

Marine fisheries declines viewed upside down: human impacts on consumer-driven nutrient recycling

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Abstract. We quantified how two human impacts (overfishing and habitat fragmentation) in nearshore marine ecosystems may affect ecosystem function by altering the role of fish as nutrient vectors. We empirically quantified size-specific excretion rates of one of the most abundant fishes (gray snapper, *Lutjanus griseus*) in The Bahamas and combined these with surveys of fish abundance to estimate population-level excretion rates. The study was conducted across gradients of two human disturbances: overfishing and ecosystem fragmentation (estuaries bisected by roads), to evaluate how each could result in reduced population-level nutrient cycling by consumers. Mean estimated N and P excretion rates for gray snapper populations were on average 456% and 541% higher, respectively, in unfished sites. Ecosystem fragmentation resulted in significant reductions of recycling rates by snapper, with degree of creek fragmentation explaining 86% and 72% of the variance in estimated excretion for dissolved N and P, respectively. Additionally, we used nutrient limitation assays and primary producer nutrient content to provide a simple example of how marine fishery declines may affect primary production. This study provides an initial step toward integrating marine fishery declines and consumer-driven nutrient recycling to more fully understand the implications of human impacts in marine ecosystems.

Key words: bottom-up; ecosystem fragmentation; estuary; food web; mangrove; nitrogen; overfishing; phosphorus; primary production; seagrass.

INTRODUCTION

Humans have radically altered the function of coastal ecosystems. Collapse of fisheries, largely driven by overexploitation and habitat alteration (Lotze et al. 2006), is one of the most troubling trends. Large predatory fishes are especially susceptible (Pauly et al. 1998), with models suggesting current abundance may be as much as 99% below historic levels in some regions (Jennings and Blanchard 2004). Loss of predatory fishes can lead to dramatic shifts in ecosystem function through cascading, top-down, mechanisms (e.g., Jackson et al. 2001). For example, overexploitation of cod has significantly altered the abundance of organisms at lower trophic levels and, through multiple pathways, affected productivity of coastal seas in which cod were once the dominant top predator (Frank et al. 2005).

In addition to top-down controls on the abundance of organisms, fishes fill other functional roles in ecosystems. Namely, through the physiological processes of consumption, assimilation and regeneration, fishes recycle nutrients into forms that are readily available for biological uptake by heterotrophic microorganisms

and primary producers (Sterner and Elser 2002). This consumer-driven nutrient recycling may contribute a substantial proportion of ecosystem nutrient demand under conditions of low ambient nutrient concentrations and/or high fish biomass (Vanni 2002, McIntyre et al. 2008). The role of fishes as nutrient recyclers has been demonstrated to be critical in many freshwater systems, supplying up to 80% of the nutrient demand for primary producers and serving as important vectors of nutrient transport across ecosystem boundaries (Vanni 2002). In marine systems, grunts (Haemulidae) are the most well-known example, whereby the fishes translocate nutrients to coral reefs after feeding bouts in nearby seagrass beds (Meyer et al. 1983). At a global scale, Maranger et al. (2008) suggested that commercial marine fisheries have altered nitrogen cycling through removal of nitrogen stored in fish tissues, which has an especially important effect in regions where anthropogenic nutrient loading is relatively low.

Our goal in this study was to bridge two focal areas in marine ecology: (1) fishery declines and (2) functional roles of fish with respect to ecosystem function. Specifically, we addressed implications of fishery declines for the role of fish in affecting nutrient availability for primary production. We quantified size-specific excretion rates of one of the most abundant fishes (gray snapper, *Lutjanus griseus*) in The Bahamas and we

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scaled these data to population-level excretion rate estimates across gradients of the two most prominent impacts to coastal ecosystems: overfishing and habitat alteration (see Plate 1). Our findings provide a novel advance in elucidating how marine fishery declines may affect ecosystem function through mechanistic pathways that remain underappreciated in marine systems.

METHODS

We used empirically derived excretion measures, and field surveys of fish abundance, to estimate mean areal (per unit area) excretion rates. Our study species was the gray snapper (*Lutjanus griseus* Linnaeus), an ecologically and economically important fish species, that is one of the most dominant fishes (in terms of abundance, biomass, and production) in Bahamian tidal creeks regardless of the degree of human impact (Layman et al. 2007, Valentine-Rose et al. 2007). Excretion rates of gray snapper were determined in situ following the methodologies of Schaus et al. (1997) as modified by Whiles et al. (2009; see Appendix A for complete methods).

To scale-up excretion rates of individual fish to areal estimates of population-level excretion, we conducted extensive visual surveys of snapper abundance in Bahamas tidal creek habitats. These systems are clear-water, mangrove-lined, ecosystems formed from scouring of calcareous rock substrate, and are dominated by marine tidal exchange with little freshwater input (Layman et al. 2007, Valentine-Rose et al. 2007, Allgeier et al. 2010). During high tide, incoming water inundates extensive, intertidal flats. During low tide, water is restricted to the main creek channels, providing permanent habitat for fishes, typically along the mangrove-lined channel fringes. Fish survey methods followed well-established protocols (Appendix A).

Across relatively small spatial scales in The Bahamas, substantial gradients exist in human population density and relative degree of human impact. This gradient is particularly pronounced on Andros, the largest Bahamian island and one of the largest in the Caribbean (Fig. 1). West Andros sites surveyed have practically no fishing pressure, with the nearest human inhabited areas >18 km by boat. Sites along the eastern coast of Andros are fished by artisanal and recreational fishers with access points to systems always < 0.1 km away from human settlements. Otherwise, creek characteristics are similar on the two sides of the island. West Andros (unfished) sites ($n = 27$) were chosen at random as part of a rapid ecological assessment (Nature Conservancy 2006), while all unfragmented tidal creeks on East Andros were surveyed ($n = 22$).

Our second measure of human impact, ecosystem fragmentation, was quantified empirically following recent studies (Layman et al. 2007). Ecosystem fragmentation results from the construction of roads, typically near the tidal creek mouth, that lack bridges

or culverts to allow for tidal exchange (Layman et al. 2004). We quantified percent fragmentation as the reduction in mean daily tidal amplitude at each survey site due to the anthropogenic source of fragmentation (Layman et al. 2007). This measure represents the overall degree of hydrologic connectivity between interior wetlands and the marine environment. All sites for the fragmentation analysis were located on East Andros to control for relative degree of fishing pressure, and we selected a subset of all available sites ($n = 11$) that best controlled for other factors (e.g., creek size, maximum depth) that may affect fish densities.

A single multivariate model, i.e., simultaneously analyzing fishing pressure and fragmentation and their interaction, was not employed because of the nature of the underlying data set. All West Andros sites have low fishing pressure and are unfragmented. As such, a gradient of fishing pressure is based only on unfragmented systems from west to east across the island. On East Andros, all sites, irrespective of fragmentation, are fished (C. A. Layman, *personal observation*). Thus, effects of fragmentation are evaluated within a subset of sites with similar fishing pressure to provide a relative indication of how fragmentation may further affect consumer nutrient recycling.

To provide an empirical example of the effects of reduced fish densities, we employed nutrient diffusing substrates (NDS) along a spatial gradient of gray snapper density within a single, unfragmented, tidal creek ecosystem. NDS are commonly used to measure nutrient limitation for primary production (Tank et al. 2007, Allgeier et al. 2010). NDS are experimental units containing a nutrient enriched agar that diffuses through a surface (fritted glass disks) upon which primary producers can colonize. The treatment that shows the greatest response of algal biomass, i.e., highest value of chlorophyll *a* per surface area, indicates which nutrient is most limiting. We used four NDS treatments: nitrogen (0.5 mol/L NH_4Cl), phosphorus (0.5 mol/L KH_2PO_4), nitrogen and phosphorus (0.5 mol/L NH_4Cl + 0.5 mol/L KH_2PO_4), and a control (agar only; see Appendix B). While NDS experiments provide an assessment of short-term limitation (days to weeks), seagrass nutrient content allows for assessment of longer term nutrient availability because of their potential for luxury nutrient uptake (Duarte 1992). We assessed nutrient content of seagrass, blade height, and blade density to provide complementary information on nutrient availability across the gradient of fish density (Appendix B). Ambient nutrient measurements were not included in this study because nutrient demand and instantaneous nutrient uptake are so high, and ambient availability is so low, that nutrient limitation assays and nutrient content of seagrasses are a better proxy for local scale nutrient dynamics (Koch and Madden 2001, Allgeier et al. 2010).

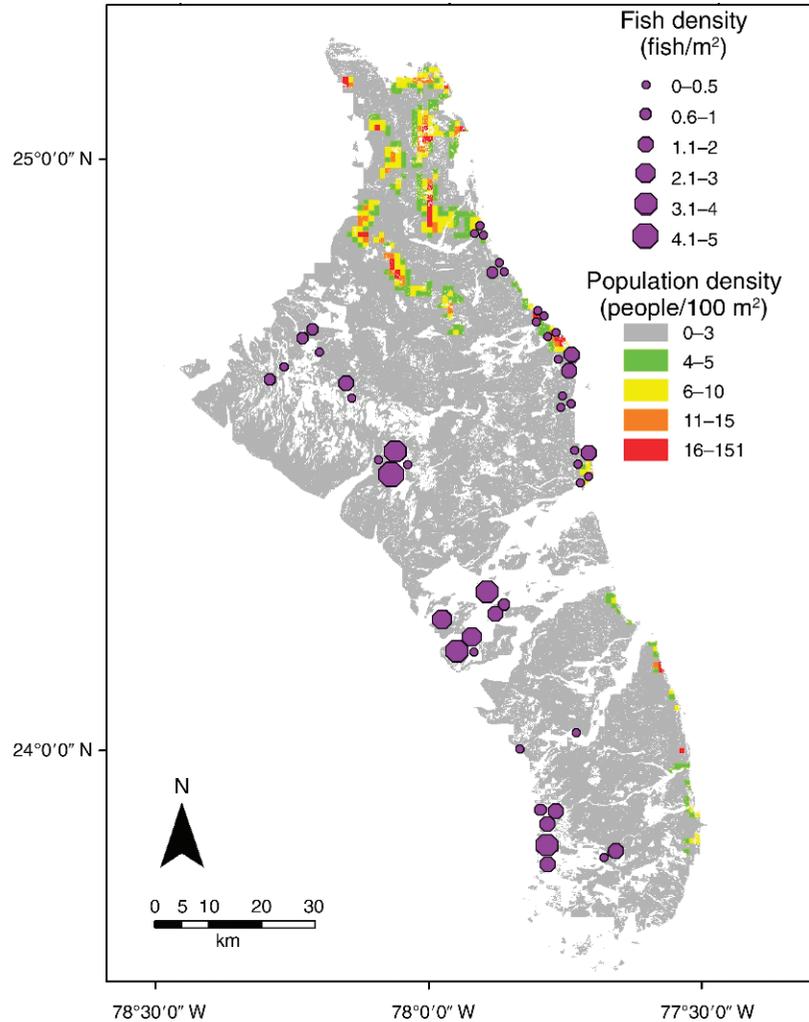


FIG. 1. Map of Andros Island, Bahamas, depicting human population density and site-specific snapper density. Population density, color coded, is concentrated along the east coast and the northern interior. Each circle represents a single survey site, and the size of the circles indicates density of gray snapper *Lutjanus griseus*.

RESULTS

We measured excretion rates of dissolved nitrogen (ammonium, NH₄-N) and phosphorus (total dissolved phosphorus, TDP-P) on 50 gray snapper ranging 80–380 mm (total length, TL) and 4.4–512 g. Estimated excretion rates of fish ranged from 128 to 12 530 μg NH₄/h and 4.3 to 596 μg TDP/h. Excretion rates were positively correlated to fish mass (NH₄ R² = 0.89, P < 0.001; TDP R² = 0.35, P < 0.001; Appendix A).

Mean fish densities were significantly greater (t = 4.1, df = 47, P < 0.001) on West Andros (unfished) than East Andros (fished) (1.35 ± 0.23 individuals/m² and 0.23 ± 0.07 individuals/m², respectively; Fig. 1). Densities were as high as 4.3 individuals/m² (337 g/m²) in unfished sites, i.e., 255 gray snapper (20 218 g) per 30 × 2 m transect. Mean density of fishes > 25 cm TL was 11× greater in west vs. east sites (0.013 large individuals/m² east side

vs. 0.16 individuals/m² west side). Size structure of east and west side populations, across all surveys sites, differed significantly (Kolmogorov-Smirnov test, D = 0.15, P < 0.001, Appendix C), largely because of the presence of individuals in larger size classes on West Andros.

Fishing pressure resulted in significantly lower estimated areal excretion rates for both NH₄ and TDP (NH₄, t = 4.2, df = 47, P < 0.001; TDP, t = 4.3, df = 47, P < 0.001; Fig. 2A, B). Mean NH₄ and TDP excretion rates were on average 456% and 541% higher, respectively, in the unfished sites (means ± SE: NH₄, 2487 ± 447 vs. 355 ± 110 μg·m⁻²·h⁻¹; TDP, 77 ± 13 vs. 11 ± 4 μg·m⁻²·h⁻¹). We estimated rates as high as 7423 μg·m⁻²·h⁻¹ NH₄ and 221 μg·m⁻²·h⁻¹ TDP in unfished sites. Examining sites only on east Andros across a gradient of fragmentation, we found that this human impact resulted in significant reductions of recycling rates



PLATE 1. (left) Overfishing and (right) habitat alteration, e.g., tidal creek fragmentation, are two of the most critical human impacts in coastal systems of The Bahamas. Photo credits: C. A. Layman.

for NH_4 (total range from 27 167 to 0 $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{hour}^{-1}$) and TDP (from 70 to 0 $\mu\text{g TDP}\cdot\text{m}^{-2}\cdot\text{hour}^{-1}$). Estimated excretion was negatively correlated with degree of creek fragmentation, with fragmentation explaining 86% and 72% of the variance in estimated excretion for NH_4 and TDP, respectively (Fig. 2C, D). This effect was driven by both reduced fish densities and shifts in size structure to smaller individuals (Appendix D).

We found a significant negative linear relationship between algal response to the combined N and P treatment and snapper biomass ($R^2 = 0.64$, $P = 0.03$; Appendix E). We also found a positive (marginally significant) linear relationship between algal response to the N treatment and snapper biomass ($R^2 = 0.47$, $P = 0.08$). These data indicate that the nature of nutrient limitation was altered across a gradient in fish biomass whereby the strength of N and P co-limitation decreased at sites with higher fish biomass and N limitation concomitantly increased (Allgeier et al. 2010). This suggests sites with higher fish biomass should have greater availability of ambient P, which is supported by the significantly higher %P content in seagrass tissues at these sites ($R^2 = 0.60$, $P = 0.04$; see Appendix E for all results). The importance of fish excretion for ecosystem function is also suggested by apparent relationships of seagrass blade density and length with gray snapper biomass (density $R^2 = 0.43$, $P = 0.09$; length $R^2 = 0.60$, $P = 0.04$).

DISCUSSION

Our study demonstrates how human impacts can dramatically alter nutrient availability in coastal ecosystems. Fish nutrient recycling is predicted to be most important under conditions of low ambient nutrient concentrations, high nutrient demand by primary producers, and high abundance and/or diversity of fishes (Vanni 2002, McIntyre et al. 2008), all of which characterize Bahamian coastal ecosystems. Shallow waters in the Bahamas are extremely oligotrophic (0.1–17 $\mu\text{g/L NH}_4\text{-N}$, 0.3–4 $\mu\text{g/L TDP-P}$; Allgeier et al. 2010,

Koch and Madden 2001), and given the extensive coverage and high biomass of seagrasses, macroalgae, and epiphytic algae (Koch and Madden 2001, Lapointe et al. 2004), uptake rates of nutrients are presumed to be high. Additionally, fish assemblages are extremely diverse (Layman et al. 2004), and secondary production is relatively high (Valentine-Rose et al. 2007), in tidal creeks. These factors, supported by previous research linking fish nutrient recycling and the incipient development of seagrass beds (Alevizon 2002) and nutrient content of seagrasses (Koch and Madden 2001), implicate consumers as an important nutrient source for primary producers in this system.

Our empirical data across a gradient of fish densities provided one example of the potential implications of reduced fish biomass for ecosystem function. Lower fish biomass (and thus lower N and P excretion rates) enhanced dual nutrient limitation. The presumed mechanism is that fish, via excretion, enrich the local environment with P to the degree that they are fulfilling the primary producer demand for this nutrient. Thus, with higher fish biomass, primary producers become less co-limited and N limitation increases. We corroborate these findings by demonstrating correlations between fish biomass and enhanced P nutrient content of *Thalassia*, as well as higher seagrass blade density and height (Appendix E). Though we did not mechanistically test implications of fish excretion through direct experimentation, our combined findings strongly support the notion that fish affect ecosystem function through the mechanism of nutrient recycling.

Gray snapper typically utilize the mangrove fringe of tidal creeks during the day as shelter, and forage by night in adjacent seagrass beds and sand flat habitats. As such, our numbers represent estimated per unit area nutrient excretion by gray snapper during their daytime shelter period. Yet, because excretion rates are directly linked to metabolism, swimming during active foraging bouts at night (over tens of meters) may enhance the

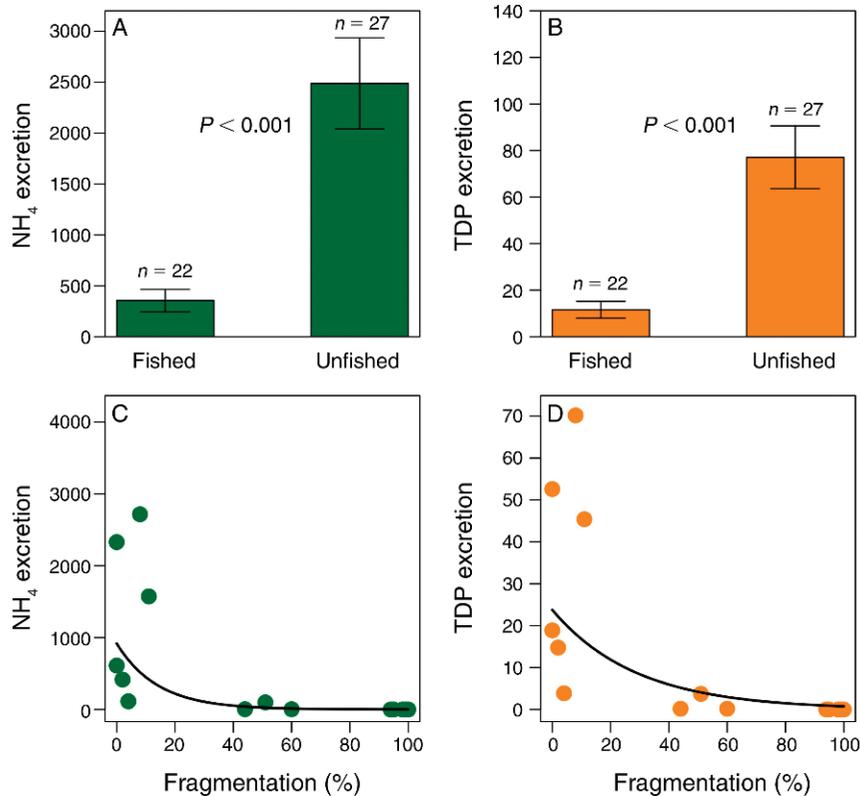


FIG. 2. Estimated excretion rates across gradients of human impact. Nutrients are measured as $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ for $\text{NH}_4\text{-N}$ and TDP-P. Graphs represent nutrient excretion rates as (A, B) a comparison between east (fished) and west (unfished) and (C, D) a function of percent fragmentation of tidal creek ecosystems on East Andros. Error bars represent $\pm\text{SE}$.

degree to which nutrients are moved across the local seascape. Traditionally, seagrass beds have been viewed as a key habitat supporting high densities of consumer fauna, but it may be equally plausible that, especially in oligotrophic systems, consumer production and associated consumer-driven nutrient recycling is necessary for dense seagrass beds to develop in the first place (Alevizon 2002). Loss of nutrient vectors may result in reduced primary production, ultimately affecting fishery production through a yet undocumented indirect pathway.

Across a relatively large geographic area, estimated mean excretion rates for gray snapper were significantly lower in sites closer to human settlements, reflecting the reduced abundance of fish and preferential loss of larger individuals in areas with higher human population density. Lower estimated excretion rates were apparent despite substantial among-site variation in fish density. Such variation likely is attributable to local habitat quality (e.g., mangrove complexity), other local seascape factors (e.g., channel bathymetry) and density of top predators (e.g., sharks), all of which cannot be controlled for in such a broad geographic study. Yet despite the other sources of variation, our results suggest even low levels of fishing pressure can lead to substantial

declines in target fish populations. Because fishing pressure on Andros is relatively low compared to other sites in the Caribbean (Kramer 2003, Newman et al. 2006), we provide a conservative estimate of loss of consumers and associated nutrient cycling.

The fragmentation component of this study provides evidence of a second way in which humans may affect consumer-driven nutrient recycling. The nonlinear relationship between excretion rates and ecosystem fragmentation (Fig. 2C, D), resemble patterns observed for reductions in gray snapper niche width (Layman et al. 2007) and secondary production (Valentine-Rose et al. 2007). The implication is that small reductions in tidal exchange following coastline development can lead to significant alterations in ecosystem function.

This study provides an interesting contrast to the widely accepted notion that human impacts on coastal ecosystems are associated with enhanced nutrient loading. Our findings suggest that, in oligotrophic systems, even apparently minor reductions in fish biomass may have important implications for ecosystem function. Yet, the importance of consumer-driven recycling decreases with increased availability of nutrients from other sources (Evans-White and Lamberti 2006), e.g., in eutrophied estuarine systems. As such, the

current study further emphasizes the complex nature of human impacts in coastal waters (Jackson et al. 2001), and that environmental context and human impacts both will mediate the relative importance of consumer-driven nutrient cycling in these systems.

Our study is a first step in integrating consumer nutrient recycling perspectives into the analysis of marine fishery declines (see also Maranger et al. 2008, Wilson et al. 2009). Our analysis was limited to a single species, but changes in community composition following over-exploitation or habitat alteration (e.g., loss of top predators leading to proliferation of organisms at lower trophic levels) may also affect consumer-driven nutrient recycling. Of particular importance are changes in the size structure of fish assemblages following human impacts. Because smaller individuals have a higher metabolic rate per unit of mass, a shift in size structure toward smaller-bodied individuals could actually increase community-wide fish excretion (Hall et al. 2007). Despite such caveats, one general conclusion seems robust: the nature of nutrient recycling, and thus ecosystem function, will change as fisheries continue to decline.

Our study focused on a relatively small-bodied species when put in the context of the complete body size range in marine fishes. However, some of the most substantial fishery declines have occurred in the largest marine taxa (Pauly et al. 1998). Jennings and Blanchard (2004) used theoretical body-mass relationships to predict historic biomass of fishes in the North Sea and suggested that fishes in the largest size classes (16–66 kg) may have declined by >99%. Losses of other large-bodied fauna (turtles, marine mammals, etc.) also have been significant (Jackson et al. 2001, Lotze et al. 2006). At a global scale, the potential loss of nutrient recycling following faunal declines is substantial. Marine fishery declines may thus portend other dire implications for ecosystem function through yet undocumented pathways.

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APPENDIX A

Methods and results for empirical estimates of gray snapper nutrient excretion rates (*Ecological Archives* A021-019-A1).

APPENDIX B

Description of methods for nutrient diffusing substrates and determination of seagrass nutrient content, blade density, and blade height (*Ecological Archives* A021-019-A2).

APPENDIX C

Size frequency histograms of snapper for surveys conducted on East and West Andros (*Ecological Archives* A021-019-A3).

APPENDIX D

Size frequency histograms of snapper for surveys conducted at each site across the fragmentation gradient (*Ecological Archives* A021-019-A4).

APPENDIX E

Linear regressions between gray snapper biomass and all treatments from the NDS experiments, seagrass nutrient content (%N, %P), density, and mean blade length (*Ecological Archives* A021-019-A5).