Subsistence harvesting by a small community does not substantially compromise coral reef fish assemblages

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Fisheries usually first remove large predators before switching to smaller species, causing lasting changes to fish community structure. Reef fish provide essential protein and income for many people, and the impacts of commercial and high-intensity subsistence fishing on reef fish are well documented. However, how fish communities respond to low levels of subsistence fishing using traditional techniques (fishing for food, few fishers) is less well understood. We use three atolls in the Marshall Islands as a model system to quantify effects of commercial and subsistence fishing on reef fish communities, compared to a near-pristine baseline. Unexpectedly, fish biomass was highest on the commercially-fished atoll where the assemblage was dominated by herbivores (50% higher than other atolls) and contained few top predators (70% lower than other atolls). By contrast, fish biomass and trophic composition did not differ between pristine and subsistence-fished atolls – top predators were abundant on both. We show that in some cases, reefs can support fishing by small communities to provide food but still retain intact fish assemblages. Low-intensity subsistence fishing may not always harm marine food webs, and we suggest that its effects depend on the style and intensity of fishing practised and the type of organisms targeted.

Keywords: apex predators, commercial fishing, conservation, coral reef, ecosystem functioning, fishing, isolation, Pacific, pristine, subsistence fishing, trophic cascade.
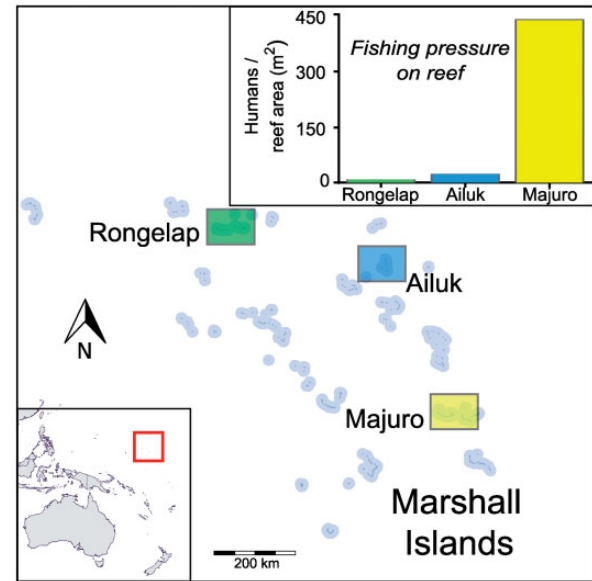
Introduction

Excessive hunting or harvesting can have detrimental effects on animal populations in all biomes (Jackson *et al.*, 2001; Myers *et al.*, 2007; Estes *et al.*, 2011; Ripple *et al.*, 2014). Typically, the first animals removed by hunting are large, long-lived species (Pauly *et al.*, 1998; Alroy, 2001; Myers and Worm, 2003). These are often top-predators and their removal by humans for trophy hunting, food, or livestock protection can result in substantial changes to entire ecosystems via altered trophic cascades (Pace *et al.*, 1999; Babcock *et al.*, 2010; Brashares *et al.*, 2010). Well-known examples of this phenomenon from around the globe include: hunting of lions and leopards in Africa (Brashares *et al.*, 2010); shooting of wolves in America (Ripple and Beschta, 2004); exclusion of dingoes in Australia (Letnic and Koch, 2010); and fishing of sharks in the North-west Atlantic (Myers *et al.*, 2007).

Top predators are harvested heavily in all marine ecosystems, and cascading effects of fishing are documented for kelp forests (Steneck *et al.*, 2004), seagrass beds (Atwood *et al.*, 2015), estuaries (Atwood *et al.*, 2015), and coral reefs (Dulvy *et al.*, 2004). Yet, many studies of the effects of fishing focus solely on commercially valuable species such as Atlantic cod (Myers *et al.*, 1997), tuna (MacKenzie *et al.*, 2009), and sharks (Baum *et al.*, 2003). Despite the encroaching footprint of commercial fishing, people in less developed countries continue to rely on subsistence fishing, where fish are captured by small communities for food (Berkes, 1988) and they can often exert considerable fishing pressure on local systems (e.g. McClanahan *et al.*, 2011; Allen, 2013; Zeller *et al.*, 2015). These fishers frequently use traditional equipment (often without modern fishing technology), catching fish from all trophic levels whilst rarely specifically targeting top-predators (although this does depend on the cultural context, for exception see Glaus *et al.*, 2015; Dalzell, 1996). Subsistence harvesting over long periods can alter food web dynamics (e.g. Simenstad *et al.*, 1978), with strongly negative ecological effects of extensive subsistence harvesting reported on land (FitzGibbon, 1998) and for some marine ecosystems (Dulvy *et al.*, 2004; Mann and Powell, 2007; Peckham *et al.*, 2007; Drew *et al.*, 2013).

Reef fish are the primary source of protein for millions of people that live on tropical islands and coral atolls, and reefs provide ~10% of all fish consumed by humans (Moberg and Folke, 1999; Albert *et al.*, 2015). The effects of fishing on coral reef ecosystems have been comprehensively assessed. Heavy fishing negatively impacts reefs by altering the structure and function of reef food webs (e.g. McClanahan, 1995; Friedlander and DeMartini, 2002; Stevenson *et al.*, 2007; D'Agata *et al.*, 2014; Fenner, 2014). The majority of studies, however, have not differentiated between small-scale artisanal fishing (small commercial operations fishing for profit), and subsistence fishing (fishing only for food, no monetary incentive to capture or refrigeration to store excess fish) that is still practised by many small coastal communities. A potential reason for this is the difficulty of quantifying fishing effort for coral reefs, it can be hard to tell if people are fishing for food, local barter or in small-scale commercial operations (Teh *et al.*, 2013). Where fishing for profit occurs, distance to the nearest market is often shown to be the strongest driver of patterns in fish assemblages (e.g. Cinner and McClanahan, 2006; Brewer *et al.*, 2012; Cinner *et al.*, 2013). Studies investigating subsistence fishing have concluded that at high levels, it can affect the size and structure of reef fish communities (Jennings and Polunin, 1996, 1997; Dulvy *et al.*, 2004a, b; Graham *et al.*, 2005). However, less is known about how subsistence fishing at very low levels compares to reefs that are truly pristine (Sandin *et al.*, 2008; Graham and McClanahan, 2013). Instead, studies often assess fishing impacts by comparing reef fish assemblages between reserve and fished areas (McClanahan *et al.*, 2011). It is, therefore, unclear if low-pressure subsistence fishing by small communities using traditional gear alters coral reef food webs from a pristine state in the same way that small and large scale artisanal fishing does.

Here, we explore how pristine reef communities are modified by fishing with respect to structure and biomass, including the entire communities of large non-cryptic species. We contrast three differently exploited remote coral atolls in the Republic of the Marshall Islands, central Pacific Ocean, to quantify the effect of low-impact subsistence harvesting on reef fish biomass and trophic composition, compared with commercial fishing and a

Figure 1. Locations of atolls surveyed and illustrative levels of fishing pressure in The Republic of the Marshall Islands (map generated using Inkscape ver. 0.48, www.inkscape.org).

near pristine baseline. By comparing differences in fish communities in a rare system containing pristine (inaccessible or uninhabited) reefs, low historical pressure, and contrasting modern fishing patterns, we provide evidence of how low-pressure fishing of relatively pristine systems affects the trophic structure and biodiversity of coral reefs. It is clear that high biomass indicates near-pristine conditions (Graham and McClanahan, 2013); however, here we provide evidence that high biomass may not necessarily indicate intact community structure, and that the low pressure exerted on reefs by small numbers of subsistence fishers does not dramatically alter reefs from a pristine state.

Methods

We consider three remote coral atolls in the Republic of the Marshall Islands on a gradient from unexploited to heavily fished (Figure 1). These atolls are exposed to similar environmental conditions (e.g. biogeography, ocean currents, and water temperatures) (Tables 1 and 2); therefore, if they were left undisturbed, they are likely to support analogous fish communities and vary only according to the size, and fishing techniques, of local human populations (Aswani and Sabetian, 2010; Cinner *et al.*, 2013; Guillemot *et al.*, 2014). Consequently, these atolls provide a natural laboratory ideal for examining fishing impacts. We surveyed complete large non-cryptic fish assemblages at three atolls: (i) a near-pristine atoll (Rongelap) that has been largely uninhabited for 60 years (Pinca *et al.*, 2004); (ii) an atoll (Ailuk) with a small human population that uses traditional subsistence fishing techniques to catch fish (mostly herbivores) from low trophic levels (Pinca, 2006); and (iii) an atoll (Majuro) with a large human population where fishing is intense (compared with other atolls in the republic) and commercial fishers target large, predatory fishes (Pinca, 2005; Table 2). Historically, all atolls have supported small human populations of around 100 inhabitants for centuries.

Table 1. Environmental similarities between atolls in the Marshall Islands relative to those in other Pacific island groups previously used to compare human drivers across islands/atolls.

	Marshall Islands		Line Islands (Stevenson *et al.*, 2007; Sandin *et al.*, 2008)		Hawaiian Islands (Friedlander and DeMartini, 2002)	
	Comparison	Greatest difference (Δ)	Comparison	Greatest difference (Δ)	Comparison	Greatest difference (Δ)
SST (°C)	Majuro vs. Rongelap	0.8	Kingman vs. Tabuaeran	0.4	Hawaii vs. Kure	2.2
Chl *a* (mg m^{-3})	Ailuk vs. Rongelap	0.09	Kingman vs. Palmyra	0.08	Hawaii vs. Kure	0.08
pH	Ailuk/Rongelap vs. Majuro	0.01	Kingman vs. Kiribati	0.01	Hawaii vs. Kure	0.02
Salinity (PSS)	Ailuk vs. Majuro	0.1	Kingman vs. Kiribati	0.4	Hawaii vs. Kure	0.5

Quantitative environment data are presented as means. Abbreviations are as follows: SST, Sea surface temperature; Chl *a*, Chlorophyll *a*; pH, potential hydrogen. Details on calculations are provided in the methods.

Table 2. Human population density, geography, fishing pressure and environmental differences across atolls.

	Geography		Human involvement			
	Reef area (km^2)	Land area (km^2)	Population		Human pressure [ind./reef area (km^{-2})]	Fishing pressure and activity
Atoll			1988	2011		
Rongelap	121	21.0	0	79	0.7[a]	Very low intensity and sporadic fishing of reef species (Pinca et al., 2004; EPPSO, 2011).
Ailuk	56	5.4	488	339	6.1	Subsistence fishing of reef species using low technology gear (e.g. outrigger canoes, throw nets, gill nets and handlines) to provide food for residents (Pinca, 2006; EPPSO, 2011). Mole (siganids) and other small herbivores are the preferred food fish on this atoll.
Majuro	64.2	9.7	19664	27797	433	Intense subsistence and commercial fishing of reef species using modern means (e.g. power craft) to provide food for nearly 30 000 locals and supply international export trade (Pinca, 2005; EPPSO, 2011).

[a]Rongelap Atoll only recently re-populated. Predominately uninhabited from 1954 to 2002 except for minor resettlement in 1957 and then re-evacuation in 1984. A small group of construction workers have been present since 2002; however these crews rely primarily on imported food.

Fish surveys

Coral reef fish assemblages were surveyed in July and August of 2014 with visual census surveys. Surveys were conducted on SCUBA at depths of both 10 and 3 m at 17 haphazardly selected outer reef crest sites spread evenly between the three atolls (Majuro: $n = 6$, Ailuk: $n = 5$, Rongelap: $n = 6$). These sites were spaced ∼10 km apart. For each site and depth, we identified, counted, and recorded the size of all fish larger than 10 cm along 3 replicate belt transects (250 m long × 5 m wide, 102 transects in total). Belt transects are known to occasionally overestimate abundance of large, mobile macrofauna such as sharks (Ward-Paige *et al.*, 2010), and underestimate timid or heavily fished species (Kulbicki, 1998; MacNeil *et al.*, 2008). For these reasons, we use longer 250 m transects to better estimate large species (Choat and Pears, 2003) instead of the 50-m long transects more typically used in coral reef fish surveys. The three SCUBA transects (10 m depth) were conducted on the same dive, with transects following the reef edge and separated by 50 m. The time required to complete transects is not reported as this varied according to the amount of fish in the area (Jennings and Polunin, 1996). Three matching transects (3 m depth) were conducted on the return swim. All counts were made by the same diver. We visually estimated fish size (to the nearest centimetre) and converted these to biomass values using published length–weight relationships (Froese and Pauly, 2000; Kulbicki *et al.*, 2005). Fishes were placed into three non-overlapping trophic groups according to trophic level values and published literature: top predators, mesopredators, and herbivores (Froese and Pauly, 2000; Palomares, 2000; Choat *et al.*, 2002; Stevenson *et al.*, 2007; for species list see Supplementary Table S1). Qualitative benthic assessments were made at 50 m intervals along each transect using visual estimates along each of these transects and included data on hard coral and algal cover (%), coral diversity and reef complexity (where 0 = no vertical relief, 1 = sparse low profile relief, 2 = widespread low profile relief, 3 = moderately complex, 4 = very complex with numerous cracks and caves, 5 = exceptionally complex with numerous caves, cracks, and overhangs).

Natural environment and human impacts on the atolls

Several recent studies have shown that fish assemblages may change between islands with different geomorphologies (e.g. Taylor *et al.*, 2015; Heenan *et al.*, 2016). Our islands, however, all have very similar geomorphologies. This is likely to have only minor effects on fish assemblages when compared with the pervasive impacts of fishing. In fact, most studies testing assembly patterns in coral reef assemblages over large geographical distances assume that changes in environmental conditions are

negligible compared with the human or other drivers being tested (e.g. Jennings and Polunin, 1996; Friedlander and DeMartini, 2002; Stevenson *et al.*, 2007; Sandin *et al.*, 2008). To confirm that this approach is indeed valid for our three target atolls, we quantified geographic and environmental attributes for each atoll (Tables 1 and 2) (*sensu* Sandin *et al.*, 2008). Key environmental attributes, sea surface temperature, chlorophyll a concentrations, pH, and salinity were extracted from BioORACLE (a global environmental dataset), with averages taken from 2002 to 2009 for each (Tyberghein *et al.*, 2012). The range in environmental variables among atolls in the current study was less than or equal to that for other island/atoll groups in the Pacific, including those previously used to test the effects of fishing such as the Line Islands (Stevenson *et al.*, 2007; Sandin *et al.*, 2008) and Hawaiian Islands (Friedlander and DeMartini, 2002). The atolls we surveyed are located within 4° of latitude, average monthly water temperature differs by <1 °C, and they are all predominantly affected by the eastward flowing North Pacific Equatorial Countercurrent. They are also relatively isolated from other nearby other atolls, and are fished primarily by local communities [although some illegal fishing does occur in the remote areas of the RMI by boats operating from Guam and the Philippines (Viegas, 2016)]. There are no confounding influences from land-based runoff, as the low-lying coral atolls of the RMI (average height is <2 m above sea level) are too small and porous to generate terrestrial sediment run-off (Table 2). The level of fishing pressure present at each atoll was determined from informal field interviews with local fisheries management staff and published data on the type of fishing, amount and species of fish harvested, and human population size at each atoll (Pinca *et al.*, 2004; Pinca, 2005, 2006; Beger *et al.*, 2008; Table 2). The small population (~144) on Rongelap Atoll was evacuated on 3 March 1954, because of fall-out from nuclear testing on nearby Bikini Atoll (Castle Bravo detonation, 1 March 1954). With the resulting lack of fishing pressure, diverse assemblages of fish and coral populations have thrived (Beger *et al.*, 2008; Houk and Musburger, 2013). The atoll has been largely uninhabited for the last 60 years except for an unsuccessful attempt at resettlement between 1957 and 1984. A small group of approximately 10–40 construction workers has worked intermittently on the atoll since 2002, but fishing pressure has remained very low because construction workers relied primarily on imported food. Ailuk Atoll currently supports a steady population of approximately 350 people who practise subsistence fishing using traditional vessels and techniques typically used in the Marshall Islands, such as throw nets, drag nets, scoop nets, hook and line, and fish traps (although gear used to make this equipment has been supplemented by modern materials; Petrosian-Husa, 2004). Fishermen on this atoll predominantly target small siganids known locally as "Mole" (*Siganus argenteus*), although any fish they catch will be consumed immediately, there is no refrigeration on the island. Majuro has a growing population of ca. 30 000 residents (EPPSO, 2011). Its reefs experience intense commercial fishing across all trophic levels, but especially targeting large predators using modern equipment such as powered vessels and depth sounders. The targeted fishing of sharks is now banned in the RMI, however, many are still caught as bycatch from longline vessels which operate throughout the entire region (Bromhead *et al.*, 2012).

Data analyses

We modelled variation in fish biomass (separately for trophic groups and all species combined) and included variables that relate to habitat attributes and putative human stressors. Habitat attributes used in models were: hard coral cover (%); reef complexity and depth (3 and 10 m). Other variables included in the models were atoll and distance to market/access point for each site. Distance to market was used on Majuro atoll (where commercial fishing occurs), whereas distance to access point was used on Ailuk and Rongelap where no fish markets were present, but locals all accessed the water from the same starting location. Generalized additive mixed models (GAMMs) were used to identify predictors of fish biomass (Wood, 2006). GAMMs were chosen to allow for potentially non-linear relationships, and to account for both fixed and random effects.

Site was included in all models as a random effect, to represent spatial variability within atolls that was not captured by our chosen predictor variables, and also account for the potential autocorrelation of sites from the same atoll. Model overfitting was reduced by running all possible combinations of ≤4 factors and by restricting the number of spline knots (individual polynomial functions that combine to form the GAMM smooth) to four or less ($k = 4$; Burnham and Anderson, 2002). Models were compared using the corrected Akaike information criterion (AICc) for small sample sizes (Burnham and Anderson, 2002). The relative importance of all variables included in each model set was calculated by summing weighted AICc values from each model containing the variable, where a higher value indicates a greater contribution (maximum of 1; Gilby *et al.*, 2015). Variables included in fixed effects components of the 'best-fit' model were also tested for significance ($p < 0.05$). To increase confidence in each best-fit model, they were compared with 'null' models and the number of models within two AICc units of each best-fit model is also reported. Models were implemented using the mgcv and the MuMIn packages in R (Barton, 2015; Wood, 2015).
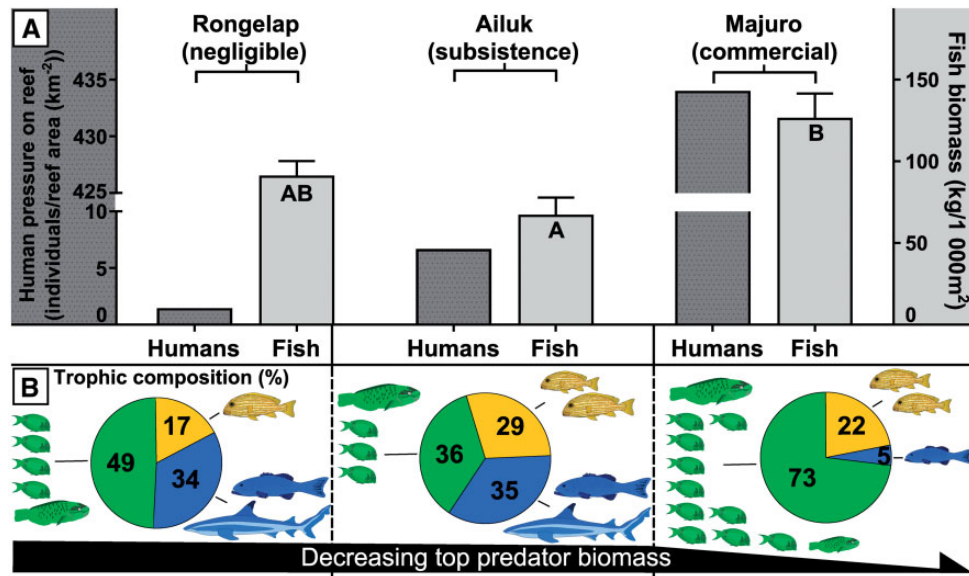
To determine if the species composition of trophic group assemblages varied among atolls, and identify species responsible for any differences, species-level biomass data were examined using permutational multivariate analysis of variance (PERMANOVA; Anderson *et al.*, 2008). Multivariate data on benthic assemblages (combined metric of coral cover, coral diversity, and algal cover) were also compared between atolls using PERMANOVA.

Pairwise tests on differences between fish assemblages for individual atolls were performed following PERMANOVA (Martin *et al.*, 2015). Canonical analysis of principal (CAP) coordinates was used to visualise differences in assemblages among atolls (Anderson and Willis, 2003). All multivariate analyses were based on modified Gower (log base 2) similarity measures, which, by allocating equal weights to compositional changes in species and doubling weight to changes in abundances, emphasize changes in species abundance and cope well with multivariate heterogeneity of variance (Anderson *et al.*, 2011). To meet normality assumptions all biomass data were transformed using an Ln ($x + 1$) transformation.

Results

Fish biomass varied among atolls for all trophic groups (Figure 2; Table 2). Overall fish biomass was highest (126 kg 1000 m^{-2}) at the commercially fished Majuro Atoll, intermediate (91 kg 1000

Figure 2. Differences in fishing pressure, fish biomass, and assemblage composition among atolls (in each panel: Rongelap, left; Ailuk, middle; Majuro, right). (a) Number of people on each atoll (dark grey bars, left *y*-axis) and corresponding fish biomass (light grey bars, right *y*-axis). Different letters at the top of bars illustrate significant differences between atolls (b). Percentage contribution of trophic groups to total fish biomass. Trophic composition did not vary between Rongelap and Ailuk ($p = 0.46$), but differed between Majuro and both Rongelap ($p = 0.01$) and Ailuk ($p = 0.02$). Symbols courtesy of the Integration and Application Network, ian.umces.edu/symbols/.

m^{-2}) at near-pristine Rongelap, and lowest (67 kg 1000 m^{-2}) at Ailuk, where subsistence fishing using traditional techniques is practised by approximately 350 locals (Figure 2).

The composition and biomass of each trophic group also differed among atolls (Figure 3). Top predators, such as grey reef sharks (*Carcharhinus amblyrhynchos*), were a dominant component of the fish community at Rongelap and Ailuk, where they comprised 34 and 35% of total fish biomass (Figures 2 and 3). In contrast, sharks and other top predators were rare at the commercially fished Majuro Atoll, where they made up only 5% of total fish biomass (Figure 2). Very low numbers of top predators on reefs at Majuro were juxtaposed by a significantly greater biomass of herbivorous fish. Herbivorous fish dominated the fish community at the commercially-fished Majuro Atoll, where they comprised 73% of total fish biomass; a substantial difference compared with the near-pristine Rongelap (49%), and subsistence-fished Ailuk (36%) atolls (Figure 2). Differences in herbivore assemblages among atolls were mainly owing to a greater biomass of surgeonfish (Acanthuridae) at Majuro Atoll (Figure 3).
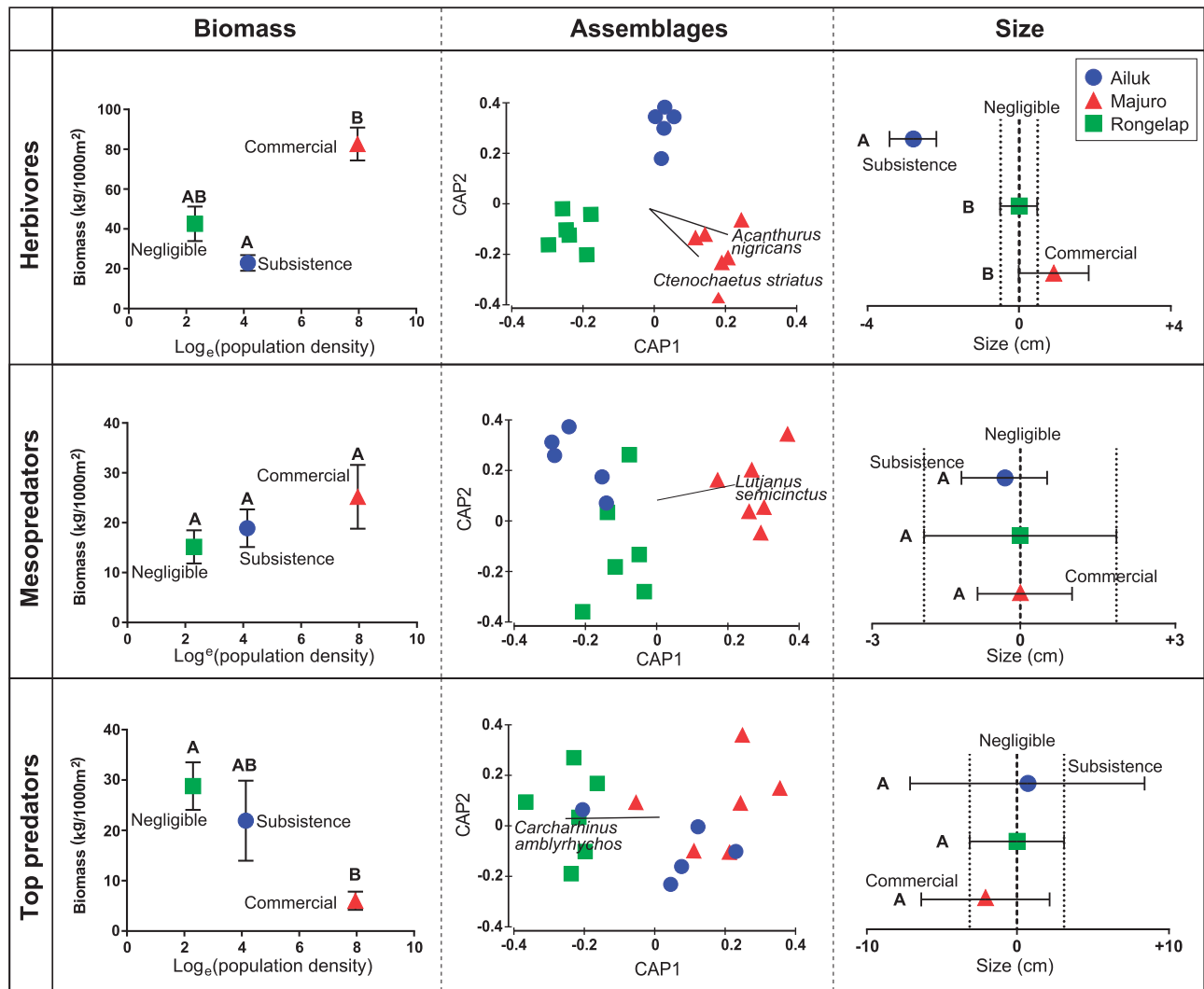
Coral cover, complexity, and depth did not significantly affect fish biomass for any trophic groups (Table 2). Distance to market/access point significantly affected all fish and mesopredator biomass (Table 2), where sites far from markets/access points had increased mesopredator and overall fish biomass (Supplementary Figure S1). Benthic reef assemblages differed between Majuro and Rongelap ($p = 0.01$) and Majuro and Ailuk ($p = 0.04$), but not for Ailuk and Rongelap ($p = 0.08$) (Figure 4; Table 3).

Discussion

This study identified fundamental differences in how commercial and subsistence harvesting affects coral reef fish on Pacific atolls in the Marshall Islands. We show that subsistence fishing by a small community using traditional gear does not dramatically alter the biomass or trophic composition of reef fish assemblages from a near-pristine state, or result in cascading ecosystem-level effects that are routinely associated with commercial harvesting of top predators. Counter-intuitively, we discover that although overall biomass was highest in the highly fished atoll of Majuro, its community was dominated by herbivores, suggesting that high overall biomass can sometimes be misleading indicator of fishing impact level. Our results suggest that impacts of fishing on reefs can depend on the style and intensity of fishing practised and the type of organisms targeted at each atoll.

Fish assemblages at Ailuk Atoll were dominated by small herbivorous fish, which are locally preferred food fishes (Petrosian-Husa, 2004). Small herbivorous fishes (i.e. rabbitfish, surgeonfish and parrotfish) typically have rapid population doubling times (between 1.5 and 4 years), which means they are less vulnerable to over-fishing than larger-bodied predators (i.e. groupers, snappers, and sharks) that grow more slowly and are longer-lived (Froese and Pauly, 2000). There are, however, two issues with harvesting fish from lower trophic levels: (i) prey limitation of predatory fishes and (ii) loss of the ecological functions these fishes perform. Higher-order predators rely on smaller fish species for food; fisheries that remove 'prey' fish can, therefore, indirectly affect populations of their predators (Smith *et al.*, 2010). Top predators were abundant under both low-pressure subsistence fishing and negligible fishing, suggesting that low levels of subsistence fishing has not reduced top-predator populations. Herbivorous fishes also maintain coral reef health by consuming algae that could otherwise overgrow corals; fisheries that remove herbivores can therefore alter reef functioning (Edwards *et al.*, 2014). There was no difference between the benthic reef assemblages of Ailuk and Rongelap atolls (Figure 4), indicating that there was no compensatory effect between atolls owing to different benthos. Given low-pressure subsistence fishing practices, and

Figure 3. Trophic group biomass, assemblage composition, and size on each of the three atolls. Fishing levels at each atoll: Ailuk, subsistence; Majuro, commercial; Rongelap, negligible. Left: biomass plots represent total biomass of each trophic group vs. human population density for each atoll. Note *x*- and y-axis scales vary among panels. Middle: constrained canonical analysis of principal co-ordinates (CAP) ordinations illustrating differences in trophic group composition among atolls. Species correlations with canonical axes are represented as vectors for species with Pearson *R* > 0.7; e.g. *Acanthurus nigricans* and *Ctenochaetus striatus* (herbivores) are positively correlated with Majuro Atoll. Right: Size plots represent average body sizes of fish plotted as differences from pristine (Rongelap). Letters above and beside data points illustrate significant differences between atolls.

isolation from commercial markets we suggest that Ailuk Atoll's fish assemblages and reefs have not been strongly and persistently altered by humans. This finding suggests that in some cases, Pacific atolls may be able to support subsistence fishing by small communities while still retaining healthy reef and fish assemblages. However, the exact thresholds in the amount of fishing that can be sustained will vary according to environmental characteristics and population sizes of atolls and will require larger sampling sizes to elucidate.
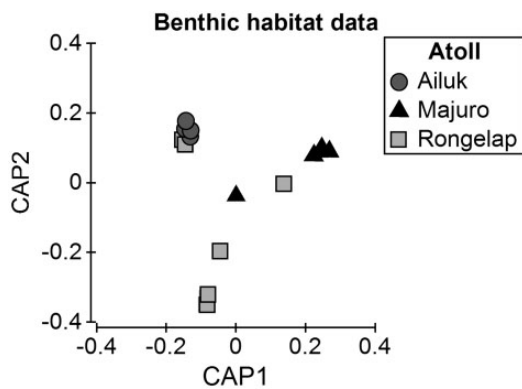
Despite having the highest fishing pressure, Majuro Atoll supported the greatest biomass of fish (39–89% higher than other atolls), a result that has not been reported on other heavily fished Pacific atolls (Friedlander and DeMartini, 2002; Stevenson *et al.*, 2007; Sandin *et al.*, 2008; Pinca *et al.*, 2012; Williams *et al.*, 2015). Reef fish assemblages at Majuro were, however, dominated by herbivores and contained far fewer top

predators (70% less) than either the unfished or low-pressure subsistence-fished atolls. This novel result challenges the perception that fished reefs support less biomass than unfished reefs (MacNeil *et al.*, 2015), therefore suggesting that studies which focus solely on total biomass changes may present a misleading picture of how fishing impacts food webs. Cascading trophic impacts from commercial fishing, such as this, are common on coral reefs and are often cited as the mechanism behind both increases in the abundance of fish from lower trophic levels (i.e. mesopredators or herbivores), and declines in the health of heavily fished reefs (Friedlander and DeMartini, 2002; DeMartini and Smith, 2015). Nevertheless, our findings suggest that fishers on Majuro Atoll have not yet started to "fish down the food web" (Pauly *et al.*, 1998). If local fishers increase their catch rates of small herbivorous fish, while continuing to remove top predators, overall fish biomass is likely to decline and

Table 3. Best-fit models for fish biomass across all atolls (site included as a random variable across all models).

Trophic group	Variables included in best fit model and their relative importance across all possible GAMM models (RVI)	R^2	AIC	Significant variables in best fit model ($p < 0.05$)
All fish	Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)	0.26	2 146	Atoll, distance to market/access point
Herbivores	Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)	0.25	2 037	Atoll
Mesopredators	Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)	0.21	2 049	Atoll, distance to market/access point
Top predators	Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)	0.13	1 653	Atoll

Relative variable importance (RVI), calculated by summing Akaike variable weights for all possible GAMM models containing that variable, is given in parentheses. Larger RVI values indicate greater correlations between variable and fish biomass (maximum of 1). All models had 10 degrees of freedom. All trophic groups had zero secondary models within two ΔAICc units of the best-fit model. In addition, null models for each trophic group were compared with the final best-fit model. In each case, null models showed vastly decreased explanatory power (>80 ΔAICc units) for each trophic group.

Figure 4. Constrained canonical analysis of principal co-ordinates (CAP) ordination illustrating the effect of atoll on benthic habitat data (normalised coral cover, coral diversity and algal cover; $\delta = 0.80$, $m = 2$, LoA = 73%).

some ecosystem functioning of Majuro's reefs may be compromised in the future (Edwards *et al.*, 2014).

The removal of top predators from reefs at Majuro Atoll may have released herbivores, like the white-cheek surgeonfish (*Acanthurus nigricans*), from top-down regulation of their abundance and biomass (Houk and Musburger, 2013). Compounding this, despite negligible sediment runoff throughout the entire RMI (owing to small land area and lack of agriculture, rivers and creeks), are strong impacts of sewage and leachates from solid waste in Majuro, which has a considerable waste management problem (Richards and Beger, 2011). Herbivores at Majuro are, therefore, also likely benefiting from an over-abundance of algae. This is supported by findings that reefs at Majuro have different benthic assemblages than those at Rongelap and Ailuk, Figure 4, which may mean that unlike at Rongelap and Ailuk, herbivore populations at Majuro are unlikely to be limited by bottom-up processes (Smith *et al.*, 2010). White-cheek surgeonfish are the dominant herbivore on reefs at Majuro; they browse on macroalgae (Choat *et al.*, 2002) and may, therefore, thrive on reefs that are impacted by nutrient stress. This has been documented on other Pacific reefs, where surgeonfish are hyper-abundant and dominate fish biomass near large human settlements (Pinca *et al.*, 2012; Houk and Musburger, 2013). The high biomass of browsing herbivorous fish at Majuro Atoll is therefore likely a joint response to the removal of their predators by humans and the positive effects of nutrients on the abundance of their food.

Human communities on coral islands rely on reef fish for their protein and income. To manage their reef fisheries effectively, it is critical that we understand how variation in the style and intensity of fishing practised and the type of organisms targeted regulate the biomass and trophic structure of fish assemblages. We show that in the Marshall Islands, commercial fishing can remove large predators, promoting populations of herbivorous 'prey' fishes and thereby enhancing total fish biomass in the system. Studies that seek to quantify fishing impacts in marine ecosystems should, therefore, test for changes in the trophic composition of assemblages rather than focusing solely on variation in fish biomass. Although exact thresholds in fishing pressure would vary between atolls, our findings suggest that isolated coral atolls may be able to support subsistence fishing by small human communities while still retaining healthy reef and fish assemblages.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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