

Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems

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Abstract. Consumer-mediated nutrient supply is increasingly recognized as an important functional process in many ecosystems. Yet, experimentation at relevant spatial and temporal scales is needed to fully integrate this bottom-up pathway into ecosystem models. Artificial reefs provide a unique approach to explore the importance of consumer nutrient supply for ecosystem function in coastal marine environments. We used bioenergetics models to estimate community-level nutrient supply by fishes, and relevant measures of primary production, to test the hypothesis that consumers, via excretion of nutrients, can enhance primary production and alter nutrient limitation regimes for two dominant primary producer groups (seagrass and benthic microalgae) around artificial reefs. Both producer groups demonstrated marked increases in production, as well as shifts in nutrient limitation regimes, with increased fish-derived nutrient supply. Individuals from the two dominant functional feeding groups (herbivores and mesopredators) supplied nutrients at divergent rates and ratios from one another, underscoring the importance of community structure for nutrient supply to primary producers. Our findings demonstrate that consumers, through an underappreciated bottom-up mechanism in marine environments, can alter nutrient limitation regimes and primary production, thereby fundamentally affecting the way these ecosystems function.

Key words: artificial reef; Bahamas; bioenergetics; bottom-up; coastal ecosystems; community structure; consumer-mediated nutrient supply; fish excretion; food web; nitrogen; phosphorus.

INTRODUCTION

Linking bottom-up mechanisms of consumer-mediated nutrient supply with nutrient constraints on primary production is a critical step in fully integrating consumers into models of ecosystem function (Vanni 2002, Evans-White and Lamberti 2006, Schmitz et al. 2010). The relative influence of consumer-derived nutrients on primary producers is dependent on multiple factors. First, nutrients must be critically limiting resources for primary production. Second, biomass of the animals must be sufficiently high to provide significant input rates of nutrients via excretion. Additionally, the strength of the consumer–producer interaction is linked to population dynamics and community structure, as primary producers can be limited by different nutrients and consumers supply nutrients differentially due to body size, identity, and diet composition (Vanni et al. 2002). Since the influence of consumers on primary production can vary as a function of such factors, additional research regarding this consumer–producer link is likely to yield novel insights into the way ecosystems function (Vanni 2002, Schmitz et al. 2010).

The strength of the consumer–producer bottom-up interaction can be quantified in three principal ways: (1) comparing animal nutrient supply rates with those from other sources in the ecosystem (e.g., Caraco et al. 1992), (2) comparing animal nutrient supply rates to nutrient demand (e.g., Grimm 1988), and (3) isolating the importance of nutrient supply by consumers through experimental manipulation (e.g., Augustine and McNaughton 2006, Evans-White and Lamberti 2006). Experimental manipulations, typically conducted with mesocosms or enclosures, have proven particularly useful in testing the consumer–producer bottom-up interaction. Yet, larger scale manipulations are lacking due to intractability associated with in situ experiments. An alternative approach is to modify the habitat template so that consumer densities vary in response to the underlying habitat structure. This gradient can be then used as an experimental context to examine the link between consumer nutrient supply and primary production.

Artificial reefs, defined as any structure (e.g., reef ball, tree stump, car, and so on) that is added to the benthic environment, are increasingly used to enhance fisheries production as part of coastal conservation and management strategies (Bohnsack and Sutherland 1985, do Carmo et al. 2011). These introduced habitats have been shown to appropriately mimic their “natural” counterparts, in that colonizing fish communities have similar

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structure and densities as those found on patch reefs (Bohnsack and Sutherland 1985, Carr and Hixon 1997). For these reasons, artificial reef habitats have been successfully used to study basic population and community dynamics (Carr and Hixon 1997, Yeager et al. 2011). Because aggregations of consumers may have direct implications for nutrient cycling, artificial reefs also provide an opportunity to quantify ecosystem function across gradients of consumer nutrient supply.

Consumers may represent an especially important nutrient source in tropical coastal environments because these ecosystems are often oligotrophic and nutrient availability limits primary production (Smith and Atkinson 1984, Duarte 1990). Previous research in tropical seagrass beds has demonstrated that colonizing seabirds (Powell et al. 1991, Herbert and Fourqurean 2008) and fishes (Alevizon 2002, Dewsbury and Fourqurean 2010) may have direct bottom-up impacts on seagrass communities. For example, nutrient inputs from roosting seabirds have been shown to cause a shift in the dominant seagrass species from *Thalassia testudinum* to *Halodule wrightii*, and to decrease seagrass species richness (Powell et al. 1991). In this study, we used artificial reefs constructed within a seagrass ecosystem matrix to directly test the strength and characteristics of the interaction between fish nutrient supply and primary production.

Using experimental artificial reefs (>two years post-construction), we tested the hypothesis that fishes, through nutrient excretion, enhance primary production and alter nutrient limitation regimes of two dominant primary producer groups: seagrass (*Thalassia testudinum*) and benthic microalgae. Nutrient supply rates for nitrogen (N) and phosphorus (P) by fishes were estimated using bioenergetics models for the 13 families of fishes present on the reefs. We then used observational (seagrass nutrient content, seagrass growth rate) and experimental (nutrient enrichment assays) tests to examine patterns of primary production and nutrient limitation. Further, because community structure can determine rates of nutrient input by consumers, we explored the relative role of fish functional feeding groups and community structure on nutrient supply rates and ratios. Finally, to contextualize our findings, we compared community-level nutrient supply rates of our study to those from other published studies in marine and freshwater ecosystems.

METHODS

The study was conducted in the Bight of Old Robinson, Abaco, Bahamas (see Plate 1), a semi-enclosed bay with a mosaic of seagrass, sand, and hard-bottom habitats (26.342791° N, 77.017655° W; Yeager et al. 2011). Artificial reefs were constructed from cinder blocks (~40 × 20 × 20 cm) in a pyramid shape in March 2009 on moderately dense seagrass habitat. Given the a priori assumption that more fish would colonize larger reefs, three configurations were

chosen: 40-cinder block reefs ($n = 10$, ~1.2 m² at the base and ~1.2 m tall), 10-block reefs ($n = 5$, ~0.75 m² at the base and ~0.40 m tall), and sites with 0 blocks for controls ($n = 5$). Initial seagrass blade density did not differ among reef sizes ($F_{3,16} = 2.47$, $P = 0.11$; for 0-, 10-, and 40-cinder block reefs, with later size class separated into two groups based on initial visual inspection of seagrass density; $n = 4$ groups total). All treatments, including the controls, will be referred to as “reefs” hereafter. These reefs have previously been used to understand aspects of community and population dynamics and colonization (Yeager et al. 2011, 2012). In this study, we tested how community and population dynamics may be linked to ecosystem processes.

Underwater visual census was used to estimate fish abundance ($n = 10$ surveys on each reef between July 2009 and August 2011). All fishes were identified to the lowest possible taxonomic level, and size (total length) of each individual was estimated to the nearest centimeter (Appendix A).

We used bioenergetics models to generate linear models of fish mass (g) and excretion rate (g nutrient-wet mass⁻¹·d⁻¹) for individuals of the 13 families in our surveys, with the exception of the family Lutjanidae, which was modeled at the generic level ($n = 14$ models total; see Appendix B: Table B1). These families represented >99% of the biomass of resident fishes on these reefs. Models were run at the family level because stoichiometry of fish excretion has been shown to vary substantially among families, but little within (Vanni et al. 2002). Models were parameterized using diet analyses of thousands of individuals from the study system, in conjunction with nutrient stoichiometry data (C, N, P) collected for this study from the 13 families of fish present on our reefs, including 252 individuals from 21 species (Appendix B: Table B2). These equations were used in conjunction with calculations of fish biomass from each reef to estimate excretion rates per reef (g nutrient/d; Layman et al. 2011). The vast majority (>90% of individuals) of fish were located within 1 m of the reef structure based on extensive daytime visual surveys (Layman et al. 2013), as such we did not present data on an areal (per meter basis) and instead as supply rate (g) per reef per day (see Appendix B for details on model parameterization).

Ambient water column nutrients are extremely low in the study ecosystem: NH₄⁺, 1–8 µg/L; NO₃⁻, 0–0.3 µg/L; soluble reactive phosphorus, 0–1 µg/L (Allgeier et al. 2011). Previous research in these highly oligotrophic ecosystems has indicated water column nutrients are not a good proxy for understanding nutrient availability for primary producers presumably because nutrient demand is greater than ambient availability and nutrient availability at these low concentrations can be patchy (Fourqurean and Zieman 2002, Allgeier et al. 2011). To further assess this assumption we examined concentrations of NH₄⁺ (the nutrient that is excreted by fish in

largest quantities) across all artificial reefs in August 2011 (Appendix C).

Nutrient limitation was investigated observationally and experimentally using two important primary producer groups, seagrass and benthic algae, respectively (Allgeier et al. 2011). It is important to note that seagrasses (macrophytic angiosperms) have fundamentally different physiological demands and requirements than benthic algae (Johnson et al. 2006), but together these groups can provide detailed insight into overall nutrient dynamics within ecosystems.

First, we examined the nutrient content and growth rate of the seagrass *Thalassia testudinum*. The nutrient content of seagrass blades has been widely used to assess nutrient availability in coastal ecosystems (Atkinson and Smith 1983, Duarte 1990, Fourqurean and Zieman 2002) and reflects ambient nutrient conditions over a relatively long time frame (i.e., months) as compared with ambient water nutrients (see Appendix D for methods). Growth rates were estimated by using the standard blade hole-punching protocol (Zieman 1974) in August 2011 (Appendix D).

We also employed nutrient diffusing substrates (NDS) on each reef unit ($n = 20$) in March 2010, May 2010, and August 2011 to assess potential effects on benthic algae. NDS are bioassays containing a nutrient enriched agar that diffuses through fritted glass disks (5.7 cm² surface area) upon which primary producers can colonize. The treatment with greatest response of algal biomass, i.e., highest value of chlorophyll *a* (chl *a*) per surface area, indicates the most limiting nutrient. NDS are commonly used to measure nutrient limitation for primary production of benthic microalgae (Tank et al. 2007), and have been informative in ecosystems similar to that in the present study (Allgeier et al. 2010, 2011, Layman et al. 2011).

We used three NDS treatments: nitrogen (0.5 mol/L NH₄Cl), phosphorus (0.5 mol/L KH₂PO₄), nitrogen and phosphorus (0.5 mol/L NH₄Cl + 0.5 mol/L KH₂PO₄), and a control (agar only; containing no other trace nutrients or sugars) on each reef (three dates; 700 total bioassays). For deployment, three NDS units of each treatment ($n = 12$ total) were attached to a polyvinyl chloride (PVC) bar with holes corresponding in size to the NDS unit. These bars were then staked into the ground ~0.5 m from artificial reefs. After ~21 d at each reef, NDS were collected and frozen for transport to Odum School of Ecology (University of Georgia, Athens, Georgia, USA). NDS were processed for chl *a* following methods by Tank et al. (2007; see also Appendix E).

Data analysis

Fish total length was converted to biomass via length-mass regressions for each of the 66 species present on the

reefs, using published data from the literature, Fishbase (*available online*),⁴ and in situ measurements (J. E. Allgeier, *unpublished data*). Biomass was used to estimate excretion rates (g nutrient/d) for N and P for each individual fish on each reef using the linear regression model of wet mass and excretion rate generated by bioenergetics models. Nutrient supply rates were estimated (for N and P per reef) by first summing excretion rates across all individuals on each reef at a given date, and then taking the average rate per reef across all survey dates. These mean values were used as the primary predictor variable for our analyses. One 40-block artificial reef was stolen from the field site during the course of our experiments, and thus was not included in the analysis.

The relationship between fish supply rates per reef (mean supply rates g nutrient/d) and all parameters of seagrass growth and nutrient limitation from seagrass (e.g., growth rates, percentage of nutrient content for N and P, and molar N:P ratio) were determined using linear regression. A multifactor analysis of covariance (ANCOVA) was used to explore the relationship between benthic microalgae chl *a* (the response variable) and the following predictor variables: date of experiment (three dates), NDS treatment (as treatment factors N, P, and N × P), fish nutrient supply per reef (mean g nutrient/d; covariate), and tide-corrected depth of each reef (to test for potential light limitation of growth; covariate). Supply rates for N and P were strongly correlated ($r = 0.98$, $P < 0.001$), and thus were used in separate models. Model results indicated that the responses of the NDS experiments did not differ across dates ($F_{2, 197} = 0.96$, $P > 0.38$); thus, chl *a* (μg/cm) for each NDS treatment type (Control, N, P, NP), was averaged across all dates for each reef and used in linear regression models to further explore the relationship between NDS treatment type and nutrient supply by fishes. When necessary, data were either log- or square root-transformed to meet model assumptions of normality and homogeneity of variance. All analyses were run in R software (R Core Development Team 2012).

Fish were separated into two functional feeding groups: herbivores (>90% of diet is primary producers, i.e., Scaridae and Acanthuridae) and mesopredators (including omnivores that had >90% animal diet). The N:P molar ratio of excreted nutrients was calculated for each group by dividing the sum of all N excreted per group by the sum of all P after converting to moles. The proportion that each group contributed to total biomass, N supply rate, and P supply rate was also calculated.

Finally, we compiled community- and population-level excretion rates from seven published studies in marine and freshwater ecosystems, to place our findings in context with other consumer nutrient supply rates. To be consistent, data from our study were converted to mg nutrient·h⁻¹·m⁻², using 16 m² as the estimate for the total area that fish occupy, including the reef, a greatly

⁴ www.fishbase.org

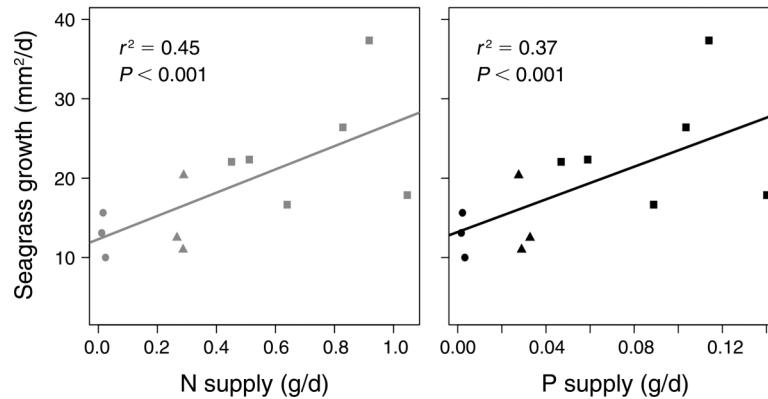


FIG. 1. Regressions between seagrass growth rates and estimated fish nutrient supply rates for N and P around artificial reefs in the Bahamas. Model statistics are for natural log-transformed data. Symbols represent controls (0-block reef; circles), 10-block reefs (triangles), and 40-block reefs (squares).

conservative estimate, as the vast majority of the fish in our surveys were within ~ 1 m of the reef (Layman et al. 2013).

We did not attempt to characterize the hydrodynamic conditions on these reefs. Uptake rates of nutrients are typically exceptionally high in oligotrophic ecosystems (Legendre and Rassoulzadegan 1995), and given the extremely nutrient-poor conditions of our study site, an a priori assumption was that the effect of fish nutrient supply should be localized around the reefs. Hydrodynamics of the study embayment are dominated by tidal and wind forces and are not unidirectional. The dispersion of nutrients around all reefs would likely be normally distributed over time thus diluting the fish-derived nutrients and, if anything, diminishing the net effect of fish nutrient supply on primary producers. In this regard our analysis is likely conservative.

RESULTS

Fish densities ranged from 0–1080 individuals per reef, an estimated 0–18 055 g of biomass. Fish biomass significantly increased with increased reef size (0-, 10-, and 40-block reefs; $F_{2,26} = 36.46$, $P < 0.001$). Mean supply rates of nutrients per reef via fish excretion rates for N and P ranged from 0–1.05 g N/d and 0–0.14 g P/d. The fish community was dominated by mesopredators (i.e., predominantly macroinvertebrates), namely, grunts (Haemulidae), snapper (Lutjanidae), and squirrelfish (Holocentridae) (Appendix B: Table B1). No significant relationship between ambient NH_4^+ in the water column and N supply rates by fishes was found (Appendix F: Fig. F1).

Seagrass growth rates ranged between 10 and 37.4 mm^2/d (18.8 ± 7.8 [mean \pm SD]). The average control site and 40-block reef growth rates were 12.9 ± 3.1 mm^2/d and 23.8 ± 7.5 mm^2/d , respectively. Relationships between fish nutrient supply rates for N and P and seagrass growth rates were significantly positive (Fig. 1).

Seagrass nutrient content ranged from 1.06% to 1.94% N ($1.34\% \pm 0.27\%$ [mean \pm SD]) and from 0.026% to

0.11% P ($0.06\% \pm 0.028\%$). These values are within range of seagrass nutrient content values found in nearby seagrass beds (Allgeier et al. 2011), but low relative to the mean nutrient content of *T. testudinum* across other study systems ($\sim 2\%$ N, $\sim 0.15\%$ P; Duarte 1990). All relationships between seagrass nutrient content (%N and %P) and fish supply of N and P were positively related ($r^2 = 0.38$, $P < 0.001$ for %N seagrass vs. P supply by fishes and $r^2 = 0.46$, $P < 0.001$ for %P seagrass vs. N supply by fishes, respectively; for other tests see Fig. 2). The molar ratio of N:P of *T. testudinum* across reefs ranged from 32.3 to 85.7, and showed a significant negative relationship with fish supply rates of P (Fig. 2) and N ($r^2 = 0.38$, $P < 0.01$).

Results from the NDS experiments showed that benthic microalgae were nutrient co-limited (i.e., the response to NP was always greater than the response to either N or P alone), across dates and experimental units ($F_{1,197} = 139$, $P < 0.01$; Appendix F: Table F3). These findings demonstrate strong nutrient limitation of benthic algae and are consistent with previous findings in similar systems (Allgeier et al. 2010, 2011). Depth was not a significant predictor of chl *a* ($P = 0.55$ and 0.67 for N and P models, respectively; Appendix F: Table F3), whereas supply rates of N and P (mean excretion per reef) were both significant predictors of chl *a* ($F_{1,197} = 7.5$, $P < 0.01$ and $F_{1,197} = 6.69$, $P < 0.01$ for N and P, respectively; Appendix F: Table F3). There was no significant interaction between NDS treatment type and supply rates of either N or P by fishes ($P > 0.2$ for all; Appendix F: Table F3), suggesting that the direction of response of benthic algae to NDS treatments was similar across sites.

Chl *a* values for both the control and P treatment ($\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$; averaged per reef across all three sample dates) on the NDS experiments were positively related to supply rates of N and P by fishes ($r^2 = 0.59$, $P < 0.001$ for P treatment and P supply rates; Fig. 2). Note that, for the regressions between the control and N and P supply, the proportion of the variance in chl *a* explained

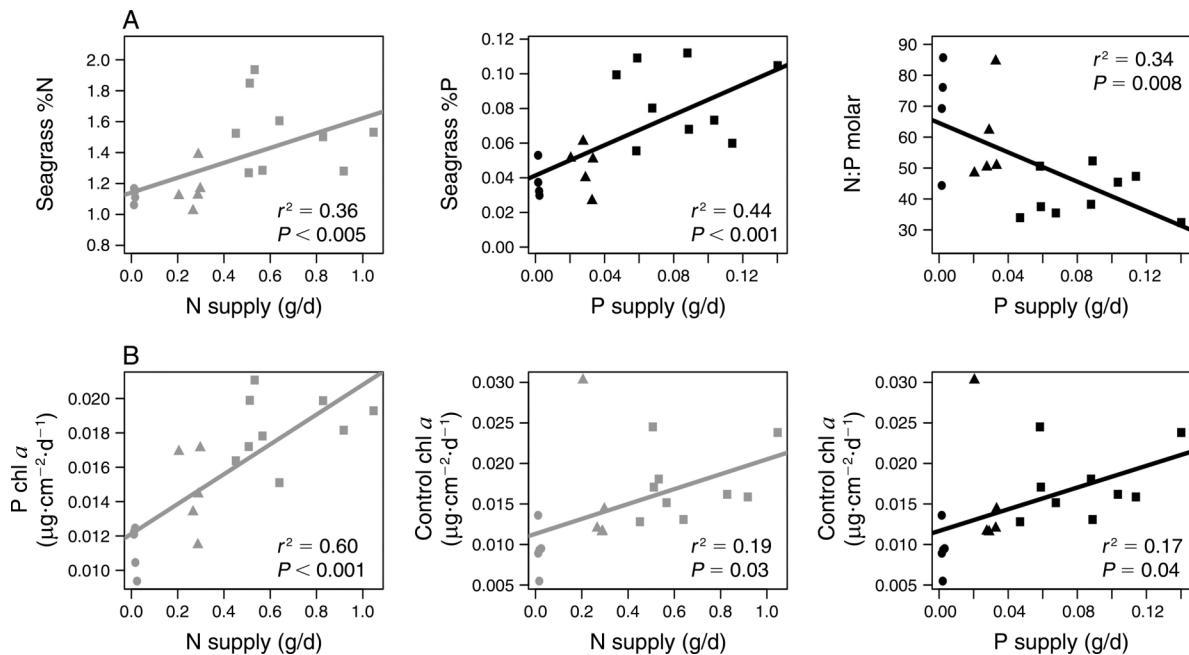


FIG. 2. (A) Regressions between seagrass characteristics (nutrient content as percentage of dry mass, N:P molar ratio), and estimated fish nutrient supply rates for N and P. (B) Regressions between chlorophyll *a* (chl *a*) responses on nutrient diffusing substrates (control and P treatment) and estimated fish nutrient supply rates for either N or P (g/d). Model statistics are for natural log-transformed data. See *Results* for other analyses. Symbols represent controls (0-block reef; circles), 10-block reefs (triangles), and 40-block reefs (squares).

by nutrient supply substantially increases after removing one apparent outlier ($r^2 = 0.55$, $P > 0.001$ and $r^2 = 0.54$, $P > 0.001$, for regressions with N and P, respectively). Relationships between chl *a* from treatment NP and N and fish nutrient supply rates were not significant ($P > 0.1$; Appendix F; Fig. F2).

Fish excretion N:P molar ratios per functional feeding group were 66.8 ± 19.4 for herbivores and 17.5 ± 2.4 for mesopredators (values calculated as mean of N:P ratios per group across reefs), indicating clear distinctions between the ratios at which the different functional groups excrete nutrients (*T* test of N:P between groups, $P < 0.001$; Fig. 3a). The disparity in N:P molar ratios of excretion becomes more apparent when assessing the proportion that each group contributes of the total nutrient supply relative to their biomass: Herbivores contribute more N, and mesopredators contribute more P, relative to body mass (Fig. 3b).

DISCUSSION

Our research directly links population, community, and ecosystem ecology by quantitatively relating estimates of consumer nutrient supply to aspects of primary production. Specifically, by allowing fishes to colonize novel habitats at various densities, we demonstrate that nutrient supply by these organisms is a regulating factor for nutrient limitation and production of dominant autotrophs within this ecosystem. Further, our research contextualizes the role of a common habitat type in coastal ecosystems, patch reefs (Adams et al. 2006), as

biogeochemical hotspots for not only fish aggregation (McIntyre et al. 2008), but ecosystem function within the seascape (Layman et al. 2013). These data underscore the magnitude at which fishes can supply nutrients to coastal marine environments, placing them among the most important sources of nutrients in coastal oligotrophic ecosystems.

Lamb-Wozniak (2006) reported loading rates from anthropogenic sources to the Florida Keys (a region with substantially greater anthropogenic influence than our study site) to be $0.00017 \text{ g N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, and all N

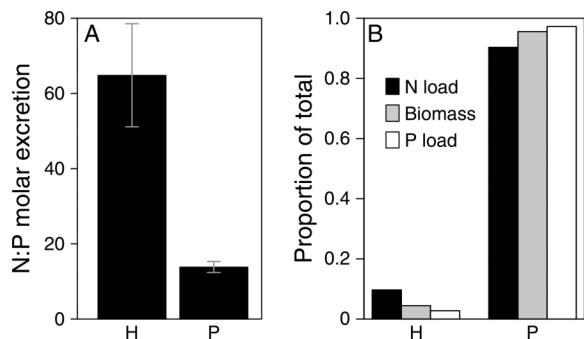


FIG. 3. (A) Estimated N:P molar ratios for excretion by the two functional feeding groups (H, herbivores, P, mesopredators), indicating their relative contribution to N and P cycling. Error bars indicate standard error. (B) Histogram of the proportion of total N (black), biomass (gray), and P (white) that each group (H and P) contribute to total.

TABLE 1. Community- and population-level excretion rates for freshwater (lake and river) and marine (all coastal) ecosystems.

Ecosystem	Spatial/temporal gradient	Assembly	Mean biomass (g)	N supply (mg N·m ⁻² ·d ⁻¹)	P supply (mg P·m ⁻² ·d ⁻¹)	Method	Citation
Freshwater							
Tropical river	riffles among same river	community	27.5	33.02	3.54	empirical	McIntyre et al. (2008)
Tropical river	riffles among same river	community	30.9	20.71	1.08	empirical	Small et al. (2011)
Temperate lake	seasons	community	NA	<0.001–0.21	<0.001–0.04	modeling	Verant et al. (2007)
Temperate lake	multiple lakes	population	NA	0.42–5	0.04–0.92	empirical	Vanni et al. (2006)
Marine							
Temperate tidal creek	single tidal creek	community	70.4	66.86	3.72	empirical	Haertel-Borer et al. (2004)
Tropical tidal creek	multiple tidal creek	population	104.7	59.69	1.85	empirical	Layman et al. (2011)
Tropical coral reef	single coral head	population	172	102.2	6.51	empirical	Meyer et al. (1983)
Artificial reef	multiple artificial reefs	community	71.35	41.67	5.32	modeling	this study

Notes: Spatial/temporal gradient refers to comparisons made within the given study. Method refers to how excretion estimates were quantified. Assembly identifies whether the study was focused on an entire community or a single population. In those studies that focused on population-level supply rates, the population examined constituted a large majority of total community biomass. Nutrient supply estimates are reported as either mean values or a range of values per study; NA indicates that data are not available.

inputs collectively (including anthropogenic influences, atmospheric deposition, nitrogen fixation, upwelling etc.) to be 0.00141 g N·m⁻²·d⁻¹. We show that fish supply 0.007–0.25 g N·m⁻²·d⁻¹ (the range of minimum and maximum loading rates on our larger, 40-block artificial reefs) representing ~5- to 177-fold increase over the estimated total N loading rates by Lamb-Wozniak (2006). While our estimates are on a much smaller spatial scale (i.e., patch/artificial reefs vs. reef complexes in The Keys), it is evident that the fish-derived nutrients on our artificial reefs is substantial relative to other sources, suggesting the importance of consumer-mediated nutrient supply for ecosystem function.

The nature of consumer nutrient supply is affected by habitat characteristics that, in turn, influence fish behavior. For example, in a lacustrine ecosystem, where fishes are typically more dispersed, the maximum values for N and P cycling reported by Vanni et al. (2006) are ~8 and ~5.5 times less than estimates reported for N and P cycling in this study, respectively (Table 1). This difference is largely attributed to the fact that fish nutrient supply on artificial reefs is estimated at a patch scale, whereas it is estimated at the ecosystem scale in lakes. This highlights the importance of artificial reefs as biogeochemical hotspots (McIntyre et al. 2008) that may function as critical ecological nodes in a larger seascape framework (Layman et al. 2013). In this sense, given their potentially critical ecological role, artificial reefs, and patch reefs more generally, warrant additional study in an ecosystem function context.

Fish nutrient supply increased seagrass growth rates likely because fishes load nutrients at low N:P ratio,

thereby reducing P nutrient limitation and, consequently, enhancing growth rates. Atkinson and Smith (1983) reported that the theoretical Redfield Ratio for seagrass (and *T. testudinum* in particular) was roughly 30:1 (N:P molar), which is similar to the molar ratio of the mean values of *T. testudinum* across various locations reported by Duarte (1990). Conceptually, this ratio provides a benchmark from which to assess nutrient limitation, indicating the approximate ratio for optimal growth (Atkinson and Smith 1983). Seagrass nutrient ratios from this study ranged from ~85 to ~32 on artificial reefs from lowest to highest nutrient supply rates, respectively. As such, in areas of the seagrass ecosystem where fish do not aggregate (represented by our control sites), seagrass appear to be P limited, and this P limitation decreases with increased nutrient supply from fishes.

While the supply of nutrients from fishes appeared to enhance net production for benthic microalgae in a similar manner as for seagrass, the effect on nutrient limitation was more nuanced. In the case of benthic algae nutrient limitation, an increase in chl *a* was found to occur on the P treatment with increased nutrient supply by fishes, suggesting enhanced P limitation. The experimental conditions of single-nutrient NDS treatments are such that, the enriched agar provides more than ample supply of the treatment nutrient (Maberly et al. 2002, Tank and Dodds 2003, Tank et al. 2007). If the ambient water conditions are oligotrophic, with low availability of the other nutrient in the water column, very little or no benthic algal biomass accrual would be predicted. However, when fish supply both N and P to the water column via excretion, an increase of algal



PLATE 1. (A) Control, (B) small, and (C) large artificial reefs used to experimentally manipulated the size of fish aggregations in the Bight of Old Robinson, Abaco, the Bahamas. Photo credit: L. A. Yeager.

biomass accrual on both treatments might be expected. Yet, only one treatment (P) responded positively to fish nutrients, suggesting that fish may be supplying sufficient N to enhance production on the P treatments, but the quantity of P supplied by fish is not sufficient to enhance the response on the N treatment. These findings underscore the importance of considering the supply ratios (community structure) and the physiological nutrient demand (producer identity) when assessing the relationship between consumer nutrient supply and primary production (DeAngelis 1992).

The rate and ratio at which nutrients are supplied are two of the most critical regulating factors for primary production in nutrient limited systems, both of which can strongly be governed by the biomass and composition of the consumer community (Vanni 2002, Vanni et al. 2002, McIntyre et al. 2007). Because diet has a strong influence on nutrient excretion by fishes (Vanni 2002, Verant et al. 2007), functional feeding groups are expected to deviate in the rate and ratios at which they excrete nutrients. We found distinct differences between nutrient excretion ratios at the functional feeding group level (Fig. 3a). For example, herbivores (e.g., parrotfish, Scaridae; surgeonfish, Acanthuridae), feeding on diets with extremely low nutrient content (typically lower in P relative to N), release nutrients at high ratios of N relative to P. In contrast, mesopredators (e.g., grunts, Haemulidae; snappers, Lutjanidae; groupers, Serranidae), typically excrete nutrients at a much lower N:P, primarily a reflection of their more P-rich diet. These factors are especially important within the context of how humans may be altering community structure by selectively removing specific functional groups (e.g., top predators).

A few caveats in our study should be noted. First, we restricted our measurements of fish contribution to nutrient input to excretion because these nutrients are in highly reduced forms that are biologically available for producers (Walsh and Wright 1995). Yet, fish egestion, i.e., particulate food matter that was not assimilated by the animal (Vanni 2002), can also provide substantial nutrient input (Meyer et al. 1983). In this sense, we generally underestimated the net nutrient input of fishes

to these ecosystems. Conversely, some (but not all) fishes move away from the reefs to forage at night (specifically, grunts; Ogden and Ehrlich 1977). Because we conducted our surveys only during daylight hours, we may have overestimated the quantities of nutrients supplied onto and adjacent the reefs by those fish. With respect to our NDS experiments, grazing and light limitation are two other factors that may have affected our results. While we show that light conditions had no statistical effect on benthic algal production across reefs by including depth as a parameter in our global model, we were unable to account for potential grazing effects on our substrates. However, the fact that the reefs with the highest fish density (and likely the largest grazing pressure) consistently had the largest NDS responses suggests that grazing was not a substantial factor affecting the overall patterns.

Our findings provide a direct linkage between consumer nutrient supply and primary production, and underscore the critical importance of this bottom-up source of nutrients in marine ecosystems. We provide evidence that fish nutrient input to the marine environment is substantial and that the high supply rate of nutrients is a critical, yet widely overlooked, aspect of ecosystem function. Our research highlights the importance of linking individual, population, and community ecology to nutrient supply, and underscores the need to emphasize bottom-up dynamics as another critical reason for conservation of animal populations.

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SUPPLEMENTAL MATERIAL

Appendix A

Supplementary methods for visual surveys ([Ecological Archives E094-043-A1](#)).

Appendix B

Supplementary methods for bioenergetics modeling ([Ecological Archives E094-043-A2](#)).

Appendix C

Water nutrient collection/analysis ([Ecological Archives E094-043-A3](#)).

Appendix D

Seagrass growth rate methods and nutrient content analysis ([Ecological Archives E094-043-A4](#)).

Appendix E

Nutrient-diffusing-substrate methods ([Ecological Archives E094-043-A5](#)).

Appendix F

Two figures showing relationship between water nutrient concentration and fish N supply, relationships between N and NP treatment and N and P supply per reef by fishes, and an ANCOVA table for both N and P excretion rates by fishes ([Ecological Archives E094-043-A6](#)).