Linking ecological and social knowledge towards sustainable coral reef fisheries

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Abstract

Overfishing on coral reefs is a key threat to the structure, function and resilience of coral reefs and the well-being of dependent human populations. Despite their global socio-economic importance and biodiversity value, knowledge of sustainable management of coral reef fisheries remains poor. I use an interdisciplinary approach to explore the consequences of exploitation of reef fisheries by integrating global-scale island nation landings statistics with local-scale social knowledge. Globally, catches of reef fishes on islands varied considerably, and increased with human population density. High-yielding fisheries were sustained by greater proportions of lower trophic level taxa, had overexploited fisheries exploitation status, and tended to be found within the Indian and Atlantic Oceans. Islands with overexploited fisheries tended to be larger, with smaller reef area: land area ratios, greater dependence on reef resources, and higher levels of socioeconomic development (GDP). Conversely, sparsely-populated Pacific islands were underexploited with larger reef area: land area ratios and lower levels of GDP. Maximum sustainable yield for island coral reef fisheries was estimated using surplus production methods, and ranged from ~8.2-22.7 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$, depending on the exploitation status of islands incorporated into the models. Results suggest yields > ~8$mt{\bullet}km^{-2}{\bullet}yr^{-1}$ may lead to overexploitation, highlighting the need to set conservative targets for their sustainable use. In contrast to global-scale spatial analyses, local social knowledge of fishers on the island of Anguilla revealed temporal declines in reef catches in recent decades, despite Anguillian reef fisheries being described as underexploited. This suggests that official landings statistics are highly conservative and highlights the importance of fisheries- independent information in understanding local-scale resource use and management on coral reefs. Sustaining reef fisheries for future generations requires an interdisciplinary approach combining ecological and societal knowledge that seeks to address the multiple underlying causes of reef degradation.

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Table of contents

Chapter 1

General Introduction

Island Harbour, Anguilla

It has become increasingly evident that rapid human population growth and economic development have caused substantial, and largely irreversible, loss of biodiversity from global ecosystems (WRI 2005). Particularly over the past 50 years, humans have altered ecosystems more rapidly and extensively than any other time in human history, with approximately 60% of all ecosystem services from fresh water, fisheries, air and water purification to the regulation of climate, believed to be severely degraded, or exploited at unsustainable levels (WRI 2005). Of all global ecosystems, coastal systems provide disproportionately more ecosystem services pertaining to human well-being than any other, and 41% of the world's population are thought to live within 100 km of the coastline (CIESIN 2003). Despite their value, and the fact that coastal ecosystems have been transformed in recent centuries, they are currently subject to more rapid and extensive changes than ever before (Vitousek 1997, WRI 2005, Lotze et al. 2006).

Marine ecosystems have particular importance for human well-being, and provide a wide variety of goods and services, in particular vital food resources for millions of people (Peterson and Lubchenco 1997, Holmlund and Hammer 1999). Consequently, marine environments worldwide are in severe decline as a result of direct anthropogenic stressors including exploitation, pollution and habitat loss (Dulvy et al. 2003, Pandolfi et al. 2003, Newton et al. 2007), coupled to the indirect effects of climate change and associated changes in ocean biogeochemistry (Hughes et al. 2003, Worm et al. 2005, Hoegh-Guldberg et al. 2007). Ecosystems such as estuaries, coral reefs, and coastal and ocean fish communities are rapidly losing biodiversity and the consequences for humanity point to the impairment of our oceans' capacity to provide food, maintain water quality and to recover from perturbations (Pandolfi et al. 2003, Lotze et al. 2006, Worm et al. 2006). In many locations globally, such losses have resulted in dramatic phase or regime shifts, whereby long lasting or irreversible shifts in species composition occur, such as those most readily observed on coral reefs (Aronson and Precht 2000, Folke et al. 2004, McManus and Polsenberg 2004).

Coral reefs are amongst the most productive and biodiverse of ecosystems and, despite covering only 0.1% of the global ocean surface, are host to nearly one third of the world's marine fishes (Smith 1978, McAllister 1991). Coral reefs are found worldwide along the coastlines of more than 100 countries in the tropics, and provide food, income, and cultural benefits to hundreds of millions of people (Salvat 1992, Moberg and Folke 1999, Whittingham et al. 2003). As they can only thrive within a narrow range of environmental conditions, coral reefs are naturally vulnerable to perturbations that may exceed their adaptive capacity, and as such are amongst the most threatened ecosystems on the planet (Nyström et al. 2000, Nystrom and Folke 2001, Hughes et al. 2003). Recent estimates suggest that approximately 20% of the world's coral reefs have already been irrevocably destroyed, and a further 60% are directly threatened from local anthropogenic sources such as overfishing, coastal development, watershed-based pollution or marine-based pollution and damage (Wilkinson 2004, Burke 2011). For example, meta-analyses have revealed that the annual rate of coral cover loss in the Caribbean between 1977 and 2001 was ~1.5%, whilst that of the Indo-Pacific region was ~1% over the last twenty years (and ~2% between 1997 and 2003), which is approximately five times the net rate of tropical deforestation (Gardner et al. 2003, Bruno and Selig 2007). Similarly, a recent study identified a staggering 50% loss of coral cover in Australia's Great Barrier Reef between 1985 – 2012, equating to a rate of ~3.38% per year (De'ath et al. 2012).

Overfishing, including the use of destructive fishing techniques, is the most pervasive threat to the world's reefs, and is thought to currently affect approximately 55% globally (Burke 2011).

This represents an 80% increase in pressure from overfishing and destructive fishing on coral reefs since ~1998 as a direct result of growth in tropical coastal populations, particularly in the Pacific and Indian Ocean regions (Burke 2011, 2012). Despite the high levels of primary productivity on coral reefs, tight recycling of nutrients within the reef ecosystem ensures that less than approximately 1% is available for export or use by humans (Hatcher 1997). Nonetheless, coral reefs support vital fisheries for millions of tropical people in the developing world, and yield an estimated global annual catch of approximately 1.4 – 4.2 million tonnes (Pauly et al. 2002, Whittingham et al. 2003). Whilst this represents only ~2-5% of global fisheries catches, their importance lies in their contribution towards the irreplaceable protein and income needs of thousands of communities and millions of tropical people (Russ 1991, Pauly et al. 2002, Sadovy and Vincent 2002). Given that 75% of the world's coral reefs exist in countries where human population is likely to double within the next 30-50 years, there has never been a greater need to understand and address the issue of overfishing (Pauly et al. 2002). Population expansion is likely to lead to more intense competition, the greater use of destructive fishing techniques such as explosives and poisons, and widespread 'Malthusian overfishing' (Pauly 1997). Despite the global socioeconomic importance of coral reef fisheries, and the impending coral reef fisheries crises in the tropics, knowledge surrounding their sustainable management remains poor (Newton et al. 2007).

The effects of intensive fishing on coral reefs have been recognised globally through comparative analyses of coral reef fish community structure along human population gradients, inside and outside of marine protected areas, and between pristine, unpopulated and densely populated coral atolls (eg.Jennings et al. 1995, Roberts et al. 2001, Sandin et al. 2008). Intensive fishing on coral reefs precipitates profound shifts in community composition and habitat structure through a reduction in the abundance, biomass, and mean size of targeted species, particularly large predatory fishes (Jennings and Lock 1996, Jennings and Polunin 1996a, 1997, McClanahan 1997). Declines in predatory species, which are intrinsically more vulnerable to exploitation, are often accompanied by increased dominance of smaller, more productive fish from lower trophic levels which are subject to top-down control (Jennings and Polunin 1997, Jennings et al. 1999, Dulvy et al. 2004). Such trophic cascades occur despite the functional redundancy of coral reef fish predators (which are represented by approximately 200 species in a typical Indo-Pacific reef system) and can have profound impacts upon reef function (Bellwood et al. 2004, Bonaldo and Bellwood 2008). Depletion of fish predators of echinoids is likely to have lead to unsustainably high densities of sea urchins in the Caribbean prior to their catastrophic mortality in the 1980's, which resulted in widespread overgrowth of macroalgae, and likely irreversible regime shifts (Lessios et al. 1984, Hughes 1994).

Despite widespread evidence of the deleterious effects of fishing on coral reef community structure and function, we are only just beginning to understand the wider geographical and taxonomic extent to which coral reef fishers are exploiting the very ecosystems on which they depend (eg.Jennings and Polunin 1996b). Using Ecological Footprint analyses, and a database of global fisheries landings statistics detailing >50 coral reef taxa, Newton et al (2007) determined that more than half (55%) of 49 island nations were exploiting their coral reef fisheries beyond sustainable limits, landing approximately 64% more than could be supported by their coral reefs. Consequently, the area of coral reef appropriated by these fisheries exceeds the available area by ~75,000km^2, or 3.7 times the area of Australia's Great Barrier Reef. Similarly, it has been ascertained that the growing international trade for live reef fishes - often associated with mobile fleets using destructive fishing techniques – also exceeds sustainable production in the Indo-Pacific and South East Asia by 2.5 and 6 times, respectively

(Sadovy and Vincent 2002, Warren-Rhodes et al. 2003). Given the worrisome scale of current overexploitation, and the expected burgeoning of human populations in the tropics, there is a clear need for further investigations pertaining to the sustainable management of coral reef fisheries, and the effects of fishing on coral reefs across similarly large taxonomical and geographical scales.

The database of global island nation coral reef fisheries landings, adapted from the Food and Agricultural Organisation of the United Nations (FAO) FISHSTAT website database (http://www.fao.org/), and used to estimate the Ecological Footprints of 49 island nation coral reef fisheries, was produced during my MSc in Applied Ecology and Conservation at the University of East Anglia. The formulation of a global coral reef fisheries landings database covering >50 coral reef taxa presented a novel opportunity to continue to explore the effects of fishing on coral reefs at greater scales than previously considered. The aim overall aim of this thesis is to use this unique database to test ecological theories pertaining to the effects of fishing on the structure and function of coral reefs, and in doing so, add to the body of knowledge surrounding the sustainable management of coral reefs for future generations.

Thesis structure

In recent years, 'marine biodiversity indicators' have become important global currency in the assessment of the impacts of fishing, the efficacy of management and the development of marine policy (Fulton et al. 2005, Litzow and Urban 2009). The most widely used marine biodiversity indicator is mean trophic level (MTL) and is derived from fisheries catches. This indicator declines with the removal of predators ('fishing down the food web'), and when yields of low-trophic level fisheries increase ('fishing through the food web') (Pauly et al. 1998, Essington et al. 2006). Catch MTL was the primary index selected by the Convention on Biological Diversity to report on the state of marine environments, and fundamentally assumes that catch MTL is a meaningful reflection of ecosystem MTL and biodiversity (Convention on Biological Diversity 2006). However, by demonstrating that catch mean trophic level (MTL) is only likely to be a useful indicator of ecosystem structure when fishing affects all trophic levels equally, recent research has called this assumption into question (Branch et al. 2010). Despite this, fisheries-independent research which documents trophic downgrading of marine environments in response to fishing suggest there is sufficient evidence to warrant further investigation of available data on catch MTL, especially in relation to coral reef fisheries which are notoriously data poor and difficult to study. Declining catch MTL has been recognised in many pelagic and demersal systems, but is less well described in coral reef ecosystems. This may be owing to the long history of exploitation on coral reefs, whereby most predators had significantly declined prior to the onset of reef research, but may also reflect the difficulty in disentangling the multitude of factors which influence species abundance (Staneck 1998, Jackson et al. 2001). Whilst there are several notable, but isolated examples of trophic downgrading of coral reef food webs (eg. Russ and Alcala 1989, Friedlander and DeMartini 2002, Mumby et al. 2012), there remains little evidence that such processes operate at large spatial scales. By considering the mean trophic level of coral reef fisheries landings, across a spatial scale of fisheries exploitation, I aim to ascertain evidence for differences in MTL in the landings of coral reef fisheries at global scale, and by doing so; provide important insights into the status of the coral reef ecosystems which support them.

Both the aforementioned estimates of global annual coral reef fisheries yields (1.4 – 4.2 million tonnes yr^{-1}), and the ecological footprint analyses which estimated the sustainability of both island coral reef fisheries and the live reef fish food trade in Asia, were all underpinned by the fundamental assumption that the maximum sustainable yield (MSY) for coral reefs is approximately 5 mt•km^{-2}•yr^{-1} (Pauly et al. 2002, Warren-Rhodes et al. 2003, Newton et al. 2007). However, yields from many coral reef fishery studies worldwide demonstrate that actual yields vary enormously, from ~0.1 to 50 mt•km^{-2}•yr^{-1}, depending upon what is defined as a coral reef area, and as coral reef fishes (Russ 1991, Dalzell 1996, McClanahan 2006, Spalding 2001). By taking an average of these studies, MSY is estimated at somewhere between 5 and 6 mt•km^{-2}•yr^{-1}, with 5 mt•km^{-2}•yr^{-1} generally been adopted as the MSY for coral reefs by the scientific community (Jennings and Lock 1996). However, given the extreme variation around this mean, and the fact that yields will vary between coral reefs depending upon factors such as variable ecological productivity, fishing effort, gears employed and targeted species, there is clearly greater research required pertaining to the estimation of MSY for coral reef fisheries, and our understanding of the factors by which it is underpinned. In Chapter 2, I use the global database on coral reef fisheries landings to estimate multispecies maximum yield using surplus production models, and go on to explore how yields for island nation coral reefs vary with two independent measures of fishing effort: the density of human populations, and the fisheries exploitation status of each island. I also explore how fisheries exploitation status, which represents a qualitative estimate of the sustainability of coral reef fisheries, impacts upon estimates of MSY.

Human population density is widely held to be the principal cause of coral reef declines, especially in the developing world (Newton et al. 2007, McClanahan et al. 2008, Mora 2008), but there is also a growing requirement for studies which help to understand how other socioeconomic factors, such as economic development, modify coral reef resource extraction (Sobhee 2004, Cinner and McClanahan 2006, Cinner et al. 2009). If we are to alleviate the growing fisheries crises in the tropics, then greater emphasis must be placed on linking social and ecological perspectives on how societies utilize and manage coral reef ecosystems (Hughes et al. 2005). In light of this, chapter 3 aims to explore some of the other factors, besides human population density, which might impact upon the way that island coral reef ecosystems are fished. In particular I focus on geographical variables, as well as more obvious socioeconomic factors such as economic development, and an estimate of how *per capita* dependence upon coral reefs, might influence yields for island nation coral reefs. Given the broad geographic and taxonomic scale of the island nation fisheries database, this should provide a novel understanding of factors beyond human population densities, which might impact upon the ways in which societies use coral reefs.

Whilst it is critical to investigate how coral reef ecosystems are exploited at broad geographic and taxonomic scales, there is also a need to balance such studies with more detailed, local-scale evidence, particularly as growing evidence points to the necessity of local-scale management of coral reef fisheries by resource users (Cinner et al. 2009). Having analysed global fisheries landings data in chapters 1- 3, chapter 4 switches the emphasis to a single island in order to investigate whether some of the broader scale findings of chapters 1 - 3, are recognisable in coral reef fisheries on the ground. In addition, rather than focusing upon landings data, chapter 4 aims to assimilate perspectives of local fishers, thereby attempting to link social and ecological knowledge; a method thought to be critical in understanding resource extraction on coral reefs (Hughes et al. 2005).

The island of Anguilla in the British West Indies was selected for study for two key reasons: (1) Coral reef fishing in Anguilla is well established, and is essentially artisanal with the majority of fishers targeting reef fish and lobster species on the inshore coral reefs close to the shore; and, (2) Anguillian reef fisheries have been previously categorised as under-exploited, based upon findings from the aforementioned Ecological Footprints study, and as such, ought to demonstrate few effects of overfishing. Evidence to the contrary would reflect underreporting of coral reef fisheries landings, and add testament to the conservative nature of previous studies depicting the scale of the coral reef crisis (Zeller et al. 2006, Newton et al. 2007, Zeller et al. 2007). Anguilla therefore, provides an ideal opportunity to explore evidence of local scale over-exploitation that does not rely upon official landings data (Newton et al. 2007).

In chapter 5, the key findings of this thesis are synthesised, and recommendations for future research priorities are discussed.

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Chapter 2

Trophic downgrading of coral reef fisheries

Small reef fish catch being prepared as bait, Anguilla

Abstract

Overfishing poses considerable threats to the structure, function and resilience of coral reefs and the well-being of dependent human populations. The selective fishing of larger, higher trophic level individuals and species can lead to increased abundance of less favourable, smaller, lower trophic level ones that are released from predation. Here, I hypothesise that such trophic downgrading will be detectable in national landings statistics and test the influence of human population density on coral reef fisheries landings, and the relationship between landings and the mean trophic level of reported landings. Across a spatial gradient of increasing human population density on 28 island nations, coral reef fisheries landings were significantly greater in more densely populated nations and appeared to be sustained by larger proportions of mid trophic level taxa, and smaller proportions of high trophic level taxa. By comparison, islands with lower population densities had higher landings of higher trophic level species, such that mean trophic level was negatively related to coral reef fisheries landings across the spatial scale of human population density. This may reflect fisheries-induced changes to coral reef food webs, and highlights the widespread, unsustainable nature of current levels of fishing on coral reefs.

Introduction

Coral reef fisheries provide an important source of food and livelihoods for tens of millions of people in the tropics (Moberg and Folke 1999, Wilkinson 2004). The continued reliance upon and extraction of coral reef resources by humans is at risk from overexploitation and habitat degradation (Newton et al. 2007, Graham et al. 2008, Wilson et al. 2010). Burgeoning human population growth, especially in the developing world, will intensify demand for coral reef resources and may lead to more frequent use of destructive fishing practices which degrade coral reef habitats and compromise productivity (Jennings and Polunin 1996b, McManus 1996). Despite their socio-economic importance, the extent to which coral reef fisheries can sustain increasing fishing pressures is poorly understood.

Evidence of overfishing on coral reefs exists throughout the world, particularly in areas of high human population density (Jackson et al. 2001, Pandolfi et al. 2003, Newton et al. 2007). At local scales, comparative analyses of coral reef fish community structure along human population gradients, inside and outside of marine protected areas (MPAs), and between pristine unpopulated coral atolls and their densely populated neighbours, demonstrate unequivocal evidence of extensive overexploitation, which typically involves the removal of apex predators (Jennings et al. 1995, Roberts et al. 2001, Friedlander and DeMartini 2002). At the global scale, an Ecological Footprint analysis of coral reef fisheries landings from 49 island nations has shown that more than half are overexploited, and that total landings are 64% higher than can be sustained (Newton et al. 2007). A further Ecological Footprint analysis focused on the increasing trade in live reef fishes for the luxury seafood restaurants in Hong Kong, and found this trade to exceed sustainable production in the Indo-Pacific and South East

Asia by 2.5 and 6 times, respectively (Warren-Rhodes et al. 2003). The live reef fish trade is a new and pernicious threat to reef sustainability, with the geographical distance of individual source nations importing into Hong Kong accelerating rapidly from ~100 km yr^{-1} in the 1970's to beyond 400 km yr^{-1} in the late 1990's, and operating on a boom and bust basis (Scales et al. 2006).

Overfishing directly influences community composition through the selective removal of more desirable, larger species and individuals at higher trophic levels (Jennings et al. 1995, Jennings and Polunin 1995). As these species are intrinsically more vulnerable to exploitation (Jennings et al. 1998, 1999a, b), and decline faster than smaller-bodied species and individuals at lower trophic levels, fish communities tend to change in a size-specific manner in response to exploitation (Jennings et al. 1999a, Jennings et al. 2002). Removal of larger-bodied predatory fishes may also elicit indirect increases in the number and biomass of prey species subject to 'top down' control (Friedlander and DeMartini 2002, Dulvy et al. 2004). Consequently, intensive fishing is thought to induce a shift in fisheries landings from large, long-lived, high trophic level, predatory fishes to small, short-lived, low trophic level species. Evaluation of the size and trophic structure of coral reef fisheries landings, at both local and national scales, may therefore provide an ideal opportunity to examine the consequences of apex-predator removal on the structure of coral reef fish communities subject to exploitation.

At local scales, fishing has been shown to influence the diversity and biomass of predatory fishes. A study in the Philippines documented temporal changes to coral reef community structure following dramatic increases in fishing pressure on a previously protected 750 km stretch of marine reserve, resulting in direct declines in targeted serranids, lutjanids and lethrinids, and significant decreases in overall species richness and density (Russ and Alcala

1989). Declining diversity and biomass of large predatory species, along with compensatory increases in number and biomass of smaller prey species have also been recorded across six Fijian islands subject to differing fishing pressures (Jennings et al. 1995, Dulvy et al. 2004). Also, comparative analyses inside and outside MPAs on the Great Barrier Reef reported predator biomass 3-4 times greater inside unfished zones, whilst prey biomass was twice that of the protected zone (Graham et al. 2003). Similarly, across a gradient of increasing fishing intensity in Kenya, declines in catch per unit effort (CPUE), mean trophic level, and the functional diversity of fished taxa were observed, coupled with compensatory elevations in prey (McClanahan et al. 2008). Additionally, comparisons between populated and unpopulated atolls in the Hawaiian islands have shown that unpopulated atolls have fish communities that are dominated by large-bodied predatory species, whilst those subject to fishing are dominated by small-bodied planktivorous fishes and fleshy macroalgae (Friedlander and DeMartini 2002).

Given the well-described evidence of the effects of fishing on coral reef fish communities at local scales, coupled with growing knowledge of the global extent at which coral reef fisheries are being overexploited, there is an urgent need to understand the extent to which trophic reorganisation of coral reef fish communities is occurring and the frequency of such changes. Here I test whether trophic reorganisation due to fishing can be detected and diagnosed using national landings statistics. I hypothesise that fisheries landings will be greater on island nations with greater human population densities, but that the landed catch will be increasingly composed of lower trophic level species. I test for these patterns using a database of coral reef fisheries landings of 56 fish taxa across 28 island nations.

Materials and Methods

Island countries and territories were selected using three criteria: (1) the presence of coral reef habitat, as defined in Spalding et al (2001); (2) presence of coral reef fisheries; and, (3) availability of fishery landings and human populations statistics for 1997 – 2001 (Newton et al. 2007). Coral reef fishery landings for island nations and territories (hereafter termed islands) were calculated from fisheries statistics reported to the FAO FISHSTAT database from 1997 – 2001 (http://www.fao.org/). For each island, landed weights of fish were categorized according to the most likely source ecosystem (coral reef, demersal, ocean, freshwater, and estuarine), and human use (consumed or destined for the aquarium trade) (see appendix A for a complete list of species categorizations). Only coral reef-associated species, i.e. those living predominantly on or near coral reef ecosystems and deriving energy from coral reefs and associated habitats for a major proportion of their lifespan, were retained for analysis. Definitions and categorizations of ecosystem and human use were provided in FishBase (Froese 2007). The coral reef-derived component of the landings was extracted for each island for each year from 1997 – 2001 and the average was expressed as $mt \bullet km^{-2} \bullet yr^{-1}$. Human population density per island was extracted from the United Nations Development Program report (2002 coral reef area was taken from Spalding et al (2001), and expressed as $people \bullet km^{-2}$ coral reef).

The trophic level of each landed fish taxon (n = 56) was taken from FishBase (Froese 2007), and 'ISCCAAP Table' of FishBase (Froese and Pauly 2000) (Table 1). The mean trophic level of landings for each island ($\overline{TL}$) per year (*Y*) was estimated as the landings-weighted mean species trophic level whereby *a* represents the trophic level of individual taxa:

$$\overline{TL} = \sum TL_a \ Y \ / \ \sum Y$$

We selected 28 island nations for which there were disaggregated coral reef fish landings data. Nine of these islands (Bahamas, Cuba, Fiji, Grenada, Guam, Mauritius, Northern Marianas Islands, Philippines and Seychelles) had fully disaggregated coral reef species landings. Of the remaining islands, 18 reported some of their coral reef fisheries landings within a generic category ""marine fishes nei""(not elsewhere included), which was problematic for the purpose of assigning trophic level (as actual species were unknown), and for estimation of absolute coral reef fisheries landings. ""Marine fishes nei"" landings were assumed to represent coral reef fish landings, providing that the islands had: 1) well-disaggregated landings of pelagic taxa; 2) few identifiable coral reef associated landings, and 3) well-known coral reef-based fisheries (Newton et al. 2007). The percentage contribution of reef-derived ""marine fishes nei"" to overall reef-derived fish landings was then calculated, and the values varied from 0 to 100%. 18 islands reported between 13.1% (American Samoa) and 97.7% (French Polynesia), and one island, Aruba in the Caribbean, did not report any ""marine fishes nei"". For the nine fully disaggregated islands, we conservatively assumed that any "marine fishes nei" did not include reef-associated taxa.

I used least squares regression to test for the overall relationship between mean coral reef fisheries landings and human population density for the 28 islands. I also tested the relationship between weighted mean trophic level and coral reef fisheries landings, and whether this was sensitive to the uncertainty resulting from the inclusion of “marine fish nei” by testing the strength of the relationship using: (a) total fisheries landings including “marine fishes nei”; and, (b) excluding “marine fishes nei”, as well as; (c) fisheries landings from only the 9 fully disaggregated islands, and Aruba which did not report any “marine fishes nei”.

Finally, coral reef fisheries landings were subdivided into trophic categories: (a) 2.0 – 2.9 (low); (b) 3.0 – 3.9 (middle); and (c) 4.0 – 4.6 (high), and both the landings of each category, and the proportion of each category relative to total landings (expressed as a percentage) were calculated for each island, and explored across the scale of landings using least squares regression models. A general linear model was then used to explore differences in the relationships between the landings of each trophic category and overall landings.

Results

Reported coral reef fishery landings varied widely across the 28 island nations, ranging over four orders of magnitude from 0.08 mt•km^{-2}•year^{-1} in New Caledonia to 56.27 mt•km^{-2}•year^{-1} in Sri Lanka. Human population density•km^{-2} coral reef also varied by three orders of magnitude from 18 people•km^{-2} coral reef in the Cook Islands to more than 28,292 people•km^{-2} coral reefs in Sri Lanka. Coral reef fishery landings were strongly and positively related to human population density, with the most densely populated islands landing four orders of magnitude more than their least densely populated counterparts (Figure 1).

Trophic levels for the 56 reported fish taxa varied from 2.0 for herbivorous surgeonfish (Acanthuridae) and parrotfish (Sparidae), to 4.6 for piscivorous snappers (Lutjanidae), wolf herrings (Chirocentridae*)* and torpedo scads (*Megalaspis cordyla)*(Table 1). Mean trophic level of the coral reef landings was significantly lower at islands with higher coral reef fish landings. This pattern was insensitive to the inclusion of '"marine fishes nei"' (Figure 2a,b). For the ten islands with well–disaggregated coral reef fishery landings (i.e. without marine fish nei), the mean trophic level of landings was consistently lower at islands with greater reported coral reef fish landings (Figure 2c).

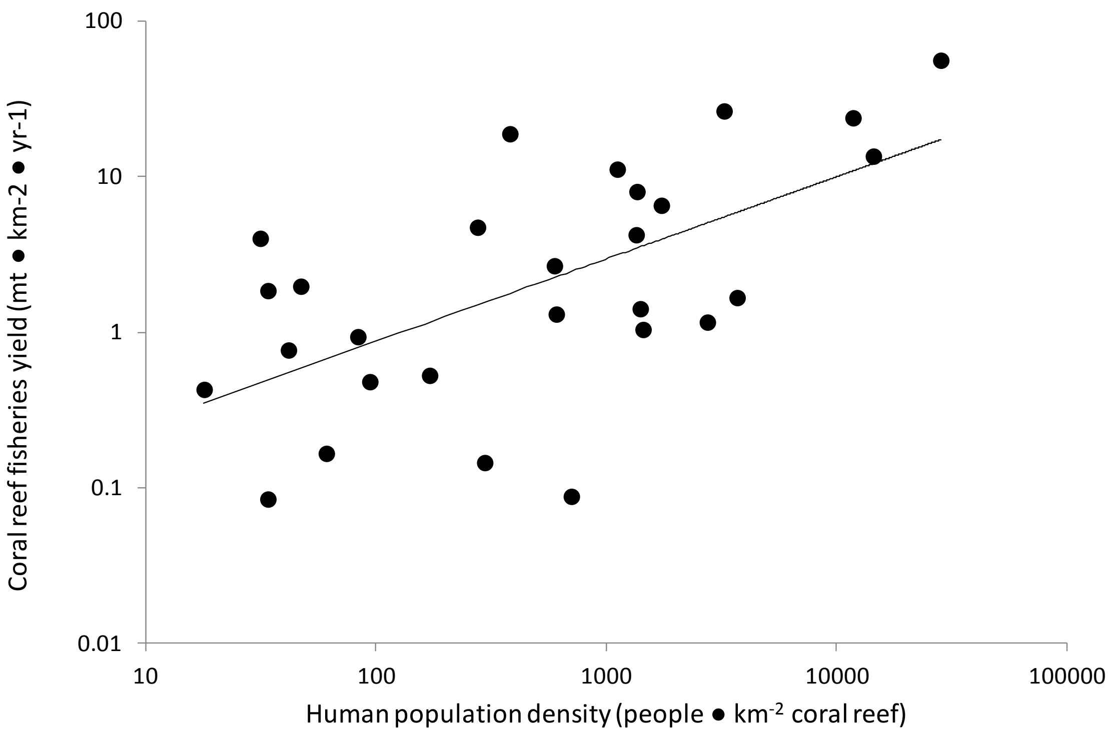

Figure 1. *Relationship between human population density and average coral reef fisheries landings (1997-2001) for 28 island nations ($log_{10}y = 0.53*log_{10}x – 1.12$; $r^2 = 0.38$; $p = 0.001$).*

Table 1. *Mean trophic level of 56 reef associated fish taxa landed by 28 island coral reef nations and reported to Food and Agricultural Organization between 1997 and 2001.*

Taxa	Trophic level
Atlantic thread herring	2.9
Barracudas nei	4.3
Batfishes	3.5
Bigeye scad	3.2
Bluestripe herring	2.8
Boxfishes nei	3.2
Carangids nei	3.3
Cardinalfishes, etc. nei	3.5
Cero	3.6
Cobia	3.3
Croakers, drums nei	3.8
Emperors(=Scavengers) nei	3.4
Filefishes, leatherjackets nei	3.4
Fusiliers	3.5
Goatfishes	3.2
Goatfishes, red mullets nei	3.2
Gobies nei	3.2
Groupers nei	3.8
Groupers, seabasses nei	3.5
Grunts, sweetlips nei	3.5
Halfbeaks nei	3.1
Jacks, crevalles nei	4
Kawakawa	3.7
Lane snapper	4.6
Largeeye breams	3.4
Lizardfishes nei	3.8
Milkfish	2
Mojarras(=Silver-biddies) nei	3.3
Moonfish	3.4
Nassau grouper	3.9
Needlefishes nei	3.55
Parrotfishes nei	2.1
Philippine catfish	3.1
Porgies	3.4
Porgies, seabreams nei	3.4
Queenfishes	3.3
Rainbow runner	3.7
Red grouper	4.3
Red hind	3.88
Scads nei	3.4
Scats	3.5
Sea chubs nei	2.24
Snappers nei	4.6
Snappers, jobfishes nei	4.6
Snooks(=Robalos) nei	3.5
Spinefeet(=Rabbitfishes) nei	2.2
Spotted sicklefish	3.4
Squirrelfishes nei	3.5
Surgeonfishes nei	2
Threadfin breams nei	3.4
Threadfins, tasselfishes nei	3.3
Torpedo scad	4.6
Triggerfishes, durgons nei	3
Wolf-herrings nei	4.5
Wrasses, hogfishes, etc. nei	3.5
Yellowtail snapper	4.6

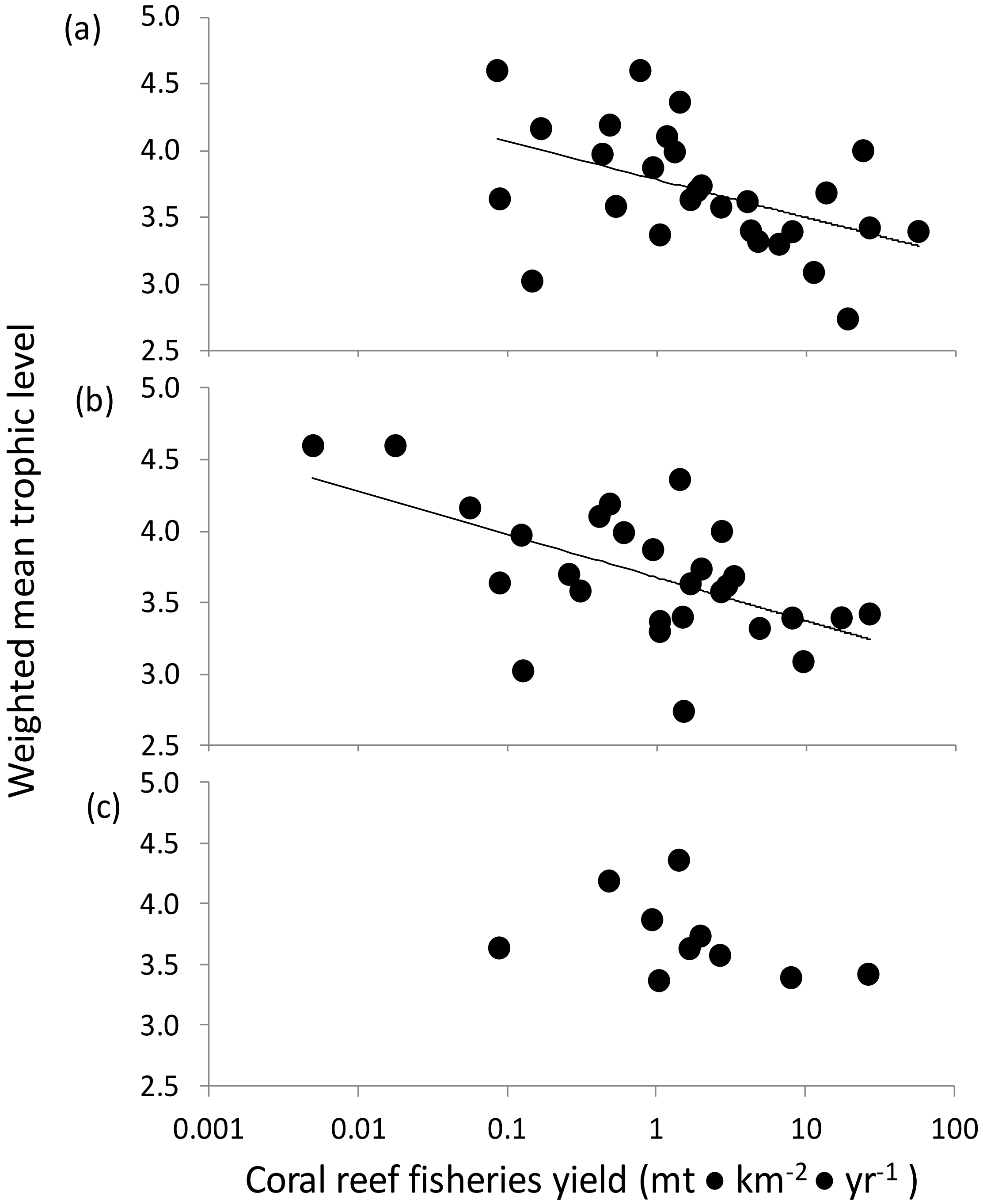

Figure 2. *Relationship between weighted mean trophic level of reported fish taxa and coral reef fish landings: (a) including "marine fishes nei" ($y = 3.78 – 0.28*log_{10}x$, $r^2 = 0.23$, $p = 0.001$ $n = 28$); (b) excluding "marine fishes nei" ($y = 3.67 – 0.30*log10x$, $r^2 = 0.34$, $p = 0.001$, $n = 28$); and, (c) from islands which reported no reef-derived "marine fishes nei" ($y = 3.76 – 0.19*log_{10}x$, $r^2 = 0.15$, $p = 0.27$, $n = 10$). Coral reef fishery landings represent mean landings of landed fish taxa reported to the Food and Agricultural Organization between 1997 and 2001 for 28 island coral reef nations.*

The pattern of coral reef fisheries landings suggests that overfishing of predators is associated with elevated landings of mesopredators (Figure 3). Whilst the proportions of lower trophic level taxa were always lower across the range of landings (0-45%; Figure 3a), the proportions of landings of mesopredatory planktivorous species were greater at higher landing islands (Figure 3b). This was mirrored by smaller proportions of predatory taxa at the highest landings islands (Figure 3c).

As would be expected, actual landings within each trophic group were higher at islands with highest total landings, and lowest at islands with lower total landings (Figure 4). However, the relationship between total landings and actual landings of mid-trophic level taxa was stronger than that between total landings and actual landings of both low and high trophic groups, suggesting that mesopredators became an increasingly large component of total landings for islands with greater coral reef fisheries landings (Table 3, Figure 4). Thus shifts in catches from apex predators to mid-level planktivorous species suggest a rise in mesopredatory species (Figure 3b, c), but does not point to a cascading effect on lower trophic level species (Figure 3a). Only some islands with depleted predatory species report higher proportions of low trophic level taxa across the spatial gradient of fisheries landings (Figures 3 and 4). For example, Palauan coral reef fisheries landed more than 58% in the lowest trophic level category (with 8.2% of total landings as predatory species), whereas the Philippines landed less than 4% in the lowest trophic category compared with 7% predatory species.

The island reporting the lowest coral reef fisheries landings, New Caledonia, reported catches comprised only of high trophic level fish taxa such as barracudas (*Sphyraenidae)* and groupers (*Epinephelinae)*, and consequently had the largest mean trophic level of 4.6 (table 2). The island with the lowest mean trophic level of 2.7, Palau, was the fourth highest landing island,

and reported greater proportions of lower to mid trophic level taxa such as emperors (*Acanthuridae*), porgies (*Sparidae*), and parrotfish (*Scaridae*) (table 2). The highest landing islands (>5 mt•km^{-2}•yr^{-1}) consistently had low to mid mean trophic levels of below 3.68, whilst mean trophic level for mid-landing islands (1 - 5 mt•km^{-2}•yr^{-1}) ranged from 3.32 to 4.36 for Antigua & Barbuda and Aruba, respectively (table 2). With the exception of American Samoa, the lowest landing islands (<1 mt•km^{-2}•yr^{-1}) had consistently high mean trophic levels above 3.58 (table 2).

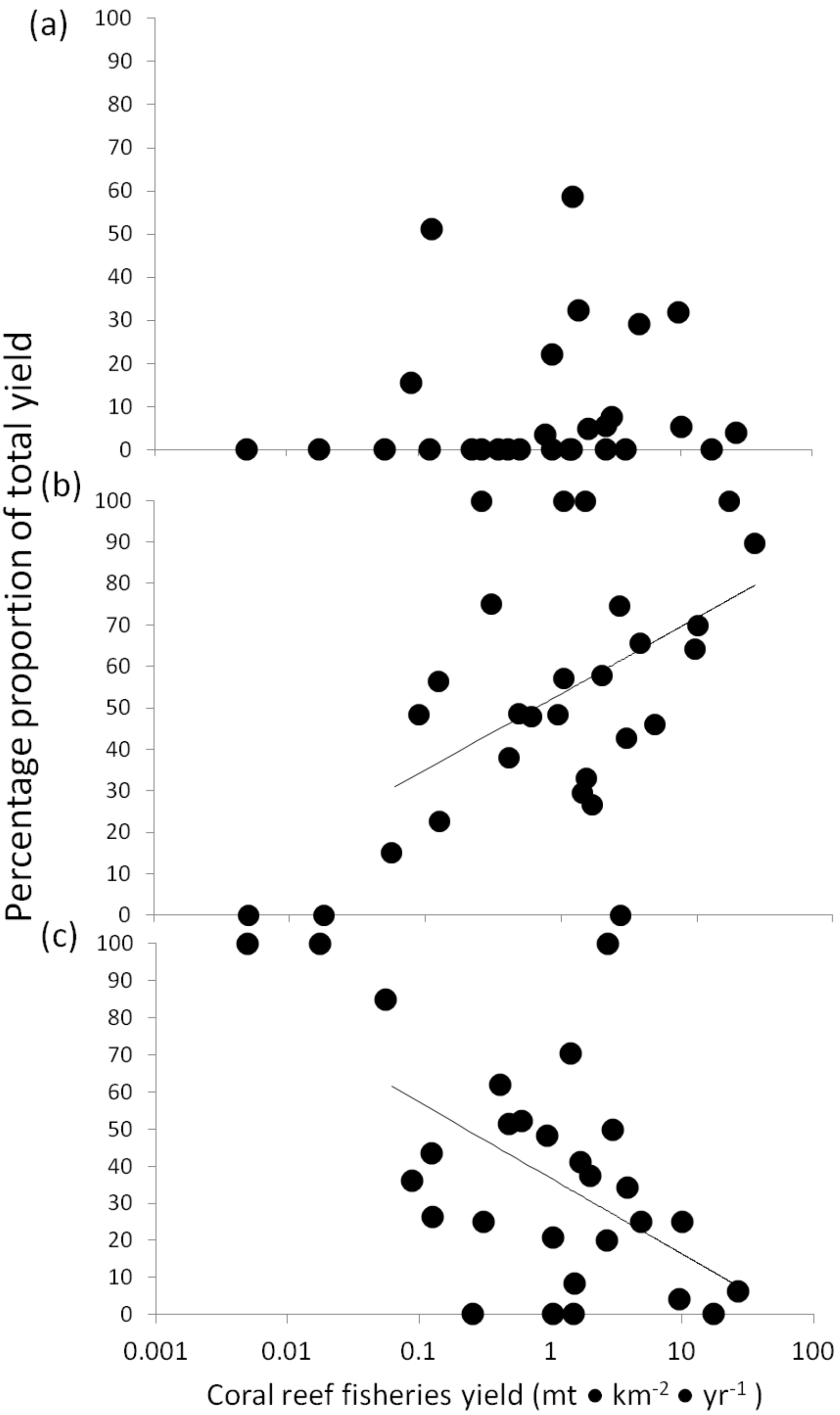

Figure 3. *Relationships between coral reef fishery landings of 28 island coral reef nations and the percentage of landings comprising fish taxa of trophic levels between (a) 2 – 2.9, (r^2 = 0.01, NS); (b) 3 – 3.9, (y = 0.02*log_{10}x -0.87, r^2 = 0.28, p = 0.004, n = 25); and, (c) 4 – 4.6, (y = 0.55 – 0.02*log_{10}x, r^2 = 0.33, p = 0.01, n = 24).*

Table 2. *Weighted MTL of coral reef fisheries fish landings, including range of trophic levels, reported to Food and Agricultural Organisation between 1997 and 2001, for 28 island coral reef nations.*

			Trophic level range	
Island	**MTL**	**landings mt•km^{-} •yr^{-1}**	***lower***	***upper***
American Samoa	3.02	0.15	2.0	4.6
Antigua	3.32	4.75	2.0	4.6
Aruba	4.36	1.42	3.8	4.6
Bahamas	4.19	0.48	3.3	4.6
Bahrain	3.09	11.21	2.1	4.6
Barbados	4.11	1.16	3.3	4.6
Bermuda	3.58	0.53	3.3	4.6
British Virgin Isl.	4.17	0.17	3.2	4.6
Comoros	3.40	4.25	3.3	3.7
Cook Islands	3.97	0.43	3.8	4.6
Cuba	3.63	1.67	2.9	4.6
Fiji	3.87	0.94	2.0	4.6
French Polynesia	4.60	0.77	4.6	4.6
Grenada	3.58	2.68	2.0	4.6
Guam	3.64	0.09	2.0	2.6
Kiribati	3.62	4.03	2.0	4.6
Maldives	3.70	1.86	3.7	3.7
Martinique	3.30	6.57	3.6	3.6
Mauritius	3.39	8.05	2.2	4.6
New Caledonia	4.60	0.08	4.6	4.6
N. Mariana Is.	3.37	1.04	2.0	4.6
Palau	2.74	18.95	2.0	4.6
Philippines	3.42	26.55	2.0	4.6
Réunion	3.68	13.60	3.3	4.6
Seychelles	3.74	1.98	2.2	4.6
Sri Lanka	3.40	56.27	3.3	3.7
Trinidad, Tobago	4.00	24.00	4.0	4.0
US Virgin Islands	3.99	1.31	3.0	4.6

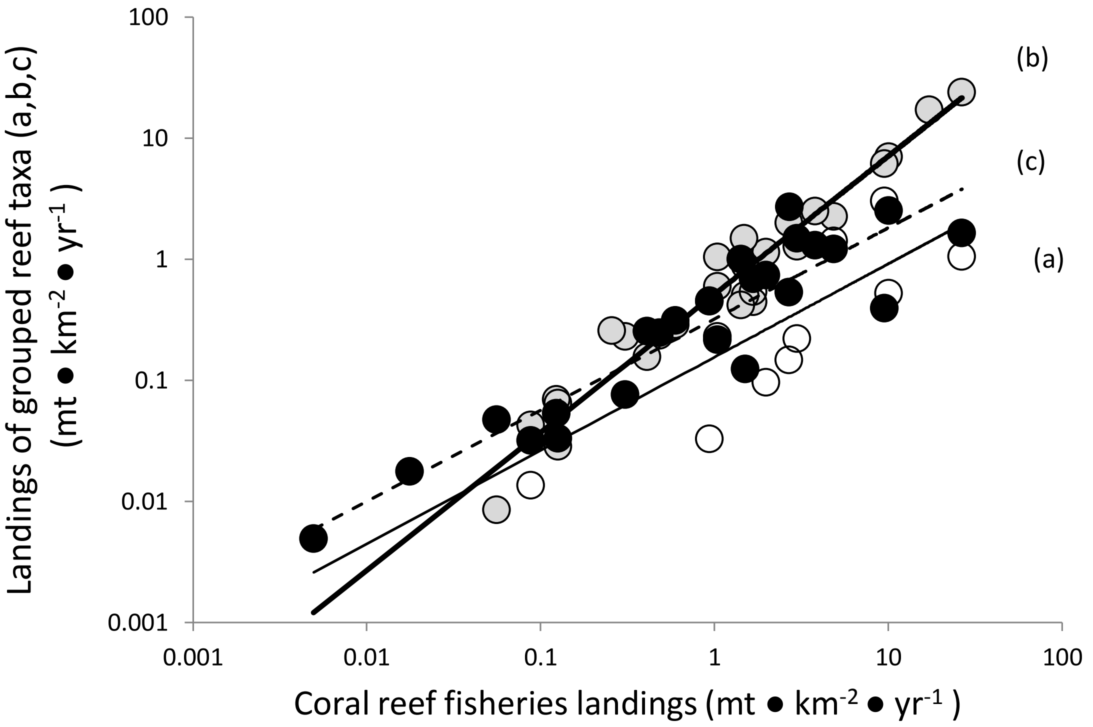

Figure 4. *Relationships between coral reef fish landings of 28 island coral reef nations and the landings of fish taxa of trophic levels between (a) 2 – 2.9, ($log_{10}y = 0.78*log_{10}x – 0.81$, $r^2 = 0.63$, $p = 0.001$, $n = 13$, open circles); (b) 3 – 3.9, ($log_{10}y = 1.14*log_{10}x – 0.29$, $r^2 = 0.95$, $p < 0.001$, $n = 25$, grey circles); and, (c) 4 – 4.6, ($log_{10}y = 0.76*log_{10}x – 0.50$, $r^2 = 0.86$, $p < 0.001$, $n = 24$, black circles). See Table 3 for statistical analysis.*

Table 3. *Summary of a general linear model of the relationship between total coral reef fisheries landings and landings of reef fish taxa in three trophic groups: (a) 2 – 2.9; (b) 3 – 3.9; and, (c) 4 – 4.6, for 28 island coral reef nations. See Figure 6.*

Source	**df**	**f**	**p**
Coral reef fisheries landings (a)	1	266.32	< 0.0001
Trophic group (b)	2	11.98	< 0.0001
a x b	2	6.82	0.002
error	56		

Discussion

Worldwide, subsistence and artisanal fisheries appear to be altering the trophic structure of island coral reef food-webs. The highest catches, at the most heavily fished islands appear to be sustained by rises in catches of mesopredatory species, probably as a result of apex predator depletion. These changes in composition of fisheries catches may well reflect changes in the underlying trophic structure of coral reef fish assemblages (Jennings and Polunin 1996a, 1997, Mumby et al. 2012).

Greater proportions of mid-trophic level species at highest yielding islands, are mirrored by smaller proportions of apex predatory species, and are consistent with a rise in mesopredatory species in response to fisheries exploitation (Prugh et al. 2009, Mumby et al. 2012). Given the strong positive relationship between human population density and coral reef fisheries landings (Figure 1), it is likely that the observed rise in the mesopredatory component of catch is driven by fisheries exploitation. Given the high vulnerability of large-bodied predatory species, and the mounting evidence suggesting that catches of predatory species cannot be maintained in overfished coral reef ecosystems, it is unsurprising to find patterns of predator depletion, previously identified in smaller scale studies, can be detected globally at the scale of islands (Jennings and Lock 1996, Jennings et al. 1999a, Cheung et al. 2007).

Previous to this study, the release of coral reef mesopredatory species in response to predator depletion has only been observed in several small-scale fish community studies. For example, the biomass of mesopredators *Cephalopholis fulvus*, *C. cruentatus*, and *Epinephelus guttatus* increased dramatically (by 880%) in response to a marked decline in the abundance of Serranids and Lutjanids, in just 7 years of intensive fishing in Belize (Mumby et al. 2012). Also, a study of remote coral reef ecosystems in Salas y Gomez, Chile, recently subjected to shark fishing, observed a large cohort of small sharks and an absence of large sharks consistent with mesopredator release (Friedlander et al. 2013). The greater component of mesopredatory species in landings reported here, for islands with highest fishing pressures and highest coral reef fisheries landings (Figure 3b), may account for the apparent absence of a cascading effect upon the lowest trophic level species, as 'prey release' could be suppressed by mesopredatory species (Estes et al. 2011, Pinnegar et al. 2000, Prugh et al. 2009,) (Figures 3 and 4). Detecting trophic cascades in coral reef ecosystems is notoriously difficult owing to the many factors that influence species abundance (Steneck 1998). Indeed, evidence for prey release in coral reef communities subject to apex predator depletion has only been weakly observed in a few localised studies (eg. Jennings et al. 1995, Friedlander and DeMartini 2002, Dulvy et al. 2004). The evidence from this study suggests that worldwide, intensive fishing of apex predators on coral reef island nations may have brought about a rise in mesopredatory species, which in turn may have suppressed prey release of low trophic level, herbivorous species (Figures 3 and 4).

The extent to which the MTL of fisheries landings is likely to reliably reflect changes to fish assemblage structure has recently been called into question (Caddy and Garibaldi 2000, Branch et al. 2010, Sethi et al. 2010). Global analyses of catch MTL, when compared with model predictions, trawl surveys and fisheries stock assessments, suggest that 'catch MTL' will often diverge from ecosystem model predictions, and may only be a useful indicator of ecosystem structure when fishing affects all trophic levels equally (Branch et al. 2010). Nevertheless, many fisheries-independent studies documenting predator depletion in response to exploitation, in both the Caribbean and Indo-Pacific regions, do suggest that the patterns observed in global coral reef fisheries landings statistics are likely to reflect those of the underlying fish community structure. In the Caribbean, such declines have been documented both historically (Jackson 1997, Pandolfi et al. 2003, McClenachan and Cooper

2008) and more recently (Hughes 1994, Hawkins and Roberts 2004, Mumby et al. 2012). Similarly, a growing number of isolated comparisons of heavily fished versus lightly fished Indo-Pacific coral reefs have recorded declining size and abundance of predatory species to be the most readily observable effects of overfishing, despite high potential functional redundancy in this region (Graham et al. 2003, Bellwood et al. 2004, Dulvy et al. 2004, McClanahan et al. 2008).

Whilst FAO provide the most extensive global time series of fishery statistics available, coral reef landings are often under- or misreported owing to the difficulties of recording landings from multispecies fisheries in remote places (Dalzell 1998, Sadovy 2005, Newton et al. 2007). Reconstructions of landings in US flag-associated islands of the western Indo-Pacific suggest that, over a 50-year time period, landings have been underestimated by 86%, 54%, and 79% for Guam, Northern Marianas islands and American Samoa, respectively (Zeller et al. 2007). As these islands form part of the analysis, it is likely that landings statistics are conservative estimates for these, and other islands considered. However, as there is no evidence of, or rationale for bias in misreporting of particular trophic levels, inaccuracies in absolute landings should not influence the trends in trophic levels reported here.

The FAO data used here pre-dates the current year by 17 years and therefore, may not be an accurate reflection of current coral reef fisheries yields. Dependence on coral reef resources and, therefore, fishing effort in the tropics is likely to have increased apace with tropical human population growth. This has been exponential in recent decades and is forecast to exceed that of the rest of the world by the late 2030s (State of the Tropics, 2014). If these analyses were repeated using today's data, greater fishing pressure coupled with the inevitable yet unclear impacts of climate change and ocean acidification on coral reef fisheries, the observed trends seen here would likely be more pronounced (Graham et al. 2008).

As trophic level estimates from Fishbase are based upon the diet composition of each species, it must be assumed that trophic level does not vary within species across size, year and geographical region. Trends arising from these 'fixed' trophic levels are therefore, likely to be conservative because trophic levels may decline within populations, as they are fished (Jennings et al, 1995)Our study supports growing evidence that many coral reef fisheries are unsustainable, and highlights the wider threat to the structure, function and resilience of reef communities (Warren-Rhodes et al. 2003, Newton et al. 2007, McClanahan et al. 2008). The implications of trophic reorganisation through fishing may be particularly severe for coral reef ecosystems, as large bodied individuals and species have disproportionate effects on key coral reef processes, such as grazing, erosion and sediment reworking (Bellwood et al. 2003, Bonaldo and Bellwood 2008). Such trophic downgrading of coral reefs may significantly impact developing nations, for whom future social and economic development depends upon healthy coral reef ecosystems (Moberg and Folke 1999).

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Chapter 3

Coral reef fisheries and maximum sustainable yield: the influence of exploitation history

Fisher preparing to 'soak' fish and lobster traps, Anguilla

Abstract

Coral reef fisheries provide a vital source of food and income for tens of millions of people in the tropics, but are severely threatened due to the effects of overfishing, pollution and climate change. Despite their global socio-economic importance and high biodiversity value, the long-term sustainable management of coral reef fisheries remains poorly understood. Maximum Sustainable Yields on coral reefs are typically assumed to be around 5 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$, yet the range of reported yields for coral reef fisheries varies greatly from 0.1 – 50 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$. One hypothesis is that part of the large range in yield is due to variation in fishing effort, with lowest yields resulting from underexploited reefs, and highest yields from fully or overexploited reefs. To address this issue, the relationship between MSY and fishing effort was considered for 49 island nations. Global island-nation-scale coral reef fisheries landings statistics were used to estimate MSY using surplus production models, and variability in two measures of fishing effort (human population density and fisheries exploitation status) were explored in relation to the yields of island coral reefs. Both measures of fishing effort were strongly related to fisheries yields, and therefore MSY estimates, with highest yields reported by densely populated over-exploited islands, and lowest yields reported by scarcely populated, under-exploited islands. Surplus production models estimate MSY to range from 8.2 to 22.7 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$ (with optimal fishing efforts (*Fmsy)* ranging from 1344 to 6953 $people{\bullet}km^{-2}$ coral reef), with an intermediate estimate of approximately 12.9 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$ (*Fmsy* = 2139 $people{\bullet}km^{-2}$ coral reef), depending upon the exploitation status of island fisheries included within the model. The highest MSYs were generated by models incorporating heavily populated, fully- and over-exploited islands, whilst the lowest MSYs resulted from models incorporating only scarcely populated, under exploited islands. Our analyses suggest that overexploitation of reef fisheries is more frequent when human population densities on

tropical islands are greater than ~1000 people•km^{-2} coral reef, where MSY would approximate 8 mt•km^{-2}•yr^{-1}, and that the likelihood of sustainable fishing declines disproportionately as MSY drops below this value. This supports previous estimates of MSY at 5mt•km^{-2}•yr^{-1} for coral reef fisheries, and suggests more recent estimates of ~15 mt•km^{-2}•yr^{-1}, if adhered too, could be deleterious to coral reef ecosystems.

Introduction

Tens of millions of people and thousands of tropical communities depend upon coral reef fisheries for both sustenance and employment (Burke et al, 2011). The future of coral reef fisheries is severely endangered by the competing pressures of overfishing, habitat degradation, and rapid human population growth (Newton et al. 2007, Knowlton and Jackson 2008, Wilson et al. 2008). Coral reefs harbour some of the highest known levels of biodiversity, especially in the Indo-Pacific Coral Triangle, adjacent to some of the poorest nations in the world (Roberts et al. 2002, Carpenter and Springer 2005). The rich diversity and associated ecosystem services on coral reefs are particularly threatened by the cascading impact of coral reef fisheries (Carreiro-Silva and McClanahan 2001, Dulvy et al. 2004a, Mora et al. 2011). Despite the global socio-economic importance of coral reef fisheries, knowledge of their long-term sustainable management remains poor.

Widespread and extensive overfishing on coral reefs has been detected through comparative analyses of fish community structure inside and outside MPAs, and along human population gradients (Jennings and Polunin 1996, Roberts et al. 2001, Russ 2002). Overfishing is known to cause direct and indirect shifts in coral reef community structure of both reef fishes, and reef communities as a whole (Russ 1991, McClanahan 1994, Dulvy et al. 2004b). Ecological Footprint analyses have shown that more than half of island nation coral reef fisheries are overexploited, and that landings destined for the live reef fish food trade exceed sustainable production in the Indo-Pacific and South East Asia by 2.5 and 6 times, respectively (Warren-Rhodes et al. 2003, Newton et al. 2007). These Ecological Footprint analyses relied on a global value of 5 $mt \bullet km^{-2} \bullet yr^{-1}$ as the maximum sustainable yield for coral reefs, which was estimated from spatially variable coral reef fisheries yields ranging from 0.1 – 50 $mt \bullet km^{-2} \bullet yr^{-1}$ (Dalzell 1996, Jennings and Lock 1996, McClanahan 2006).

Spatial variation in yield estimates can be influenced by differences in environmental productivity, catch rates and gear selectivity, the history of fishing on the coral reef, and fishing effort (Dalzell 1996, McClanahan 2006). Fishing effort is arguably the most fundamental factor influencing yields, and is highly variable among coral reef fisheries. Two ways of measuring fishing effort on coral reefs include consideration of differences in human population densities, and fisheries exploitation history or status. Numerous previous studies have expressed fishing effort as the number of people per unit length or area of coral reef (e.g. Jennings and Polunin 1997, Dulvy et al. 2004a, Stallings 2009). Fisheries exploitation status has been described as a qualitative estimate of sustainability defined for island coral reef fisheries, generated through combined analyses of localised literature, datasets and communications with fisheries officers (Newton et al. 2007). Exploitation status represents a stage in the development and demise of a coral reef fishery through time, from under- to fully-, to over-exploited and collapsed (Newton et al. 2007) (Figure 1). Knowledge of the underlying response of fisheries landings to changes in fishing effort and/or sustainability is important for fisheries management, especially where maximum sustainable yield is sought through control of fishing effort (McClanahan et al. 2008, Cinner et al. 2009).

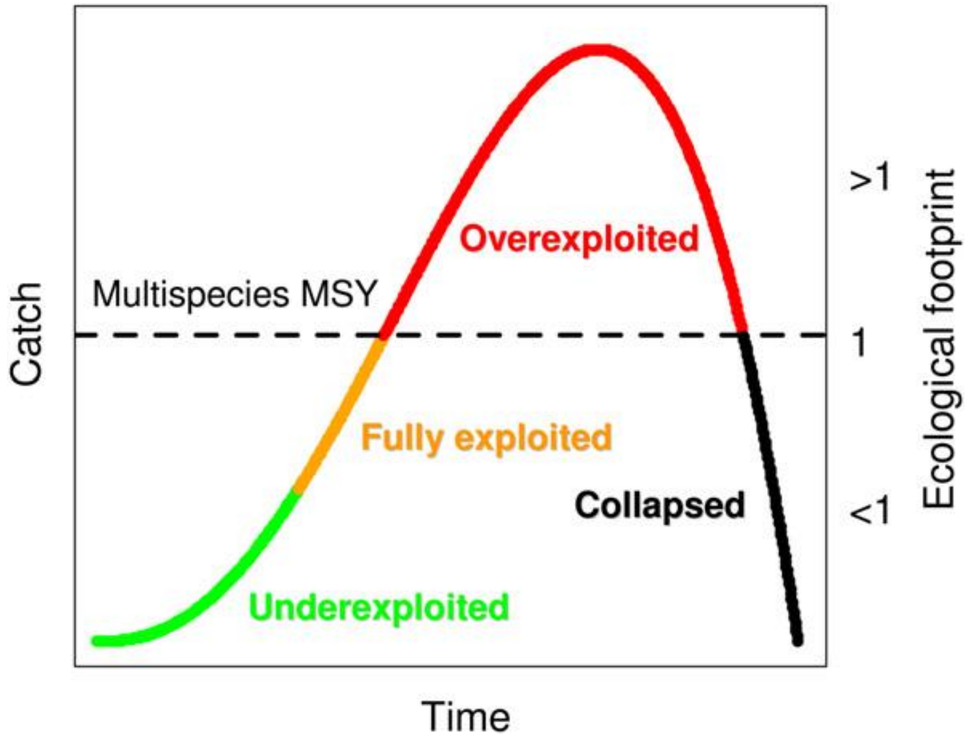

Figure 1. *Schematic representation of the development of a coral reef fishery and its Ecological Footprint through time (Newton et al. 2007) .*

The most widely used method for estimating maximum sustainable yield (MSY) relies on fitting a surplus production model to the relationship between fishing effort and yield of single species over time. However, as such data are rarely available, the method more typically applied is to aggregate multispecies data across a spatial gradient of fishing pressure (e.g. Ralston and Polovina 1982, Munro and Thompson 1983, Koslow et al. 1994). These spatial comparisons of catch and effort can provide useful surrogates for data-scarce ecosystems such as coral reefs, and variability in scale is dealt with by standardising both yield and effort by reef area (Hilborn and Walters 1992). This method assumes that all processes affecting system production are captured within the overall relationship between yield and effort. Despite concerns regarding equilibrium conditions, which assume that yield will be balanced by production; such an approach offers a workable alternative to complex models with elaborate data requirements. A final assumption of this model is that fishing mortality and effort are proportional to each other, such that:

$$F \; = Q * f$$

Where F = fishing mortality (or Fmsy), f = fishing effort (or Emsy), and Q = the catchability quotient (the efficiency of a particular fishery). Fishing mortality (or Fmsy) describes the maximum rate of fishing mortality (the proportion of a fish stock caught and removed by fishing), yet the model actually measures fishing effort (or the expected level of fishing that will produce the maximum sustainable yield). Therefore, it is assumed that the efficiency of each coral reef island fishery (*Q)* is constant. The effect of variable fishing effort on yield has been recently compared for 79 Asian and Caribbean coral reef-based fisheries, using aggregate surplus production models which incorporate human population density as a measure of fishing effort. This analysis suggested a multispecies maximum sustainable yield of approximately 15 mt•km^{-2}•yr^{-1} which occurred at a fisher density of 640 people km^{-2} (Halls et al. 2006). This is similar to a previous estimate for reef fishery MSY of 16.4 mt•km^{-2}•yr^{-1} at a fisher density of 581 people km^{-2}, which was calculated using coral reef fish yields from approximately 40 South Pacific Islands (Dalzell and Adams 1997). However, to date there remains no comprehensive global-scale overview of maximum sustainable yield, and the effect of variability in fishing effort on coral reef fisheries yields.

Here FAO fisheries landing statistics of coral reef fishes, molluscs and crustaceans are used to estimate the multispecies maximum sustainable yield across 49 island nations, using surplus production models. We also explore how yield varies with two independent measures of fishing effort: the density of human populations and fisheries exploitation status, and consider how exploitation status impacts upon estimates of MSY.

Methods and materials

Island countries and territories were selected for study on the basis of three criteria: presence of a coral reef as defined in Spalding et al (2001); availability of Food and Agriculture Organisation (FAO) fishery landings for 1997-2001; and evidence of a coral reef fishery as defined by Food and Agriculture Organisation (FAO) FISHSTAT database. Coral reef fishery landings for island nations and territories (hereafter termed islands) were calculated from fisheries statistics reported to the FAO FISHSTAT database from 1997 – 2001 (http://www.fao.org/). For each island, landed weights of fish, molluscs and crustaceans were categorized according to the most likely source ecosystem (coral reef, demersal, ocean, freshwater, and estuarine) and human use (consumed or destined for the aquarium trade) (Appendix A). Only coral reef-associated species, i.e. those living predominantly on or near coral reef ecosystems and deriving energy from coral reefs and associated habitats for a major proportion of their lifespan, were retained for analysis. Definitions and categorizations of ecosystem and human use were provided in FishBase (Froese 2007). The coral reef-derived component of the landings was extracted for 49 islands and the average was calculated from 1997 – 2001 and expressed as $mt \bullet km^{-2} \bullet yr^{-1}$. Crustaceans and molluscs were included in these analyses so that the metrics reflected total yields.

Two indicators of fishing pressure were calculated: human population density per unit of reef area and exploitation status. Human population densities were extracted from the United Nations Development Program report (2002), and expressed as $people \bullet km^{-2}$ coral reef. Coral reef area was extracted for each island from Spalding et al (2001). Fisheries exploitation status were extracted from Newton et al (2007) and represent data collated from primary and secondary literature, and from global and regional fisheries databases. Four stages of fisheries development were recognized: (1) under-exploited; (2) fully- exploited; (3) over-exploited; and, (4) collapsed (Figure 1). Islands were conservatively scored as under- or fully-exploited if there was only localized evidence of overfishing. Over-exploited islands which were low yielding (yields < than sustainable production) were assigned the collapsed status, as per Newton et al. (2007). Coral reef fishery landings were then divided by human population density to generate catch per unit effort (CPUE) values, expressed as kg•person^{-1}•km^{-2}•yr^{-1}.

Maximum sustainable yield for island coral reef fisheries was estimated by fitting a surplus production model using least squares regression, for which the null expectation was a negative linear relationship between CPUE and fishing effort (e.g. Schaefer 1967). For island coral reef fisheries, this was dependent upon a log transformation of human population densities, producing a variant of the Schaefer model (e.g. Koslow et al. 1994) such that:

Coral reef fisheries yield = $af + bf\ \log_{10}f$

Where f = human population density•km^{-2} coral reef.

Relationships between CPUE, human population density and exploitation status were also explored using General Linear Models with CPUE as the dependent variable, human population density as a covariate and exploitation status as a fixed factor. Non-significant variables were removed by sequential backwards deletion.

Island nations were then grouped into one of three groups according to their individual exploitation status: fully- and over-exploited islands (Group 1); under-, fully-, over-exploited and collapsed islands (Group 2); and under-, fully- and over-exploited islands (Group 3). MSY's were then calculated for each group using the above method, and resulting MSYs were tested for their sensitivity to the removal of the extremely high yielding Sri Lankan coral reef fishery (56 mt•km^{-2}•yr^{-1}).

Relationships between mean coral reef fisheries yields per island, human population density and exploitation status were explored using general linear models with yield as the dependent variable, human population density as a covariate and exploitation status as a fixed factor.

Finally, we plotted the relationship between the percentages of islands fishing unsustainably (i.e. above maximum sustainable yield) across a range of theoretical maximum sustainable yield estimates.

Results

For the 49 island nations considered here, coral reef fisheries yields averaged 6.4 mt$\bullet$km$^{-2}\bullet$yr^{-1} (± 1.5 SE) but ranged widely from 0.1 – 56.2 mt$\bullet$km$^{-2}\bullet$yr^{-1} reported by Marshall Islands and Sri Lanka, respectively. Human population densities per unit area of reef also varied greatly and ranged from 11 to 28,292 people$\bullet$km^{-2} coral reef (Marshall Islands and Sri Lanka, respectively), with a mean of 1836 people$\bullet$km^{-2} coral reef (± 678.8 SE) (Figure 2).

Both measures of fishing effort were strongly related to coral reef fisheries yield (Figure 3a). Yields were significantly and positively related to human population densities on islands, and differed significantly between island nations with differing exploitation status, with lowest yields on lightly populated underexploited islands and highest yields on densely populated, fully exploited islands (Figure 3a; Table 1). Collapsed islands had mostly intermediate population densities, with fisheries yields below the average for such densities, whilst the most densely populated, overexploited islands reported yields consistently in excess of the average for that density (Figure 4).

Table 1. *Summary of a general linear model testing the relationship between coral reef fisheries yields, human population density (people•km^{-2} coral reef) and fisheries exploitation status for 49 island coral reef nations. Coral reef fishery yield estimates represent mean landings of fish taxa reported to the Food and Agricultural Organisation from 1997 – 2001*.

Source		*df*	F	P
(a)	Exploitation status	3	5.51	0.003
(b)	Human population density	1	13.90	0.01
	a x b	3	8.23	0.001
	Error	41		

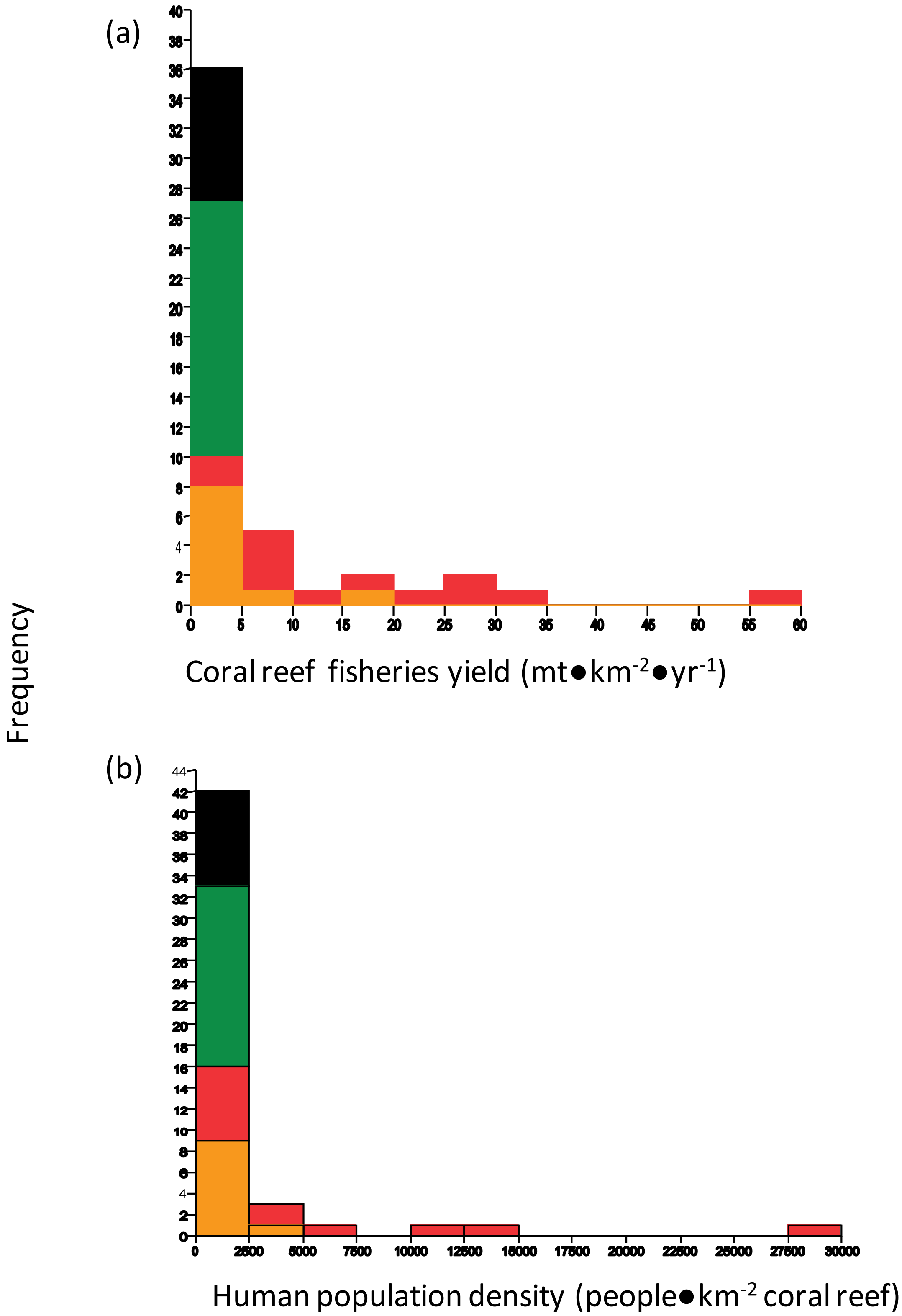

Figure 2. *Frequency distributions of (a) coral reef fisheries yields and (b) human population densities of island nations with reef fisheries of differing exploitation status (red = over-, orange = fully-, green = under-exploited, black = collapsed).*

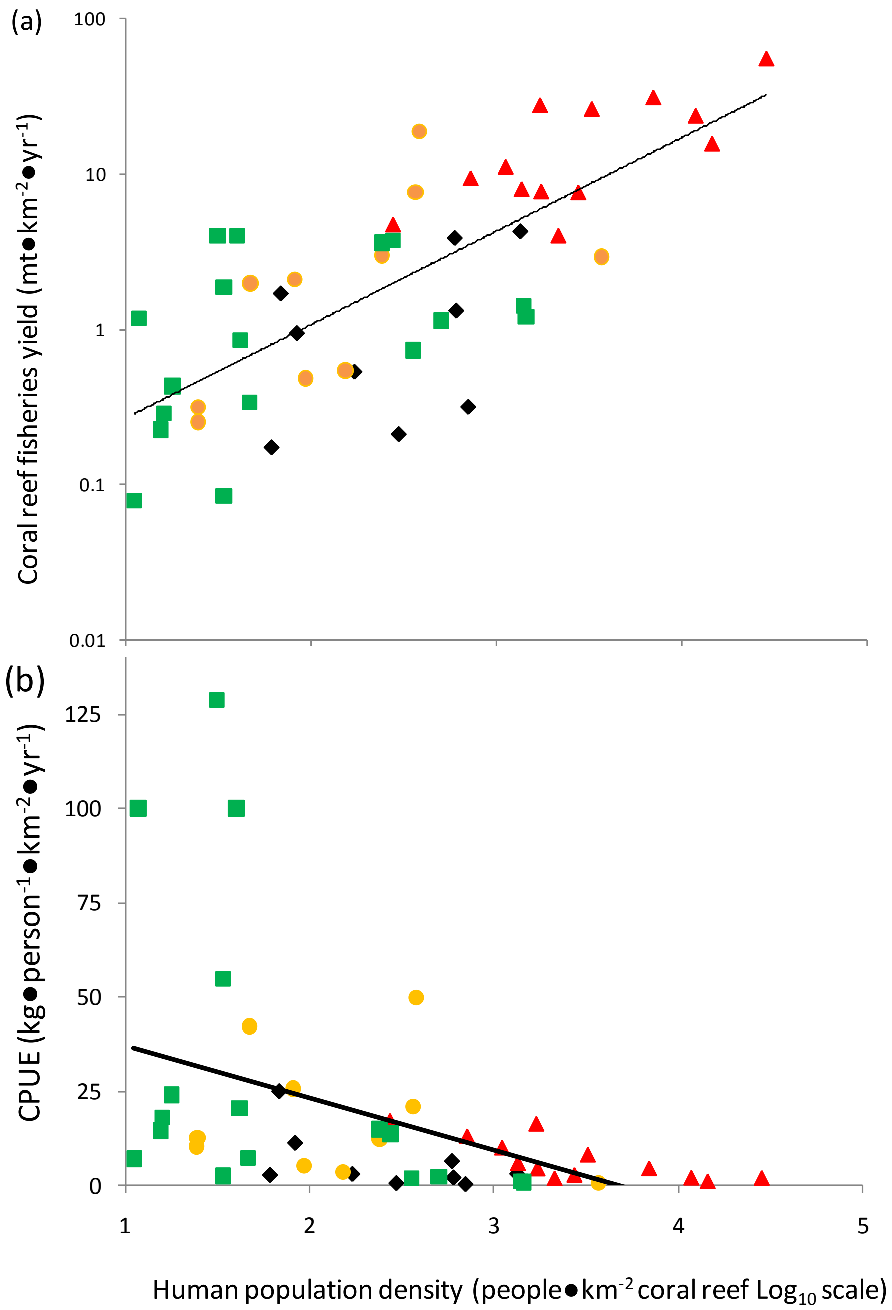

Figure 3. *Relationships between human population density and (a) coral reef fisheries yield ($Log_{10}y = 0.60*log_{10}x – 1.17$; $r^2 = 0.55$, $p < 0.0001$); and (b) catch per unit effort, CPUE ($y = 0.05 – 0.02*log_{10}x$; $r^2 = 0.45$, $p = 0.001$) for 49 island coral reef nations with coral reef fisheries of differing exploitation status (red triangles = over-, orange circles = fully-, green squares = under-exploited, black diamond's = collapsed). Coral reef fishery yield estimates represent mean landings of fish taxa reported to the Food and Agricultural Organisation from 1997 – 2001.*

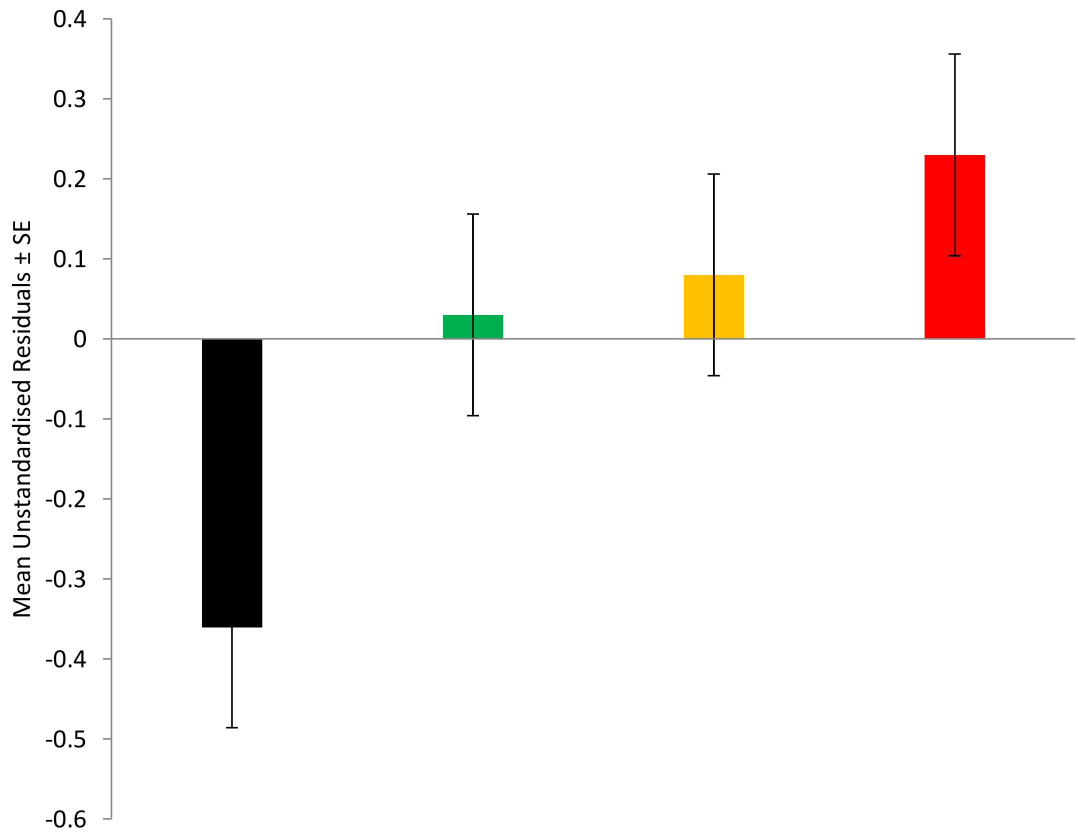

Figure 4. *Variation among islands of differing exploitation status in coral reef fisheries yields for a given human population density (measured as residual variation of the overall relationship between human population density and coral reef fisheries yield) for 49 island coral reef nations. Red = over-, orange = fully-, green = under-exploited, black = collapsed).*

Table 2. *Summary of parameters of least squares regression surplus production models,(coral reef fisheries yield =* $af + bf\ log_{10}f$ *, where f = human population density•km^{-2} coral reef), for different combinations of reefs differing in exploitation status (U = underexploited islands, F = fully exploited islands, O = overexploited islands, and C = collapsed islands), with resulting estimates of maximum sustainable yield (MSY) and optimal fishing effort (Fmsy),* with upper and lower 95% CIs. *Models are presented including and excluding the very high-yielding Sri Lankan fishery.*

			Parameter estimates		**Upper CI**		**Lower CI**							
Model	**N**	***R^2***	***a***	***b***	***a***	***b***	***a***	***b***	***MSY***	***Upper MSY***	***Lower MSY***	***Fmsy***	***Upper Fmsy***	***Lower Fmsy***
U,F,O,C	49	0.21	0.051	-0.014	0.072	-0.006	0.030	-0.022	**9.8**	1281.350	0.077	**1704**	28292	11.00
U, F, O	40	0.22	0.054	-0.014	0.078	-0.005	0.031	-0.023	**16.090**	1577.045	0.002	**2740**	28292	11.00
F,O	23	0.26	0.033	-0.007	0.050	-0.002	0.016	-0.013	**56.054**	1162.708	-0.050	**14420**	28292	11.00

Exc. Sri Lanka			**Parameter estimates**		**Upper CI**		**Lower CI**							
Model	**N**	***R^2***	***a***	***b***	***a***	***b***	***a***	***b***	***MSY***	***Upper MSY***	***Lower MSY***	***Fmsy***	***Upper Fmsy***	***Lower Fmsy***
U,F,O,C	48	0.21	0.053	-0.015	0.074	-0.006	0.031	-0.023	**8.163**	707.246	0.077	**1344**	14420	11
U, F, O	39	0.21	0.056	-0.015	0.080	-0.005	0.031	-0.024	**12.934**	853.739	0.065	**2139**	14420	11
F,O	22	0.24	0.034	-0.008	0.052	-0.001	0.015	-0.014	**22.685**	689.867	-0.108	**6953**	14420	11

When considering all islands together, and therefore all exploitation status, catch per unit effort (CPUE) was negatively related to human population density for the 49 island coral reef fisheries considered here, although this explained only 21% of the variation in yield (Figure 3b; Table 2; F = 6.12, *df* = 2, p = 0.02). The highest CPUE occurred at lowest human population densities in the most sustainably exploited islands. The lowest CPUE occurred at the least sustainable islands with the highest human population densities (Figure 3b). However, the relationship between CPUE and human population density did not vary significantly between island nations of differing exploitation status categories, as the interaction between human population density and exploitation status was not significant (Figure 3b; F = 0.82 , *df* = 2, p = 0.49).

MSY estimates ranged widely depending upon the exploitation status of the islands included in each model (Figure 5). The highest MSY was estimated for group 1 (fully- and over-exploited islands) at 22.7 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$ with an optimal fishing effort (*Fmsy*) of 6953 $people{\bullet}km^{-2}$ coral reef. Inclusion of all exploitation status (group 2) in the model resulted in the lowest MSY estimate (8.2 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$, *Fmsy* = 1344 $people{\bullet}km^{-2}$ coral reef), and an intermediate MSY of 12.9 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$ (*Fmsy* = 2139 $people{\bullet}km^{-2}$ coral reef) was derived when collapsed islands were removed and only under-, fully- and over-exploited fisheries were included (group 3). Estimates of MSY were higher when Sri Lankan coral reef fishery yields were included (56.1, 9.8, and 16.0 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$, for groups 1 – 3, respectively).

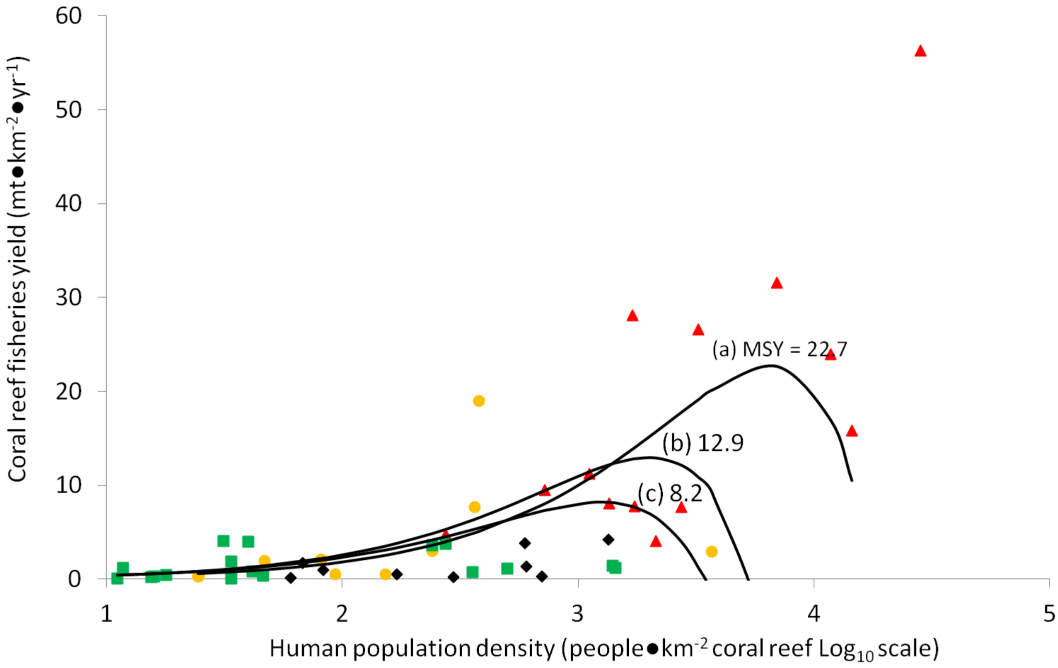

Figure 5. *Relationships between estimates of maximum sustainable coral reef fisheries yields calculated using adapted surplus production models (yield = af + bf ($log_{10}f$)), for island nations with (a) fully- and over-exploited (n = 22); (b) under-, fully-, and over-exploited (n = 39); and, (c) under-, fully-, over-exploited and collapsed (n = 48) fisheries exploitation status. Red triangles = over-, orange circles = fully-, green squares = under-exploited, black diamond's = collapsed islands. Coral reef fishery yield estimates represent mean landings of fish taxa reported to the Food and Agricultural Organisation from 1997 – 2001. Human population density extracted from United Nations Development Program report (2002). The extremely high yielding (56.2 mt•km^{-2}•yr^{-1}) Sri Lankan coral reef fishery is excluded from MSY estimations.*

The relationship between theoretical maximum sustainable yield and the proportion of islands fishing unsustainably was negative and non-linear (Figure 6). Between hypothetical MSYs of ~10 to 25 mt•km^{-2}•yr^{-1}, the percentage of unsustainable fisheries increased at a slower rate (from ~10 to 15%) than for lower values of MSY ranging from 0 – 10 mt•km^{-2}•yr^{-1}, where there were rapid increases in the percentage of unsustainably fished islands (from ~15 to 65%). The most rapid increase in the probability of unsustainable fishing occurs at ~8 mt•km^{-2}•yr^{-1}, where the non-linearity of the relationship indicates that for every further drop in MSY, the percentage of islands fishing unsustainably increases disproportionately. This concurs with Figures 3 and 5, which indicate that islands yielding > 8 mt•km^{-2}•yr^{-1} tend to have overexploited fisheries status.

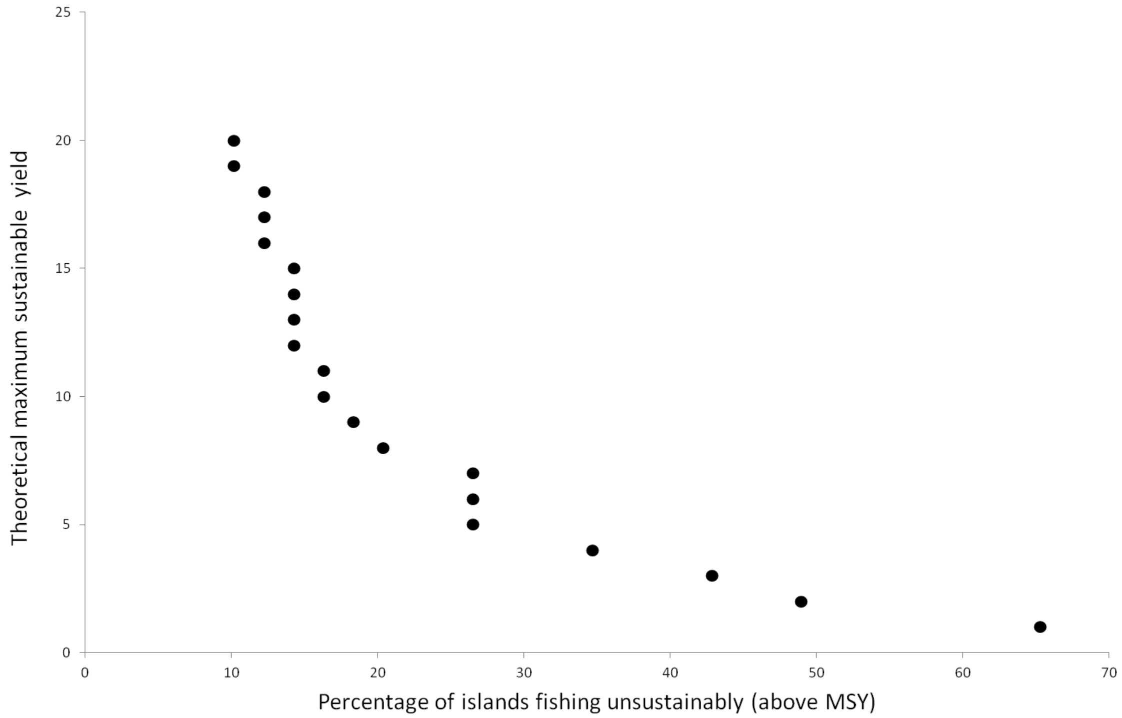

Figure 6. *Percentage of 49 island coral reef fisheries estimated to be unsustainably exploited under a range of hypothetical maximum sustainable yield estimates. Coral reef fishery yields derived from coral reef fish taxa reported to the Food and Agricultural Organisation between 1997 and 2001.*

Discussion

These analyses demonstrate the considerable variability in coral reef fisheries yields between island coral reef nations, and show that densely populated islands tend to be overexploited and high yielding, whilst sparsely populated islands tend to be underexploited and low yielding. The link between human population density, exploitation history and yield goes on to strongly influence estimates of maximum sustainable yield, and our adapted surplus production models estimate multispecies MSY for island coral reef fisheries to vary between 8.2 mt•km^{-2}•yr^{-1} (with an optimal fishing effort (*Fmsy*) of 1344 people•km^{-2} coral reef) and 22.7 mt•km^{-2}•yr^{-1} (*Fmsy* = 6953 people•km^{-2} coral reef), with an intermediate estimate of 12.9 mt•km^{-2}•yr^{-1} (*Fmsy* = 2139 people•km^{-2} coral reef), depending upon the exploitation status of coral reef fisheries incorporated into the model. The highest estimates were derived from models which contained only the most densely populated, fully- or over-exploited islands, whilst the lowest estimates resulted from models which contained only the least populated, under-exploited or collapsed islands. However, this study suggests that yields > ~8 mt•km^{-2}•yr^{-1} tend to be reported from islands which are considered to be overexploited, and thus MSYs approaching or exceeding 8 mt•km^{-2}•yr^{-1} may lead to greater risk of unsustainability. The intermediate MSY of 12.9 mt•km^{-2}•yr^{-1} was derived when collapsed islands were removed and only under-, fully- and over-exploited fisheries were included (group 3). This may be an appropriate estimate of MSY given that landings from collapsed island fisheries are low yielding (because they are unsustainably fished) and therefore negatively bias MSY estimates (i.e. lead to underestimating MSY). Conversely, the inclusion of extremely high yielding Sri Lanka into the models may lead to overestimates of MSY for coral reef fisheries (56.1, 9.8, and 16.0 mt•km^{-2}•yr^{-1}, for groups 1 – 3 respectively). However, Figures 3 and 5 show that islands yielding > ~8 mt•km^{-2}•yr^{-1} tend to have overexploited fisheries status, suggesting MSYs of 12.9 mt•km^{-2}•yr^{-1} may be too high in the context of island coral reef fisheries. This demonstrates that MSYs calculated using fisheries statistics from both extreme yields and high yielding over-exploited islands must be viewed with caution, as the yields, whilst large (as they are heavily overfished by the greatest population densities), are likely to be unsustainable and heading towards collapse. This interpretation is supported by the prevalence of collapsed islands at intermediate human population densities, as their distribution suggests that degradation of coral reef fisheries can occur at lower levels of yield and effort than reported here. Yields from collapsed islands range from between 0.17 to 4.24 mt•km^{-2}•yr^{-1} in the British Virgin Islands and the Comoros respectively, with population densities ranging from 61 to 1344 people•km^{-2} coral reef. Evidence of overexploitation of island fisheries with lower population densities and fisheries yields, suggests that MSY for coral reefs could be much lower than these analyses predict, and points to the difficulties of applying a single MSY to islands with coral reefs subject to vastly differing socioeconomic threats such as fishing pressure, coastal development and habitat degradation. Given the predominance of collapsed islands at intermediate population densities, the higher yields observed in the densely populated, over exploited islands may well be inaccurate or artificially inflated by the inclusion of molluscs and crustaceans, such as lobster. This would in turn have overestimated the MSY values generated here. The wide range of MSY estimates demonstrates the difficulty in calculating an exact MSY appropriate for every island, but also indicates the importance of including islands of every exploitation status into the model. Excluding collapsed islands (to generate our intermediate MSY) leads to overestimates of MSY, which could be detrimental to island reef fisheries if adhered to. The MSY of 12.9 mt•km^{-2}•yr^{-1} is closer in value to previously reported estimates by Dalzell and Adams (1997) of 16.4 mt•km^{-2}•yr^{-1} at 581 people km^{-2}, and by Halls et al (2006) of 15 mt•km^{-2}•yr^{-1} at 640 people km^{-2}, although optimal fishing effort for the coral reef islands reported here is 3.7 and 3.3 times greater than that suggested by Dalzell and Adams (1997) and Halls et al (2006), respectively. The differences between our estimates and those of Dalzell and Adams (1997) and Halls et al (2006) are likely a result of the differing scale and quality of data sources used. While the FAO provide the most extensive global time series of fishery statistics available, yield estimates for island coral reef fisheries reported here are likely to be conservative owing to well documented under-reporting of multispecies, multi-geared fisheries in remote tropical regions (Dalzell 1998, Sadovy 2005, Newton et al. 2007). Extensive underreporting of coral reef species has been shown through reconstructions of landings in several Indo-Pacific islands as well as small-scale fisheries in Tanzania and Mozambique (Zeller et al. 2006, Jacquet et al. 2010). Using the surplus production model method to generate an MSY for hypothetically large yields would likely have led to commensurately larger MSYs (as demonstrated by removing the extremely high yielding island of Sri Lanka from the analyses), which may have been more in line with the estimates of both Halls et al. (2007) and Dalzell and Adams (1997). However, given due consideration to fisheries exploitation status, it may be argued that higher yields would not be sustainable in the long term. Equally, if our estimates are conservative, yields reported here would have likely been achieved at lower human population densities, suggesting that over-exploitation would occur before populations reached ~1000 people$\bullet$km^{-2} coral reef.

Estimates of MSY reported here are approximate, not least because of the equilibrium assumptions behind the model fitting method, i.e. that observed catches are sustainable at observed levels of effort (Hilborn and Walters 1992). The model assumes that all species respond similarly to exploitation, yet larger, less productive species are known to be more susceptible to fishing, and may be quickly overexploited at effort levels required to maximise yield in a multispecies assemblage (Jennings et al. 1999). Equally, the concept of maximum sustainable yield is less appropriate for short-lived, highly fecund species for which yield is more dependent upon recruitment, and therefore other environmental factors that can strongly influence recruitment (Hilborn and Walters 1992). Also, whilst human population density represents a reliable indicator of dietary reef fish requirement per island, is does not accurately reflect the number of active fishers on the ground. It also does not account for the vast variation in gears, gear numbers, fishing intensity (number of fishing trips per fisher), and skill levels which characterises multigeared, multispecies coral reef fisheries. Similarly, whilst we used the most up to date information regarding coral reef area per island, we cannot claim that each island reports yields from fishing grounds fitting the same description. Furthermore, coral reef fisheries are dynamic and many other contributory factors likely affect the relationship between human population density and yield, such as island size and geomorphology, as well as wide ranging socio-economic factors which influence fisher behaviour (eg. Dalzell 1996, Cinner and McClanahan 2006, McClanahan 2006).

This study demonstrates that the highest yielding island coral reef nations have the greatest human population densities, and tend to be overexploited, whereas islands with sparser human population densities tend to have lower yielding coral reef fisheries and be underexploited. Despite the upward trend in yield along the human population gradient (Figure 3a), the distribution of exploitation status suggests the highest yielding fisheries are unsustainable. The range of MSY estimates described here encompasses previous estimates (Halls at al. (2006) and Dalzell and Adams (1997)) but varies considerably as a consequence of extremely variable yields between islands. Differences from previous estimates may also be a result of the wider geographic scale of our data, which incorporate both densely populated Caribbean and Indian Ocean islands, and the less populated Pacific islands which make up the majority of the above studies. Furthermore, datasets used in Dalzell (1996) differ in timescale by 20 years in some cases, ranging from 1977 to 1995, whereas our data represent more recent landings from 1997 to 2001. Rapid human population growth and increasing dependency on coral reef fisheries may influence the differences in reported yields, and therefore MSY estimates.

Whilst MSY is an important tool in the sustainable use of coral reef fisheries, these analyses demonstrate the complexity involved in estimating a reliable value of MSY, and provide an insight into the potential pitfalls in adopting MSY as a sole management option. Principally, as seen here, overestimation of MSY could have an adverse effect on sustainable fishing. There are, however, alternative methods to reduce catch and effort, such as restrictions on numbers of people or boats, time spent fishing, areas closed to fishing, gears, and species and sizes of fishes allowed to be caught (McClanahan, 2006). It is generally held that combinations of these measures are required to sustain coral reef fisheries, subject to appropriation and enforcement success (Acala et al, 2006).

These analyses suggest that yields from coral reefs which exceed ~8 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$ tend to indicate overexploitation, and therefore that an MSY of 8.2 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$ is too optimistic. Previous estimates of 5 $mt{\bullet}km^{-2}{\bullet}yr^{-1}$ which have been used in other analyses, such as Newton et al (2007), may be a better approximation, although it is evident that MSY will vary according to the history or exploitation status of component fisheries. This in turn, will vary according to other attributes such as island size, reef area, species richness, and the MTL of catch, again indicating the need for multiple and context-specific reef management measures.

Sri Lankan fisheries yields were extremely large, principally because of the extremely high human population density, but arguably because the Exclusive Economic Zone (EEZ) or fishing area of Sri Lanka is larger than its land area, with coastal fisheries providing ~70% of the annual fish production (Samaranayake 2003). The introduction of motorised crafts and synthetic nets in the 1990’s is thought to have revolutionised Sri Lankan fisheries, which have expanded from traditional fishing grounds in lagoons, and inshore waters, extending their operating radius to exploit species on the outer ridge of the continental shelf.

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Chapter 4

Linking fisheries yield and economic development within island coral reef nations

Conch fisherman, Anguilla

Abstract

Overfishing severely threatens coral reef ecosystems which provide vital goods and services for hundreds of millions of dependent people in the tropics. Human population density is a major driver of overexploitation and the associated degradation of coral reef ecosystems. Given strong evidence linking human population density and coral reef fisheries yields, it is difficult to disentangle other drivers which are likely to influence levels of resource exploitation on coral reefs. For 49 island coral reef nations worldwide, we explore how human population density and the associated influence on coral reef fisheries yields and fisheries sustainability (measured as fisheries exploitation status) vary in relation to geographic location (oceanic basin), land area (island size), reef area: land area (as a proxy for reef dependence), and gross domestic product (GDP). The most densely populated islands tend to have overexploited fisheries exploitation status and are generally found within the Atlantic and Indian Ocean basins. They tend to be larger islands, with smaller reef area: land area ratios (and arguably greater *per capita* dependence on reef resources), and have higher levels of socioeconomic development (GDP). Conversely the least densely populated islands with underexploited fisheries exploitation status tend to be found within the Pacific Ocean, have greater land areas and reef area: land area ratios, and lower levels of socioeconomic development. Economic development of island coral reef nations globally may therefore be associated with increased extractive practices on coral reefs, as densely populated islands with high coral reef fisheries yields and unsustainable fishing practices tend to be wealthier, whilst the least densely populated islands, characterised by low yields and sustainable fishing practices tend to be poorer. At broad geographic scales, these insights provide evidence that economic development plays a role in the way different societies utilize coral reefs, and suggests that

increasing affluence does not necessarily lead to improved environmental quality for coral reefs. Sustaining coral reef fisheries for future generations requires a greater emphasis on understanding how socio-economic factors influence resource use, and how such factors link with ecological impacts on coral reefs.

Fisher residence, Sandy Ground, Anguilla

Introduction

Coral reef fisheries are critical to the well-being of millions of tropical people, but are severely endangered due to overexploitation, habitat degradation and rapid human population growth (Moberg and Folke 1999, Newton et al. 2007, Wilson et al. 2010). Overfishing on coral reefs has detrimental effects on the structure, function and resilience of reef fish communities (Friedlander and DeMartini 2002, Newton et al. 2007, Chapter 2). However, knowledge surrounding the influence of other socio-economic characteristics on patterns of extraction and degradation of coral reef resources remains poor. Conserving coral reef ecosystems, and managing the growing fisheries crises in the tropics, is likely to require a greater emphasis on understanding relationships between socio-economic drivers and resource use on coral reefs (Newton et al. 2007, Cinner et al. 2009, Chapter 3).

Clear relationships between human extractive practices and the degradation of coral reef ecosystems have been established in multiple studies worldwide (eg. Friedlander and DeMartini 2002, McClanahan et al. 2008, Mora 2008). Deleterious shifts in the structure of reef communities as a result of fishing have been recognized through comparative analyses along human population gradients, between protected and unprotected areas, and populated versus unpopulated coral reefs (Roberts et al. 2001, Friedlander and DeMartini 2002, Dulvy et al. 2004). Ecological Footprint analyses, which represent the ratio of coral reef fisheries' consumption (landings) to sustainable production, have also shown that more than half of island nation coral reef fisheries for which relevant data are available are overexploited as a result of human population pressures, and that these findings are consistent with another measure of fisheries sustainability; fisheries exploitation status (Newton et al. 2007). Fisheries exploitation status has been described as a qualitative estimate of sustainability defined for island coral reef fisheries, generated through combined analyses of localised literature, datasets and communications with fisheries officers (Newton et al. 2007). Exploitation status represents a stage in the development and demise of a coral reef fishery through time, from under- to fully-, to over-exploited and collapsed (Newton et al. 2007, Chapter 3). However, there remains a need to explore further influences on island coral reef fisheries yields, such as socio-economic factors which may determine patterns of extraction on coral reefs.

There are few studies which consider socio-economic factors beyond human population densities on coral reef resource use. For example, proximity to markets in Papua New Guinea was shown to be a better indicator of overfishing than human population size, whilst inequality of income was linked to overexploitation of coral reefs in Mauritius (Sobhee 2004, Cinner and McClanahan 2006). A recent study has suggested that the relationship between socio-economic development and coral reef fisheries may follow a U-shaped environmental Kuznets curve, whereby increasing socio-economic development results in resource degradation until a point where environmental quality improves as a result of increased societal affluence and demand (Arrow et al. 1995, Grossman and Krueger 1995). One study focussed upon five countries within the Indian Ocean, and showed that targeted fish biomass in fished areas was best explained by a U-shaped relationship with local-scale socio-economic development, whereas human population density was only weakly negatively related to fish biomass (Cinner et al. 2009).

Coral reef fisheries yields may also vary geographically, both as a consequence of differences in densities of human populations, but also potentially through differing coral reef species richness between major ocean basins (Mora et al. 2003). Largely owing to the evolutionary history of isolation and loss of taxa in the Caribbean basin, coral reef diversity is greatest in the central Indo-Pacific ‘Coral Triangle’ and decreases with increasing distance from the Indo-Australian archipelago (Bellwood and Wainwright 2002, Hughes et al. 2002, Plaisance et al. 2011). It has been argued that the markedly differing species richness and taxonomic composition of coral reef functional groups - and therefore, reduced functional redundancy and resilience - between the Caribbean region, and those of the Indo-Pacific, may render Caribbean reefs more susceptible to human impacts, thereby reducing coral reef productivity and potential fisheries yields (Bellwood et al. 2004).

Species richness within tropical fish communities has also been shown to vary as a consequence of habitat availability, both within the Indo-Pacific, and the Caribbean region (Bellwood and Hughes 2001, Sandin et al. 2008). Bellwood and Hughes (2001) found the availability of shallow water habitat explained much of the variation in regional-scale reef biodiversity across the Indian and Pacific Oceans, whilst Sandin et al (2008) showed how the diversity of reef-associated fishes increased strongly with both increasing island area, and decreasing isolation from other islands. Island area is thought to reflect both habitat availability and habitat diversity, such that larger islands ought to have a greater range of habitats suitable for reef fishes, such as mangroves, estuaries and sea grass beds, than smaller islands with comparable total reef areas. Sandin et al (2008) found reef area to be a poorer predictor of species richness than land area, and suggested this reflects the ability of certain reef species to shift to less preferred habitats such as rocky reefs. If species richness, and therefore functional redundancy, confers greater resilience in tropical reef fish communities, then yields from larger islands (with greater species richness) may reflect this.

In the aforementioned Ecological Footprint analysis of island coral reef fisheries (Newton et al. 2007), eleven potential correlates of coral reef productivity, and therefore fisheries sustainability were considered. Besides human population density and coral reef area, these correlates included continental shelf area, coral reef health, mangrove forest area, oceanic primary production, maximum elevation, average precipitation latitude, and fish and coral species richness. The two most significant predictor variables of Ecological Footprint - or fisheries sustainability - were human population density and coral reef area. Here, using a database of coral reef fisheries landings and fisheries exploitation status for the same 49 island coral reef nations, the variation between islands in human population densities per reef area (termed human population density from here on in) in the Atlantic, Indian, and Pacific Ocean basins, and between islands with collapsed, fully-, over- and under-exploited fisheries exploitation status are explored. In addition, the influence of Gross Domestic Product Purchasing Power Parity (GDP), an indicator of island wealth, island size, and the proportion of reef area relative to land area available to each island, are also investigated.

Methods and materials

Island countries and territories were selected for study on the basis of three criteria: 1) presence of a coral reef as defined in Spalding et al (2001); 2) availability of FAO fishery landings for 1997-2001; and, 3) evidence of a coral reef fishery. Coral reef fishery landings for island nations and territories (hereafter termed islands) were calculated from fisheries statistics reported to the Food and Agriculture Organisation (FAO) FISHSTAT database from 1997 – 2001 (http://www.fao.org/). For each island, landed weights of fish were categorized according to the most likely source ecosystem (coral reef, demersal, ocean, freshwater, and estuarine) and human use (consumed or destined for the aquarium trade) (Appendix A, table 1.). Only coral reef-associated species, i.e. those living predominantly on or near coral reef ecosystems and deriving energy from coral reefs and associated habitats for a major proportion of their lifespan, were retained for analysis. Definitions and categorizations of ecosystem and human use were provided in FishBase (Froese 2007). The coral reef-derived component of the landings was extracted for each of the 49 islands and the average was calculated from 1997 – 2001 and expressed as $mt \bullet km^{-2} \bullet yr^{-1}$.

For each island, coral reef area (extracted from Spalding et al (2001) and human population densities (extracted from the United Nations Development Program report (2002)) were used to calculate $people \bullet km^{-2}$ coral reef, termed human population density from here on in.

Land area for each island was extracted from the CIA World Fact book, https://www.cia.gov/library/publications/the-world-factbook, and expressed as km^2. The relative proportion of coral reef area relative to land area per island, expressed as a percentage, was calculated as below:

$$\underline{Coral\ reef\ \ area \div (coral\ reef\ \ area\ + total\ land\ area) \times 100}$$

Data on the number of MPAs was extracted from http://www.wri.org/project/earthtrends/, and expressed as the absolute number of MPAs, the number of MPAs per coastline area, and the number of MPAs per reef area.

Fisheries exploitation status were taken from Newton et al (2007). Fisheries exploitation status represents a qualitative estimate of sustainability and a ‘snapshot’ view of a particular stage in the development and demise of a coral reef fishery through time, from under- to fully-, to over-exploited and collapsed. Primary and secondary literature pertaining to the status of coral reef fish and fisheries resources were collated and searched, along with global and regional fisheries databases. This information was used along with opinions of local scientists and fisheries officers in order to describe the four stages of fisheries development (details in Newton et al. 2007). Islands were conservatively scored as under- or fully-exploited if there was only localized evidence of overfishing. Over-exploited islands with an Ecological Footprint < 1 were given the collapsed status. See Appendix B, figure 1 for a global map of island coral reef nations and their respective exploitation status.

Gross domestic product (GDP) or value of all final goods and services produced within a nation in a given year, expressed as GDP at purchasing power parity (PPP) was extracted from the CIA World Fact Book (https://www.cia.gov/library/publications/the-world-factbook) for the year 2008 (which was the year closest to the other variables considered in this analysis). A nation's GDP at purchasing power parity (PPP) exchange rates is the sum value of all goods and services produced in the country valued at prices prevailing in the United States. This is the preferred economic measure for consideration of *per capita* welfare and for comparisons of resource use across countries.

In order to assess and describe the differences among island nations, the variation in mean human population density and total reef area among exploitation status groups and ocean basins were compared using one-way ANOVA analyses and Kruskal-Wallis tests. Secondly, general linear models were constructed to explore the influence of human population density and fisheries exploitation status on GDP. Non-significant variables were removed by sequential backwards deletion. General linear models were also used to explore relationships between human population density, island size, and exploitation status, as well as the relationship between human population density, the proportion of reef area relative to land area, and exploitation status. Again, non-significant variables were removed by sequential backwards selection.

Results

For the 49 island nations considered here, human population densities per km^{-2} coral reef varied greatly and ranged from 11 – 28,292 people•km^{-2} coral reef (Marshall Islands and Sri Lanka, respectively), with a mean of 1836 people•km^{-2} coral reef (± 678.8 SE), whilst mean coral reef fisheries yield for the 49 islands was 6.4 mt•km^{-2}•yr^{-1} (± 1.5 SE) (Chapter 1, Figure 1). Coral reef fisheries yields were very wide-ranging, with the lowest yields reported by the Marshall Islands (0.1 mt•km^{-2}•yr^{-1}), whilst the highest yields (56.2 mt•km^{-2}•yr^{-1}) were recorded in Sri Lanka.

The land area (size) of each island also varied greatly, from 12 – 581,540 km^2 (Tokelau and Madagascar, respectively), with a median of 717 km^2 (mean of 33,414.78 km^2 (± 15,913.19 SE)). Total reef area per island varied from 50 to 25,060 km^2, with a median of 570 km^2 (mean of 2404.08 km^2 (± 635.75 SE)), whilst the proportion of reef area relative to land area available to each island ranged widely from 0.38 – 97.12 % (Madagascar and the Marshall Islands, respectively).

Mean GDP for the 49 islands in 2008 was US$14.93 billion (±7.11 SE), and varied considerably from US$1.5 million for Tokelau in the South Pacific to US$324.4 billion for the Philippines. However, 42 of the 49 islands had estimated GDP values lower than US$10 billion (Figure 1).

Table 1. *Summary of a general linear model of the influence of human population density (people • km $^{-2}$ • coral reef, and fisheries exploitation status, on economic development (GDP purchasing power parity, \$ Billion US log $_{10}$ scale), for 49 island coral reef nations.*

Source	*df*	F	P
Human population density	1	40.13	0.01
Error	47		

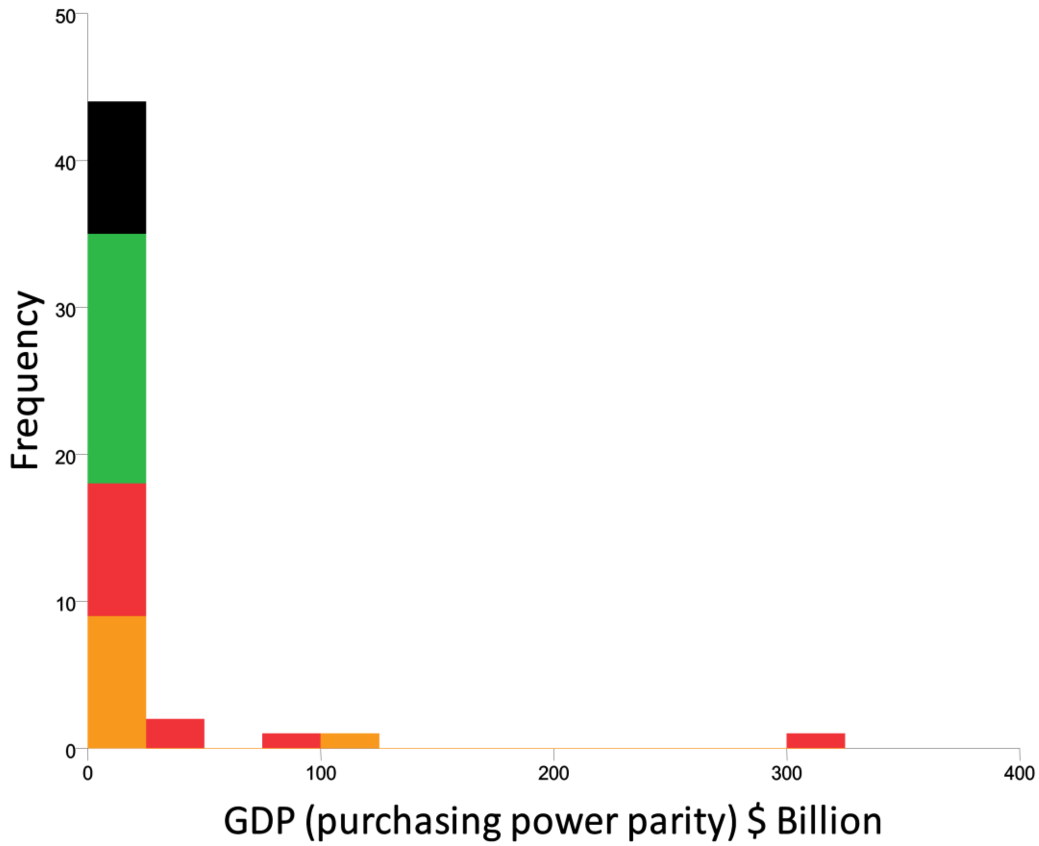

Figure 1. *Variation in GDP purchasing power parity (\$ Billion US log $_{10}$ scale) among 49 island coral reef nations of differing reef exploitation status (red = over-, orange = fully-, green = under-exploited, black = collapsed). GDP purchasing power parity estimates taken from CIA World fact book, 2008.*

Mean human population density varied significantly between islands with differing fisheries exploitation status groups, and between islands located in the Atlantic, Indian, and Pacific Ocean basins, whereby overexploited islands were significantly more populated than their under-, fully – and collapsed island counterparts ($F_{3, 45} = 16.47$, $p < 0.0001$; Figure 2), and Pacific islands were significantly less populated than islands found within both the Indian, and Atlantic Ocean basins ($F_{2, 46} = 11.93$, $p < 0.0001$; Figure 3).

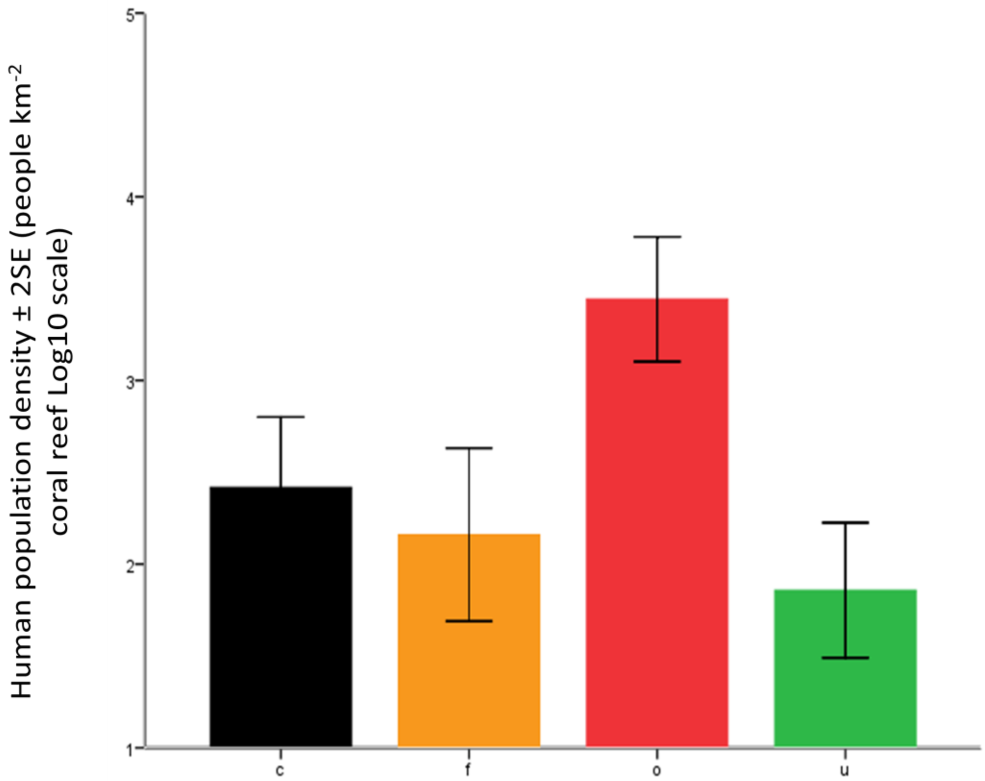

Figure 2. *Mean human population density (people •km^2 coral reef Log$_{10}$ scale) for 49 coral reef islands with collapsed (black, n = 9), fully-exploited (orange, n = 10), over-exploited (red, n = 13), and underexploited (green, n = 17) coral reef fisheries exploitation status.*

Human population density per km^{-2} coral reef was positively related to economic development (GDP) for the 49 island coral reef nations, with islands with denser human populations tending to be wealthier (Figure 4). Wealthier islands also tended to have overexploited fisheries exploitation status, whilst less wealthy islands tended to have underexploited fisheries exploitation status (Figure 4). Overexploited fisheries were mainly found on islands with human population densities greater than ~1000 people•km^{-2}•coral reefs, and GDP values of greater than US$ 10 billion, whilst underexploited fisheries tended to be on islands with human population densities less than ~1000 people•km^{-2}•coral reef, and GDP values of less than US$ 10 billion. However, islands with fully exploited and collapsed fisheries tended to have intermediate human population density and GDP values of ~10 – 1000 people•km^{-2}•coral reef and ~US$ 0.1 – 10 billion, respectively. Consequently, whilst GDP was strongly correlated with human population densities per island, this relationship did not vary significantly between the four exploitation status categories (table 1). GDP per capita values were also considered with respect to human population densities, and the resulting analyses did not differ. GDP per capita was strongly positively correlated with human population densities, such that islands with high population densities tended to have higher per capita GDP values (r^2 = 0.67, p = 0.01, n = 49).

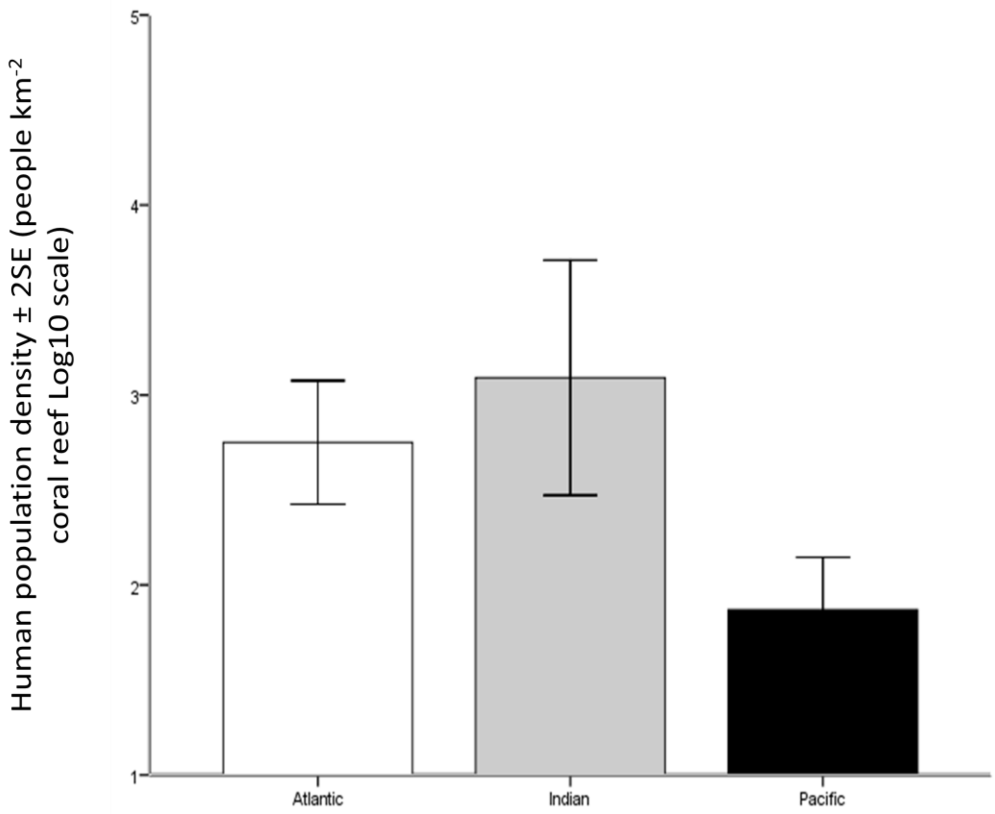

Figure 3. *Mean human population densities (people •km^2 coral reef Log$_{10}$ scale) for 49 coral reef islands located in the Atlantic (white, n = 18), the Indian (grey, n = 10), and the Pacific (black, n = 21) ocean basins.*

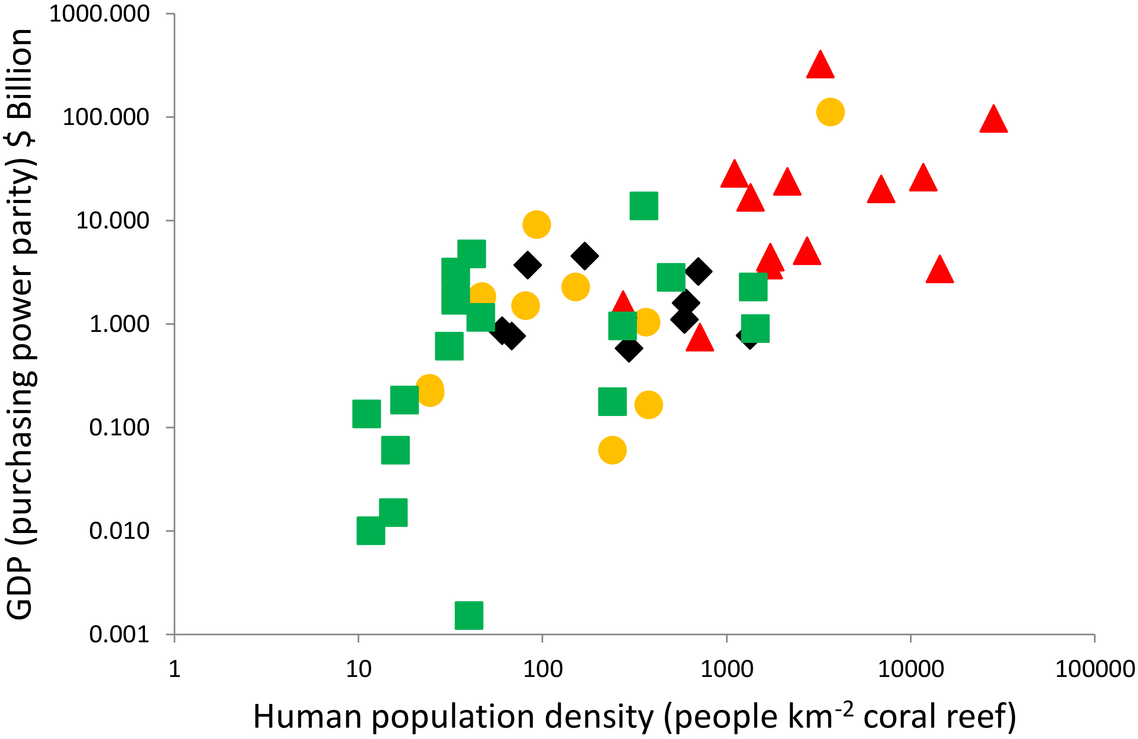

Figure 4. *Relationship between human population density per km^{-2} coral reef and economic development (GDP power purchasing parity, $ Billion US log$_{10}$ scale) for 49 island coral reef nations, across four fisheries exploitation status. Colours and shapes indicate fishery exploitation status of each island nation: under-exploited (green squares, n = 17), fully-exploited (orange circles, n = 10), over-exploited (red triangles, n = 13) and collapsed (black diamonds, n = 9).*

The density of human populations on each island varied strongly and positively with island size (land area) with smaller islands having less dense human populations compared with large islands that had high human population density (Figure 5). This relationship also varied systematically with exploitation status, with larger islands with denser human populations tending to have over-exploited fisheries exploitation status (Table 2, Figure 5). Islands with collapsed, and underexploited fisheries exploitation status were predominantly less than 1000 km^2, with human population densities < 1000 people• km^2•coral reef, whilst overexploited islands were all >1000 km^2 with human population densities >1000 people•km^2•coral reef. Fully exploited islands ranged greatly in both land area, and human population densities (~10 - 100,000 km^2, and ~10 - 10,000 people•km^2•coral reef respectively).

Table 2. *Summary of a general linear model testing the variation in human population density (people • km $^{-2}$ • coral reef) in relation to land area (km ^{2}) and fisheries exploitation status for 49 island coral reef nations.*

Source	df	f	p
Land area	1	4.47	.040
Exploitation status	3	13.01	<0.0001
Error	44		

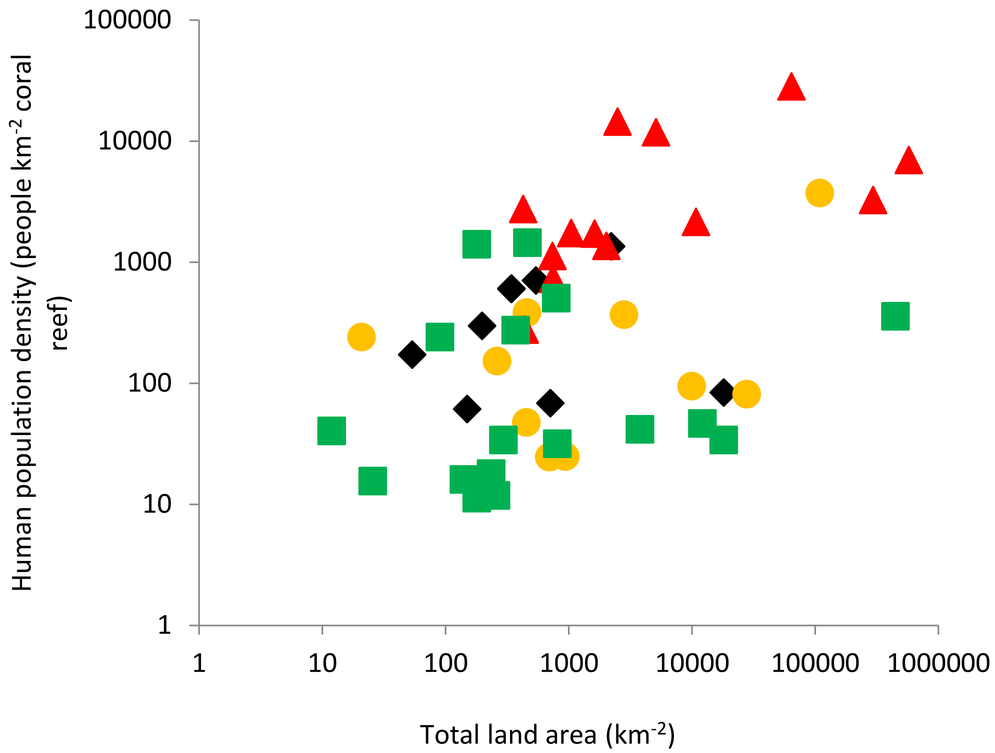

Figure 5. *Relationship between total land area (km^2) and human population density (people •km^2 coral reef) for 49 island coral reef nations across four fisheries exploitation status. Colours and shapes indicate fishery exploitation status: under-exploited (green squares, n = 17), fully-exploited (orange circles, n = 10), over-exploited (red triangles, n = 13) and collapsed (black diamonds, n = 9).*

There was no significant difference between the total area of coral reef available to islands within the Atlantic, Indian and Pacific Ocean basins, (X^2_2 = 0.44, p = 0.93), however total reef area did vary significantly between islands within differing exploitation status groups, (X^2_3 = 9.67, p = 0.02), with fully-exploited islands having significantly greater reef areas that their under-, over-exploited and collapsed island counterparts (fully-exploited islands mean = 2425.34 km^2 ± 7403.0 SE; collapsed islands mean = 202.58 km^2 ± 611.0 SE, over-exploited islands mean = 592.32 km^2 ± 1516.92 SE, under-exploited islands mean = 407.49 km^2 ± 1091.18 SE).

There was a negative relationship between the ratio of reef area: land area and human population density, with larger islands with denser human populations (Figure 6) tending to have smaller reef area: land area ratios. This relationship also varied systematically with exploitation status, whereby densely populated, overexploited islands had the smallest reef area: land area ratios (Table 3, Figure 6). All of the overexploited islands had less than ~45% reef area: land area, whilst ratios for fully- and under-exploited islands varied greatly from ~5 - 97% reef area: land area. Reef area: land area also varied greatly for islands with collapsed status, from ~15 - 85%.

Table 3. *Summary of a general linear model testing the variation in human population density (people • km $^{-2}$ • coral reef) in relation to reef area: land area (%) and fisheries exploitation status for 49 island coral reef nations.*

Source	df	f	p
Reef: Land area (%)	1	39.44	<0.0001
Exploitation status	3	13.01	<0.0001
Error	44		

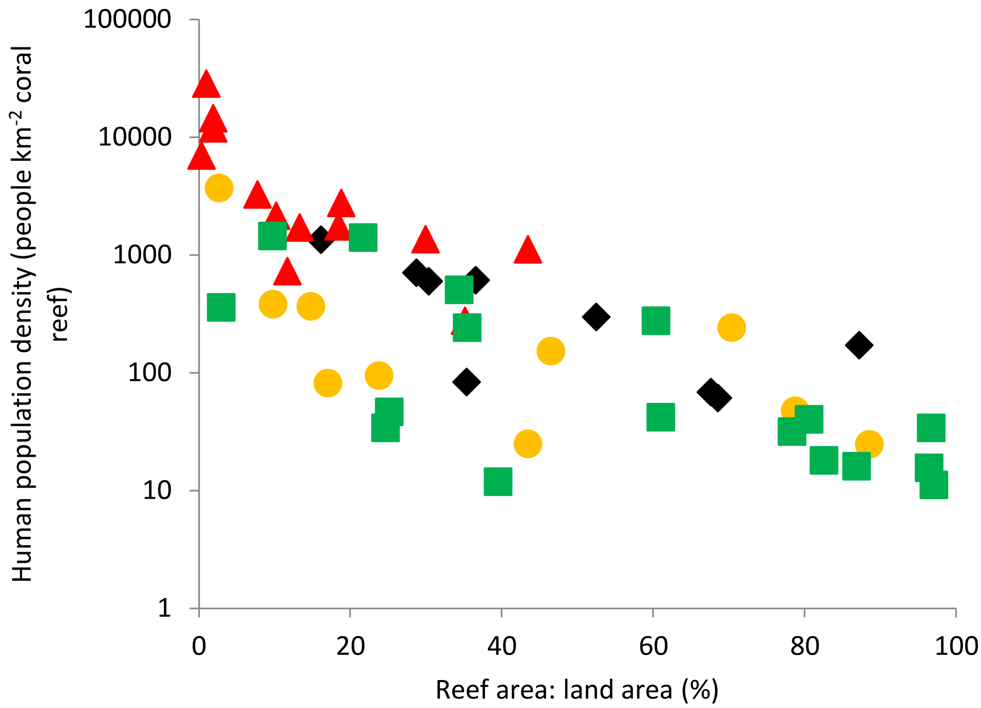

Figure 6. *Relationship between reef area: land area (%) and human population density (people •km^{2} coral reef) for 49 island coral reef nations across four fisheries exploitation status. Colours and shapes indicate fishery exploitation status: under-exploited (green squares, n = 17), fully-exploited (orange circles, n = 10), over-exploited (red triangles, n = 13) and collapsed (black diamonds, n = 9).*

Discussion

Throughout the world, coral reef island nations vary greatly in the extent to which their reef fishery resources are exploited, with densely populated islands exploiting these resources to a greater extent. Here we describe how islands differing in population density and fishery exploitation status also vary geographically, biologically, and socioeconomically. The most overfished islands, with dense human populations and overexploited fisheries exploitation status, tend to be found within the Indian and Atlantic Ocean basins, whilst the least densely populated islands and less exploited fisheries are found within the Pacific Ocean. The most densely populated, over-exploited islands are also wealthier, with significantly higher GDP values than their less populated, underexploited island counterparts. Wealthier islands with high human population densities and overexploited fisheries also tend to be larger, with smaller ratios of reef area: land area, and therefore, arguably greater *per capita* dependence on coral reef resources.

Given the extensive global scale of the study, it was interesting to find that islands with the highest human population densities and most overexploited coral reef fisheries were found within the Caribbean and the Indian Ocean islands, especially as there were no significant differences between the area of coral reef available between islands in differing ocean basins, which might artificially inflate human population densities per unit area of coral reef. If coral reef fisheries yields were influenced by geographic variation, it might be expected that those of the Caribbean were significantly lower than those of the Indian and Pacific Ocean basins on account of regional differences in the species richness, functional composition and resilience of reef systems (eg.Bellwood et al. 2004). It is thought that lower biological diversity in Caribbean systems may contribute to weakened ecosystem resilience and response diversity to both environmental perturbations and human activities such as overfishing (McCann 2000, Hooper et al. 2005, Cardinale et al. 2006). This was demonstrated on Caribbean reefs when overfishing led to the sea urchin *Diadema* becoming the dominant herbivore, precipitating rapid phase shifts to dominance by macro-algae following their die-off in 1983 (Lessios et al. 1984, Knowlton 1992, Hughes 1994). However, the link between species richness and resilience on coral reefs remains equivocal, as it is recognised that particular species and functional groups perform disproportionately important functional roles (Bellwood et al. 2003, Bellwood et al. 2006, Hughes et al. 2007). Nevertheless, given that the sparsely populated, yet highly biologically diverse islands within the Pacific Ocean are considered to be underexploited, it is unlikely that differences in coral reef fisheries yields as a result biogeographical differences can be detected through these analyses.

The positive relationship between island size and human population density is likely to be largely geographical, as larger islands have more space for human populations to expand. Denser human populations have been shown to strongly and positively influence coral reef fisheries yields (eg.Newton et al. 2007). However, greater yields from larger islands may also be a consequence of higher fish diversity in line with 'island biogeography theory', which predicts that species richness will increase with increasing habitat area and therefore habitat complexity (MacArthur and Wilson 1967). This effect has been recognised for coral reef systems, both in the Indo-Pacific and the Caribbean ocean basins, where larger populations in greater areas of habitat have greater genetic diversity, and reduced probability of extinction (Palumbi 1997, Bellwood and Hughes 2001, Sandin et al. 2008). Nevertheless, given that the largest islands have predominantly overexploited fisheries exploitation status, it is impossible to disentangle the effect of fishing effort as a driver of yield in this study. Given islands with smaller reef area: land area ratios are the most densely populated, and tend to have overexploited fisheries exploitation status, it seems unlikely that the effect of habitat area (and therefore species richness) has positively increased coral reef fisheries yields. Sandin et al (2008) suggested that, for the Caribbean, reef area was a poorer predictor of species richness than island area, given the facultative nature of many reef species, and that land area is most likely to reflect both habitat diversity and availability. Nevertheless, we might expect that larger reef areas, with greater diversity and resilience, would yield larger catches, which is the opposite of what is found. The most parsimonious explanation is that the reef area: land area ratio is a measure of the *per capita* dependence on coral reef resources per island, with larger, more densely populated islands having a greater requirement for reef resources, which is reflected both in yield and in the overexploited status of the majority of these islands.

The strong positive relationship between human population density and GDP may imply a link between socio-economic development and coral reef fisheries for island nations, such that affluence could be positively influenced by reef fishing. Figure 4 suggests that heavily populated islands with greatest yields and least sustainable fishing practices are most affluent, whilst the sparsely populated islands, with lowest yields, and most sustainable fishing practices are poorer. This relationship differs somewhat from the U-shaped curve described by Cinner et al (2007) in their study of how local scale socioeconomic development influenced reef fish biomass in the Indian Ocean. Here it appears the most affluent nations have increased, rather than decreased, the scale of their extractive practices on reefs, which contradicts the environmental Kuznets curve hypothesis that suggests wealthier nations reduce environmental impacts through improved technologies, reduced dependence on primary resource extraction, shifts to service industries, and through displacement of local impacts by taking resources from poorer, less regulated areas (Arrow et al. 1995, Grossman and Krueger 1995, York et al. 2003). This may be a consequence of scale, given that the present study considers 49 global island nations, whereas the Cinner et al (2007) study considers 5 countries within the Western Indian

Ocean. Nonetheless, Figure 4 may imply that increasingly wealthy nations have greater capacity to expand their extractive practices over larger areas through improved access to more efficient technologies (Arrow et al. 1995, Berkes et al. 2006). This could account for the predominance of islands with overexploited fisheries status on highly-developed islands, perhaps indicating that greater levels of access to boats with engines may allow for widespread overexploitation further afield. This may be increasingly common given the growing, unsustainable global trade in live reef fishes, which yields approximately 30,000 tonnes annually, with an estimated trade value of approximately US$810 million (Sadovy et al. 2003, Warren-Rhodes et al. 2003). Conversely, less-developed islands may be largely underexploited as a consequence of technological constraints such as fewer boats with engines, but may also be subject to social institutions such as taboos, which are widespread in the Indo-Pacific where many of these islands are located (Johannes 1997). However, the majority of underexploited islands are relatively sparsely populated, and likely to be subject to less fishing pressure, despite a likelihood of higher dependence on fishing as a primary occupation. Nevertheless, given the strong relationship between human population density and coral reef fisheries yields across the 49 islands, and given that there would likely be a strong relationship between human population density and GDP regardless of coral reef fisheries, it is extremely difficult to decouple fishing effort as a driver of yield, from the socioeconomic benefits/disadvantages of overfishing island coral reefs.

The scale and quality of the data sources used here must be given some consideration. Firstly, while the FAO provide the most extensive global time series of fishery statistics available, coral reef landings are often under or misreported owing to the difficulties of recording landings from multispecies fisheries in remote places (Dalzell 1998, Sadovy 2005, Newton et al. 2007), as shown by reconstructions of landings in US flag-associated islands of the western Indo-

Pacific. These analyses suggest that, over a 50-year time period, landings have been underestimated by 86%, 54%, and 79% for Guam, Northern Marianas islands and American Samoa, respectively (Zeller et al. 2007). Secondly, our measure of economic development (GDP Power Purchase Parity) is notoriously difficult to compute as a US dollar value has to be assigned to all goods and services in the country regardless of whether these goods and services have a direct equivalent in the United States. Also, many countries do not formally participate in the World Bank's PPP project that calculates these measures, so the resulting GDP estimates for these countries may lack precision. However, given the wide geographic and monetary scales represented in this analysis, absolute accuracy of data is less important than the overall trends observed, and there is no reason for systematic bias in GDP estimates with respect to fisheries yields or exploitation status.

These analyses provide a novel understanding of how a range of geographical, biological, and socioeconomic factors may affect the distribution of human population densities within coral reef island nations, and therefore, their potential impact upon respective coral reef fisheries yields.

At broad geographic scales, our data may suggest that growing affluence among island coral reef nations tends towards greater resource extraction, unsustainable fisheries and therefore environmental degradation. We observe no evidence for any improvement in resource conditions with increasing socio-economic development, as suggested by the environmental Kuznets curve hypothesis. Given predictions for human population growth in future years, especially in the developing world where 75% of coral reefs occur, the implications of this study may be grave for the future of coral reef fisheries. As well as the expansion of extractive practices, growing societal wealth has wider consequences for the health of coral reefs through increased coastal development, pollution and carbon emissions (York et al. 2003, Dietz et al. 2007). Sustaining coral reef fisheries for the future will require greater consideration to the interaction of socio-economic and ecological factors which influence resource use on coral reefs (Bellwood et al. 2004).

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Chapter 5

Fishers' perceptions of change in coral reef ecosystems

Coral reef fisher, Sandy Ground, Anguilla

Abstract

Coral reefs support vital fisheries for millions of tropical people in the developing world, but are acutely endangered by multiple stressors. In particular, overfishing threatens the structure, function and resilience of coral reef ecosystems as tropical coastal populations continue to expand. Despite the global socioeconomic importance of coral reef fisheries, there remains insufficient knowledge pertaining to their sustainable management. Whilst broad-scale studies of fisheries landings data have provided vital insights into the changes in reef communities as a consequence of fishing on coral reefs, finer-scale fisheries-independent evidence of such effects may be more relevant for understanding the status of individual fisheries and reef environments. In particular, locally sourced evidence from coral reef fisheries that are not yet overexploited can provide useful insights into the factors that characterise local-scale fishing effects. Here, evidence of such change is explored on the Caribbean island of Anguilla, which has been previously described as having underexploited inshore coral reef fisheries. By assimilating the perceptions of local stakeholders engaged in coral reef fishing over a period of four decades, evidence for changes in absolute catches, target species, size and abundance are explored. The insights of local fishers point strongly to marked declines in catches, and highlight the disappearance of highly favoured species, coupled with substantial expansion of fishing effort and an overall concern for the status of the Anguillian inshore coral reef fishery. This investigation reveals extensive over-exploitation that is manifest in current and historical coral reef fishing on Anguilla, and points to the difficulties of drawing inferences on fisheries' exploitation status from landings data which are frequently misreported.

Introduction

Coral reef ecosystems are home to extremely high levels of biodiversity, and are found along the coastlines of more than 100 of the world's poorest developing nations (Roberts et al. 2002, Carpenter and Springer 2005). Consequently, tens of millions of people are thought to be entirely dependent upon extractive practices such as fishing for both food and livelihoods (Whittingham et al. 2003, Burke 2011). The continued supply of coral reef resources is endangered by multiple stressors including overfishing, habitat degradation, climate change and rapid human population growth (Newton et al. 2007, Graham et al. 2008, Knowlton and Jackson 2008, Wilson et al. 2010). In particular, the cascading effects of overfishing on coral reefs may have considerable repercussions for ecosystem function and therefore fisheries potential (Carreiro-Silva and McClanahan 2001, Dulvy et al. 2004a, Mora et al. 2011). Despite the global socio-economic importance of coral reef fisheries, the extent to which they can continue to sustain human extractive practices is poorly understood.

Overfishing on coral reefs causes a reduction in abundance, biomass and mean size of targeted species within the coral reef community (Russ 1991, Jennings et al. 1995, Jennings and Lock 1996). Fishing can directly impact community structure through the selective removal of larger-bodied species and individuals at high trophic levels which are generally most desirable and easiest to catch (Jennings et al. 1995, Jennings and Polunin 1995, Jennings and Kaiser 1998). Additionally, such species are also intrinsically more vulnerable to fishing than their smaller-bodied, lower trophic level relatives, and decline faster in response to exploitation

(Jennings et al. 1998, Jennings et al. 1999b). Consequently fish communities tend to change in a size-specific manner in response to fishing (Jennings et al. 1998, Jennings et al. 1999a, Jennings et al. 2002). Removal of larger-bodied predatory fishes may also elicit indirect increases in the number and biomass of prey species subject to 'top down' control (Dulvy et al. 2004b). Consequently, intensive fishing is thought to induce a shift in fisheries landings from large, long-lived, high trophic level species to small, short-lived, low trophic level species (Pauly et al. 1998).

The effects of overfishing on coral reefs have been detected throughout the tropics, and are thought to be strongly determined by the density of human populations (Newton et al. 2007)(Chapter 1). Ecological Footprint analyses have shown that more than half of island nation coral reef fisheries are overfished, and that the live reef fish food trade exceeds sustainable fisheries potential in the Indo-Pacific and South East Asia by between ~2.5 and 6 times (Warren-Rhodes et al. 2003, Newton et al. 2007). Comparative analyses of coral reef fish assemblages inside and outside of MPAs, between pristine and densely populated coral atolls, and along spatial gradients of fishing pressure have also identified fisheries-induced coral reef degradation (Jennings et al. 1995, Roberts et al. 2001, Sandin et al. 2008).

Whilst large-scale catch and survey data provide strong evidence of global declines in coral reef fisheries, additional perspectives may be gained through considering local-scale evidence of changes on reefs. In particular, locally-sourced evidence from underexploited coral reef fisheries may identify declines sooner than broad scale landings data, and additionally might provide insights into the processes that characterise the development of fisheries from under- to fully-exploited. Underexploited coral reef fisheries have been described in Ecological Footprint analyses as those in which resource consumption is lower than sustainable reef production (i.e. Ecological Footprint < 1; assuming a sustainable yield of 5 mt•km^{-2}•yr^{-1}) and there is only local-scale evidence of overexploitation (Newton et al. 2007). As such, underexploited coral reef fisheries should demonstrate few effects of overfishing. Evidence to the contrary may reflect widespread underreporting of coral reef fisheries landings, and add testament to the conservative nature of previous studies depicting the scale of the coral reef crisis (Zeller et al. 2006, Newton et al. 2007, Zeller et al. 2007). However, long-term, local-scale studies of coral reef fisheries, let alone underexploited ones, are rare.

An alternative approach to evaluating changes in coral reef community structure is to consider perceptions of local resource users, in particular those engaged in reef fisheries, which can provide important insights in data-poor contexts (Johannes 1998, Folke 2004). Growing evidence suggests that fisheries-induced reef degradation can and should be managed at local scales, and must involve those participating in fisheries (Cinner et al. 2009). Perceptions of local resource users may be critical in linking social and ecological systems, which is vital in understanding the complex patterns of resource use on coral reefs, and the effective management of the growing fisheries crisis (Hughes et al. 2005, Cinner et al. 2009).

Here, I present a study of the evidence for fisheries-induced coral reef degradation on the Caribbean island of Anguilla, using local fishers' perceptions of changes over the last four decades. In a previous study, the coral reef fisheries in Anguilla have been categorised as underexploited, based upon landings statistics reported to the Food and Agriculture Organization (FAO) FISHSTAT database (Newton et al. 2007). These fisheries therefore provide an ideal opportunity to explore evidence of local-scale levels of exploitation that do not rely upon official landings data (Newton et al. 2007). I aim to explore evidence of changes to the coral reef fish community structure, and associated coral reef fisheries yields of Anguilla over a period of 40 years, through the insights of fishers, and to identify key characteristics of: (a) fishers, fishing effort and fishing methods; (b) catches, i.e. target species, size and abundance, and overall yields; and how each of these have changed over the last four decades.

Methods and materials

Study site

This study was undertaken in Anguilla, British West Indies (Figure 1). Fishing in Anguilla is essentially artisanal, is concentrated on 2000 km^2 of submerged shelf within the Economic Exclusion Zone (EEZ), and employs approximately 300 outboard-powered open-topped fishing vessels which average between 12 – 50 feet in length (Mukhida and Gumbs 2008). The majority of fishers operate close to shore, but many vessels have expanded their range to within an approximately 65 km radius of the island (Mukhida and Gumbs 2008). The inshore reef fishery principally targets the Caribbean spiny lobster (*Panulirus argus)* and the spotted lobster (*Panulirus guttatus),* known locally as crayfish, as well as many reef fish species such as snappers (*Lutjanidae*), surgeonfish (*Acanthuridae*), triggerfish (*Balistidae*), parrotfish (*Scaridae*) and groupers (*Serranidae*), and coastal pelagics such as jacks *(Carangidae*). Anguilla has few technical restrictions on the fishery, but there is a ban on taking egg-bearing lobsters (*P. argus* and *P. guttatus*), a minimum size and weight restriction for *P. argus*, a minimum fish trap mesh size and a ban on the use of gillnets and poison for fishing. There are no no-take areas or closed fishing seasons (Dr S. Wynne, personal communication 2008), although there are five marine parks, with several other sites in the waters surrounding the island designated as no-anchoring zones.

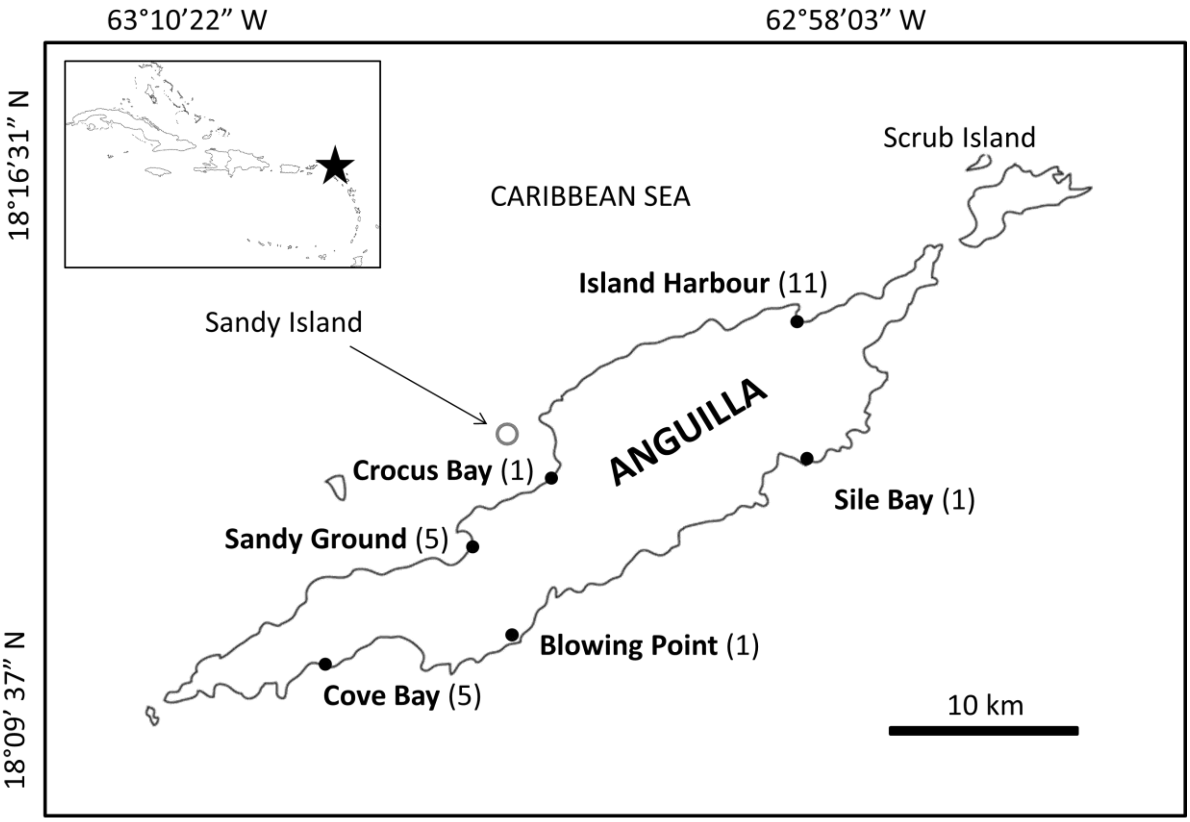

Figure 1. *Anguilla, British West Indies. The location and names of the fishing harbours studies are indicated, with the numbers of respondents interviewed at each site. The inset shows the location of Anguilla within the Caribbean region.*

Study subjects

Interviews were conducted with 23 fishers from six harbours, between February and April 2008 (see Figure 1 for study sites, and Appendix C for respondent details and codes). All fishers relied on fishing the inshore coral reefs for all or part of their income, and used both fish and lobster traps as well as hand-lines as their principal fishing methods. Respondents were chosen on the basis of recommendations from key informants (senior employees from the Anguilla Department for Fisheries and Marine Resources (DFMR), and experienced local fishers), and through snowball sampling (whereby respondents recommended further potential interviewees; Bunce et al. 2000). Each respondent was given a consent form, which described the study, to sign prior to the interviews (Appendix D), and the confidential treatment and storage of the data was fully explained.

Interviews consisted of both highly structured closed questions to generate quantitative data on relevant variables such as age, gender, and family status; and open-ended, semi-structured questions to provide complementary qualitative data on fishing practices and strategies. Fishers were also asked to indicate on maps (1:50,000 and 1:175,000 scale) of Anguilla where they currently fished (see Appendix C for full interview guides). Interviews were tape-recorded and transcribed verbatim, then systematically coded and analysed using an 'open coding' method. This methodology involves breaking down the transcripts in order to label and define data concepts, and in turn develop categories based on their properties and dimensions. This is the most appropriate method when using 'open-ended questions' to generate qualitative data (see Bryman 2004). Although all questions were asked of all fishers, not all questions were answered in sufficient detail to allow coding of answers, sample sizes vary between questions. Triangulation was used to confirm and validate the interview responses by reviewing and vetting specific information such as fishing yields, boat sizes, and target species with other interviewees, key informants from the fishing community, government officials from the DFMR and through personal observation for approximately 8 weeks during February and March, 2008 (Bunce et al. 2000).

Reef fish and lobster fisher interviewed at Island Harbour, Anguilla

Results

The fishers

All 23 fishers interviewed in this study were male Anguillan nationals ranging in age from 18 to 65, with the average age being 44 (± 14 SD). The majority of the fishers were aged from 45 to 54 (n = 8), and only 5 were younger than 35 years. All but one of the fishers had lived in Anguilla all of their lives, and most fishers began fishing for income as a teenager (mean age ± SD, 18 ± 6 years). Fishing careers of interviewees ranged from 5 to 40 years, with the mean number of years spent fishing being 25 years (± 12 SD), with 95% (n = 22) having a family link to the industry, with fathers and grandfathers having fished the inshore coral reefs before them. Of the 23 fishers, 74% (n = 17) considered fishing to be their full time occupation, but

52% (n = 12) subsidised their income with construction work, private boat charters and other employment.

Fishing strategies

All respondents fished with their own boats, which averaged 29.3 feet in length (± 5.8 SD) and were typically made of wood and fibre glass, and powered by out-board motors ranging in size from 10 to 250 Horse power. Thirteen fishers operated their vessels alone, whilst eight fished with a member of their family, and a further two fished with friends. Average boat length did not constrain the number of traps employed by each fisher because traps are usually deployed once or twice a year, and stay in the water for routine hauling. Interviews revealed that species-specific survival rates determined the hauling frequency ('soak' times) for traps, with lobster traps being hauled on average once a week and reef fish traps every 2-3 days.

Fish traps, Island Harbour

Of the 23 respondents, 47.8% (n = 11) consistently targeted both coral reef fishes and lobsters at the same time throughout any year, whereas 13% (n = 3) of fishermen target only lobster, and 21.7% (n = 5) of fishers target coral reef fishes exclusively. The remaining 17.3% (n = 4) of fishers alternated their fishing strategies with the seasons; fishing for lobster typically between November and April, and coral reef fishes for the remaining months. These fishers often used the same traps, with adapted funnels which are larger during lobster season to accommodate the Caribbean spiny lobster.

Figure 2. Fish trap with adaptable 'funnel'

Fishing gears employed in Anguilla consist mainly of lobster and coral fish traps, deep slope coral reef fish traps (which are up to four times larger than reef fish traps), hand lines, long lines, and fish aggregation devices (FADs). For the two month duration of the study, the mean number of lobster and fish traps employed by each fisher was 85 (± 78 SD) but varied considerably, ranging from 0 to 380. The mean number of lobster traps in use for the duration of the study ranged from 0 – 300 with a mean of 52 (± 70 SD), whilst the average number of fish traps employed by each fisher was 31 (± 24 SD), and ranged from 0 to 80. Only one of the fishers interviewed used FADs, and these were employed largely to catch oceanic pelagic species such as tuna (*Scombridae*) and dolphin fishes (*Mahi mahi).* These catches were excluded from the study*.* Only 8.7% (n = 2) of fishers owned deep slope coral reef fish traps, whereas 61% (n = 14) engaged in hand and long-lining for species such as the yellowtail snapper (*Ocyurus chrysurus*).

Fisher preparing a type of long-line fishing gear known locally as 'rigging'

Fishers were based at eight different harbours around the island; although they were fairly homogenous with respect to the inshore fishing grounds they targeted (Figure 3). Fishing grounds to the North and West of Anguilla were used by all of the respondents for trap fishing of both fish and lobster, whereas deeper fishing grounds along the 'Anguilla Bank' in the North was targeted by six respondents for deep slope species such as red snapper, using either deep slope fish traps, or long lining.

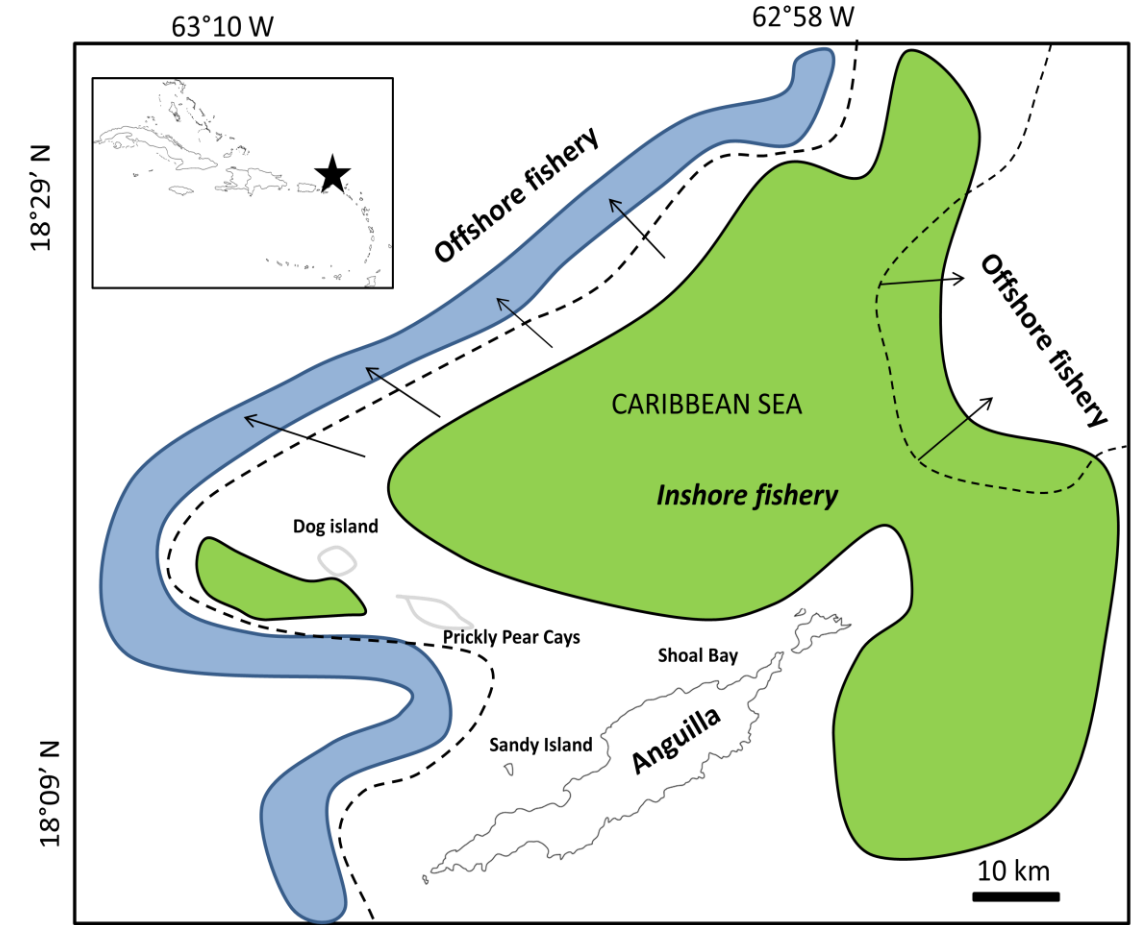

Figure 3. *Locations of fishing activity around Anguilla, British West Indies, as indicated by interviews with local stakeholders. The inshore fishery (green) is targeted by all coral reef fish and lobster fishers (n = 23) whilst 6 fishers target deep slope and pelagic species towards the offshore areas and the deep slope bank (blue). The oceanic shelf is indicated by the dashed line and signifies the outer reaches of the inshore fishing grounds. The inset indicates the location of Anguilla within the Caribbean region.*

Catches

Estimates of daily current lobster and fish catches were obtained through the open question "*What is your average daily catch for lobsters and reef fishes?*"

The mean estimated daily catch of the 23 fishers across all fishing methods was 86.1 kg day^{-1} (± 34.0 SD) but varied considerably between fishers from 18.1 to 158.8 kg day^{-1} (units were converted from lbs to kilograms). Mean estimated daily lobster catch of the 23 fishers was 30.3 kg day^{-1} (± 30.9 SD), ranging from 0 to 90.7 kg day^{-1}, whereas mean estimated daily fish catch was 55.9 kg day^{-1} (± 32.9 SD), and varied from 0 to 140 kg day^{-1}. The number of traps per fisher was significantly and positively related to the weight of estimated daily catch per fisher when considering lobster catches (number of traps = 0.48*catch weight +11.73, r^2 = 0.66, n = 23, p = 0.001), but not to total catch weight, i.e. lobster and reef fishes (r^2 = 0.02, p = 0.74), or reef fish catches alone (r^2 = 0.01, p = 0.48), as 61% of fishers supplement their reef fish catches with hand or long lining.

Typical fishing boats, Island Harbour, Anguilla

Fishers' perceptions of changing catches and abundance of lobster and reef fishes in recent decades:

The day's fish catch by Cove Bay fisher, Anguilla

Catches per trap

Anecdotal evidence for considerable declines in typical catches over recent decades was revealed through the open question "*has the weight of your average catch changed over the last 40 or so years?*"

Through memory, seven respondents were able to provide estimates of typical lobster catches per trap for past decades, and five provided past catches from coral reef fish traps (Figure 3). The estimated weights of lobster catch declined significantly from 1970 to present day ($r = -0.77$, $n = 34$, $p < 0.001$), as did that of reef fish catches ($r = -0.73$, $n = 22$, $p < 0.001$) (Figure 3). Whilst there was only a single estimate of lobster catch in 1970 (45 kg $trap^{-1}$), this high value was corroborated by several other fishermen who remarked upon it, and considered it not too atypical of the time (see quotes below). Between 1975 and 1990, estimates ranged from 5 to 20 kg $trap^{-1}$, whilst those between 1990 and 2000 did not exceed ~6 kg $trap^{-1}$. Mean estimated weight of lobster catch for the current period was 0.88 kg $trap^{-1}$ (± 1.87 SD), but varied greatly from 0 to 6.8 kg $trap^{-1}$, whereas mean estimated weight of coral reef fish catch per trap was 1.4 kg $trap^{-1}$ (± 1.6 SD) and also ranged from 0 to 6.8 kg $trap^{-1}$. In general, current estimates of typical catch weight did not exceed ~4 kg $trap^{-1}$, although two of the respondents claimed to be able to catch similar quantities of lobster in 2008 (6.8, and 6.51 kg $trap^{-1}$ respectively), as was estimated to be a typical catch between 1990 and 2000. However, the remaining lobster fishermen catch considerably less, with only three fishermen landing more than approximately 1 kg $trap^{-1}$. Similarly, one fisherman claimed to land large coral reef fish catches (6.8 kg $trap^{-1}$) which were equivalent to typical catches for years between 1990 and 2000. The remainder of the respondents landed < 3.8 kg $trap^{-1}$. If the one high estimate of current fish catch is excluded (6.8 kg $trap^{-1}$), the mean estimated catch per trap for reef fishes is considerably lower than the 1990 – 2000 estimate, at 1.16 kg $trap^{-1}$ (± 1.06 SD; $n = 15$).

Fisher quotes regarding changes in catch weights:

"Hope Webster once hauled 950lbs with 10 pots. There was so many lobsters they would hang onto the outside of the pots, but that was many, many years ago" (IH4)

"In the 60's and 70's, my grandfather used to go out in his row boat in the evening to his fish traps with a torch, and there were so many lobsters he could just pick one from the water with his hand, and I mean big lobsters, 6-8 lbs, there was so much lobsters". (IH7).

"I remember pre 1980's, one friend had 13 pots, and they caught more than 6-700 lbs of lobster". (IH8).

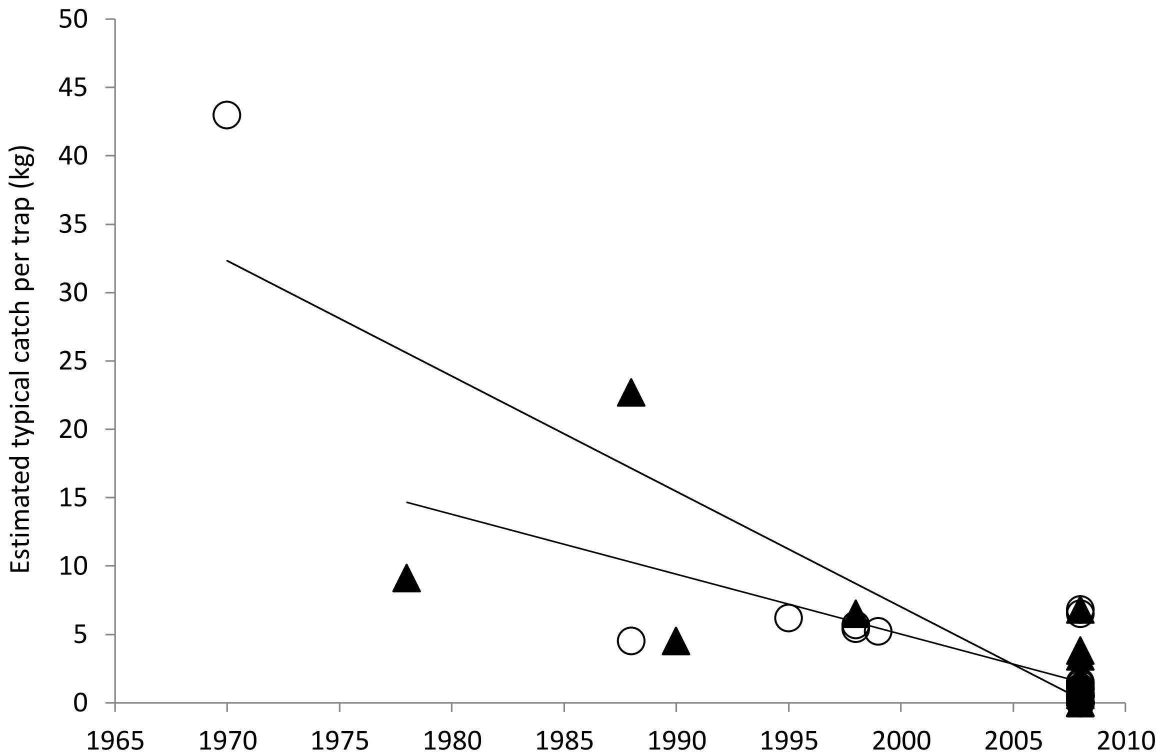

Figure 3. *Estimates from 23 Anguillian fishers of typical lobster (open circles) and coral reef fish (open triangles) catches per trap which they achieved at different times over the past four decades.*

As well as declining catches, respondents also reported that the general abundance of both lobsters and coral reef fish species had decreased from the inshore waters of Anguilla in recent decades (Table 1).

Table 1. *Fisher responses to the open question "Has the abundance of fish and lobster around the island changed over the past 40 years?" The number and percentage of fishers that mentioned each response is reported.*

Fisher response	**Number of responses**	**Percentage of responses**
There are much less fish and lobsters, and many more fishermen	4	17.4
There are much less fish and lobsters	12	52.2
Most species have declined	3	13.0
There has been no change in the time that I've been fishing	4	17.4

The majority of respondents (82.6%) said that the abundance of both fish and lobsters has declined substantially during the past 20 to 30 years of fishing. Of the four respondents who suggested there has been no change, their respective ages were 18, 22, 37 and 65, and two of them would therefore not have witnessed declines within their lifetimes. Overall, interview responses suggest that the scale of declines in fish and lobster abundance in Anguillan coral reefs has been widespread and extensive over recent decades.

Table 2. *Selected remarks made by fishers during semi-structured interviews in response to the open question "Has the abundance of fish and lobster around the island changed over the past 40 years?"*

Selected examples of fisher responses
"20 yrs ago, 25 pots would haul 200 lbs lobster and I hauled every 3 days. Now, 25 pots would haul 40 lbs if you are lucky and that is hauling once a week".
"My grandfather, when he used to fish, they used to catch a lobster, bust them with a club; throw them back in the pot to catch triggerfish, because there were so many lobsters".
"When I was a boy, we used to go spearfishing and we'd be kicking parrotfish out of the way, now it can take you an hour to spear 6".
"In the olden days when we had fish in abundance [30 yrs ago] one trap was enough for any one fisherman, but they still had 6 or 7. They would bring it [reef fish] to shore and leave it to rot. They

overfished the fishing grounds from way back then. They had so much fish you didn't have to buy it".

"Shoal bay should be closed down to any kind of fishing, absolutely. I used to swim there as a boy over those reefs, and now you can hardly see a fish in the area".

Target species

In response to the open question *"Have your target species changed in the past 40 years?"* Fishers suggested there have been subtle changes in recent decades (Table 3). Twenty percent (n = 4) claimed that declining lobster catches had forced them to switch to coral reef fishes in order to maintain landings (Table 3), whilst 25% (n = 5) commented that they now catch more red hind (*E. guttatus*) and fewer groupers (*Serranidae*). A further 25% (n = 5) claimed that species caught are generally similar but volumes are considerably lower. The five respondents which answered "not in the time frame which I've been fishing" were below 35 years old and had only been fishing for an average of 9 years (± 4.3 SD). However, in response to a further open question regarding target species *"are there species which you can no longer, or rarely catch, which used to be a regular part of your haul?",* respondents revealed further detail on the loss of both groupers (*Serranidae*) and parrotfishes (*Scaridae*) from regular catches (Table 8).

Table 3. *Fisher responses to the open question "have your target species changed in the past 40 years". 20 responses were obtained. The number and percentage of respondents that mentioned each response is reported.*

Fisher response	Number of responses	Percentage of responses
Declining lobster led me to catch more fish	4	20
No, I catch the same species	1	5
I catch the same species just less of them	5	25
I catch more red hind and less grouper	5	25
Not in the time frame which I've been fishing	5	25
Total number of	**20**	

Fishers' perceptions of changing fishing methods

With respect to fishing methods, respondents reported that fishing gears have remained the same in recent decades despite the switch from sail-powered to outboard motor-powered vessels in the 1970s and 80s. This had little effect on fishermen other than to reduce their time at sea. However, 78% (n = 18) of respondents, all of whom were older than 35, remarked that the number of traps each fisherman owned was considerably more than in recent decades, whereas 26% (n = 6) spent longer fishing in order to maintain catches. As well as declining catches per trap, 30% (n = 7) of respondents also reported that they now have to travel further to maintain their catches.

Table 4. *Respondent remarks during semi-structured interviews with respect to distances travelled to fish.*

Selected examples of fisher responses
"We don't fish inshore with traps anymore as there are no fish, and there are too many traps down there already. We moved offshore to catch more fish."
"We used to be able to fish in the shallows - now we have to go all the way to the glass point. You had to keep moving on, travelling further."
"[There is] much less fish, much less lobsters. There are no fishes left in West End where there is a concentrated fishing effort."
"Now I have to travel further, use more traps, and catch much less fish! I catch on average, 30lbs less fish now than 10 years ago for the same effort."
"In that time [30yrs ago], you'd go fishing and you wouldn't see another boat. You could catch the lobsters from the land, now you go 20 miles out to catch them."

Table 5. *Fisher responses to the open question "have your fishing methods changed over the past 40 years".*

Selected examples of fisher responses
Fishing has changed a lot. I only used to have 5 traps and each one would haul about a potato bag of fish. That's about 50lbs. Now I have 65 fish traps and haul about two coolers [200lb]"
"I only needed 7 traps when I started. I built them up to make up for catching less"
"20 yrs ago, no one would have had more than 30 traps, you just didn't need them. Things have now changed dramatically, some fishermen have 300 traps"
"You need more traps now to catch the same amount of fishes"
"There are much more traps in the water fishing the same grounds"
"Much less traps needed to catch the same amount of fishes 20 yrs ago"
"I fish for about 6, 7 maybe 8 hours a day now. 20, 30 years ago, we'd spend 3 hours at the most on the sea".
"Sometimes we don't catch much at all, we have to stay out longer".
"20 years ago I'd spend 3 hours on the sea; now it's more like 5 or 6"
"I have to fish for much longer now as all the lobsters are gone".
"You need to go out many more times now to catch the same amount of lobster".

Fishers' perceptions of changes in the size of target species

Of the 23 interviewees, 43.5% said that both fish and lobster were much smaller today, compared with 20 to 30 years ago, whereas 26.1% suggested that some, but not all, species were smaller (Table 6). The two youngest fishermen both remarked that older fishermen talked of how fish and lobster used to be larger many years ago.

Table 6. *Fisher responses to the open question "Has the average size of fish and lobster changed over the past 40yrs?" The number and percentage of respondents that mentioned each response is reported.*

Fisher response	Number of responses	Percentage of responses
Both fish and lobsters are much smaller than they used to be	10	43.5

Some species are smaller, but others are the same	6	26.1
They are about the same size	5	21.7
Older fishermen remark that fish and lobster used to be larger	2	8.7

Overall, interview responses suggest that both fish and lobster caught in recent years were considerably smaller than those caught by either themselves, or their fathers/grandfathers (Table 6, 7).

Table 7. *A selection of fisher responses to the open question "Has the average size of fish and lobster changed over the past 40 yrs?"*

Selected examples of fisher responses
"Fish are all much, much smaller now. I've been fishing on the local reefs all of my life and the difference scares and concerns me deeply".
"I remember fishing with my father when I was a small boy, and we would catch anything up to 10 large [Nassau] grouper (Epinephelus striatus) *weighing 60lbs each. Now you don't catch them. If you do they are more like 6lbs".*
"Certainly, we are catching less, and the fish are getting smaller and smaller."
*"Rainbow parrotfish [*Scarus guacamaia], *midnight parrotfish [*Scarus coelestinus*] they are all smaller, you don't see them like before. You don't see much cobbler fish [*Alectis ciliaris] *no more either. You see lots of smaller ones!"*
"The fish are much, much smaller these days. That is a fact. 30 yrs ago, you might have 20 hinds [Epinephelus guttatus] *in a trap, each weighing 3, 4, 5, up to 8 lbs. Today if you find a hind that weighs 1lb, you are lucky. So yes, they are enormously smaller".*
"Lobsters are many, many times smaller than they used to be when I was a boy".

Fishers' perceptions of declines in particular species

Of all 23 interviewees, 65% said they can no longer catch groupers, or do so very rarely, and five respondents specifically named the mutton grouper (*Epinephelus striatus*), the rock grouper *(Epinephelus adscensionis*) and the black grouper (*Mycteroperca bonaci*) as being particularly scarce compared with recent decades. Sixteen percent of respondents said that parrotfish are also caught much less frequently relative to 20 – 30 years ago, with Rainbow parrotfish (*Scarus guacamai*), midnight parrotfish (*Scarus coelestinus*) and the blue parrotfish (*Scarus coeruleus*) recognised as being particularly rare (Table 8).

Interview responses suggest that the abundance and biomass of both groupers and parrotfish, both of which used to be an integral part of the inshore reef fisheries catch, have significantly declined from Anguillan reef fish communities in recent decades (Table 8, 9).

Table 8. *Fisher responses to the open question "are there species which you can no longer, or rarely catch, which used to be a regular part of your haul?" The number and percentage of respondents that mentioned each response is reported.*

Fisher response	**Number of responses**	**Percentage of responses**
Not in the time frame that I've been fishing	3	7.9
Groupers, (*Epinephelinae*)	15	39.5
Mutton grouper, (*Epinephelus striatus)*	2	5.3
Rock grouper, *(Epinephelus adscensionis)*	2	5.3
Black grouper, (*Mycteroperca bonaci)*	1	2.6
Parrotfish, (*Scaridae)*	6	15.8
Rainbow parrotfish, *(Scarus guacamaia*)	3	7.9
Midnight parrotfish, (*Scarus coelestinus)*	4	10.5
Blue parrotfish, *(Scarus oeruleus)*	2	5.3

Fishers' perceptions of the fishing industry in Anguilla

Whilst fishers were not asked any direct questions about the status of the fishing industry, nine respondents remarked that they were concerned about the extent to which the inshore coral reef has been overfished in recent years. One fisherman expressed concern about the lack of controls in place on mesh sizes and the illegal taking of berried female lobsters. The majority of respondents (n = 16), however, claimed to engage in discarding of small fish, lobsters and berried lobsters and at least two fishermen owned callipers which were employed to measure small lobsters to ensure they were of legal size (personal observation). Two of the youngest fishers said they retained small fishes for use as bait.

Table 9. *A selection of fisher responses to the open question "Are there species which you can no longer, or rarely catch, which used to be a regular part of your haul?"*

Selected examples of fisher responses
"You don't see grouper no more. My father used to catch a lot of grouper; rock grouper, mutton grouper, black grouper, you don't see them no more".
*"I remember fishing with my father when I was a small boy, and we would catch anything up to 10 large mutton grouper [*Epinephelus striatus*] weighing 60lbs each. Now you don't catch them. If you do they are more like 6lbs."*
"You don't see as much grouper as you used to see, back in the days, in my dad's days. He used to have at least 6 or 7 groupers in each trap. Today if you are lucky, you might see one in a trap".
"Groupers are very, very scarce now. You might catch a grouper once a year. 30 yrs ago you always caught them."
*"You don't see the rainbow [parrotfish] [*Scarus guacamaia*], or the blue bitch [*Scarus coelestinus]. [I] h*aven't seen one for 6 or 7 years. Fishermen used to be able to lean out of the boat and shoot 'em".*

Table 10. *Selected remarks made by fishers about the status of the fishing industry in Anguilla during semi-structured interviews.*

Selected examples of fisher responses
"We have destroyers, not fishermen on this island. Spear fishing ought to be banned".
"Shoal bay is a problem, it is more than overfished."
"The guys from the east, they used to catch the grouper, chunk it up, throw it in the pot to catch the lobster. Ignorance in some facts and not being too wise has really messed with the sea."
"Younger fishermen have a sense of greed."
In the next 20 years, I guarantee you; you won't be catching any more fish in these surrounding islands. The amount we is fishing today, the multiplication [of effort] just cannot add up."
"Fish are declining because there's too much fishing and the wire's too small [mesh size]. Lots of people use illegal wire, and no one's checking it."
"[There are] much more traps in the water fishing the same ground, and yes we are bothered by this."

Discussion

The perceptions of local stakeholders directly engaged in coral reef fishing on the Caribbean island of Anguilla strongly suggest marked declines in catches, sizes and abundance of targeted fish and lobster species, coupled with increases in the quantity of gears employed, distances travelled to fishing grounds and time spent fishing, over a period of ~40 years. Their testament also provides evidence for the disappearance of several highly favoured species, as well as widespread concern for the expansion and status of the fishery. This investigation suggests that extensive over-exploitation is manifest in current coral reef fishing in Anguilla, and has occurred historically at the scale of decades.

Given global declines in coral reef fisheries, and widespread fisheries-induced degradation of Caribbean coral reefs, it is unsurprising to find putative evidence of extensive overfishing in Anguilla by way of declining catches, size and abundance of targeted species (Burke and Maidens 2004, Newton et al. 2007, Mora 2008). The patterns reported here for Anguilla have been documented in many other studies of Caribbean coral reefs both historically (Jackson 1997, Pandolfi et al. 2003, McClenachan and Cooper 2008), and more recently (Hughes 1994, Hawkins and Roberts 2004, Mumby et al. 2012). Whilst not all fishers were able to provide estimates of catches from previous decades, those that could reported strong declines in average catch per trap for both fish and lobster, from as much as 45 kg $trap^{-1}$ in 1970, to current estimates of ≤~4kg $trap^{-1}$. These historical testimonies were also corroborated by other fishers who remembered similar catches within the fishing community in recent decades, and the general consensus was that catches have been steadily declining since the 1970's. These reports were further supported by more than 80% of respondents acknowledging that the general abundance of target species has significantly declined from inshore coral reef areas in recent decades.

Sixty-five percent of fishers acknowledged the almost complete loss of previously abundant, large, piscivorous groupers from their catches in recent years, coupled with the general decline in desirable, large parrotfish species such as *Scarus guacamaia.* In a recent study of a Belizean coral reef fishery, Mumby et al. (2012) identified a similar rapid decline in grouper species, coupled to a marked increase in the abundance of several mesopredators, in just 6 - 7 years of fishing. In Anguilla, the widespread loss of three, large-bodied, piscivorous groupers (*Epinephelus striatus, E. adscensionis, and Mycteroperca bonaci)*, coupled to an increased abundance of smaller *Epinephelus guttatus (*reported by twenty percent of Anguillian fishers), mirrors the Belizean study and suggests a similar trophic cascade in response to increasing fishing pressure, and a reduction in predation pressure from large piscivores (Pauly et al. 1998, Dulvy et al. 2004b, Mumby et al. 2012). In support of this, almost half of Anguillian fishers agreed that targeted species of both fish and lobster were significantly smaller than in recent years, whilst more than 25% suggested some were larger but others remained the same. In particular, one fisher (CB2) suggested that *E. striatus*, has declined in size by an order of magnitude (from ~60 lb to 6 lbs), whilst another said that *E. guttatus* had declined from approximately 8 lb to 1 lb per fish, despite their increased catch frequency.

Substantial expansion of fishing effort in order to maintain catches in Anguillian fisheries lends further evidence to suggest widespread over-exploitation of coral reef communities on the island. This was manifest in longer times spent fishing, distances travelled, and greater numbers of fish and lobster traps employed by each fisher. The scaling up of effort in recent decades represents a typical response to declining coral reef resources, whereby increasingly determined stakeholders can be driven to more intensive, and sometimes destructive fishing practices (McManus et al. 2000, McClanahan and Mangi 2004, McClanahan et al. 2008). Whilst the types of fishing gears employed have remained largely the same over the last 20-30 years, the use of illegally sized mesh for both fish and lobster traps in Anguilla appears to have become more prevalent, as well as the taking of small, and berried lobsters. The retention of small reef fishes for use as bait is also now commonplace (personal observation 2008). Additionally, many respondents attested to the marked increase in numbers of fishers in recent years, presumably as it became an increasingly attractive livelihood option. Owing to the development of high-end tourism and an increased demand for expensive seafood, fishing can be extremely profitable in Anguilla, with many earning thousands of US dollars each month (Mukhida and Gumbs 2008). Finally, it was evident that fishers have to travel considerably further than in recent decades, in order to maintain fisheries yields as a result, they believed, of declining resources and intense competition between fishers . This is of particular concern as the spatial expansion of exploitation can mask local declines in targeted species (as catches are maintained), preventing feedback within the fishing community and the incentive to consider conservation initiatives (Myers and Worm 2003, Berkes et al. 2006). This is further supported by comparing the size of the inshore fished areas as described by Anguillian fishers (~400km^2, Figure 3) with that of the total reef area as reported by Spalding et al (2001) (~50km^2). The disparity in these estimates may well reflect the discourse of the fishers attesting to spatial expansion of Anguillian reef fisheries (Table 4), especially as reef fishing in Anguilla has largely become a commercial enterprise driven by tourism, as opposed to the small scale subsistence, shallow water fishing of past years (Tables 4 and 5).

It is difficult to estimate how such expansion could influence sustainable production for Anguilla, and elsewhere, primarily because the calculation of this hinges upon the area specific assumption that reefs can yield 5 mt•km^{-2}•yr^{-1} , and doesn't account for reef species caught off- shore. In a previous study based on landing statistics (and the assumption of 5 mt•km^{-2}•yr^{-1} as the MSY for coral reef fisheries) it was suggested that Anguillian reef fisheries were underexploited (Newton et al 2007). Given the much larger size of the fished area, this suggests that the true yields from these fisheries were underreported to the FAO, which is supported by the communications of the fishers attesting to degraded reefs and declining catches despite increased fishing effort.

Declining catches in Anguilla are likely compounded by the local degradation of coral reefs as a direct result of destructive fishing techniques and powerful hurricanes (Mukhida and Gumbs 2008). Trap fishing, which is the predominant method employed in Anguilla, is both highly effective and unselective, and directly damages corals and other bottom living organisms when traps are dropped onto the reef (Yoshikawa and Asoh 2004, Hawkins et al. 2007). Also, hurricanes, such as Luis and Lenny in 1995 and 1999, respectively, which devastated fishing grounds in Anguilla, can destroy complex reef structures that serve as habitats for demersal fishes and lobsters, and may cause mobile species to move further afield. Following Hurricane Luis, Anguillian fishers remarked upon the loss of structural complexity, in the form of broken tabular corals and the filling of 'fish holes' with sand, and how they believed that fish had moved in order to find refuge. The importance of coral morphology for fish communities has been demonstrated for both small, site-attached, as well as large, mobile reef species, in both the Indo-Pacific (Wilson et al. 2008, Coker et al. 2009, Kerry and Bellwood 2012) and the Caribbean (Luckhurst and Luckhurst 1978, Pittman et al. 2007). However, the relationship between coral cover, architectural complexity and fish density remains equivocal, especially in the Caribbean, where region-wide loss of coral cover and architectural complexity over the last three decades, has resulted in only modest declines in reef fish density in the last decade (Gardner et al. 2003, Paddack et al. 2009, Alvarez-Filip et al. 2011).

Whilst the underlying causes of declining coral reef fisheries are notoriously difficult to decouple, this study presents strong evidence for the role of overfishing in local scale deterioration of coral reefs in Anguilla. Given that Anguillian coral reef fisheries have been previously described as 'underexploited', the apparent disconnect between true yields in Anguilla, and those reported to the FAO suggests that misreporting may well be problematic for the other island nations considered in this study. This investigation demonstrates the conservative nature of official coral reef fisheries reporting, and highlights the importance of local-scale analyses in the evaluation of fisheries-induced coral reef declines and the broader context of the global coral reef crisis (Bellwood et al. 2004, Newton et al. 2007, Cinner et al. 2009).

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Chapter 6

Concluding remarks

Reef fishing boats returning home, Cove Bay, Anguilla

Worldwide declines in coral reefs require urgent improvements to our understanding of both the large-scale ecological processes which underpin reef ecosystems, and the influence of humanity on these processes (Bellwood et al. 2004). Overfishing remains a principle threat to the world's reefs, causing profound direct and indirect shifts in coral reef community structure (Russ 1991, McClanahan 1994, Dulvy et al. 2004). Using an interdisciplinary approach, this thesis explores the consequences of exploitation by integrating global-scale island nation coral reef fisheries landings statistics with local-scale social knowledge. The broad geographic and taxonomic extent of these landings presented a novel opportunity to investigate evidence of the effects of fishing at differing scales, with the aim of identifying patterns of human-associated change that could be applied and understood globally. Importantly, insights gained through global fisheries data have been balanced by assimilating the objective viewpoints of experienced reef fishers operating locally.

Overfishing on coral reefs is widespread and extensive, and has been recognised worldwide (Warren-Rhodes et al. 2003, Newton et al. 2007). Chapter 2 provides another sombre assessment of the scale at which humans are overexploiting coral reefs. This chapter demonstrates that catches of coral reef fishes increase with increasing human population density on islands, and provides evidence of fisheries-induced changes to reef fish communities at vast geographic and taxonomic scales. Using the global landings database to estimate weighted MTLs of island coral reef fish catches, Chapter 2 also identifies declines in MTL (MTL) of landings with increasing yields, and shows that these catches were sustained by greater proportions of lower trophic level taxa and smaller proportions of high trophic level species. The most sobering aspect of this research was that trophic cascades on coral reefs are evident at such large scales, using data that are likely to be highly conservative (Newton et al. 2007). Underreporting of coral reef fish yields to fisheries agencies is commonplace worldwide, and reflects the difficulties associated with recording catches from spatially diverse, multispecies and multi-geared fisheries (Dalzell 1996, Zeller et al. 2006, Zeller et al. 2007). Therefore, given the likely vagaries of official, global-scale coral reef fisheries landings, the patterns observed in Chapter 2 are likely to be even more extreme and widespread.

An additional impediment to Chapter 2 was the considerable reporting of fish taxa within the unidentified category, “marine fishes nei”. As the determination of weighted MTL required knowledge of the component trophic levels making up absolute catch, the number of islands suitable for inclusion in the analysis dropped from 49 to 28. Whilst the trends in declining MTL were evident regardless of whether the overall catch included or excluded these landings, it would have been compelling to explore these relationships at even broader geographic scales.

Notwithstanding the debate that surrounds the use of ‘catch MTL’ as a reliable indicator of ecosystem trophic level (Branch et al. 2010), given the extensive body of literature which demonstrates the effects of fishing on community structure on coral reefs, it is very likely that the composition of coral reef fisheries landings on islands reflect those of the reef fish communities (eg.Russ 1991, Jennings and Lock 1996, Sandin et al. 2008a). To find a systematic global relationship between the densities of human populations, yields and the apparent structuring of fish communities on coral reefs is worrisome - not least because of the ongoing expansion of human populations - and highlights the urgent, worldwide need to bolster management efforts for coral reefs (Bellwood et al. 2004, Hughes et al. 2005, Knowlton and Jackson 2008).

Management of coral reef fisheries is fraught with difficulties, but typically hinges on the restriction of catch and effort though limiting numbers of people or boats, time, area and gears, and the size and species that can be targeted (McClanahan 2006). However, as coral reefs continue to decline, successful management of reef resources will require greater understanding of how these factors influence yields (Newton et al. 2007, McClanahan et al.

2008). The number of MPAs globally is rising rapidly, but the extent to which they fulfil their ecological potential can be influenced by many factors, such as illegal or destructive harvesting, emigration of stocks across boundaries, and inadequately sized reserves (Edgar et al 2011, Mora et al. 2006, Babcock et al, 2010). Understanding the potential for rebuilding reef fish abundances through MPAs and gear restrictions is a vital research area, and has been recently addressed through a global study of 832 coral reefs across 64 countries. This study showed that, on average, if protected from fishing, fish biomass on reefs had the potential to recover within 35 years for moderately degraded systems, and less than 60 years if reef abundance is severely eroded (MacNeil et al. 2015).

Large-scale closures to fishing are thought by some to be essential for conserving fish biomass, but others suggest such closures could reduce catch levels where effective management already exists (e.g. Roberts et al, 2005, Buxton et al, 2014). These hypotheses were addressed in a recent study of the potential fishery benefits of a large-scale closure of an additional 28.4% of the Great Barrier Marine Park (GBRMP) of Australia in 2004. Under Government initiatives, the area closed from fishing rose from 4.6 to 33% of the GBRMP, a total area of 117,000km^2, to form one of the largest no-take areas in the World. It was expected that following an initial reduction of ~10% in catch and value, recovery of catches would become apparent after three years because of increased juvenile recruitment and adult spill over, However, following the closure, initial net reductions were estimated at ~35%, and there was no sign of recovery in total catch levels nine years on. This study highlighted the importance of the critical evaluation of realistic outcomes of MPAs, opposing the notion that large-scale closures will inevitably benefit, or at least have neutral impacts on surrounding fisheries, and supporting evidence that MPAs will reduce overall catch if effective fisheries management alternatives already exist (Walters et al. 2007, Buxton et al, 2014,).

There are however, numerous studies which have shown that well-managed MPAs can increase fish biomass inside the MPA (Halpern, 2003; Lester et al., 2009), and can contribute to fish production outside the MPA through improved recruitment and spillover, although this has been observed mostly at smaller scales (Garcia et al., 2013). A good example of spillover has been recognised in Apo Island Marine Reserve in the Philippines where increased biomass inside the MPA has benefited those fishing outside the reserve (Russ et al., 2004).

For some species, such as the charismatic Eastern Blue Grouper (*Achoerodus viridis*), small-scale MPAs have been shown to be highly effective. Owing to long residency times and high site fidelity, a Australian study has shown that a relatively small protected area (0.16 km^2) was effective in meeting the spatial requirements of adult Eastern Blue Grouper, which is useful information for garnering public support for the designation of MPAs (Lee at al. 2015).

Whilst there is widespread agreement that MPAs can be an extremely important conservation tool, for fisheries management they are often difficult to implement because of social and political issues surrounding people who depend heavily on reef resources (McClanahan 2011). Indeed, the majority of MPAs fail to meet their management objectives – an issue recently highlighted by a study of the effectiveness of MPAs across 7 sites in the Philippines, which showed that huge improvements are necessary in areas of resource conflict, and in the relationships between stakeholders and those managing MPAs (Tupper et al, 2015).

The obvious challenge of managing the trade-offs between conservation priorities and fisheries requires new policies which can converge both issues, but the successful management of reef fisheries must include a combined approach which includes garnering a greater understanding of the potentially sustainable yields on coral reefs.

Given the strong relationship between coral reef fisheries yields and human population densities identified in Chapter 2, Chapter 3 aimed to explore the influence of the relationship between fishing effort and yield on estimates of the sustainable limits for coral reefs fisheries, or maximum sustainable yield (MSY). Estimating how much can be extracted from fish stocks without adversely affecting future reproduction and recruitment is especially difficult in tropical fisheries, owing to the difficulties in recording long-term, temporal catch and effort data (Hilborn and Walters 1992, Dalzell 1996, Dalzell et al. 1996). Comparisons of previously published estimates from spatially variable coral reef fisheries have suggested that MSY for coral reefs is approximately 5mt•km^{-2}•yr^{-1} (Dalzell 1996, Jennings and Lock 1996, McClanahan 2006). Here, the FAO landings database presented a novel opportunity to estimate maximum sustainable yield for coral reef fisheries at broad spatial and taxonomic scales, using surplus production models of aggregated multispecies data across a spatial gradient of fishing pressure (human population density). Using this method, estimates of MSY varied considerably, from 8.2 - 22.7mt•km^{-2}•yr^{-1}, which is considerably higher than previously suggested values of 5mt•km^{-2}•yr^{-1}. However, yields greater than ~8mt•km^{-2}•yr^{-1} tended to be reported from islands which are considered to be overexploited, which suggests yields approaching ~8mt•km^{-2}•yr^{-1} may lead to a greater risk of unsustainability. Critically, this study emphasised the complexity of estimating MSY using surplus production methods and highlights that resulting estimates are extremely dependent upon the exploitation status of the reefs which are included in the models. Therefore, whilst this study may support previous estimates of 5mt•km^{-2}•yr^{-1} as an approximate MSY for coral reefs, given the evidence for overfishing globally, it also highlights the pressing need for a conservative approach towards the setting of targets such as MSY (eg. Newton et al. 2007, Mora 2008, Sandin et al. 2008a).

Whilst Chapters 2 and 3 affirmed a strong positive relationship between the densities of human populations on islands and their respective coral reef fisheries yields, Chapter 4 aimed to explore the geographical, biological, and socioeconomic factors that may characterise reef fisheries of differing exploitation status. Geographically, the most overfished islands, with the densest human populations and overexploited fisheries exploitation status, tended to be found within the Indian and Atlantic Ocean basins. Given that Caribbean coral reef ecosystems are thought to have weaker resilience to human activities on account of lower biological diversity, it is unsurprising that high-yielding fisheries in this region have overexploited fisheries exploitation status (McCann 2000, Hooper et al. 2005, Cardinale et al. 2006). Conversely, Pacific Ocean islands, with higher biological diversity, are the least densely populated and tend to have underexploited status (Carpenter and Springer 2005). Human population density (and therefore, to some extent, coral reef fisheries yield) was also significantly positively related to GDP, an indicator of the wealth of these island nations. Whilst it is likely that GDP and human population density are intrinsically linked for a variety of factors, reef fisheries have considerable economic importance in both the commercial and subsistence sectors (eg. McManus 1996). Demand from overseas markets, and the increasing wealth of East and South East Asia ensure that reef fishing, especially the export of live reef fish, continues to be a lucrative business (Sadovy and Vincent 2002, Warren-Rhodes et al. 2003). Wealthier fishers with greater access to effective fishing gears and motorised boats, coupled with the commercial incentive to fish intensively is likely to lead to overexploitation (Arrow et al. 1995, McClanahan et al. 2008). Given that wealthier islands tend to have overexploited reef fisheries, GDP for island nations may well therefore, be positively influenced by reef fishing. However, wealthier islands with high human population densities and overexploited fisheries also tend to be larger. Whilst island area might positively influence biological diversity (and potentially yields) on account of greater habitat availability for fish communities, larger islands also tended to have smaller ratios of reef area: land area, and therefore, arguably greater *per capita* dependence on coral reef resources (Bellwood and Hughes 2001, Sandin et al. 2008b). Whilst the strong relationship between island nation coral reef fisheries yields and humans confounds definitive identification of other controlling factors, it also adds to the body of literature citing humans as a principle driver of declines in reef ecosystems worldwide (eg. Newton et al. 2007, Mora 2008, Mora et al. 2011). It also clearly demonstrates the difficulties associated with differentiating between the complex factors which influence both the structure and functioning of coral reef ecosystems, and the way in which humans utilize them (Bellwood et al. 2004, Hughes et al. 2005, Knowlton and Jackson 2008).

Findings from Chapters 2, 3 and 4 have provided compelling evidence of extensive and widespread overexploitation of island coral reef fisheries at a global scale, using broadly-scaled geographic and taxonomic data, and have attempted to understand some of the key principles by which reef fisheries, and their respective fish communities, operate at large scales. In contrast, Chapter 5 used a different approach in both scale and method, by considering a single fishery on the Island of Anguilla, and a process of assimilating the viewpoints and perceptions of local stakeholders. Anguilla provided an ideal study site because it has a well-established reef fishery, which had been previously described as underexploited by Newton et al. (2007). This provided a novel opportunity to explore fisheries-independent evidence of local-scale exploitation which might add testament to the conservative nature of previous studies describing the scale of the coral reef crisis (Baisre et al. 2003, Newton et al. 2007, Zeller et al. 2007). Interviewing, and conversing with the local fishers throughout the key fishing grounds in Anguilla, was very revealing and provided important insights and details which could not be detected in global studies that depend upon large-scale - and inevitably coarse - , data. Critically, the Anguillian fishers identified an alarming estimate of temporal declines in fish and lobster catches in recent decades, which appeared to be mirrored by increasing effort, expansion of gears and numbers of new fishers entering the fishery. Vivid descriptions of how fish communities appear to have completely changed in the inshore fishing grounds were particularly disconcerting. For example, accounts that spear fishers used to have to “kick parrotfish [species] out of the way", as they were so plentiful and so much bigger than in recent decades. A particularly salient observation during my study was that the true extent of the fisheries landings was undetectable to the fisheries agencies on the ground. As far as I could establish, there were no records kept by either the fishers, or the appropriate agencies, and equally no management of the considerable number of 'recreational' fishers who have alterative livelihoods, but still targeted reef species in their spare time. I was also discouraged by the apparent disparity in attitudes between the older, experienced fishers and their younger contemporaries, towards sustaining and conserving the inshore fishing grounds. The problem of shifting baselines will inevitably lie at the heart of future interpretations of the major factors driving coral reef declines - in Anguilla and elsewhere - and may ultimately govern the way in which societies choose to respond (Jackson et al. 2001, Knowlton and Jackson 2008).

Whilst coral reef ecosystems decline at unprecedented rates, and the scale of human societies on which they depend multiply, it is clear that coral reef fisheries worldwide face an uncertain future (Gardner et al. 2003, Bruno and Selig 2007, Burke 2011). The extent to which coral reefs can continue to provide ecosystem services to humans looks increasingly bleak as the pace of combined stressors including overexploitation, pollution, habitat loss and climate change persist (eg. Hughes et al. 2003, Pandolfi et al. 2003, Wilson et al. 2010). Understanding and moderating the profound influence of people on the functioning of coral reef ecosystems is an urgent and worldwide challenge (Bellwood et al. 2004, Hughes et al. 2005). This thesis has provided a sombre assessment of the extent to which island coral reefs throughout the world are being overexploited, and points to the decline in fish communities on coral reefs as a result (Chapter 2). The difficulties and complexities in determining sustainable limits for coral reefs have also been addressed, and analyses suggest that, even at relatively low yields, coral reef fishing can result in the degradation of reef ecosystems (Chapter 3). This may have a particular bearing on the management of coral reefs, especially when fisheries agencies seek to control fishing by setting maximum limits on yields (McClanahan et al. 2008, Cinner et al. 2009). Chapter 3 underlines the distinct relationship between humans and the pattern of resource use on coral reefs, and demonstrates the difficulties and complexities of disentangling the many factors which likely influence their structure, function and resilience (Mora 2008, Mora et al. 2011). Finally, by linking the complex global patterns observed in Chapters 2, 3and 4, chapter 5 acknowledges the requirement to link ecological analyses with complex social knowledge, and demonstrates the importance of local scale, fisheries-independent information in our understanding of resource use on coral reefs (Hughes et al. 2005). Sustaining reef fisheries for future generations will no doubt require an interdisciplinary approach combining ecological and societal knowledge that seeks to address the multiple underlying causes of reef degradation.

Reef fishers sorting the day's catch, Sandy Ground, Anguilla

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Appendices

My field assistant Evie Newton (aged 2), hard at work in Anguilla

Appendix A

Table 1. *The Categorization of FAO Landings by ecosystem, taxon, and human Use*

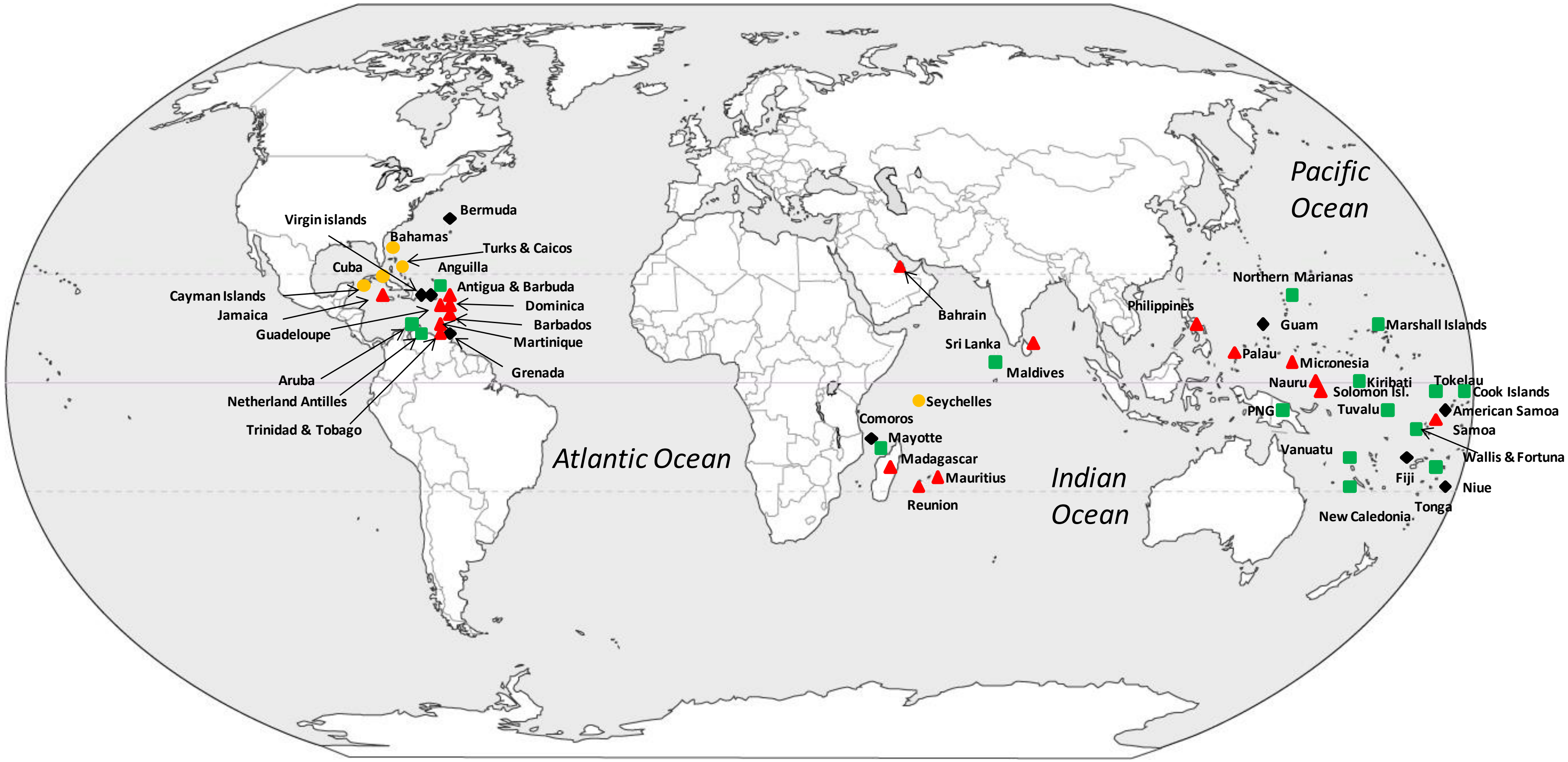
FAO Landings Category	Ecosystem	Taxonomy	Use	FAO Landings Category	Ecosystem	Taxonomy	Use
				Mackerels nei	o	f	c
Abalones nei	dm	mo	c	Mangrove cupped oyster	m	mo	c
Albacore	o	f	c	Marine crabs nei	e	cr	c
Alfonsinos nei	dm	f	c	Marine crustaceans nei	dm	cr	c
American eel	fw	f	c	“marine fishes nei”	o	f	c
Anadara clams nei	r	mo	c	Marine molluscs nei	dm	mo	c
Anchovies, etc. nei	o	f	c	Marine shells nei	r	mo	t
Angelfishes nei	dm	f	t	Marine turtles nei	r	f	t
Aquatic invertebrates nei	r	inv	c	Marlins, sailfishes, etc. nei	o	f	c
Ark clams nei	r	mo	t	Milkfish	r	f	c
Atlantic bluefin tuna	o	f	c	Mojarras (=silver-biddies) nei	r	f	c
Atlantic bonito	o	f	c	Moonfish	r	f	c
Atlantic moonfish	e	f	c	Mozambique tilapia	fw	f	c
Atlantic sailfish	o	f	c	Mullets nei	e	f	c
Atlantic seabob	o	f	c	Narrow-barred Spanish mackerel	o	f	c
Atlantic thread herring	r	f	c	Nassau grouper	r	f	c
Atlantic white marlin	o	f	c	Natantian decapods nei	dm	cr	c
Banana prawn	dm	cr	c	Needlefishes nei	r	f	c
Barracudas	r	f	c	Needlefishes, etc. nei	r	f	c
Barramundi	e	f	c	Nile tilapia	fw	f	t
Batfishes	r	f	c	Northern pink shrimp	dm	cr	c
Bigeye scad	r	f	c	Oceanian crayfishes nei	fw	cr	c
Bigeye tuna	o	f	c	Octopuses, etc. nei	r	mo	c
Black marlin	o	f	c	Opah	o	f	c
Black stone crab	dm	cr	c	Parrotfishes nei	r	f	c
Blackfin tuna	o	f	c	Patagonian toothfish	dm	f	c
Blacklip abalone	r	mo	c	Pearl oyster shells nei	r	mo	t
Blacktip shark	r	e	c	Penaeus shrimps nei	dm	cr	c
Blue crab	e	cr	c	Percoids nei	o	f	c
Blue marlin	o	f	c	Philippine catfish	r	f	c
Blue swimming crab	e	cr	c	Pomfrets, ocean breams nei	o	f	c
Blue tilapia	fw	f	c	Ponyfishes (=slipmouths)	r	f	c
Bluestripe herring	r	f	c	Porgies	r	f	c
Boxfishes nei	r	f	c	Porgies, seabreams nei	r	f	c
Brazilian sardinella	o	f	c	Portunus swimcrabs nei	e	cr	c
Broad-striped anchovy	o	f	c	Queenfishes	r	f	c
Butterfishes, pomfrets nei	o	f	c	Rainbow runner	r	f	c
Carangids nei	r	f	c	Rainbow sardine	r	f	c
Cardinalfishes, etc. nei	e	f	t	Rays, stingrays, mantas nei	r	e	c
Caribbean spiny lobster	r	cr	c	Red grouper	r	f	c
Cephalopods nei	o	mo	c	Red hind	r	f	c
Cero	r	f	c	Red seaweeds	r	p	c
Chacunda gizzard shad	e	f	c	River and lake turtles nei	fw	r	c
Chub mackerel	o	f	c	River eels nei	fw	f	c
Cichlids nei	fw	f	c	River prawns nei	fw	cr	c
Clams, etc. nei	r	mo	c	Round sardinella	o	f	c
Clupeoids nei	o	f	c	Ruffs, barrelfishes nei	o	f	c
Cobia	r	f	c	Sardinellas nei	o	f	c
Common dolphinfish	r	f	c	Scads nei	r	f	c
Common squids nei	o	mo	c	Scaled sardines	o	f	c
Conger eels, etc. nei	dm	f	c	Scallops nei	dm	mo	c
Croakers, drums nei	r	f	c	Scats	r	f	c

Cusk-eels, brotulas nei	dm	f	c
Cuttlefish, bobtail squids	r	mo	c
Cyprinids nei	fw	f	c
Demersal percomorphs	dm	f	c
Diadromous clupeoids	o	f	c
Dogtooth tuna	o	f	c
Echinoderms	r	ec	c
Emperors (=scavengers)	r	f	c
Endeavour shrimp	o	cr	c
False trevally	o	f	c
Filefishes, leatherjackets	r	f	t
Flatfishes nei	dm	f	c
Flyingfishes nei	o	f	c
Freshwater crustaceans	fw	cr	c
Freshwater fishes nei	fw	f	c
Freshwater gobies nei	fw	f	c
Freshwater molluscs nei	fw	f	c
Freshwater prawns	fw	cr	c
Frigate and bullet tunas	o	f	c
Fusiliers	r	f	c
Gastropods nei	r	mo	c
Giant river prawn	fw	cr	c
Giant tiger prawn	dm	cr	c
Glassfishes	fw	f	c
Goatfishes	r	f	c
Goatfishes, red mullets	r	f	c
Gobies nei	r	f	c
Green mussel	fw	mo	c
Green seaweeds	r	p	c
Green turtle	r	r	c
Groupers nei	r	f	c
Groupers, seabasses	r	f	c
Grunts, sweetlips	r	f	c
Gudgeons, sleepers nei	fw	f	c
Hairtails, scabbardfishes	dm	f	c
Halfbeaks nei	r	f	c
Hawksbill turtle	r	r	c
Indian mackerel	o	f	c
Indian mackerels nei	o	f	c
Indian pellona	fw	f	c
Indo-Pacific king mackerel	o	f	c
Indo-Pacific sailfish	o	f	c
Indo-Pacific swamp crab	m	cr	c
Indo-Pacific tarpon e	e	f	c
Jacks, crevalles nei	r	f	c
Japanese eel	fw	f	c
Jellyfishes	o	f	c
Kawakawa	dm	f	c
King mackerel	o	f	c
Lane snapper	r	f	c
Large-eye breams	r	f	c
Little tunny (Atl. black skipj)	o	f	c
Lizardfishes nei	r	f	c
Loggerhead turtle	r	r	c
Longbill spearfish	o	f	c
Longtail tuna	o	f	c
Sea catfishes nei	e	f	c
Sea chubs nei	r	f	c
Sea cucumbers nei	r	ec	t
Sea urchins nei	r	e	c
Seerfishes nei	o	f	c
Sergestid shrimps nei	dm	cr	r
Serra Spanish mackerel	o	f	c
Sharks, rays, skates, etc. nei	o	e	c
Short mackerel	o	f	c
Short neck clams nei	dm	mo	c
Shortbill spearfish	o	f	c
Shortfin mako	o	e	c
Silky shark	o	e	c
Sillago-whitings	dm	f	c
Silversides (=sand smelts)	fw	f	c
Silver-stripe round herring	o	f	c
Skipjack tuna	o	f	c
Slipper cupped oyster	m	mo	c
Slipper lobsters nei	dm	cr	c
Snappers nei	r	f	c
Snappers, jobfishes nei	r	f	c
Snooks (=robalos) nei	r	f	c
Southern bluefin tuna	o	f	c
Southern red snapper	dm	f	c
Spinefeet (=rabbitfishes) nei	r	r	f
Sponges	r	s	t
Spotted sicklefish	r	f	c
Squillids nei	o	cr	c
Squirrelfishes	r	f	c
Stolephorus anchovies	o	f	c
Streaked seerfish	o	f	c
Striped marlin	o	f	c
Striped snakehead	fw	f	c
Stromboid conchs nei	r	mo	t
Surgeonfishes nei	r	f	c
Swordfish	o	f	c
Threadfin breams nei	r	f	c
Threadfins, tasselfishes nei	r	f	c
Tilapias nei	fw	f	c
Torpedo scad	r	f	c
Torpedo-shaped catfishes nei	fw	f	c
Triggerfishes, durgons nei	r	f	c
Trochus shells	r	mo	c
Tropical spiny lobsters nei	r	cr	c
Tuna-like fishes nei	o	f	c
Unicorn cod	o	f	c
Various squids nei	o	mo	c
Wahoo	o	f	c
Wolf-herrings nei	r	f	c
Wrasses, hogfishes, etc. nei	r	f	c
tuna	o	f	c
Yellowtail snapper	r	f	c

Key to ecosystems: r = reef associated, dm = demersal marine, o = oceanadromous, fw = freshwater, and e = estuarine. Key to taxa: f = fish, mo = mollusc, cr = crustacean, ec = echinoderm, and e = elasmobranch. Key to human use: c = consumed and t = traded

Appendix B

Figure 1. *Global distribution of island nations. Colours and shapes indicate fishery exploitation status of each: under-exploited (green squares, n = 17), fully-exploited (orange circles, n = 10), over-exploited (red triangles, n = 13) and collapsed (black diamonds, n = 9).*



Appendix C

Fisher's livelihood survey 2008

A: Identification

Date of interviewer:

		/			/	**0**	**8**

Surveyor's name: ______________________

Survey site: ______________________ Survey number: ______________________

Respondent's name: ______________________

Start time: ______________________ Finish time: ______________________

B: Respondent general characteristics

1. Gender: Male: ☐ Female: ☐

2. Age: 15-18 19-24 25-30 31-35 36-40 41-45 46-50 51-55 56-60 61-65 66-70 70+

3. Marital status

4. # of dependents in family (i.e. wives/husbands & children under age x)_________

5. Nationality: ________________________

6. How long have you lived in Anguilla? Always: ☐ No. years: ☐

7. What is the highest level of education you have reached?

   Never Primary Junior

   Secondary University Post-graduate

8. How many people live with you now?

9. How many sleeping rooms are there in your house?

10. What are the outer walls of your home made from?

    Wood concrete concrete & wood other________________________

Occupation(s):

1. Is fishing your only occupation?

2. What other livelihoods do you undertake? How long do you spend in each one?

3. Which is the most important livelihood and why?

4. How does this vary in and out of the hurricane season?

5. Why do you fish?

6. How long have you fished for a living?

7. What occupation did you have before you began fishing?

8. What is the family history of fishing?

9. Does your father/grandfather still fish?

Fishing effort:

1. What fishing gear do you own?

2. What fishing methods do you use? How long do you spend with each method/gear type?

3. Have your fishing methods altered over the last 20 years? Why?

4. Do you fish alone or with others? Why?

5. What boat do you use? Do you own this? Outboard motor?

6. How long does it take you to prepare gears/bait for each fishing trip?

7. How many hours a day/week/month do you spend fishing?

8. What determines this?

9. Are there constraints on your time spent fishing?

10. How does this vary in and out of the hurricane season?

11. Has this changed over the last 40 years? Why?

12. Has fishing effort changed over the last 40 years? Why?

Fishing location:

1. Where do you fish, and when?

    a. Show map, and ask the respondent to mark on the map their fishing ground, with the number of traps or fishing gear.
    b. How many of these traps do you check each day at this time of year?
    c. How about next month, and the next etc…show the respondent the seasonal timeline and ask the respondent to mark how many time these traps are checked for each month of the year, and also where they are checked on the map.

2. Have you always fished there?

3. Why?

Catches and perception of fish abundance:

1. What are your target species? Does this vary in and out of the hurricane season?

2. Have these changed in the past 40 years? Why?

3. Are there any more/less fishes than 40years ago?

4. Do you switch your target species according to times of year?

5. Can you always land target species, or do you catch whatever you can?

6. Are target species smaller and rarer than they were 40 years ago?

7. Are there fishes that you can no longer catch, but which used to regularly caught?

8. What is your average catch per trip (weight, species, $).

9. Has this changed over the last 20 years? Why?

10. What is a ‘good’ and ‘bad’ haul?

11. Can you remember your worst and best ever catch? When were these?

12. Do you throw any of your catch back into the sea?

13. Are there any constraints on fishing in Anguilla – e.g. seasonal bans on FSAs?

14. Would you be happy for me to weigh your catch daily/weekly?

Destination of catches (using market chain sheets):

1. What quantity and species do you sell on versus retain for personal consumption?

2. How much fish does your household eat now compared to 40 years ago?

3. How has this pattern changed over the last 40 years?

4. What are the sources of conflict with the system?

Table 1. *Interview respondent codes for fishers (Chapter 5). Prefix letters refer to the harbour at which each is based. Interview date, fishing harbour and fishing strategies used are listed.*

Interview date	respondent code	Fishing grounds	Fisher strategy
27.02.08	C1	Crocus Bay	fish/lobster traps, inshore line fishing
05.03.08	S1	Sile Bay	lobster traps
10.03.08	CB1	Cove Bay	fish traps, deep slope line fishing
13.03.08	IH2	Island Harbour	lobster traps
13.03.08	IH3	Island Harbour	fish/lobster traps
13.03.08	IH4	Island Harbour	fish/lobster traps
19.03.08	IH5	Island Harbour	fish/lobster traps
20.03.08	IH6	Island Harbour	fish/lobster traps
20.03.08	CB2	Cove Bay	fish/lobster traps
21.03.08	IH7	Island Harbour	fish/lobster/crayfish traps, inshore line fishing
21.03.08	IH8	Island Harbour	fish/lobster/crayfish traps, inshore line fishing
31.03.08	IH9	Island Harbour	fish/lobster traps, inshore line fishing
01.04.08	SG1	Sandy Ground	fish/lobster traps, deep slope line fishing
01.04.08	CB3	Cove Bay	fish/lobster traps, inshore line fishing
02.04.08	CB4	Cove Bay	fish/lobster traps, inshore line fishing
03.04.08	IH10	Island Harbour	fish/lobster traps, inshore line fishing
03.04.08	IH11	Island Harbour	fish/lobster traps, inshore line fishing
08.04.08	BP1	Blowing Point	fish/lobster traps, deep slope line fishing
08.04.08	SG2	Sandy Ground	fish/lobster traps
08.04.08	SG3	Sandy Ground	fish traps, inshore line fishing
08.04.08	CB5	Cove Bay	fish/lobster traps
10.04.08	SG4	Sandy Ground	fish/lobster traps, deep slope line fishing
10.04.08	SG5	Sandy Ground	fish/lobster traps, deep slope line fishing

Appendix D

Consent form for fishers interviews

Thank you for participating in this survey. It provides me with invaluable data for my PhD research at the University of East Anglia.

Purpose of the study
The purpose of this study is to explore key factors influencing the future sustainability of coral reef dependent livelihoods in Anguilla under environmental change. To achieve
this I will be assessing the extent to which the inshore coral reef fishery in Anguilla has been influenced by previous hurricane events and the changes these events have had on fishing practices. The types of questions I will be asking will relate to the day-to-day aspects of your work, past experiences, future aspirations, and the seasonality of your job. I hope that these interviews will provide a clearer understanding of the types of decisions that fishers make, the constraints they face and the potential for adaptation, particularly in the face of changing environmental pressures on marine ecosystems in Anguilla. This information can then be used to develop more sustainable marine management, which takes into consideration the incentives and decisions of fishers.

Right to refuse or end participation in the study
If you agree to join this study, we can agree a time for an interview that is convenient for you. You can decide to participate in this study or not and have the right to refuse to answer any questions, or withdraw from the interview completely.

Study procedures
I will contact you to arrange a time and a place to meet. I expect the interview may take approximately an hour. My contact details are XXX@uea.ac.uk and my Anguilla phone number is XXX if you have any questions about this study, please don't hesitate to contact me.

Confidentiality
Your name or any facts that could identify you will not appear in any report of this study. All of your answers will be kept confidential and cannot be traced back to you. The interview notes will be kept in a safe place that only I have access to.

Agreement
The project information was read and explained clearly, anything I didn't understand was explained to me and all my questions were answered.
Respondent agrees to participate? YES NO
Signature of participant: ________________________________ Date: _________
OR verbal consent given, date/time/place ________

Appendix E

Table 1. Characteristics of the island nations from which FAO data on reef fisheries were used for analyses in this thesis. Exploitation status (c: collapsed, o: overfished, f: fully fished, u: under-fished) is from analyses in Newton et al. (2007).

country	Exploitation status	Population	Ocean	Fisheries yield (mt●km-2●yr-1)	Mean trophic level	GDP -PPP ($ Billion)	land area (km-2)	Coastline (km)	Reef area (km-2)
American Samoa	c	65000.0	Pacific	46.2	3.5	0.6	199.0	116.0	220.0
Anguilla	u	12000.0	Atlantic	180.0	3.0	4.5	54.0	103.0	50.0
Antigua and Barbuda	o	66000.0	Atlantic	1139.6	3.2	0.9	151.0	80.0	240.0
Aruba	u	70000.0	Atlantic	71.0	4.4	0.8	2235.0	340.0	50.0
Bahamas	f	294982.0	Atlantic	1518.4	3.3	3.7	18274.0	1129.0	3150.0
Bahrain	o	634000.0	Indian	6391.2	3.1	1.1	344.0	121.0	570.0
Barbados	o	274000.0	Atlantic	766.4	3.7	3.2	544.0	125.5	100.0
Bermuda	c	62997.0	Atlantic	195.8	3.6	0.8	717.0	419.0	370.0
British Virgin Islands	c	20000.0	Atlantic	57.0	3.5	1.6	346.0	188.0	330.0
Cayman Islands	f	35000.0	Atlantic	125.0	n/a	9.1	10070.0	3542.0	230.0
Comoros	c	578000.0	Indian	1826.0	3.4	2.3	264.0	160.0	430.0
Cook Islands	u	20000.0	Pacific	481.4	3.1	110.9	109820.0	3735.0	1120.0
Cuba	f	11142000.0	Atlantic	8864.4	3.3	0.2	702.0	6112.0	3020.0
Dominica	o	72000.0	Atlantic	946.4		0.1	21.0	30.0	100.0
Fiji	c	832494.0	Pacific	9402.8	3.2	0.2	459.0	1519.0	10020.0
French Polynesia	u	249000.0	Pacific	5099.6	2.9	1.0	2821.0	403.0	6000.0
Grenada	c	89000.0	Atlantic	577.2	3.6	1.8	455.0	491.0	150.0
Guadeloupe	o	426000.0	Atlantic	7020.0	3.0	1.5	27986.0	5313.0	250.0
Guam	c	154623.0	Pacific	69.2	3.7	0.2	948.0	389.0	220.0
Jamaica	o	2652689.0	Atlantic	4990.2	2.0	1.5	442.6	153.0	1240.0
Kiribati	u	92000.0	Pacific	11840.0	3.4	28.3	741.0	161.0	2940.0
Madagascar	o	15506000.0	Indian	70361.8	2.7	5.1	430.0	97.0	2230.0
Maldives	u	301475.0	Indian	16558.8	3.7	0.7	751.0	148.0	8920.0
Marshall Islands	u	68000.0	Pacific	480.0	2.1	3.7	1628.0	581.0	6110.0
Martinique	o	415000.0	Atlantic	1864.0	2.7	23.8	10831.0	1022.0	240.0
Mauritius	o	1179000.0	Indian	7004.6	3.6	20.2	581540.0	4828.0	870.0
Mayotte	u	156000.0	Indian	2140.0	n/a	4.4	1060.0	350.0	570.0
Micronesia (Fed. States of)	f	133000.0	Pacific	1380.0	2.3	16.7	2030.0	177.0	5440.0
N Marianas	u	72000.0	Pacific	60.4	3.5	324.4	298170.0	36289.0	50.0
Nauru	f	12000.0	Pacific	150.0	n/a	3.4	2507.0	207.0	50.0
Netherlands Antilles	u	210000.0	Atlantic	478.0	2.0	96.6	64630.0	1340.0	420.0
New Caledonia	u	202000.0	Pacific	506.6	2.4	26.2	5128.0	362.0	5980.0
Niue	u	2000.0	Pacific	200.0	n/a	0.2	91.0	61.0	170.0
Palau	f	19000.0	Pacific	947.9	2.8	2.3	180.0	68.5	50.0
Papua New Guinea	u	4926984.0	Pacific	10100.0	2.4	0.2	236.0	120.0	13840.0

Philippines	o	81159644.0	Indian	665698.2	3.4	4.7	3827.0	2525.0	25060.0
Reunion	o	721000.0	Indian	791.4	3.7	0.6	811.0	1143.0	50.0
Samoa	f	179000.0	Pacific	3761.0	2.1	1.7	298.0	644.0	490.0
Seychelles	f	79326.0	Indian	3348.2	3.7	0.1	181.0	370.4	1690.0
Solomon Islands	f	466194.0	Pacific	12000.0	2.0	1.0	374.0	185.2	5750.0
Sri Lanka	o	19238575.0	Indian	38266.0	3.3	2.8	800.0	364.0	680.0
Tokelau	u	2000.0	Pacific	200.0	n/a	3.2	18275.0	2254.0	50.0
Tonga	c	102000.0	Pacific	2535.8	2.7	0.0	260.0	64.0	1500.0
Trinidad and Tobago	o	1176000.0	Atlantic	2399.6	4.0	0.9	464.0	1482.0	100.0
Turks and Caicos Islands	f	18000.0	Atlantic	230.0	2.1	13.7	452860.0	5152.0	730.0
Tuvalu	u	11000.0	Pacific	160.0	n/a	0.0	12.0	101.0	710.0
United States Virgin Islands	c	120917.0	Atlantic	262.2	3.8	0.0	26.0	24.0	200.0
Vanuatu	u	190000.0	Pacific	1380.0	2.1	1.2	12189.0	2528.0	4110.0
Wallis and Futuna Islands	u	15000.0	Pacific	269.2	2.2	0.1	142.0	129.0	940.0