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Size-structural shifts reveal intensity of exploitation in coral reef fisheries



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ABSTRACT

Fisheries exploitation represents a considerable threat to coral reef fish resources because even modest levels of extraction can alter ecological dynamics via shifts of stock size, species composition, and size-structure of the fish assemblage. Although species occupying higher trophic groups are known to suffer the majority of exploitative effects, changes in composition among lower trophic groups may be major, though are not frequently explored. Using size-based biomass spectrum analysis, we investigate the effects of fishing on the size-structure of coral reef fish assemblages spanning four geopolitical regions and determine if patterns of exploitation vary across trophic groups. Our analyses reveal striking evidence for the variety of effects fisheries exploitation can have on coral reef fish assemblages. When examining biomass spectra across the entire fish assemblage we found consistent evidence of size-specific exploitation, in which large-bodied individuals experience disproportionate reductions. The pattern was paralleled by and likely driven by, strongly size-specific reductions among top predators. In contrast, evidence of exploitation patterns was variable among lower trophic groups, in many cases including evidence of reductions across all size classes. The breadth of size classes and trophic groups that showed evidence of exploitation related positively to local human population density and diversity of fishing methods employed. Our findings highlight the complexity of coral reef fisheries and that the effects of exploitation on coral reefs can be realized throughout the entire fish assemblage, across multiple trophic groups and not solely restricted to large-bodied top-predators. Size-specific changes among fishes of lower trophic groups likely lead to altered ecological functioning of heavily exploited coral reefs. Together these findings reinforce the value of taking a multi-trophic group approach to monitoring and managing coral reef fisheries.

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1. Introduction

Body size is a fundamental attribute of an organism and thus size distributions have important meaning to the structure and dynamics of ecological communities (Calder, 1984; Kleiber, 1947; Peters, 1983). Many life history characteristics including growth, age at maturity, reproductive output, and lifespan are related to body size. For example, large-bodied species tend to exhibit slow growth, late maturation, and long lifespan (Adams, 1980; Stearns, 1992). Additionally, body size has important implications for predator-prey dynamics, foraging behavior, home range, and interspecific competition (Calder, 1984; Peters, 1983). Large-bodied species play a fundamental role in structuring communities because they tend to forage over large areas, occupy higher trophic levels, and can be better competitors for resources (Jennings et al., 2001; Peters 1983).

However, many of these ecological characteristics make larger-bodied species vulnerable to exploitation and extinction (Dulvy et al., 2003; Zgliczynski et al., 2013).

The role that humans play in extinctions and defaunation has been the topic of considerable debate (Barnosky et al., 2004; Koch and Barnosky 2006). Today it is widely accepted that the global geographic expansion of humans is closely linked with the loss of many species from ecological communities (McCauley et al., 2015; Sandom et al., 2014). These losses can be attributed to the modernization of size-selective hunting practices that tend to target large-bodied species that often occupy higher trophic levels (Darimont et al., 2015; Jennings and Kaiser 1998; Worm 2015). In doing so, the animal assemblage shifts to one that is characterized by smaller-bodied lower trophic level species (Pauly et al., 1998; Terborgh and Estes 2010). Thus, size-based and trophic-based assessments of species assemblages serve as an important metric for assessing the effects of exploitation.

In marine communities size-based assessments have proven to be invaluable analytical tools for assessing the effects of fisheries

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exploitation (Dulvy et al., 2004; Graham et al., 2005; Jennings et al., 2002). However, in most cases, size-based assessments are conducted on entire fish assemblages, ignoring possible differences in size–frequency relationships between different trophic groups (e.g., predators versus herbivores). The rationale here is that higher trophic levels are composed of larger-bodied individuals, a pattern that is common in many pelagic fisheries (Jennings et al., 2001). Such positive scaling of body size and trophic level is expected in single-channel trophic systems (e.g., single primary food source and step-wise predation through subsequent trophic levels). The positive scaling is further reinforced among fishes, where predation is realized through gape-limited predation, namely only prey that fit whole (or mostly whole) in the predator's mouth. However, such a clear linkage between body size and trophic level breaks down in many coastal fish assemblages, likely linked with the availability of more diverse trophic resources (e.g., plankton, benthic primary producers, benthic infauna). With more trophic pathways, there is capacity for the development of broad size distributions among fishes in multiple trophic groups. As such, size-based assessments without regard for trophic groupings may be insufficient to interpret fully the specifics of exploitation, especially when attempting to separate patterns of exploitation as a function of size versus a function of trophic level.

On coral reefs, systems with little-to-no exploitation are characterized by an abundance of large-bodied predatory species that compose a significant proportion of total fish biomass (Friedlander and DeMartini, 2002; Sandin et al., 2008) (Fig. A1). As exploitation increases, the resultant structure of the assemblage becomes less dominated by large-bodied fishes and predators, and shifts to an assemblage comprised of small-bodied fishes and lower trophic level species (Dalzell, 1996; Jennings and Polunin, 1996a,b; Munro 1996). Many assessments of size-structural shift among reef fisheries thus focus the conclusions primarily on the importance of removal of large-bodied predators (Graham et al., 2007; Polunin and Roberts 1996). However, important fisheries exist for many taxa on coral reefs, including but not limited to predators (Dalzell 1996; Dalzell et al., 1996; Fenner 2014). For instance, in many regions, spear fisheries and the live reef fish trade target “dinner plate sized” fishes across trophic groups (Edwards et al., 2014; Sadovy et al., 2003; Sadovy de Mitcheson and Yin, 2015). Traps and nets are known to capture fishes almost indiscriminately across size and trophic group (Dalzell 1996; Dalzell et al., 1996; Hawkins et al., 2007; Jennings and Kaiser 1998; Mahon and Hunte 2001;), and small-scale and artisanal fisheries rarely discard non-target landings (Hawkins and Roberts, 2004; Jacquet and Pauly, 2008). At the further extreme of size-structure, active ornamental fisheries for aquaria can target even the smallest fishes (Fujita et al., 2014; Rhyne et al., 2012; Tissot and Hallacher 2003). Thus, analyses focused purely on shifts in total biomass or reductions of predator stocks lack resolution to explore emergent multi-trophic impacts of exploitation within diverse reef fisheries.

Size-based assessments have gained popularity over last decade and much of their attention has focused the direct effects of exploitation to the fish community. However, an important question remains – how are the effects of fisheries exploitation revealed across and within trophic groups of the fish assemblage? Is there evidence of variation in size-based change that is distinct across trophic groups or that is linked to intensity of exploitation? To address these questions we explore the effects of varying levels of exploitation on the size-structure of coral reef fish assemblages at both a whole-assemblage and a functional group (trophic group) resolution across four geopolitical regions of the tropical Pacific. Using metrics derived from size-based biomass spectrum analysis, we examine the effects of exploitation on the size-structure of reef fish assemblages and determine if there is evidence multiple forms of fishing realized in coral reef ecosystems, and if so whether there

is variation of patterning linked with region-specific patterns of exploitation.

2. Materials and methods

2.1. Study sites

To examine changes in the size-structure of reef fish assemblages we analyzed quantitative survey data collected from 49 islands, atolls and reefs (hereafter referred to as islands) spanning the equatorial Pacific (Fig. 1; Appendix A of Supplementary material). These islands are located within 4 distinct geopolitical regions: American Samoa, Hawaiian Archipelago, Mariana Archipelago, and the Pacific Remote Islands. Within each geopolitical region we analyzed multiple elements of the fish assemblage, contrasting assemblage structure between inhabited and remote islands. As such, we present four parallel sets of analyses, one for each region, using island-scale means of assemblage structure as statistical replicates.

Islands were classified as either “inhabited” ($n = 19$) or “remote” ($n = 30$) based on the supposition that human population presence serves as a first-order proxy for fisheries exploitation (DeMartini et al., 2008; Williams et al., 2011). Islands were classified as remote if they supported no permanent human population, were geographically located at least 100 km away from population centers, or had management plans in place restricting nearshore fisheries (e.g., Marine National Monument or National Wildlife Reserve). Conversely, islands were classified as inhabited if they supported permanent human populations and there was a documented or reasonable expectation that the islands were exposed to fisheries exploitation. Each region, included at least two island replicates of each population classification (i.e., inhabited and remote). See Appendix A of Supplementary material for further details regarding island classifications.

2.2. Survey methods

Quantitative underwater surveys (belt transect surveys) of reef fish assemblages were conducted at all islands with the methodological details described elsewhere (DeMartini et al., 2008; Friedlander et al., 2010; Sandin et al., 2008). Belt transect surveys are a reliable fishery independent method of assessing density of non-cryptic fish taxa, enumerating the vast majority of biomass density of fishes in nearshore environments (Edgar et al., 2004; Mapstone and Ayling, 1998). The reported underestimation of cryptic fishes by underwater visual surveys (Willis, 2001) involve principally the smallest size classes of the fish assemblage (<5 cm Total Length) that contribute very little to the biomass density (Bellwood and Alcala, 1988). In practice, belt transect are reported to be the most commonly used methods for underwater visual censuses of reef fishes (Caldwell et al., 2016).

Surveys were restricted to the forereef slope at depths between 8 and 15 m. The unit of replication within islands was the station. A total of 1307 stations were included in this assessment, 787 stations from remote islands and 520 from inhabited islands. Data were aggregated from multiple region-specific research expeditions across the study timeline (2002–2012), with an average of 3.8 (1.7 SD) survey time points (or sampling years) completed per island. Note that there were no dramatic shifts in levels of island habitation or of fish assemblage structure across survey years for any island in this study. Fishes identified during surveys were assigned to one of five trophic groups (Top-predators [Sharks], Top-predators [Bony Fishes], Mid-level Carnivores, Planktivores, and Herbivores) based on web-based (i.e., www.fishbase.org) and published references (Myers 1999; Randall 2005, 2007).

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