areas (Epstein et al. 1999). The few studies that provided appropriate inside-outside or before-after comparisons clearly did not address the full range of issues associated with tourism in NTAs and adjacent human communities, and additional appropriately designed studies are necessary.

Human well-being

The establishment of NTAs involves reallocation of ownership and use rights and may therefore influence socioeconomic conditions, including employment, income, patterns of consumption, and material assets (Mascia & Claus 2009). The reallocation of use rights consequently results in winners and losers within and among social groups and may also have secondary effects (e.g., migration of fishers to other grounds) (Figure 3). Few studies, however, have examined the effects of NTAs on aspects of well-being such as community values, poverty, human health and empowerment (Table 1).

Values

In Kenya, government-managed NTAs generally have high-value tourism and are located near urban centres, leading to higher total economic value than community-managed NTAs or comanaged areas (Hicks et al. 2009). However, these government-managed sites lacked key community-level values, such as cultural values (associated with folklore and tradition) and bequest (desire to maintain the ecosystem for future generations), and had lower social capital (relationships, rules and trust within a community) between resource users (Hicks et al. 2009). Along the Kenyan coast, fishers living adjacent to NTAs have lower occupational diversity, higher expenditures, and greater ecological knowledge than fishers living far from NTAs, but these differences may be confounded by urbanization near the NTAs in Kenya (Cinner et al. 2010).

Human health

NTAs may provide human health benefits to adjacent human communities by improving fisheries and providing alternative incomes, such as from tourism (Hatcher & Hatcher 2004, Figure 3). However, few studies have empirically explored this relationship. Two studies in our review provided contrasting conclusions. Energy and protein intake were generally higher in Solomon Islands villages where NTAs were more effectively managed and lower in villages with no NTAs or ineffectively managed NTAs (Aswani & Furusawa 2007). In contrast, across 40 community-based NTAs in the Philippines, large fines for violations of NTA rules were associated with deteriorating child nutrition over 2 years (Gjertsen 2005).

Empowerment

One aspect of NTAs that has generated much interest is the potential to empower communities through collaborative comanagement arrangements (e.g., Pomeroy et al. 2001, Jentoft 2005, Figure 3). These comanagement arrangements are hypothesized to enable communities to participate, control and influence the decision-making process affecting their lives (Maliao et al. 2009a). Capacity building and institution building (nurturing, enhancing and utilizing the skills and capabilities of people and institutions) can facilitate participation and secure rights and hence may enable empowerment (Jentoft 2005). A wide range of actions could promote empowerment when NTAs are established and managed, such as improving community access to information and services, ensuring community participation, raising awareness of people and businesses, and securing control over the use and management of natural resources (Pomeroy et al. 2001).

Empirical studies have shown that the establishment of NTAs, as part of a comanagement framework, can have both positive and negative effects on the empowerment of local resource users. A meta-analysis of indicators of empowerment (participation of users in comanagement, influence over comanagement, control over coastal resources, conflict management, and user compliance with fisheries rules) at 16 sites in the Philippines showed higher empowerment scores after the establishment of NTAs with comanagement programmes (Maliao et al. 2009a). The Philippines has a formal decentralized governance structure that facilitates the adoption of community-based and comanagement frameworks (Christie & White 2007). However, the potential of NTAs to engender empowerment is not always realized. In eastern Africa, despite legislation conducive

to comanagement (Cinner et al. 2009c), NTAs have usually not resulted in community empowerment, often due to a lack of community involvement in the establishment process (Francis et al. 2002, Tobey & Torell 2006).

The establishment of NTAs can, conversely, marginalize local users by exacerbating conflicts over coastal resources, curbing ownership and use rights, and reducing participation in decision making (Christie 2004, Mascia & Claus 2009, Figure 3). For example, a zoning system in the Gili Islands, Indonesia, restricted access rights to fishing grounds in favour of tourism activities, which led to the marginalization of fishers (Satria et al. 2006). Conflicts among stakeholders have also been reported elsewhere in Indonesia and in the Philippines (Christie 2004, Oracion et al. 2005, Majanen 2007). These conflicts are often characterized by unequal power relationships, which relate to the perceived limitations that conservation efforts impose on fishers' livelihoods, disagreement over NTA management (sometimes controlled by tourism interests), displacement of ownership and user rights, and lack of benefits for local residents from the tourism sector (Christie 2004, Majanen 2007, Mascia & Claus 2009). Clearly the potential benefits or costs of NTAs for human well-being are extremely context specific.

The effects of climate change

Climate change is affecting the world's oceans in many ways, including an increase in the frequency and magnitude of sea-surface temperature anomalies and increasing ocean acidification (Hoegh-Guldberg et al. 2007). Climate change impacts have not been dealt with specifically in the previous sections as the literature on the effects of climate change on NTAs is currently limited, and the impacts are likely to be realized over the coming decades. Ocean acidification is expected to reduce coral skeletal accretion and have an impact on physiological and behavioural attributes of reef fishes (Kleypas et al. 1999, Munday et al. 2008). However, there is no reason to suspect that these impacts will differ between NTAs and fished areas (Hughes et al. 2003). More is known about thermally induced coral bleaching events. Changes in temperature, photosynthetic activity and ultraviolet radiation exposure are known to cause bleaching and subsequent mortality of reef-building invertebrates due to loss and *in situ* degradation and death of their symbiotic dinoflagellate algae (Dunn et al. 2004). Fundamentally important questions are to what extent NTAs can offer any resistance to coral bleaching events or enhance recovery rates.

On the GBR, the 1998 bleaching event caused severe bleaching on 35% of protected reefs and 39% of fished reefs, indicating little difference (Oliver & Berkelmans 2001). In both Kenya and Seychelles, coral cover in the mid-1990s was higher in NTAs (McClanahan & Mutere 1994, Graham et al. 2007); however, after the 1998 bleaching event, coral cover declined more in NTAs than fished areas due to higher cover of susceptible taxa such as *Acropora* and *Montipora*, essentially homogenizing the seascape in terms of coral cover and benthic composition (Graham et al. 2007, McClanahan 2008, Darling et al. 2010). A meta-analysis of studies at several locations in the western Indian Ocean showed no significant differences in bleaching effects on benthic communities between NTAs and fished areas (Graham et al. 2008). Another meta-analysis of Pacific and Caribbean reefs showed that the benefits of the buildup of coral cover through time with protected area status was lost following a bleaching event because there are often higher rates of coral mortality in areas with high initial coral cover, resulting in similar low cover between protected and fished sites following bleaching (Selig & Bruno 2010). These findings are not surprising as the boundary of an NTA cannot prevent the buildup of warm water that causes coral bleaching and mortality (Jameson et al. 2002, Hughes et al. 2003).

The timescale of most studies assessing recovery of coral cover from coral bleaching is limited to the period since the devastating global bleaching event of 1998. The majority of these studies that included 7–9 years postbleaching data indicated that recovery is not faster in NTAs compared to fished areas. In Kenya, recovery rates between fished and protected areas did not differ

(McClanahan 2008). In fact, coral recruitment and survivorship of small colonies were lower in NTAs than in fished areas (McClanahan et al. 2005, Mangubhai et al. 2007). Herbivory rates were about 30 times higher in NTAs than in fished areas (McClanahan 2008), possibly resulting in higher incidental losses of coral recruits by herbivores. There may also have been higher direct predation by corallivores inside the NTAs. More broadly in the western Indian Ocean, a study assessing 66 sites in seven countries 7 years after the 1998 bleaching event found no evidence of faster recovery in NTAs (Graham et al. 2008). Disturbed reefs on the GBR also showed no difference in rate of recovery between protected and general-use areas over a 6- to 10-year period (Myers & Ambrose 2009). Similarly, Selig & Bruno (2010) found no differences in recovery in the 7 years following the 1998 bleaching as a function of protection status. In contrast, one recent study found that increases in coral cover were significantly higher within an NTA in the Bahamas than in adjacent fished areas, but the fastest recovery was an increase in absolute cover of only 2% after 2.5 years (Mumby & Harborne 2010). It may be that differences in recovery processes between protected and fished areas take decades to eventuate, or the benefits of NTAs only become apparent following extreme degradation of fished areas. Given that mass coral bleaching is predicted to become more frequent, differences in recovery between protected and fished reefs may not be as relevant as larger geographic predictors of coral mortality and recovery (Graham et al. 2008), such as the thermal history of a site, acclimation history, proximity to deep-water coral refuges, the initial species composition or the proximity of the site to sources of propagules for replenishment (i.e., connectivity). Furthermore, recent findings suggest that coral-host productivity and resilience under different environmental conditions may be linked to the symbiont type associated with geographically distinct areas (Berkelmans & van Oppen 2006, Abrego et al. 2008, Cantin et al. 2009). These are important considerations for NTA planning in the face of global climate change.

Evidence for declines in reef fish diversity and abundance and changes in size structure associated with coral mortality events is growing (Wilson et al. 2006, Pratchett et al. 2008). As discussed, NTAs offer little immediate protection against bleaching-induced mortality of reef corals. In Kimbe Bay, Papua New Guinea, reef fish species richness declined in both fished areas and NTAs in response to severe coral mortality (Jones et al. 2004). Similarly, in the inner Seychelles Islands, more than 90% coral mortality resulted in structural collapse of the reef matrix (Graham et al. 2006). This led to reduced fish species richness and a reduction in abundance of many reef fish groups, particularly small-bodied species and those reliant on live coral for food, shelter or settlement (Graham et al. 2006). These effects were not distinguishable between NTAs and fished areas, with greater declines in certain fish groups in NTAs associated with a higher initial cover of corals (Graham et al. 2007). Furthermore, a change in the size structure of the fish assemblage, whereby individuals less than 35 cm long declined in abundance and individuals longer than 45 cm increased, was apparent in both fished and protected areas (Graham et al. 2007). Negative effects on the fish assemblage inside and outside NTAs were apparent across the entire western Indian Ocean following the 1998 bleaching event, suggesting that NTAs offer no protection to reef fish assemblages following bleaching events (Graham et al. 2008). Habitat-mediated changes to fish assemblages may therefore override fishing-induced changes for many groups, but larger fishery-target species will likely still benefit from reduced fishing (Wilson et al. 2008, 2010).

If the ecology of coral reefs is fundamentally changed through climate warming, and these impacts are felt in NTAs and fished areas, there will also be a negative impact on many of the other benefits of NTAs. For example, pools of genetic diversity may be lost, a negative impact on organism physiology may occur, harmful microbial communities may increase, fisheries may decline and tourists will be less willing to pay for diving experiences. For example, 80% of tourists visiting Bonaire would not be willing to return at the same cost if mass coral bleaching damaged the reefs (Uyarra et al. 2005). Furthermore, predicted migrations of people to coastal zones in response to unfavourable farming conditions inland as a result of climate change will put more pressure on

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coral reef resources and associated management regimes (Daw et al. 2009). Clearly, a great deal more research is needed to assess whether NTAs may continue to provide benefits in the face of increasing climate disturbance. This will likely require revisiting the placement and design of NTA networks (West & Salm 2003, Game et al. 2008).

Conclusions and future directions

The greatest benefits of coral reef NTAs are increased abundance of target species of fishes and invertebrates and overall increases in the economic revenue derived from reef-based tourism, with smaller effects on the reef benthos and fisheries, and variable effects on microbial communities, genetic diversity, marine megafauna and various indicators of social well-being (Table 1). These benefits align well with the five categories of expectation of NTAs (tourism, fisheries, biodiversity, resilience and human well-being), all of which have fish or motile invertebrates as key priorities of protection (Figure 2). However, the present review suggests that the evidence is weakest for the resilience and well-being expectations.

The effects of NTAs on fish, and to a lesser extent motile invertebrates, have received the most research attention. However, even within these groups, most studies assessed diversity, density and biomass, with less attention on trophic interactions, life history traits and adult and larval export. Surprisingly, the impacts of NTAs on the coral reef benthos are not well studied in most regions, and again those studies available focused on fairly simplistic measures, such as percentage cover. Effects on other aspects, such as megafauna abundance, microbes, genetic diversity and most of the social factors assessed in the previous discussion have also received limited attention. Although all of these areas deserve a great deal more research, some key research questions have been identified as a result of the present review that represent critical gaps in coral reef NTA science and deserve prioritization (Table 2). Other critical gaps in coral reef NTA science have been identified elsewhere (Sale et al. 2005, Wilson et al. 2010).

The ecological and economic benefits of coral reef NTAs may be enhanced or undermined by ongoing climate change. It is now widely accepted that climate change is a major threat to coral reefs (Hughes et al. 2003, Hoegh-Guldberg et al. 2007) and may have unknown effects on many aspects of the success of NTAs, from reducing coral cover and fish diversity, to eroding social capital through the migration of people to coastal zones. There are indications that large NTAs may offer some ecological resilience to climate impacts (Mumby et al. 2006, Mumby & Harborne 2010). However, in most tropical countries, NTAs only occupy a small proportion of the total reef area (Wood et al., 2008), compliance with management rules is often inadequate (McClanahan et al. 2009, Pollnac et al. 2010), and the costs of substantially increasing NTA coverage are not politically and socially realistic. Small and medium-size NTAs may not offer much resilience to climate change in the short term (Ledlie et al. 2007, Graham et al. 2008, Darling et al. 2010, MacNeil & Graham 2010, Selig & Bruno 2010), and we currently do not know the value of NTAs in the long-term management of coral reefs in the face of a changing climate. It is possible that NTAs placed in locations known to escape climate disturbances will be a useful strategy (West & Salm 2003, Game et al. 2008), but this would still leave large areas of reef vulnerable.

NTAs are clearly an important part of the conservation toolbox and have many benefits but will not work in isolation. There is a growing realization that a range of other management tools, such as fishing gear restrictions, devolution of power structures and catchment management, targeting areas outside NTAs will also be necessary in conjunction with NTAs (Hughes et al. 2005, Graham et al. 2008, McClanahan et al. 2008b, Mumby & Steneck 2008, Cinner et al. 2009a,b). For the most part, NTAs ensure persistence of populations and communities within their boundaries should overexploitation and other anthropogenic pressures cause localized extinction in unprotected areas. However, there is also a cost associated with establishing NTAs (e.g., fishing pressure is concentrated into a smaller area, thereby limiting sustainability of catches if fishing effort is not reduced in

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Table 2 Critical knowledge gaps in the science of coral reef NTAs**Habitat**

1. Do NTAs enhance the surface complexity of the reef substratum?
2. Do NTAs increase the fitness of benthic populations contained within them, and can they influence the demography of the metapopulation?
3. Are ecological communities within NTAs more or less susceptible to disturbance?
4. Do coral assemblages recover faster from major disturbances inside or outside NTAs?
5. What facets of benthic biodiversity are promoted by NTAs?
6. How are productivity and energy fluxes at multiple levels changed by NTAs?

Motile organisms

1. To what extent do NTAs, specifically enhanced habitat structure, influence target and non-target invertebrates?
2. How do cryptic reef fish and invertebrate communities respond to NTAs?
3. Do NTAs enhance larval input to fished areas?
4. How do fisheries target species influence the abundance of destructive invertebrate species, including urchins and crown-of-thorns starfish?
5. How do connectivity patterns differ among species, and how will this influence network design for multiple species on timescales that are relevant to life histories of the species?

Social

1. How do NTAs affect the socioeconomic value associated with adjacent fisheries?
2. How does the establishment of NTAs influence community well-being (e.g., health, empowerment, poverty)?
3. Do NTAs attract more tourists than fished areas, and if so, why?
4. Who are the winners and losers from tourism developments resulting from NTAs?
5. What are the economic costs and benefits of NTAs in addition to fisheries and tourism?
6. What are the goods and services that NTAs provide aside from fisheries and tourism?

conjunction with NTA implementation), and further work is required to establish the optimal size, area and shape of NTAs, and spatial arrangement of NTA networks, to balance often-conflicting demands of conservation of biodiversity versus fisheries management. Furthermore, where climatic disturbances are predicted to be large in the future, and societal adaptive capacity to change is low, NTA management will likely not be appropriate at all; rather donor aid to reduce human reliance on natural resources, build social capital and diversify livelihoods will be necessary (McClanahan et al. 2008a). Incorporating NTAs and other forms of management in the context of local social characteristics and environmental conditions will provide the most successful conservation outcomes.

Acknowledgements

We thank the Australian Research Council's (ARC) Centre of Excellence scheme for funding workshops and collaborations that led to this review. We also acknowledge fellowships from the ARC and the Queensland Smart Future Fund. The manuscript was improved through comments from Terry Hughes and Tim McClanahan.

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