

The roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems

HILLARY S. YOUNG,^{1,2,3,7} DOUGLAS J. MCCAULEY,^{4,5} ROBERT B. DUNBAR,⁶ MICHAEL S. HUTSON,¹
ANA MILLER TER-KUILE,¹ AND RODOLFO DIRZO¹

¹Biology Department, Stanford University, 371 Serra Mall, Stanford, California 94305 USA

²Division of Vertebrate Zoology, Smithsonian Institution, Washington, D.C. 20013 USA

³Center for the Environment, Harvard University, 24 Oxford Street, Cambridge, Massachusetts 02138 USA

⁴Hopkins Marine Station, Stanford University, 120 Oceanview Boulevard, Pacific Grove, California 93950 USA

⁵Department of Environmental Science, Policy, and Management, University of California, 130 Mulford Hall, Berkeley, California 94720 USA

⁶Department of Environmental Earth System Science, Stanford University, Stanford, California 94305 USA

Abstract. Many different drivers, including productivity, ecosystem size, and disturbance, have been considered to explain natural variation in the length of food chains. Much remains unknown about the role of these various drivers in determining food chain length, and particularly about the mechanisms by which they may operate in terrestrial ecosystems, which have quite different ecological constraints than aquatic environments, where most food chain length studies have been thus far conducted. In this study, we tested the relative importance of ecosystem size and productivity in influencing food chain length in a terrestrial setting. We determined that (1) there is no effect of ecosystem size or productive space on food chain length; (2) rather, food chain length increases strongly and linearly with productivity; and (3) the observed changes in food chain length are likely achieved through a combination of changes in predator size, predator behavior, and consumer diversity along gradients in productivity. These results lend new insight into the mechanisms by which productivity can drive changes in food chain length, point to potential for systematic differences in the drivers of food web structure between terrestrial and aquatic systems, and challenge us to consider how ecological context may control the drivers that shape food chain length.

Key words: ecosystem size; food chain length; food web structure; islands; Palmyra Atoll; productivity.

INTRODUCTION

Understanding the forces that determine food chain length (FCL; the number of trophic exchanges between the top and bottom of a food web) and explain natural variation in FCL across ecosystems was a prominent aim of early ecologists (Elton 1927, Lindeman 1942, Hutchinson 1959) and is an issue that continues to be debated today (Pimm 1982, Post 2002, Calcagano et al. 2011). Food chain length is a fundamental architectural property of ecosystems that carries strong implications for a wide range of ecosystem functions and properties (DeAngelis et al. 1989, Cabana and Rasmussen 1994, McIntyre et al. 2007). While multiple potential drivers of variation in FCL have been proposed (Schoener 1989, Post 2002, McHugh et al. 2010, Calcagano et al. 2011), three of them (ecosystem size, productivity, and environmental stochasticity [disturbance]) have received the majority of research attention and support.

Productivity was an early and intuitive explanation for observed variation in food chain length (Hutchinson 1959, Pimm 1982). Based largely on theoretical grounds, the suggestion of this energy limitation hypothesis was that more productive ecosystems could support a greater biomass of both consumers and their predators, ultimately allowing higher trophic levels to persist. Results from microcosm experiments and some early, detailed food web analyses corroborated these theoretical predictions, illustrating that productive ecosystems could support longer food chains (Jenkins et al. 1992, Kaunzinger and Morin 1998, Townsend et al. 1998). Despite the theoretical and small-scale experimental support for the connections between productivity and FCL, multiple studies, including several larger scale field comparisons, have failed to identify productivity alone as a primary driver of increased FCL (Briand and Cohen 1987, Vander Zanden et al. 1999, Post et al. 2000, Sabo et al. 2010). Similarly mixed results have emerged from the studies of the role of disturbance on FCL, with studies finding negative (Townsend et al. 1998, McHugh et al. 2010, Sabo et al. 2010), positive (Parker and Huryh 2006, Marty et al. 2009), and no effects (Takimoto et al. 2008) of disturbance on FCL. In contrast to the highly variable responses of FCL to productivity alone or to

Manuscript received 4 May 2012; revised 8 October 2012; accepted 22 October 2012. Corresponding Editor: N. J. Sanders.

⁷ Present address: Center for the Environment, Harvard University, 24 Oxford Street, Cambridge, Massachusetts 02138 USA. E-mail: hyoung@fas.harvard.edu

environmental stochasticity, ecosystem size, or size mediated productivity (called productive space), has been a relatively reliable and frequently observed driver of FCL (Schoener 1989, Spencer and Warren 1996, Post et al. 2000, Post et al. 2007, Vander Zanden and Fetzer 2007, Takimoto et al. 2008, McHugh et al. 2010, Sabo et al. 2010). These studies do not suggest that ecosystem size or size-mediated productivity is likely to be the only explanatory driver of FCL, and indeed, there is growing agreement that there are generally likely to be multiple interacting drivers of FCL. However, cumulatively, these findings have led to the suggestion that ecosystem size is typically the strongest and most consistent driver of FCL. Yet, the variable results from large-scale studies on the drivers of FCL emphasizes how little we still know about the processes and mechanisms underlying these relationships and how crucial it is to explore multiple contexts to understand where and when various controls on FCL are most important (McHugh et al. 2010).

Even in systems where primary drivers of FCL have been identified, detailed mechanisms underlying these patterns are generally poorly understood (Post et al. 2000, Takimoto et al. 2008). Three non-mutually exclusive possible explanations underlying changes in FCL were proposed by Post and Takimoto (2007): (1) new higher level predator species are added (additive mechanism); (2) the diversity or relative abundance of intermediate consumers increases (insertion mechanism); (3) the consumers diet changes either by growing larger and feeding on larger and potentially higher trophic position prey, or by purely behavioral shifts toward specialization allowing for more trophic exchanges within the food web (omnivory mechanism). However, the relative roles of these mechanisms in driving FCL, particularly the latter two, have received little attention. Understanding the mechanisms by which FCL changes is critically important to any effort to understand the variability in drivers across ecosystems, and how ecological context might determine observed variation in drivers of FCL.

Nearly all large-scale, ecosystem-level FCL studies exploring the drivers of FCL have come from freshwater, and mostly lacustrine, ecosystems (Vander Zanden et al. 1999, Post et al. 2000, Thompson and Townsend 2005, Doi et al. 2009, McHugh et al. 2010, Sabo et al. 2010). Aquatic food webs likely differ fundamentally from terrestrial ones in many ways that could affect the functioning of the various mechanisms driving variation in FCL. For example, aquatic food webs may diverge regarding the relative importance of top-down ecological controls (Shurin et al. 2002, Borer et al. 2005), body size ratios and the degree of size structuring across food webs and trophic levels (Brose et al. 2006, Shurin et al. 2006), the relationship between productivity and diversity (Mittelbach et al. 2001, Partel et al. 2007), and in the relative abundance of generalist consumers (Hairston and Hairston 1993, Thompson et al. 2007). Moreover,

many terrestrial ecosystems, as well as many marine ecosystems, are much larger than most lake and riparian systems, and often lack the relatively clearly defined boundaries of many freshwater environments, perhaps reducing the likelihood that ecosystem size might limit FCL (Post et al. 2007). Given these multiple, systematic differences between the aquatic systems from which so many of our conclusions about FCL have been derived, and other ecological contexts, there is a strong need for additional examination of the drivers of FCL, and the mechanisms by which these drivers operate, outside the freshwater environment.

To take up this task, we first measured average FCL across a series of topographically and geologically similar islets of a single tropical atoll. The islets are positioned across large and independent gradients of productivity and size, but yet span only a very small geographic area under the same climatic conditions. We then compared a series of models including productivity, ecosystem size, and productive space for their ability to explain observed variation in total FCL and trophic position of each consumer species. We found strong evidence that productivity alone drives FCL in these systems. We also explored the mechanisms underlying changes in FCL through detailed surveys of consumer abundance, diversity, body size, and diet across the productivity gradient. We found no support for changes in predator identity in explaining observed gradients in FCL. However, we did see support for the role of increased species richness in explaining these changes, as well as for the role of behavioral and morphological changes in consumers. Cumulatively these small shifts may be driving the large overall shift in FCL across this tropical terrestrial productivity gradient.

METHODS

The fieldwork was conducted across a series of islets ($n=23$) at Palmyra Atoll ($5^{\circ}53' N$, $162^{\circ}05' W$), a remote, wet tropical atoll in the central Pacific Ocean (see Plate 1). All islets are low lying (<2 m above sea level), consist of coral reef-derived materials overlying limestone basement, and are located in close proximity to one another (all within a 20-km^2 area). Islet area (used as a metric of ecosystem size) varied nearly four orders of magnitude, from 5.29×10^2 to $2.60 \times 10^6 \text{ m}^2$. Measured productivity varied 14-fold, from 2.20×10^{-4} to $3.20 \times 10^{-3} \text{ g foliar N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, while available soil nutrients ("potential productivity," as used in other studies) varied ~ 100 -fold from 8 to 786 μg plant available NO_3^- , NH_4^+ , and PO_4^- per gram of dry mass soil. Variation in productivity across islets was derived from variation in abundance of nesting and roosting seabirds on the atoll (Young et al. 2010a), and there was no significant relationship between ecosystem (islet) size and productivity ($R^2=0.05$, $P=0.76$). Due to their very close geographic proximity, and the open ocean surroundings, the islets likely experience little natural,

systematic variation in disturbance over long time periods.

Characterization of productivity and ecosystem size

Many different approaches have been used to estimate productivity or energy availability of systems in FCL studies, including direct measurements of productivity (e.g., $\text{mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ [Thompson and Townsend 2005, Sabo et al. 2010]), nutrient limitation (e.g., $\mu\text{g P/L}$ [Post et al. 2000]), precipitation index [Arim et al. 2007]), or, most recently, realized resource availability (e.g., $\mu\text{g edible C/L}$ [Doi et al. 2009]). We elected to estimate productivity as $\text{g foliar N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ produced in controlled growth experiments on site. In Appendix A we provide details on methods of this growth experiment, confirm that this metric is strongly correlated to alternative metrics of productivity, and demonstrate that the use of alternative metrics, including limiting nutrients, do not change our conclusions. Ecosystem size for each islet was directly measured via ArcGIS (ESRI 2008). We used the product of productivity and ecosystem size as a metric of productive space (Post 2007).

Collection and measurement of isotopic samples

The length of the food chain on each islet was approximated using the trophic position of the highest level predator in that system (generally geckos or spiders). The trophic position of consumers was calculated as the mean increase in $\delta^{15}\text{N}$ between that consumer and the base of the food web, corrected for changes in consumer dietary sources using a mixing model, and calibrated by average fractionation of consumers (Appendix B). The isotopic baselines of each food web were defined using an integrated sample of three common plant species on each islet. The marine baseline of each food web was characterized as an integrated sample of marine wrack collected across the atoll system (Appendix B contains details on isotopic baseline characterizations). On each islet we attempted to sample nine different species of the most common consumers including four predators (*Heteropoda venatoria*, *Neoscona theisi*, *Lepidodactylus lugubris*, *Lepidodactylus* sp. nov.), two omnivores (*Rattus rattus*, *Ornebius* sp.), and three herbivores (*Stoerberhinus testaceus*, *Dysmicoccus* sp., and *Agonexana argaula* larvae). Between 3 and 10 individuals per species were sampled at each islet when present, although not all species were found at all islets. *R. rattus* was sampled only at a subset of 10 islets. For isotopic analysis of consumers we used whole animals for insects and arachnids, except for the abdominal cavity (to avoid sampling gut contents); for geckos we used tail tips; and for rats we used whole muscle tissue. *R. rattus* and *Lepidodactylus* spp. tissue samples were stored frozen, freeze-dried, ground, lipid extracted (using chloroform–methanol extraction), and oven dried prior to analysis (Catenazzi and Donnelly 2007). Plant tissue, insects, and marine wrack were dried

at 55°C for 48 h, and ground to a powder. All individuals within a given taxonomic group collected on a given islet were pooled prior to isotopic analysis, except for *R. rattus* and *Lepidodactylus* spp., where all individual animal samples were analyzed separately, as part of another study, and data were then pooled subsequent to analysis (see Appendix C: Table C1 for sample sizes). Stable-isotopic ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed using a Carlo Erba CN analyzer coupled to a ConFlo open split interface (Carlo Erba, Milan, Italy) feeding either a Thermo Finnigan Delta-Plus IRMS or a Thermo Delta V Advantage isotope-ratio mass spectrometer (IRMS; Thermo Fisher Scientific, Bremen, Germany). Analytical error was $<0.2\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. All samples for these analyses were collected over a four-month period in 2010.

Consumer abundance, diversity, and diet

To explore mechanisms potentially driving patterns of increased FCL, we surveyed arthropod (primarily insect) abundance and diversity across islets using three different methods: (1) blacklight traps, (2) standardized vegetation surveys, and (3) targeted surveys of abundance of *Dysmicoccus* sp. and *Phisis holdhausi*, two particularly abundant and easily surveyed insects in the system (sampling details for all methods in Appendix C). We focused on arthropods as they make up the vast majority of free-living terrestrial diversity in this system and include consumers at all trophic levels. While certainly there are many taxa not captured via these three methodologies, it was not feasible to comprehensively inventory biodiversity at all islets. We thus assume that changes consistently observed across the diverse group of species that we captured using these surveys are likely to be representative of changes in entire islet food webs. We also surveyed body mass (± 0.01 g) of the larger predators occurring on the atoll (*L. lugubris*, *Lepidodactylus* sp. nov., *H. venatoria*, and diurnal spiders) from hand-collected animals (the only terrestrial vertebrate that occurs in this system that was not included in our sampling was *Hemidactylus frenatus*, an invasive gecko that occurs only on a few islets). Finally, we analyzed stomach contents from a subset of surveyed individuals of *Lepidodactylus* spp. (both species pooled, $n = 115$), and quantified the frequency with which other predators were found in the gut contents (details in Appendix C). In order to limit the amount of lethal sampling of *Lepidodactylus* spp., these diet analyses were conducted only on a subset of extremely high- and low-productivity islets (defined using top and bottom quartile of productivity).

Calculating food chain length

We calculated food chain length per islet as the trophic position of the apex predator. Trophic position of the organisms examined in this study was calculated to be $\lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}})/\Delta$, with Δ equaling fractionation and λ representing the trophic position of

TABLE 1. Effects of productivity, island size (measured in m²), and productive space (the product of these terms) on insect abundance, insect diversity, and predator body size.

| Response metric | No. islets sampled | Productivity (g N·m ⁻² ·d ⁻¹) | | | log ₁₀ (island area) | | | Productive space | | |
|--|--------------------|--|------------------|----------------------|---------------------------------|------|-------------|------------------|-------------|------------------|
| | | R ² | P | Coefficient | R ² | P | Coefficient | R ² | P | Coefficient |
| Total insect abundance | | | | | | | | | | |
| Blacklight surveys (log biomass) | 14 | 0.31 | 0.04 | 244.8 ± 106.6 | 0.18 | 0.13 | 0.3 ± 0.2 | 0.41 | 0.01 | 0.5 ± 0.2 |
| Vegetation surveys (log biomass) | 18 | 0.29 | 0.02 | 268.0 ± 104.6 | 0.03 | 0.51 | 0.1 ± 0.2 | 0.15 | 0.11 | 0.2 ± 0.1 |
| Scale surveys (% rosettes occupied) | 18 | 0.22 | 0.05 | 312.2 ± 148.3 | 0.01 | 0.68 | 0.2 ± 0.2 | 0.05 | 0.36 | 0.1 ± 0.2 |
| Targeted <i>Phisis holdhausi</i> surveys (log count) | 18 | 0.65 | <0.001 | 269.9 ± 50.0 | 0.01 | 0.75 | 0.0 ± 0.1 | 0.09 | 0.11 | 0.1 ± 0.1 |
| Diversity | | | | | | | | | | |
| Blacklight traps (species richness) | 14 | 0.38 | 0.02 | 5.6 ± 2.1 | 0.01 | 0.74 | 1.0 ± 2.9 | 0.40 | 0.02 | 6.0 ± 2.1 |
| Body size | | | | | | | | | | |
| <i>Lepidodactylus lugubris</i> | 16 | 0.26 | 0.04 | 123.1 ± 55.9 | 0.02 | 0.62 | -0.1 ± 0.1 | 0.01 | 0.77 | 0.0 ± 0.1 |
| <i>L. sp. nov.</i> | 8 | 0.00 | 0.87 | 34.9 ± 201.8 | 0.01 | 0.84 | 0.0 ± 0.2 | 0.00 | 0.97 | 0.1 ± 0.3 |
| <i>Heteropoda venatoria</i> | 16 | 0.28 | 0.04 | 290.1 ± 125.5 | 0.01 | 0.74 | 0.0 ± 0.2 | 0.01 | 0.81 | 0.0 ± 0.2 |
| Web-building spiders | 16 | 0.05 | 0.41 | 100.4 ± 119.3 | 0.09 | 0.23 | 0.1 ± 0.1 | 0.06 | 0.36 | 0.2 ± 0.1 |

Notes: Significant effects are shown in boldface. Regression coefficients are shown ±SE.

baseline (taken to be 1; e.g., Post et al. 2000, Takimoto et al. 2008). The base of the food web ($\delta^{15}\text{N}_{\text{base}}$) used in determining trophic position for all higher omnivores and predators (*H. venatoria*, *N. theisi*, *L. lugubris*, *Lepidodactylus* sp. nov., and *R. rattus*, and *Ornebius* sp.) was calculated using a two-end member mixing model (Fry and Sher 1984, Post 2002), with marine wrack and plant material as two potential sources according to the following formula:

$$\delta^{15}\text{N}_{\text{base}} = (\delta^{15}\text{N}_{\text{plant material}} \times \alpha + \delta^{15}\text{N}_{\text{marine wrack}} (1 - \alpha)) / \Delta$$

where

$$\alpha = \frac{(\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{marine wrack}})}{(\delta^{13}\text{C}_{\text{plant material}} - \delta^{13}\text{C}_{\text{marine wrack}})}$$

(Appendix B: Fig. B1 shows isotopic values of end members and of seabird guano as a reference point.) This accounts both for changes in plant baseline $\delta^{15}\text{N}$ levels across islets due to varying plant uptake of high $\delta^{15}\text{N}$ guano on some islets, and for the potential of diet shifting by consumers to marine food sources on some islets (Catenazzi and Donnelly 2007). This model assumes no trophic fractionation of $\delta^{13}\text{C}$ (as in other studies of FCL, e.g., Post 2002); previous work has demonstrated that estimates of trophic position using this methodology are relatively insensitive to estimates of the trophic fractionation of $\delta^{13}\text{C}$ (Post 2002). For obligate herbivores (*S. testaceus*, *A. argaula*, and *Dysmicoccus* sp.), we used terrestrial plants as the sole baseline for calculating trophic position (as they are not known to consume marine wrack). For all species we estimated fractionation as 3.4‰ for $\delta^{15}\text{N}$ (Takimoto et al. 2008). In Appendix C we demonstrate that using other standard values of trophic fractionation of $\delta^{15}\text{N}$ or species-specific fractionation values (from literature and directly measured in the laboratory) do not alter our general conclusions. As C₄ plants are relatively uncommon on Palmyra (Young et al.

2010b), we assumed no variation in carbon from variability in $\delta^{13}\text{C}$ in terrestrial plants.

Statistical analyses

To analyze the relative role of each potential driver in explaining FCL and trophic position of each consumer, we constructed a series of multiple linear regressions that included productivity, ecosystem size, and the product of these terms as predictor variables. We selected the best model using the stepwise method based on Akaike’s information criterion (AIC_c) and tested if the results fit models using an *F* test. These models were repeated for total FCL measurements and for trophic position of each consumer. We reran analyses with varying assumptions of fractionation, foliar nutrient baselines, and metrics used to estimate productivity, and confirmed our conclusions (Appendix B: Table B1). We used multinomial logistic regressions to test if there was a significant relationship between either productivity or ecosystem size and the identity of the predator at the top trophic position on each islet. For consumer abundance, diversity, and body size, we used multiple regressions; abundance data for each consumer type was log-transformed prior to analysis (except for *Dysmicoccus* sp. surveys, as this was not a raw abundance metric, but rather a metric of the percentage of rosettes occupied). The R² values presented in Table 1 are for each term, and the productive space term (product of productivity and area) does not control for main effects. All statistical analyses were performed in R version 2.13.12 (R Development Core Team 2012).

RESULTS

We found that FCL varied by approximately three trophic levels between islets. Investigation of the relative importance of productivity, ecosystem size, and productive space on FCL demonstrated that productivity alone

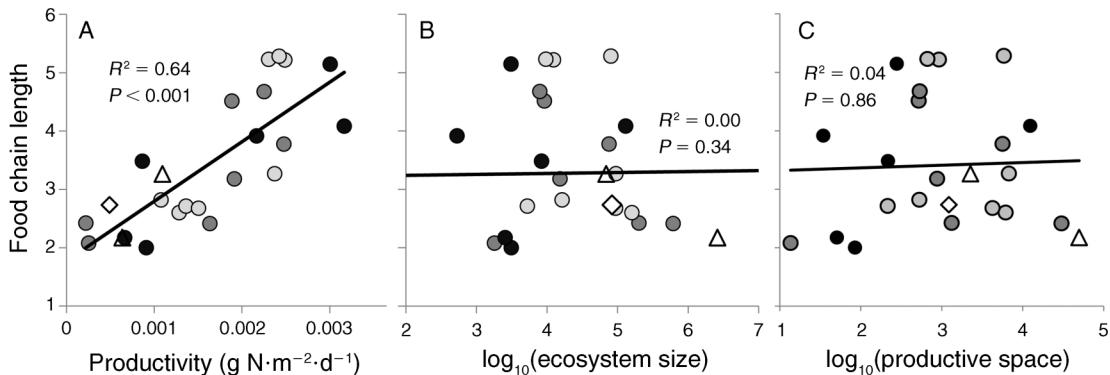


FIG. 1. Maximum trophic position by ecosystem properties. Maximum trophic position (highest mean trophic position of any consumer species) was used to approximate food chain length in our study islets. (A) It had a strong positive relationship with ecosystem productivity as estimated by $\text{g N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ but showed no significant relationship with (B) ecosystem size (measured in m^2) or (C) productive space (the product of productivity and ecosystem size). Along the productivity gradient, omnivores (open triangles) and herbivores (open diamonds) were found occupying the maximum trophic position only at low-productivity sites, but there were no other significant overall relationships between the maximum trophic position of the islet and the identity of the predator (*Neoscona theisi*, light-gray circles; *Lepidodactylus* spp., medium-gray circles; and *Heteropoda venatoria*, dark-gray circles).

was the best predictor of variation of FCL ($R^2 = 0.64$, $P < 0.0001$; Fig. 1). F test results indicated that the addition of ecosystem size ($F_{1,21} = 1.50$, $P = 0.23$) or of productive space ($F = 2.39$, $P = 0.14$) to the linear model did not significantly improve upon the model based on productivity alone. Use of alternative values for fractionation, or alternative metrics of productivity, do not substantively change the conclusions about drivers of FCL, but do alter the magnitude of total FCL change observed (Appendix B)

Multinomial logistic regressions showed no relationship between productivity and the identity of the apex predators ($R^2 = 0.09$, $\chi^2 = 5.07$, $P = 0.17$). Likewise, adding the identity of the apex predator to the best models of FCL did not improve overall model fit ($F_{3,18} = 0.39$, $P = 0.81$). Measurements of the trophic position of four top predators, two omnivores, and three herbivores revealed strong increases in trophic position with increasing productivity for all predators (Fig. 2A) and a significant increase for one of the two omnivores with the second omnivore, *R. rattus*, only marginally nonsignificant and showing similar patterns ($P = 0.06$; Fig. 2B), but no increase in trophic position for any of the herbivores, as would be predicted given that the trophic position of obligate herbivores is fixed (Fig. 2C). There was no effect of productive space or ecosystem size on trophic position of any consumer (Appendix B: Table B1).

To understand how changes in productivity could engender these changes in FCL we examined changes in consumer abundance, body size, and diet. With regard to consumer abundance, we found increased abundance of insects on islets with higher productivity in all three of the abundance measurements we employed (Table 1). In contrast, there was no significant effect of either island area or productive space on most metrics of abundance, although productive space was positively correlated to

abundance of insects in blacklight surveys (Table 1). With regard to species richness of insects in blacklight traps, this was also significantly higher on more productive islets; species richness was also positively correlated with productive space, but not with ecosystem size (Table 1). Species richness was analyzed only for the one trapping method (blacklight trapping) where we had sufficiently high taxonomic resolution to analyze diversity.

With regards to morphological or behavioral shifts in consumers along the productivity gradient, we observed significant increases in average body size with increasing islet productivity levels for two of the four top predators (or predator groups) we examined: Both *L. lugubris* and the *H. venatoria* showed significant increases in body size with productivity (Table 1). Smaller, web-building spiders showed no significant increase in mean body size with productivity (Table 1). Body size of *L. sp. nov.* was not significantly correlated with any of the metrics examined; however, this species is not as widespread at Palmyra and thus islet sample size was low ($n = 8$). None of the predator species showed any relationship of body size to either productive space or island area.

Finally, we also saw direct evidence of increased intra-guild predation in the geckos, *Lepidodactylus* spp., the only taxa for which diet contents were readily examinable. These predatory *Lepidodactylus* spp. showed small but significant increases in the frequency of occurrence of other predators in their diet in high-productivity islets as compared to low-productivity islets (13% vs. 0% of individuals contained intra-guild predators in their stomach contents on high- vs. low-productivity islets; Fisher's exact test, $P = 0.025$).

DISCUSSION

We found that productivity alone explained >60% of the variation in FCL observed across our study system. Neither ecosystem size nor productive space was

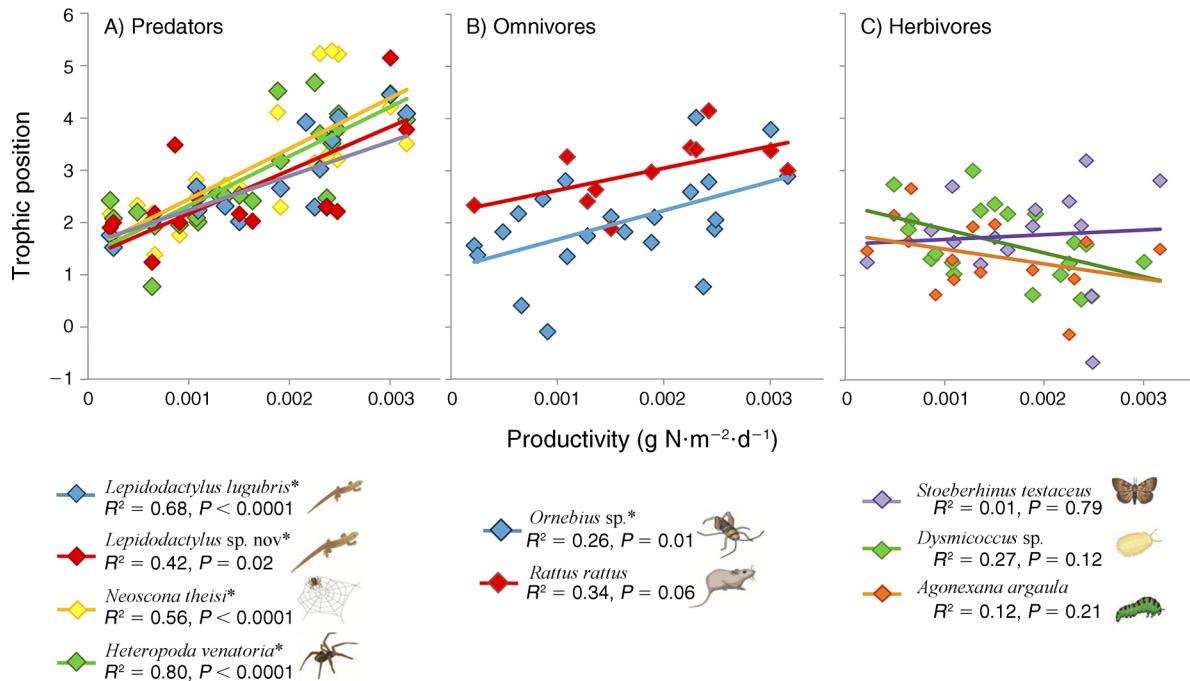


FIG. 2. Average trophic position by consumer taxa and ecosystem properties. Average trophic position of a given consumer on each islet is strongly correlated to productivity (as estimated by $\text{g N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) for (A) all four predators and for (B) one of the two omnivores (results are only marginally nonsignificant for *R. rattus*), but (C) not for any of the measured herbivores. Significant relationships are marked with an asterisk.

* $P < 0.05$.

effective in explaining FCL variability. This result strongly contrasts with results from many other studies that found ecosystem size to be a dominant factor in explaining FCL (reviewed in Takimoto and Post 2012). While the strong observed response of FCL to productivity is highly consistent with the early energy limitation hypotheses, the mechanisms suggested by our results differ somewhat from those predicted by the proponents of this theory (e.g., Hutchinson 1959), which suggest that limitations to FCL by productivity are due to the fact that low-productivity systems simply cannot support top predator species because of the energy losses associated with multiple trophic transfers. In contrast to the expectations of the energy limitation hypothesis, we found no difference in identity of top predators across the productivity gradient and no evidence that the addition of new top predators played any role in the observed lengthening of food chains (as observed in Post et al. [2000], and McHugh et al. [2010]).

If new predators were not added at more productive sites, the question remains: How were the pronounced increases in FCL that we observed achieved? The increases in trophic position within the same species of predators and omnivores (but not of herbivores) across the productivity gradient strongly suggest that changes in FCL took place due to a series of changes *within* the existing food web network rather than by new additions to the top of the food web (consistent with Post and

Takimoto [2007], Post et al. [2007], Takimoto et al. [2008], Sabo et al. [2010]). Likewise, the strong increases in total insect abundance we observed in high-productivity systems using multiple survey techniques suggests that the increased productivity is directly stimulating consumer abundance, providing opportunity for food chain lengthening. This is consistent with early conceptual understandings of energetic constraints to FCL (e.g., Schoener 1989), with more energetically rich islets supporting more animals and ultimately longer interaction chains. To understand how such changes in productivity and consumer abundance might translate to increased FCL, we examined two avenues of change in food web structure that might change total FCL without changes in apex predator identity (the additive mechanism): (1) the insertion mechanism, in which increases in diversity of consumers in high-productivity sites supports longer food webs; and (2) omnivory mechanisms, in which consumers shift in their amount of omnivory, achieved either by changes in morphology of consumers facilitating consumption of larger, potentially higher trophic-level prey items, or by behavioral shifts alone, with consumers targeting higher trophic-level prey (Appendix C: Fig. C2).

We found some support for each of the two mechanisms considered. With regards to the omnivory mechanism, we found increases in predator body size with increasing productivity, although not for all

predators. Two of the consumers for which body size was examined (*L. lugubris* and *H. venatoria*) had significantly larger sizes in more productive islands. Results were not significant for *Lepidodactylus* sp. nov., but this may be due to the very small sample size for this consumer; they were also not significant for web-building spiders, which are less likely to have increased hunting efficacy with increased body size. An increased body size of predators could allow a given species of predator to realize a higher trophic position if it allows them to increase the size and type of prey they target: By increasing intra-guild predation and cannibalism, larger animals can operate functionally like the addition of a new species (Woodward et al. 2005). Increases in trophic position with increasing body size have been shown for many predators, particularly smaller bodied ones (Cohen et al. 1993, France et al. 1998, Woodward and Hildrew 2002). We also found significant, albeit small, changes in the diet of predators for the one group where it was examined. *Lepidodactylus* spp. had higher proportions of intra-guild predators in their stomach contents when found on high-productivity islets as compared to low-productivity islets. Sample size was limited in this analysis, and more extensive diet analysis in this group of consumers and others would help confirm this conclusion. However, these results are consistent with those observed in other studies. Predators and omnivores have previously been shown to exhibit greater diet specialization, selectively feeding on higher trophic-level prey, in more productive systems (Arim et al. 2007, Stenroth et al. 2008). Increases in body size may drive this change, as larger body size facilitates cannibalism and intra-guild predation (Cohen et al. 1993, Woodward and Hildrew 2002).

With regard to the insertion mechanism, in our examination of changes in consumer diversity with productivity, we found support for the hypothesis that diversity may also be elevated in more productive islets in this system, potentially providing internal diversification of food webs. While a wide variety of productivity–diversity relationships have been observed and the universality of these relationships is much contested (Adler et al. 2011), there is some suggestion that this relationship may be generally positive in terrestrial tropical systems (Partel et al. 2007). While increases in diversity need not be correlated with increased FCL, increases in functional diversity, particularly within intermediate consumers, is a major proposed mechanism for increases in FCL (Post and Takimoto 2007). Such changes have been shown to be associated with increased FCL in other systems (e.g., Vander Zanden et al. 1999, Parker and Hury 2006, McHugh et al. 2010). When such a positive relationship occurs, it will likely lead to stronger FCL–productivity relationships.

While both insertion and omnivory mechanisms are likely to result in small individual shifts in trophic position, when taken cumulatively across multiple steps in the food web, the additive effect could cause large

effects on FCL without requiring changes in the identity of the apex predators. However, much more detailed studies of diet and behavior of consumers in this system and others would be needed to document the relative importance of each of these pathways, and to ascertain if these two mechanisms are sufficiently powerful to explain observed changes on the productivity gradient.

Equally intriguing as the strong positive response of FCL to productivity is the lack of any effect of any metric of ecosystem size (either directly or integrated into productive space) on FCL. While this lack of response to ecosystem size was observed in a global review of FCL and ecosystem size (Vander Zanden and Fetzer 2007), it is at odds with a robust literature documenting strong effects of ecosystem size or productive space on FCL in other, predominantly freshwater, systems (Takimoto and Post 2012). Indeed, not only is there no suggestion of any trend toward increasing FCL with ecosystem size at Palmyra, but some of the largest islets in the atoll complex actually have some of the lowest measured FCLs. Why did an explanation that plays such an obvious and important role in controlling the food chain length of lakes fail to be important in this terrestrial context? We argue that the explanation likely derives from several fundamental differences between the terrestrial context in which we conducted this study and other aquatic systems in which the majority of other work has been conducted.

There are many systematic differences documented, or hypothesized, in the functioning of terrestrial and aquatic ecosystems that could account for the variation of our results from those derived primarily from freshwater systems (Chase 2000, Shurin et al. 2006). Here, we focus upon three such potential pathways. First, differences in feeding constraints in consumers in aquatic vs. terrestrial systems may make terrestrial systems less likely to be constrained by size limitations of predators. In aquatic systems, and particularly for fish, feeding (particularly maximum prey size) is often constrained by gape size ratios leading to strongly size-structured food webs (Jennings et al. 2001). In comparison, terrestrial systems, where grasping and behavioral innovations (e.g., spider webs) may allow greater predation within a size class and within a feeding guild (Hairston and Hairston 1993, Brose et al. 2006), large size may not be needed to obtain a high trophic position. Consistent with this mechanism, freshwater systems show higher predator:prey body size ratios than terrestrial systems (marine systems are similar to terrestrial systems in this regard, but this may be confounded by a preponderance of benthic samples in these compendiums of marine data which often are not as heavily fish dominated; Brose et al. 2006). Thus, in terrestrial systems, relatively small animals, with smaller energetic needs and home ranges, could occupy higher trophic positions, potentially dampening the influence that increases in ecosystem size have on FCL. However, this difference is not absolute; gape-limited predators in

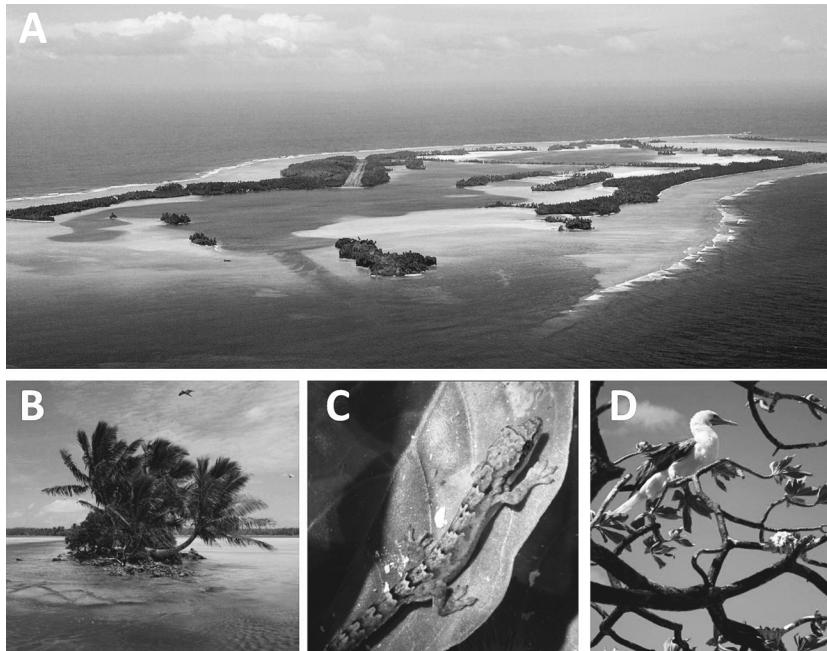


PLATE 1. The study system of Palmyra Atoll. (A) Palmyra consists of 23 islets ranging from (B) 0.05 ha to over 250 ha. The islets have relatively simple food chains with various species of (C) geckos and spiders as top predators. (D) Islets span a tenfold gradient in productivity that is driven by variation in seabird density and associated nutrient inputs. A color version of the plate is available in Appendix D. Photo credits: (A) K. Pollock, (B) G. Carol, (C) S. Hathaway, (D) H. Young.

terrestrial systems should still gain in trophic position with increased body size. There is some evidence for this in our results from Palmyra. *Lepidodactylus* (geckos, which are likely gape limited) and *H. venatoria* (a spider species that does not build webs) both showed body size increases on more productive islets. By contrast, as might be expected, primarily web-building spiders did not show size increases, but still showed similar changes in trophic position. In summary, it seems that, while body size may matter less, on average, for terrestrial system FCL than in aquatic systems, it may still play an important role in increasing trophic position of individual consumers and thus increasing overall FCL.

A second possible systemic difference between aquatic and terrestrial systems of importance to FCL may be in relationships between productivity and diversity. If productivity–diversity relationships are generally positive in terrestrial tropical systems (Partel et al. 2007), as appears may be the case in this study system too, but unimodal or nonexistent in many aquatic systems (Mittelbach et al. 2001), and if changes in species diversity increases FCL, such variation in productivity–diversity relationships could explain variation in importance of productivity as a driver in FCL.

Another final possible important difference between freshwater and terrestrial systems in driving FCL is in the nature of ecosystem boundaries and the relative size of systems, potentially explaining the lack of observed response of FCL to productive space. Both productivity

and productive space as drivers of FCL rest on similar theoretical underpinnings: principally that increasing the amount of energy or limiting resources in a system should increase the ability of the system to support top predators. Since productive space encapsulates whole-system energy availability, it is intuitively more connected to the system-wide metric of FCL than is the per unit area measurement of productivity. However, at some spatial scale, which should greatly exceed top predator home range size, predators should not be affected by further increases in productive space, as no additional energy would be available to them with increasing ecosystem size. In such cases only the per unit area productivity should matter. We suggest that this may explain the lack of response of predators to productivity in this system: Because Palmyra's top predators (geckos, spiders), as well as many of the other consumers in this system, have very small home range sizes, increases in islet size beyond a very small level are unlikely to increase the energy resources available to top predators. Thus, even though Palmyra's islets are very small, because the atoll, for biogeographic reasons, has few far-ranging animals, the relationship between predator home range and ecosystem size may be more similar to that found in many natural terrestrial systems (e.g., Arim et al. 2007), and may deviate from that of many lacustrine systems of similar area. Also of importance in terrestrial systems is that many predators (e.g., migratory passerines and birds of prey, notably

lacking from Palmyra) will regularly use multiple habitats, easily crossing spatial and energetic boundaries (McCauley et al. 2012), thus making ecosystem size more difficult to delimit. Freshwater systems are, of course, also intimately energetically linked to surrounding terrestrial habitats by predators (e.g., raccoons, ospreys, bears) and a great deal of nutrient movement (e.g., litterfall, leaching), making measurements of ecosystem size difficult even in these most cleanly demarcated systems. However, the boundaries are generally much clearer in most freshwater systems than in many terrestrial and marine habitats, where it is often challenging to conceptualize productive space (or ecosystem size; Post et al. 2007). The lack of response of FCL to ecosystem size or productive space in this terrestrial system and in a global review (Vander Zanden and Fetzer 2007) may thus reflect underlying differences between terrestrial and freshwater systems in the importance of size constraints on food web structure and FCL. However, these ideas will require further substantiation in other terrestrial settings, particularly in continental environments or in other contexts in which the scale of ecosystem size exceeds that explored in this work.

The observations we report from this study of terrestrial ecosystems contribute to our growing awareness that there is no universal driver of FCL and suggest that considerations of ecological context must be taken into account when identifying dominant drivers. Our results indicate that productivity may play an underappreciated role in structuring FCL in certain ecosystems, particularly in terrestrial settings, consistent with early energetic-limitation hypotheses. By providing some preliminary mechanistic support for how such changes in productivity can effect changes in FCL, these results offer insight into how different drivers may achieve primacy in various systems. While it seems likely that drivers of FCL vary both within and among systems, the responses observed here seem inconsistent with the spectrum of responses observed in most aquatic systems (e.g., Takimoto and Post 2012). However, there may be significant overlap in drivers of FCL across systems. Extending these studies to other terrestrial systems, as well as to other larger systems not constrained by size and dispersal limitations, will be important to understanding in what contexts productivity is likely to have its strongest impact on trophic architecture. Yet, cumulatively, these observations suggest that some of the drivers of FCL that have been derived from aquatic systems, and held to be largely universal, may not have the same explanatory power in terrestrial settings.

ACKNOWLEDGMENTS

We thank the National Science Foundation (#0639185), the Woods Institute for the Environment, the National Geographic Society, the Bishop Museum, and the U.S. Fish and Wildlife Service for support on this project. We are grateful to P. Vitousek, N. Cormier, D. Croll, R. Fisher, S. Hathaway, C. France, C. Chu, and A. A. Briggs for data, advice, and field

assistance. We also thank D. Post, and three anonymous reviewers for their careful reviews of earlier versions of the manuscript, which greatly improved this paper. Vector images are courtesy of Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary). This is publication number PARC-0092 of the Palmyra Atoll Research Consortium.

LITERATURE CITED

- Adler, P. B., E. W. Seabloom, E. T. Borer, H. Hillebrand, Y. Hautier, A. Hector, W. S. Harpole, L. R. O'Halloran, J. B. Grace, and T. M. Anderson. 2011. Productivity is a poor predictor of plant species richness. *Science* 333:1750–1753.
- Arim, M., P. A. Marquet, and F. M. Jaksic. 2007. On the relationship between productivity and food chain length at different ecological levels. *American Naturalist* 169:62–72.
- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* 68:528–537.
- Briand, F., and J. E. Cohen. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1867.
- Brose, U., et al. 2006. Consumer-resource body-size relationships in natural food webs. *Ecology* 87:2411–2417.
- Cabana, G., and J. B. Rasmussen. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255–257.
- Calcagano, V., F. Massol, N. Mouquet, P. Jarne, and P. David. 2011. Constraints on food chain length arising from regional metacommunity dynamics. *Proceedings of the Royal Society B* 1721:3042–3049.
- Catenazzi, A., and M. A. Donnelly. 2007. The *Ulva* connection: marine algae subsidize terrestrial predators in coastal Peru. *Oikos* 116:75–86.
- Chase, J. M. 2000. Are there real differences among aquatic and terrestrial food webs? *Trends in Ecology and Evolution* 15:408–412.
- Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldaña. 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology* 62:67–78.
- DeAngelis, D. L., S. M. Bartell, and A. L. Brenkert. 1989. Effects of nutrient recycling and food chain length on resilience. *American Naturalist* 134:778–805.
- Doi, H., K. K. Chang, T. Ando, I. Ninomiya, H. Imai, and S. Nakano. 2009. Resource availability and ecosystem size predict food chain length in pond ecosystems. *Oikos* 118:118–144.
- Elton, C. 1927. *Animal ecology*. Sidgwick and Jackson, London, UK.
- ESRI. 2008. ArcGIS. Environmental Systems Research Institute, Redlands, California, USA.
- France, R., M. Chandler, and R. Peters. 1998. Mapping trophic continua of benthic food webs: body size– $\delta^{15}\text{N}$ relationships. *Marine Ecology Progress Series* 174:301–306.
- Fry, B., and E. B. Sher. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* 27:13–47.
- Hairton, N. G., and N. G. Hairton. 1993. Cause-effect relationships in energy-flow, trophic structure, and interspecific interactions. *American Naturalist* 142:379–411.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia; or why are there so many kinds of animals? *American Naturalist* 93:145–159.
- Jenkins, B., R. L. Kitching, and S. L. Pimm. 1992. Productivity and food web structure at a local spatial scale in experimental container habitats. *Oikos* 65:249–255.
- Jennings, S., J. K. Pinnegar, N. V. C. Polunin, and T. W. Boonin. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic

- structuring in fish communities. *Journal of Animal Ecology* 70:934–944.
- Kaunzinger, C. M. K., and P. J. Morin. 1998. Productivity controls food chain properties in microbial communities. *Nature* 395:495–497.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–418.
- Marty, J., K. Smokorowski, and M. Power. 2009. The influence of fluctuating ramping rates on the food web of boreal rivers. *River Research and Applications* 25:962–974.
- McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* 22:1711–1717.
- McHugh, P. A., A. R. McIntosh, and P. G. Jellyman. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters* 13:881–890.
- McIntyre, P. B., L. E. Jones, A. S. Flecker, and M. J. Vanni. 2007. Fish extinctions alter nutrient recycling in tropical waters. *Proceedings of the National Academy of Sciences USA* 104:4461–4466.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396.
- Parker, S. M., and A. D. Huryn. 2006. Food web structure and function in two arctic streams with contrasting disturbance regimes. *Freshwater Biology* 51:1249–1263.
- Partel, M., L. Laanisto, and M. Zobel. 2007. Contrasting plant productivity-diversity relationships across latitude: the role of evolutionary history. *Ecology* 88:1091–1097.
- Pimm, S. L. 1982. Food webs: population and community biology series. Chapman and Hall, London, UK.
- Post, D. M. 2002. The long and short of food chain length. *Trends in Ecology and Evolution* 17:269–277.
- Post, D. M. 2007. Testing the productive-space hypothesis: rational and power. *Oecologia* 153:973–984.
- Post, D. M., M. W. Doyle, J. L. Sabo, and J. C. Finlay. 2007. The problem of boundaries in defining ecosystems: A potential landmine for uniting geomorphology and ecology. *Geomorphology* 89:111–126.
- Post, D. M., M. L. Pace, and N. G. Hairston. 2000. Ecosystem size determines food chain length in lakes. *Nature* 405:1047–1049.
- Post, D. M., and G. Takimoto. 2007. Proximate structural mechanisms for variation in food chain length. *Oikos* 116:775–782.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Sabo, J. L., J. C. Finlay, T. Kennedy, and D. M. Post. 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science* 12:965–967.
- Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* 70:1559–1589.
- Shurin, J. B., E. S. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785–791.
- Shurin, J. B., D. S. Gruner, and H. Hillebrand. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B* 273:1–9.
- Spencer, M., and P. H. Warren. 1996. The effects of habitat size and productivity on food web structure in small aquatic microcosms. *Oikos* 75:419–430.
- Stenroth, P., N. Holmqvist, P. Nyström, O. Berglund, P. Larsson, and W. Grandéli. 2008. The influence of productivity and width of littoral zone on the trophic position of a large-bodied omnivore. *Oecologia* 156:681–690.
- Takimoto, G., and D. M. Post. 2012. Environmental determinants of food-chain length: a meta-analysis. *Ecological Research*. <http://dx.doi.org/10.1007/s11284-012-0943-7>
- Takimoto, G., D. A. Spiller, and D. M. Post. 2008. Ecosystem size, but not disturbance, determines food chain length on islands of the Bahamas. *Ecology* 89:3001–3007.
- Thompson, R. M., M. Hemberg, B. M. Starzomski, and J. B. Shurin. 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology* 88:612–617.
- Thompson, R. M., and C. R. Townsend. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108:137–148.
- Townsend, C. R., R. M. Thompson, A. R. McIntosh, C. Kilroy, E. Edwards, and M. R. Scarsbrook. 1998. Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters* 1:200–209.
- Vander Zanden, M. J., and W. W. Fetzner. 2007. Global patterns of aquatic food chain length. *Oikos* 116:1378–1388.
- Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rasmussen. 1999. Patterns of food chain length in lakes: a stable isotope study. *American Naturalist* 154:406–416.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20:402–409.
- Woodward, G., and A. G. Hildrew. 2002. Body size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology* 71:1063–1074.
- Young, H. S., D. J. McCauley, R. D. Dunbar, and R. Dirzo. 2010a. Plants cause ecosystem nutrient depletion via interruption of bird-derived spatial subsidies. *Proceedings of the National Academy of Sciences USA* 107:2072–2077.
- Young, H. S., T. K. Raab, D. J. McCauley, A. A. Briggs, and R. Dirzo. 2010b. The coconut palm, *Cocos nucifera*, impacts forest composition and soil characteristics at Palmyra Atoll, Central Pacific. *Journal of Vegetation Science* 21:1058–1068.

SUPPLEMENTAL MATERIAL

Appendix A

Evaluating islet productivity ([Ecological Archives E094-060-A1](#)).

Appendix B

Calculating food chain length ([Ecological Archives E094-060-A2](#)).

Appendix C

Surveying consumer abundance, diversity, and body size ([Ecological Archives E094-060-A3](#)).

Appendix D

A color version of Plate 1, showing images from Palmyra atoll study system ([Ecological Archives E094-060-A4](#)).