Effects of Productivity on Aquatic Food Webs

by

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ABSTRACT

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Ecologists have long sought to understand the effects of productivity on community structure, and the question remains an issue of pressing importance given contemporary patterns of anthropogenic change. Extensive debate has revolved around bottom-up (resource limitation) and top-down (predation) hypotheses for community response to productivity, with the latter now dominating our conceptualization of this question, especially in aquatic ecosystems. Key to this discourse is the principle that top-down control is a fundamental response of communities to rising productivity, and, in the absence of bottlenecks to energy flux, becomes stronger across productivity gradients. I argue that this principle, when projected onto commonly occurring food web motifs, readily predicts (a) common violations of assumptions of classical top-down hypotheses, and (b) that community responses to rising productivity are not conserved across productivity gradients, but are instead context-dependent.

Here I use this principle to predict and explore the context-dependent nature of aquatic food web structure across large gradients of productivity. I show that food webs increasingly depart from the fundamental assumptions of classical top-down hypotheses with rising productivity (i.e. strong consumer-resource (especially producer-herbivore) interactions, linearity and singularity of food chains, rarity of omnivory, and productivity-driven lengthening of food chains). Alternative energy channels which arise with productivity subsidize generalist predators, which in turn mediate community structure. I demonstrate this at the scale of large, whole-ecosystem food webs, where increasing productivity is directed into bottom-up controlled detritus channels as primary producers become less edible, subsidizing generalist predators, which in turn exert top-down control on herbivores in an apparent trophic cascade. I also demonstrate this phenomenon in food webs at a sub-ecosystem scale, where subsidies from an alternative energy channel facilitate community compositional turnover from edible to less edible consumers across productivity gradients. I further show that rising productivity causes food chain length to decline as increasing energy flux begets top-heavy biomass pyramids, which favour omnivory. Overall this thesis suggests that, in contrast to conventional thinking, mechanisms of community response to productivity are not conserved across productivity gradients, and instead may be readily predicted by a simple framework for energy flux.
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# Table of Contents

Prologue.................................................................................................................................................. 1

Chapter 1. HSS Revisited: Bottom-up control in Detritus-based food chains facilitates Top-down control in Grazing Food Chains across a Productivity Gradient................................. 12
  1.1 Abstract.............................................................................................................................................. 12
  1.2 Introduction....................................................................................................................................... 13
  1.3 Methods ........................................................................................................................................... 15
  1.4 Results ............................................................................................................................................. 18
  1.5 Discussion ....................................................................................................................................... 19
  1.6 References....................................................................................................................................... 25
  1.7 Figures ............................................................................................................................................. 30

Chapter 2. A Mechanistic Theory for Food Chain Length ..................................................................... 35
  2.1 Abstract ........................................................................................................................................... 35
  2.2 Introduction ....................................................................................................................................... 36
  2.3 A Mechanistic Theory for Food Chain Length .................................................................................. 37
    2.3.1 Towards a General Theory for Food Chain Length ................................................................. 37
    2.3.2 Species Richness and FCL Mechanisms .................................................................................... 37
    2.3.3 An Energy-Driven Mechanism for Food Chain Length .......................................................... 38
    2.3.4 The Relationship between Existing Hypotheses and Energy-Driven FCL Theory .............. 41
    2.3.5 The Context Dependency of FCL: Ecosystem Size or Productivity? ................................. 42
    2.3.6 Summary .................................................................................................................................... 44
  2.4 Empirical Methods .............................................................................................................................. 45
    2.4.1 Food Web Data ........................................................................................................................... 45
2.4.2 Evaluating support for the Species Richness Mechanism for Food Chain Length ................................................................. 46

2.4.3 Evaluating predictions for the Energy Flux theory for Food Chain Length ....... 47

2.5 Empirical Results ................................................................................................................................................................................. 49

2.6 Discussion ........................................................................................................................................................................................................... 51

2.7 References .................................................................................................................................................................................................................. 54

2.8 Figures .................................................................................................................................................................................................................. 59

Chapter 3. Seagrass Benthic Community Response to Eutrophication is characterized by
Rising Dominance of an Inedible Consumer ................................................................. 65

3.1 Abstract ........................................................................................................................................................................................................... 65

3.2 Introduction ....................................................................................................................................................................................................... 66

3.3 Diamond modules in natural settings............................................................................................................................................... 68

3.4 Methods ........................................................................................................................................................................................................ 70

3.4.1 Study System ...................................................................................................................................................................................................... 70

3.4.2 Field Collections ..................................................................................................................................................................................................... 72

3.4.3 Stable Isotope Analysis ................................................................................................................................................................. 74

3.4.4 Statistics ...................................................................................................................................................................................................... 75

3.5 Results ........................................................................................................................................................................................................ 78

3.5.1 Eutrophication Gradient ................................................................................................................................................................... 78

3.5.2 The Focal Diamond Module......................................................................................................................................................... 78

3.5.3 Alternative energy channels............................................................................................................................................................. 79

3.5.4 Generalist consumer coupling into alternative energy channels ................................................................. 79

3.5.3 Compositional Turnover ............................................................................................................................................................. 80

3.6 Discussion ....................................................................................................................................................................................................... 81
List of Figures

Fig. 1.1. Predicted patterns for alternative hypotheses for trophic control in coupled grazing and detritus-based energy channels across a productivity gradient..................................................30

Fig. 1.2. Relationships between total primary production and functional group biomass... 31

Fig. 1.3. The relationship between total primary production and the fraction of top predator diets derived directly or indirectly from detritus.................................................................32

Fig. 1.4. The relationship between total primary production and the fate of primary production. ..........................................................................................................................33

Fig. 1.5. The relationship between total primary production and a) total herbivory among grazing channel consumers, and b) total predation on grazing channel consumers. ........34

Fig. 2.1. Equilibrium results from Eqn. 2.1 for the effect of increases in any a, e, or K on a) biomass pyramid shape, b) omnivory, c) food chain length, and d) stability (for systems with and without omnivory)........................................................................................................59
Fig. 2.2. The simultaneous effects of increasing ecosystem productivity (i.e. increasing $K$) and decreasing ecosystem size (i.e. increasing $a_{pc}$) on biomass pyramid shape, omnivory, and food chain length. ................................................................. 60

Fig. 2.3. Summary of the context-dependent nature of food chain length across gradients of increasing energy availability ........................................................................................................... 61

Fig. 2.4. The relationship between food chain length and fish species richness in a) marine bounded systems and b) lakes .................................................................................................................. 62

Fig. 2.5. The relationships between environmental gradients mediating energy flux and biomass pyramid shape, fish omnivory, and food chain length for marine bounded systems. ........................................................................................................................................... 63

Fig. 2.6. The relationships between food chain length and environmental gradients mediating energy flux for lake systems ........................................................................................................... 64

Fig. 3.1. Predicted outcomes of rising productivity in a focal diamond module .......... 89

Fig. 3.2. Locations of *Halodule* and *Thalassia* meadows sampled ................................ 90

Fig. 3.3. $\delta^{15}$N values of epiphytic algae indicate gradients of increasing eutrophication in *Halodule* and *Thalassia* systems ........................................................................................................... 91

Fig. 3.4. The relationship between eutrophication and biomass of members of the focal diamond module in *Halodule* and *Thalassia* systems: .............................................................. 92
Fig. 3.5. The relationship between eutrophication and biomass of members of the alternative epiphytic algae energy channel: .................................................................93

Fig. 3.6. The relationship between eutrophication and coupling of diamond module consumers into alternative energy channels. .................................................................94

Fig. 3.7. Benthic community composition across eutrophication gradients in Halodule and Thalassia systems.............................................................................................................95

Fig. 3.8. Conceptual representation of seagrass community structure across the eutrophication gradient in Halodule systems sampled in 2010. .................................................................96
**Prologue**

How does productivity structure ecological communities? This question has been a central focus of inquiry in ecology for 175 years (e.g. Liebig 1840, Haeckel 1866, Lotka 1925, Elton 1927, Volterra 1926, Lindeman 1942, Hutchinson 1959, Slobodkin 1961, Fretwell 1977, Persson et al. 1996) and remains a question of pressing importance given contemporary patterns of global change (e.g. anthropogenic changes in the cycling of limiting nutrients; Vitousek et al. 1997, Rabalais et al. 2009).

The notion that resources limit the biomass and diversity of consumer populations, first articulated as Liebig’s Law of the Minimum (1840), was widely accepted and underlay ecologists’ conceptualization of nature for a century. This concept was later extended and formalized as the bottom-up control hypothesis (Elton 1927, Lindeman 1942), which predicted cascading bottom-up effects on the biomass of consumers at successive trophic levels (e.g. Elton’s pyramid of numbers). This bottom-up view of ecological communities was challenged when Hairston, Smith, and Slobodkin (‘HSS’; 1960), noting a ‘green world’ and pondering why herbivores do not simply remove all plant biomass, posited that predation prevents herbivore biomass from reaching levels permitting runaway grazing. Later refinement to this top-down control hypothesis recognized that energy transfers between trophic levels are inherently inefficient and therefore limiting. Rising energy inputs should therefore result in the addition of successive trophic levels of consumers, which would, in turn, control the trophic level immediately below, resulting in alternating patterns of top-down and bottom-up control of producer biomass with rising productivity and successive predator additions (Fretwell 1977, Oksanen et al. 1981, Oksanen & Oksanen 2000; the ecosystem exploitation hypothesis, or ‘EEH’).
This top-down (EEH) theory builds from 4 key assumptions:

(i) that consumptive links between consumers and their resources, especially the link between herbivores and plants, are always strong,

(ii) that food chains are linear, or that communities are accurately represented as single, unbranched food chains,

(iii) that omnivory is rare, and

(iv) that changes in productivity manifest foremost as changes in vertical diversity (i.e. the addition and subtraction of trophic levels, which alter food chain length) but not functional horizontal diversity (i.e. the addition and subtraction of parallel food chains).

This top-down control theory has come to underlie much of our conceptualization of community structure and response to changing productivity, especially in aquatic ecosystems. However, the hypothesis has been controversial and has generated substantial debate. Primary producers and consumers often employ chemical, morphological, and behavioural defenses against grazing and predation, and rising productivity can facilitate the dominance of these defended groups (e.g. Phillips 1974, Lubchenco & Gaines 1981, Leibold 1989 & 1996, Van Donk et al. 2001, Karban et al. 2014). Because these defenses necessarily weaken consumptive interactions, their existence contradicts the fundamental assumption of the HSS and EEH hypotheses that consumer-resource links are always strong. Among producers, these defenses result in the accumulation of unconsumed biomass, which becomes detritus on senescence and fuels detritus-based food chains (Cyr & Pace 1993, Cebrian 1999). Grazing channels are often characterized by factors which facilitate top-down control, while detritus channels are often characterized by factors which facilitate bottom-up control (Strong 1992, Hairston & Hairston 1993, Polis & Strong 1996, Cebrian 1999, Shurin et al. 2006, De Bruyn et al. 2007); moreover,
generalist consumers often couple parallel grazing and detritus channels (Polis & Strong 1996, Rooney et al. 2006). As such, communities may not be accurately represented by linear food chain models, thus violating assumption (ii). The widespread prevalence and functional importance of omnivory (Polis & Strong 1996, Thompson et al. 2007) contradicts assumption (iii). Finally, empirical tests have both supported and refuted the assumption that rising productivity increases food chain length (e.g. Vander Zanden et al. 1999, Post et al. 2000, Pimm 2002, Takimoto & Post 2013). Moreover, for biogeographic and physiological reasons it is infeasible that pools of potential colonizers are available to sequentially add top predators to food chains ad infinitum (Pimm 2002). Collectively, these departures from assumptions of top-down theory have called into question the accuracy and utility of top-down theory. However, a well-developed literature from experimental and natural settings has documented the presence and importance of top-down control (e.g. Terborgh et al. 2001, Borer et al. 2006, Gruner et al. 2008), and a more limited literature has demonstrated its utility across productivity gradients (e.g. Persson et al. 1992, Jeppesen et al. 2000; but see Borer et al. 2005, Gruner et al. 2008). The challenge, then, to ecologists is to reconcile these ostensibly contradictory findings.

Of fundamental importance to understanding the role of productivity in structuring communities is that:

(a) consumers are not the source of top-down control, but rather that rising productivity necessarily gives rise to top-down control, and

(b) this holds true unless energy is diverted from vertical transfer, increasing the importance of bottom-up control (de Bruyn et al. 2007).

Such energetic diversions can arise from inefficient conversion of ingested prey into biomass (i.e. inefficient movement of energy through trophic levels; for example, metabolic constraints,
density-dependence, poor resource quality), or from impeded transfer of energy between trophic levels (i.e. weakly connected pathways; for example, inedible or inaccessible prey, consumer interference). This concept – that top-down control is a fundamental response of communities to rising productivity, and that top-down control becomes stronger with rising productivity – I refer to henceforth as the ‘productivity / top-down principle’ (PTP).

Fundamental to understanding the implications of the PTP for community-level responses to productivity is that there are relatively few configurations in which constituents of ecological communities are repeatedly arranged (i.e. community modules or food web motifs; for example, the food chain, apparent competition, predation on competing prey, intraguild predation; Holt 1997, Milo et al. 2002, Bascompte & Melian 2005). A well-developed set of theory (henceforth ‘community module theory’; Holt 1997), now well supported by experimental evidence from simple systems, predicts effects of rising productivity on these motifs and in turn provides a structure on which the PTP can be mapped.

Here I posit that the PTP, informed by predictions from community module theory, can provide a central organizing framework which readily predicts violations of EEH assumptions and realized effects of productivity on community structure. A key outcome of this framework is that these predictions are not conserved across productivity gradients, but are instead context-dependent on productivity levels. For instance, productivity-driven shifts in importance from competition to predation can cause food chain length to peak at intermediate productivity (the intraguild predation hypothesis; Holt & Polis 1997), and can cause resource biomass to increase but become less edible with rising productivity (the diamond module hypothesis; Leibold 1989, 1996, Holt 1997). While the EEH recognized the PTP, importantly, it did not incorporate the context-dependent nature of the PTP’s implications across large gradients of productivity;
instead the EEH assumed that effects of rising productivity are uniform across all levels of productivity.

This thesis uses the PTP, informed by predictions from community module theory, to predict and explore the context-dependent nature of food web structure across large gradients of productivity in natural settings. I document and evaluate the implications of violations of the fundamental assumptions of the EEH, and evaluate the implications of rising strength and importance of top-down control for aquatic food web response to rising productivity.

Productivity is the rate at which primary producers generate new biomass. Owing to logistical constraints productivity per se is rarely measured directly, and is instead typically estimated using various proxies. In this thesis I use several proxies of productivity, depending on the research question and ecosystem type. Because food web structure can influence primary production rates (Carpenter & Kitchell 1988, Power 1992), productivity is often estimated using the concept of potential productivity (the maximum rate of primary production possible in a given ecosystem; Oksanen & Oksanen 2000), which is often treated conceptually as carrying capacity (K) and estimated empirically as availability of the resource most limiting to primary production (typically nutrients, in aquatic systems). I adopt the potential productivity approach in Ch. 2, where I use theory to generate predictions for the effect of productivity on food web topology and food chain length using carrying capacity, K, and where I evaluate these predictions across a gradient of total phosphorus concentration in lakes. This limiting nutrient approach to productivity is suitable for systems such as lakes, where primary production is typically dominated by a single producer group (phytoplankton) whose productivity scales linearly and positively with availability of the producer’s most limiting nutrient. However, in
systems where multiple producer groups make important contributions to total ecosystem productivity (e.g. coastal marine ecosystems), availability of a limiting nutrient is not necessarily a strong predictor of total ecosystem productivity. Instead, rising availability of a limiting nutrient can be associated with contrasting shifts in production of producer groups – for instance, in coastal marine systems, rising availability of nitrogen is often associated with rising dominance of epiphytic and planktonic primary production and declining macrophytic production (Cloern 2001). This shift in producer group dominance with changing nutrient availability highlights one way in which eutrophication (the addition of limiting nutrients) and productivity are distinct concepts. Therefore, for marine systems (Ch. 1 & 2), I use realized total productivity – the summed annual primary production of all autotrophs in each ecosystem. For these ecosystems, the influence of food web structure on primary production rates is likely not problematic, because I show in Ch. 1 that herbivores do not control producer biomass in these systems. Finally, in Ch. 3 I evaluate the implications to food web structure of a eutrophication-driven shift in the dominant source of productivity. Here, I use the ratio of $^{15}$N / $^{14}$N stable isotopes, a known correlate of anthropogenic wastewater inputs to coastal ecosystems (McClelland et al. 1997, Cole et al. 2004).

In the first chapter, I explore the implications of well-known productivity-driven violations of EEH assumptions (i) and (ii). I show that the producer-herbivore trophic link is weakened with rising productivity due to a herbivore-mediated shift to inedible producer dominance and increasing predator suppression of herbivores with rising productivity. Because this unconsumed producer biomass accumulates and increasingly fuels bottom-up controlled detritus channels with rising productivity, and because grazing and detritus channels exhibit contrasting directions of trophic control, the assumption that food webs are accurately
represented by single linear food chains is increasingly violated with rising productivity. I show that detritus and grazing food chains are linked by top predators in a manner analogous to the apparent competition module, and that this coupling of food chains increasingly transmits bottom-up effects of productivity from detritus channels to top-down control of grazing channels (an apparent trophic cascade). This chapter demonstrates that although grazing channel biomass qualitatively matches predictions of the HSS and EEH, this outcome is in fact mediated by bottom-up processes in detritus channels.

In the second chapter, I evaluate the assumption that rising productivity begets rising vertical diversity (rising food chain length) and explore the implications of the PTP for food chain length. I first show that food chain length and diversity are unrelated in natural settings. Instead, using simple consumer-resource models, I show that rising vertical energy flux through food webs increases the strength of top-down control, eventually rendering omnivory energetically beneficial to predators and thereby reducing food chain length. I further show that environmental conditions other than productivity (e.g. ecosystem size) can also mediate the magnitude of energy that is transferred vertically through food webs, and that these conditions have context-dependent effects on food chain length. Overall this chapter demonstrates that, in contrast to predictions of the EEH, rising productivity results in declining food chain length.

In the third chapter, I explore how (the presence of) multiple parallel energy channels (a violation of EEH assumption ii) influence community module response to rising productivity in food webs at a sub-ecosystem scale. Similar to the first chapter, I show that energy channels which rise in importance with productivity subsidize generalist predators, which in turn facilitate community compositional turnover from edible to less edible consumers. I further show that this shift occurs at a lower threshold of energy input in communities with greater overall resource
availability.

References


Haeckel 1866


Chapter 1. HSS Revisited: Bottom-up control in Detritus-based food chains facilitates Top-down control in Grazing Food Chains across a Productivity Gradient

1.1 Abstract
Classical food web theory holds that grazing channels are regulated by top-down control with rising productivity. However this hypothesis does not consider the existence of parallel detritus-based energy channels that can fuel generalist top predators, altering trophic control in grazing channels. Using large marine food webs, we show that food web responses to increasing productivity are consistent with the Apparent Trophic Cascade hypothesis (ATCH) – rising productivity fuels bottom-up control in detritus channels, subsidizing generalist predators, and thereby strengthening top-down control in grazing channels. This pattern is likely mediated by the redirection of primary production from grazing to detritus channels as producers become less edible and as rising top predator biomass increasingly holds grazers in check. These results testify to a fundamental role of detritus channels in mediating food web responses to productivity and demonstrate that the ATCH provides an alternative explanation for classical predictions of top-down control in grazing channels.
1.2 Introduction

The nature and strength of trophic control in grazing food chains has long been a subject of debate among ecologists, with contrasting theories for the effect of resource availability on the direction of trophic control. Bottom-up responses to productivity (Elton 1927, Lindeman 1942) were thought to be ubiquitous until seminal papers by Hairston et al. (1960) and Oksanen et al. (1981) proposed that predators limit herbivore densities, allowing primary producers to remain at high biomass (i.e. the Green World Hypothesis; otherwise known as the Hairston, Smith and Slobodkin Hypothesis or ‘HSS’), and that this pattern prevails with rising productivity (the Ecosystem Exploitation Hypothesis; ‘EEH’). While top-down responses to productivity have since been documented in grazing chains (e.g. Carpenter et al. 1987, Persson et al. 1992, Wootton & Power 1993, Jeppesen et al. 2000), these classical hypotheses are based largely on simple, linear conceptualizations of grazing pathways, and do not consider the existence of parallel and interconnected detritus-based pathways (Polis & Strong 1996).

Making a call to arms for an integrative, multi-channel approach to food web ecology, Polis & Strong (1996) postulated a central role of detritus and detritus-based food chains as alternative energy pathways in food webs (i.e. the Apparent Trophic Cascade hypothesis (ACTH), whereby donor-controlled, bottom-up forcing in detritus pathways subsidizes top predator biomass, which in turn exerts top-down control in coupled grazing channels). Here we suggest that this hypothesis may be extended to predict the effect of rising productivity on trophic control in grazing channels. To build this argument, we first note 2 elements of food web structure and function:

i) Grazing channels, especially those in aquatic ecosystems, tend to be characterized by
factors which facilitate strong vertical transfers of energy (e.g. strong size structure, high producer and consumer edibility and nutritional quality; Peters 1983, Hairston & Hairston 1993, Cebrian 1999, Elser et al. 2000, Shurin et al. 2006) and thereby render food chains prone to top down control (De Bruyn et al. 2007). Conversely, detritus channels are often characterized by donor control and / or factors which promote impeded or inefficient trophic transfers (e.g. resource inedibility, consumer interference, density-dependence; Strong 1992, Polis & Strong 1996), thereby rendering food chains prone to bottom up control (De Bruyn et al. 2007).

ii) Higher-order consumers routinely couple grazing and detritus channels (Polis & Strong 1996, Moore et al. 2004, Rooney et al. 2006). This linked configuration and its flexible nature (owing to dietary generalism among predators) may facilitate the transmission of trophic dynamics between parallel pathways (Wollrab et al. 2012).

Given these phenomena, we identify 2 potential mechanisms underlying the ATCH, both giving rise to a decoupling of the herbivore-producer trophic link and a consequent redirection of rising primary production from grazing to detritus channels. First, if a grazing channel is top-down controlled, then across a productivity gradient top predators should impede rises in herbivore biomass, releasing producers from herbivore control. Producer biomass should therefore accumulate with rising productivity and become detritus upon senescence. Second, rising productivity can facilitate the dominance of less edible primary producers. This phenomenon can arise from the herbivore-mediated turnover in producer species composition along productivity gradients, where grazing defenses are constitutively expressed and the most edible species are preferentially consumed by herbivores, leaving less palatable species to persist and dominate as productivity rises (Phillips 1974, Lubchenco & Gaines 1981, Leibold 1989 & 1996,
Leibold et al. 1997, Chase et al. 2000). It can also arise without shifts in species compositional turnover from the induction of morphological, chemical and life history defenses in response to herbivore presence and grazing activity (Van Donk et al. 2001, Karban et al. 2014). This material is less susceptible to herbivory and, consequently, fated to become detritus. From both of these mechanisms it follows that ecosystems with high productivity may experience substantial detritus inputs, with this energy available for subsequent transmission through detritus-based pathways to subsidize higher trophic levels that would otherwise depend solely on energy from the grazing pathway (a detritus shunt, sensu Polis & Strong 1996), and ultimately facilitate stronger top-down control in the grazing channel with rising productivity.

Here we evaluate 3 alternative hypotheses for the effect of primary production on the direction of trophic control in ecosystems with parallel grazing and detritus-based energy channels linked by the fate of primary production and by top predators: Top-down response in both channels, Bottom-up response in both channels, and Apparent Trophic Cascade (Fig. 1). Using 18 marine food webs situated across a natural productivity gradient, we evaluate the effect of annual primary productivity on i) trophic level biomass in grazing and detritus channels, ii) the fraction of top predator diets ultimately derived from detritus, and iii) the fate of primary production. Finally, we evaluate whether there is evidence for a role of the herbivore suppression (top-down control) or declining producer edibility mechanisms in these processes.

1.3 Methods
Food web data were obtained from Ecopath network models identified from Ecopath.org, from a literature search of the Web of Science database (1996-2012) for the term ‘EcoPath’, and from references cited in Rooney et al. (2006) and other literature retrieved from these searches. Of > 120 food webs returned by these searches our selection criteria yielded 18 marine food
webs which were retained for analysis (see Appendix 1 and Table A.1).

Support for the 3 alternative hypotheses was evaluated relative to the predictions shown in Fig 1.1. To evaluate the direction of trophic control in grazing and detritus-based channels we evaluated the relationship between total primary production and functional group biomasses (Primary Producer, Detritus, Intermediate Consumers in Grazing and Detritus-based pathways, and Top Predators). The productivity gradient represented the summed annual primary production of all autotrophs in each ecosystem. In offshore systems, phytoplankton contributed 100% of summed primary production. In coastal and estuarine systems, phytoplankton contributed on average 61% (±9%) of summed primary production, benthic and epiphytic microalgae 24% (±9%), and macroalgae and seagrass 15% (±6%). There was no trend in autotroph functional group contribution across the productivity gradient. Consumers with trophic position ≥ 3.5 were considered top predators. Because top predator diets were comprised of both primary (TP 2 - 2.5) and secondary (TP 2.5 – 3.5) consumers (on average 33% and 58%, respectively), primary and secondary consumers were pooled into a single Intermediate Consumer trophic group with trophic position 2 – 3.5. Intermediate consumers were considered to be in grazing or detritus channels if ≥60% of their diet was derived directly or indirectly from primary producers or detritus respectively. In cases where producer or detritus biomass was not derived from a local estimate, where upper trophic levels appeared to be overly aggregated (e.g. benthic and pelagic fish aggregated into a single functional group), or where some higher order consumers appeared to be excluded from the food web model, the trophic group in question was omitted from analysis but remaining data from the ecosystem were included in analyses.

To evaluate whether the fraction of top predator diets ultimately derived from detritus varied with primary productivity, we evaluated the relationship between primary production and
the proportion of higher order consumer diets ultimately derived from detritus, calculated as

\[ DC_d = \sum_{i=1}^{n} DC_{ji} \cdot R_{id} \]

where \( R_{id} \) is the proportion of prey item \( i \)'s diet that is derived from detritus either directly (via detritivory) or indirectly (via consumption of detritivores and their consumers). \( DC_d \) was calculated for all consumers with TL \( \geq 3.5 \) and a weighted mean was computed according to the fraction of total predator biomass represented by a given predator.

To evaluate whether the fate of primary production shifted with rising productivity we evaluated the relationship between primary production and the fraction of primary production consumed. To evaluate support for the herbivore suppression (top-down control) mechanism for the ATCH, we evaluated the relationship between primary production and total predation on intermediate consumers in the grazing channel exerted by top predators. If predators are capable of holding grazing channel consumers in check with rising productivity, predation on grazing channel consumers should rise across the productivity gradient. To evaluate support for the declining producer edibility mechanism for the ATCH, we evaluated the relationship between primary production and total herbivory exerted by intermediate consumers in the grazing channel. Given that total consumption by intermediate consumers in grazing channels is the product of the grazer attack rate on producers (a), grazer biomass (H), and producer biomass (P) (i.e. aHP in a Type I functional response), the rise in producer biomass and herbivore suppression that we observe with rising productivity (Fig. 1.2b,d) should result in an increase in total consumption by grazing channel consumers with rising productivity. If a bottom-up mechanism impedes this increased consumptive response (i.e. causes the attack rate to decline, e.g. all new producer biomass is inedible), then this increased consumption will be muted. Thus, any non-positive change in herbivore total consumption is evidence for a bottom-up (declining producer edibility) effect.
Proportional data (i.e. % primary production consumed) were logit-transformed prior to analysis. All hypotheses were evaluated across a gradient of primary production using the `lm()` function for linear models in the statistical software R 2.15 (R Core Development Team, 2011).

### 1.4 Results

The food web functional group biomass and top predator diet origin results support the extended Apparent Trophic Cascade hypothesis (ACTH). Across the productivity gradient detritus-based energy channels exhibited bottom-up control (Fig. 1.2c, e) while parallel grazing channels exhibited top-down control (Fig. 1.2 b, d). Among intermediate consumers (trophic position 2-3.5), the majority of biomass was in the grazing channel at low productivity and conversely in the detritus channel at high productivity (Fig. 1.2 b, c). Top predator biomass rose (Fig. 1.2a) and predators derived an increasing fraction of their diet from detritus with rising productivity (Fig. 1.3); values ranged from 6% at low productivity to 82% at high productivity, with most food webs falling in the range of 30 – 70%.

The fate of primary production shifted from grazing to detritus channels with rising productivity. The fraction of primary production consumed by herbivores declined with rising productivity (Fig. 1.4). Although we lack independent estimates of detritus production, it can be inferred that the unconsumed primary production flowed to detritus, increasing detritus production across the productivity gradient. This inference is supported by a marginally significant rise in detritus standing stock across the productivity gradient, despite small sample size (Fig. 1.2e). Considered with the declining ratio of grazing consumer to producer biomass (Fig. 1.2b,d) with rising productivity, these results collectively suggest that the herbivore-producer link became decoupled with rising productivity.

Herbivory exerted by intermediate consumers in the grazing channel showed no trend
with productivity (Fig. 5a) despite an increase in producer biomass with increased primary production (Fig. 1.2d), while predation on intermediate consumers in the grazing channel by top predators showed a marginally significant positive trend (Fig. 1.5b), suggesting that both the herbivore suppression (top-down) and producer edibility mechanisms contributed to decoupling of the herbivore-producer link with rising productivity.

1.5 Discussion

Our results indicate that ecosystem response to rising productivity is consistent with the Apparent Trophic Cascade Hypothesis (ATCH). Across the productivity gradient, top predators progressively coupled into increasingly productive detritus channels, thereby inflating predator biomass, which in turn facilitated top-down control of intermediate consumers in parallel grazing channels (Fig. 1.2). This result confirms a long-standing, but as-yet untested, hypothesis about the importance of multi-channel dynamics involving the detritus shunt in complex empirical food webs (Polis & Strong 1996), and in broader terms, highlights the capacity and significance of alternative energetic pathways as indirect regulators of focal food chains. In most aquatic and terrestrial communities, primary production becomes detritus and detritus comprises the majority of total ecosystem organic matter (Lindeman 1942, Polis & Strong 1996, Cebrian & Lartigue 2004, Moore et al. 2004). Given the abundant, donor-controlled nature of detritus in most ecosystems, it is not surprising that detritus-based pathways can be important alternative conduits of energy in food webs. Our result is corroborated by a recent meta-analysis which found positive effects of detritus on detritivores and generalist predators (and evidence for bottom-up control in detritus channels), a positive but non-significant effect on producers (although sample size may have been too small to detect a significant effect), and no effect on herbivores in aquatic systems (Hagen et al. 2012, their Table 4). Because detritus production is
ultimately driven by primary production (Cebrian & Lartigue 2004, this study), Hagen and coauthors’ results match the predictions for the Apparent Cascade Hypothesis. Our result also matches the theoretical predictions of Wollrab et al. (2012, their Fig. 4b) for the response of linked grazing and detritus channels to enrichment when the producer-detritus link is donor-controlled and the per capita effect of predators on consumers is greater in grazing than detritus channels (i.e., when vertical energy transfer is greater in grazing than detritus channels – a realistic representation of most aquatic and terrestrial ecosystems). Non-energetic effects of detritus (e.g. nutrient recycling, habitat provision and refugia for detritivores and predators; DeAngelis 1992, Moore et al. 2004, Hagen et al. 2012) may be reflected in our results as well, however these effects are likely driven by primary production in its capacity as a driver of detritus production.

Overall, our results suggest that grazing channels exhibit classic (HSS) top-down trophic control driven more by within-channel processes at low productivity and by progressively more coupled, multi-channel processes with rising productivity. At low productivity, grazing and detritus-based energy channels were less coupled – weaker herbivore control by predators and higher producer edibility resulted in greater flows of primary production to herbivores (Fig. 1.4) and consequently lower flows of production to detritus, and top predators linked grazing and detritus-based channels only weakly, deriving their energy almost exclusively from grazing channels (82 – 94% of top predator diets were ultimately derived from autotrophs in the 2 food webs with the lowest productivities; Fig. 1.3). Conversely, with rising productivity, grazing channels were increasingly driven by multi-channel Apparent Trophic Cascade processes, as grazing and detritus-based channels became increasingly linked – strong suppression of herbivores by predators and declining producer palatability resulted in greater flows of primary
production to detritus and top predators increasingly coupled into detritus-based channels (on average only 32 – 57% of top predator diets were ultimately derived from autotrophs in food webs with intermediate to high productivity).

This flexibility in energy channel use (shift towards detritus-based energy channels) was manifest among consumers at all trophic levels. In addition to diet shifts among predators towards detritus-based carbon, there was a shift in consumer feeding along the productivity gradient - most consumer biomass was in the grazing channel at low productivity and conversely in the detritus channel at high productivity (Fig. 1.2b, c). With rising productivity some consumers incorporated more detritus or detritivorous prey into their diets while remaining in the grazing channel, while others became channel couplers (i.e. obtained resources from both channels), or even switched channels to consume largely from the detritus channel. This pattern was especially apparent among benthic and demersal consumers. No consumer groups shifted towards the grazing channel with rising productivity. These patterns may have been attributable to top-down suppression of grazing channel consumers, to a rise in dominance of obligate members of detritus-based channels (e.g. deposit-feeding polychaetes), or to diet shifts towards detritus or detritivores among generalist consumers. Importantly, all of these mechanisms support the general result of a restructuring of food webs from grazing- to detritus-based energy channels with rising productivity.

This rising importance of detritus channels likely arose from a progressive decoupling of the herbivore-producer link with rising productivity and associated redirection of primary production from grazing to detritus channels. Our results suggest that this phenomenon was mediated both by increasingly stronger top-down control within grazing channels (predator suppression of grazing channel intermediate consumers) and by declining producer edibility.
across the productivity gradient, with both mechanisms exerting positive feedbacks on the process. Classical top-down hypotheses for top-down control in grazing channels (i.e. HSS, EEH) have long been criticized because they do not consider the existence of grazing defenses. Intriguingly, our results suggest that producer edibility, via its contribution to decoupling of the producer-herbivore link, can in fact contribute to top-down control in grazing channels.

Decoupling of the producer-herbivore link with rising primary production has been documented in aquatic and terrestrial systems by meta-analyses and unmanipulated field studies conducted across natural productivity gradients (Brett & Goldman 1997, Micheli 1999, Chase et al. 2000, Jeppesen et al. 2000, Schmitz et al. 2000, Burkepile & Hay 2006), and has been linked to producer quality (Jeppesen et al. 2000, Cebrian & Lartigue 2004, Cebrian et al. 2009, but see Gruner et al. 2008). As we have already noted, our evidence for the producer edibility mechanism arises from an indirect inference about herbivore attack rates (a). Because this metric is a measure of herbivore effectiveness, it may reflect processes that influence producer accessibility to herbivores other than producer edibility. Herbivores may experience reduced grazing success with rising productivity if ecosystems become dominated by producers with high lignin content (i.e. macrophytic producers; seagrass and macroalgae). However neither macrophytic producer biomass, nor the fraction of total primary producer biomass represented by these groups, rose across the productivity gradient in our systems. Consumer interference or density-dependence may also reduce producer accessibility to herbivores, however this mechanism can be ruled out because herbivore biomass was invariant across the productivity gradient ($p = 0.21$). As such, it is unlikely that these alternative processes underlie our metric of producer accessibility to herbivores, and producer edibility instead offers the most compelling explanation for the pattern we observe.
Our grazing channel results align qualitatively with the predictions of the classic EEH model of top-down, single-channel responses to rising productivity (Fig. 1.2a,b,d). However, importantly, for the EEH model of top-down responses to rising productivity to be accurate, increases in productivity must be transferred up food chains without encountering impediments to energy flow (e.g. resource inedibility, declining herbivory, density-dependence, consumer interference; de Bruyn et al. 2007). Our data instead suggest that top-down control in grazing channels with rising productivity in fact arises from the cycling of this productivity through the detrital compartment and consequent subsidization of top predators (Fig. 1.3). Currently, empirical support for the EEH prediction of top-down responses to productivity derives largely from ecosystems with low productivity (e.g. oligotrophic lakes: Persson et al. 1992, Carpenter et al. 1995; temperate streams: Wootton & Power 1993; high-latitude tundra: Oksanen et al. 1981, Aunapuu et al. 2008) and from experimental communities with simple, single food chains characterized by uniform producer edibility or poorly developed grazing defenses (e.g. Kaunzinger & Morin 1998, Kneitel & Miller 2002). Studies that have failed to detect top-down control in grazing channels with rising productivity have found or speculated a role of inedible producers (Brett & Goldman 1997, Micheli 1999, Schmitz 1994, Chase et al. 2000, Schmitz et al. 2000). Collectively, these findings are in agreement with the conceptual result we present here – that top-down control in grazing channels is driven more by within-channel processes at low productivity and by progressively more multi-chain processes as productivity rises.

Our analysis evaluated dynamics in marine ecosystems, but our results likely hold in freshwater ecosystems too, which have similar food web characteristics to marine systems. In terrestrial systems, for a given level of productivity, herbivore control of producers is generally weaker (Strong 1992, Polis & Strong 1996, Shurin et al. 2002, but see Schmitz et al. 2000) and
producers generally have lower palatability (Cebrian & Lartigue 2004) than in aquatic systems. Terrestrial food webs may therefore exhibit a more bottom-up driven response in the classical grazing channel as well as the detrital channel, or may shift from single (grazing) -chain to multi-chain dynamics at a lower threshold of productivity than aquatic systems. It follows that for a given level of productivity, detritus-based pathways should be even more important in terrestrial than aquatic systems – a phenomenon that has indeed been reported (Strong 1992, Polis & Strong 1996).

The parallel, linked configuration of grazing and detritus channels characteristic of the Apparent Trophic Cascade is likely a stabilizing feature in food webs. Relative to grazing channels that are often characterized by pulsed production, detritus-based channels are likely to be more stable (i.e. less variable over time) owing to their slower turnover rates, greater diversity, donor-controlled nature, and relative lack of pulsed production (Moore et al. 2004, Rooney et al. 2008, Rooney & McCann 2012). By allowing detritus channels to sustain higher order consumers during temporal (e.g. seasonal) fluctuations in adjacent grazing channels, and by virtue of the flexible nature of this coupling (that is, top predators’ ability to shift their consumption between grazing and detritus channels with changing environmental conditions), the Apparent Trophic Cascade’s linking of these stable (detrital) and less stable (grazing) channels likely confers stability to food webs (Post et al. 2000, Rooney et al. 2006, McCann & Rooney 2009). Additionally, the detritus shunt inherent in the Apparent Trophic Cascade likely allows the relative stability of detritus channels to buffer food webs against instabilities associated with rising primary production in parallel, less stable grazing channels – that is, as rising energy inputs are transmitted through detritus instead of grazing channels, the slower turnover of detritus channels may allow this excess energy to dissipate more slowly than it would
in simple, unbranched grazing channels. These mechanisms are likely reflected in Moore et al.’s (2004) finding that the Apparent Trophic Cascade configuration is often stabilizing to food webs. Collectively, the flexible coupling of these structurally and dynamically diverse pathways allows for plasticity in community-level responses to varying environmental conditions conferring stability to food webs.

In conclusion, our results support an Apparent Trophic Cascade hypothesis – with rising primary productivity, donor-controlled bottom-up forcing in detritus-based energy channels subsidizes top predator biomass, which in turn exerts top-down control in coupled grazing channels (Fig. 1.2, 1.3, 1.5). We find evidence for a decoupling of the producer-herbivore link with rising productivity and an associated shift in the fate of primary production from grazing to detritus channels, likely due to the combined effects of herbivore suppression and declining producer edibility with rising productivity. Our results testify to a fundamental role of detritus-based pathways in mediating – and potentially buffering – food web responses to changing primary production, and highlight the importance and capacity of alternative energetic pathways as indirect regulators of dynamics in focal food chains. Importantly an Apparent Trophic Cascade, and the associated decoupling of the producer-herbivore link, yield the same patterns of trophic level biomass in grazing channels predicted by classical top-down theories (HSS, EEH), demonstrating that the Apparent Trophic Cascade provides an alternative explanation for classical predictions of top-down control in grazing food chains.

1.6 References


Fig. 1.1. Predicted patterns for alternative hypotheses for trophic control in coupled grazing and detritus-based energy channels across a productivity gradient. Dotted line: top down trophic control in both channels, solid black line: bottom-up trophic control in both channels, solid grey line: apparent trophic cascade. a) Functional group biomass, b) the fraction of predator diets ultimately derived directly or indirectly from detritus.
Fig. 1.2. Relationships between total primary production and functional group biomass. a) Top predators (TL > 3.5; \( p = 0.020 \), \( R^2 = 0.349 \), \( F = 6.98 \), \( n = 15 \)), b) intermediate consumers in grazing food channel (TL 2.0 – 3.49; \( p = \text{not significant} \) (regression line shown for effect), \( n = 16 \)), c) intermediate consumers in detritus-based food channel (TL 2.0 – 3.49; \( p = 0.004 \), \( R^2 = 0.449 \), \( F = 11.39 \), \( n = 16 \)), d) total primary producers (\( p < 0.001 \), \( R^2 = 0.656 \), \( F = 28.57 \), \( n = 17 \)), e) detritus (\( p = 0.099 \), \( R^2 = 0.388 \), \( F = 3.8 \), \( n = 8 \)).
Fig. 1.3. The relationship between total primary production and the percent of top predator diet (biomass-weighted means) derived directly or indirectly from detritus ($p = 0.018$, $R^2 = 0.341$, $F = 7.228$, $n = 16$). Values < 40% indicate ecosystems with top predators supported primarily by grazing channels, values > 60% indicate ecosystems with top predators supported primarily by detritus-based channels, and values 40-60% indicate ecosystems with top predators supported by both grazing and detritus-based channels.
Fig. 1.4. The relationship between total primary production and the fate of primary production (the percent of total primary production consumed; $p = 0.023$, $R^2 = 0.284$, $F = 6.345$, $n = 18$).
Fig. 1.5. The relationship between total primary production and a) total herbivory among grazing channel consumers ($p = $ not significant; regression line shown for effect); b) total predation on grazing channel consumers ($p = 0.073$, $R^2 = 0.244$, $F = 3.87$, $n = 14$).
Chapter 2. A Mechanistic Theory for Food Chain Length

2.1 Abstract

Multiple hypotheses propose an ostensibly disparate array of drivers of food chain length (FCL), including resource availability, dynamic stability, and aspects of ecosystem size. These hypotheses are supported in experimental in vitro and in silico systems, however, patterns in natural settings are contradictory. Here, we posit that these hypotheses effectively argue for two underlying mechanistic drivers of FCL: species richness and food web topology. For the case where species richness is constant, we show that FCL is readily predicted by a simple conceptual framework for the effect of changes in vertical energy flux on food web topology. Using a tri-trophic Lotka-Volterra model, we show that rising energy flux gives rise to increasingly top-heavy biomass pyramids, which render omnivory energetically beneficial, in turn reducing FCL. We then consider this theory in terms of two empirically documented drivers of food chain length, productivity and ecosystem size. We show that rising productivity drives declining FCL, and, moreover, that effects of productivity and ecosystem size on FCL are context-dependent. We test these predictions using empirical data from 50 lake and 9 marine food webs. We show that the species richness mechanism is not supported in natural settings, and instead that ecosystem size is the most important driver of FCL in low-productivity systems, while productivity is most important in large and high-productivity systems. These results stand in contrast to classical hypotheses which predict a positive effect of productivity on FCL, and provide a mechanistic explanation for the Dynamic Stability hypothesis. Moreover, these results provide a unifying framework for drivers of FCL and reconcile the seemingly contradictory nature of published results for effects of productivity and ecosystem size on FCL.
2.2 Introduction

Ecologists have long sought to understand the nature and origin of variation in food chain length (the maximum trophic position among all members of a food web) because of its potential to influence the direction of trophic control, nutrient cycling, and other ecosystem services. Multiple hypotheses propose a diverse array of potential drivers – classical hypotheses emphasize the importance of resource availability (Elton 1927, Hutchinson 1959, Slobodkin 1961, Fretwell 1977, Oksanen et al. 1981, Schoener 1989) and the dynamic stability of food web configurations (Pimm & Lawton 1977, but see Sterner et al. 1997), while recent work posits roles of body size and physiological design constraints (Pimm 2002), intraguild predation (Holt & Polis 1997, Diehl & Feissel 2001, Post & Takimoto 2007, Takimoto et al. 2012), and ecosystem size (Cohen & Newman 1992, Holt 1996, McCann et al. 2005). Experimental evidence supports most of these hypotheses in simple in vitro and in silico systems, however, results from natural settings are contradictory. In natural settings food chain length has consistently been positively related to ecosystem size (Post et al. 2000, Thompson & Townsend 2005, Takimoto et al. 2008, Sabo et al 2010, Tunney et al. 2012, Takimoto & Post 2013), while positive, negative, or no relationship has been documented with productivity (Persson et al. 1992, Townsend et al. 1998, Vander Zanden et al. 1999b, Pimm 2002, Thompson & Townsend 2005, Takimoto & Post 2013). Several mechanisms may underlie these results and their relative importance remains unclear; moreover, drivers of food chain length may be context-dependent (Post 2002).

Here, we posit that these hypotheses effectively argue for two underlying mechanistic drivers of food chain length: species richness and food web topology. Using data for lake and marine food webs, we show that the species richness mechanism is not supported in natural
settings. We develop a simple, general energy-related theory for food chain length for the case where species richness is constant. We use this theory to demonstrate the implications of changing energy flux within food webs (e.g. changing attack rates, resource carrying capacity) on food chain length. We then consider this theory in terms of two empirically documented drivers of food chain length (productivity and ecosystem size) and evaluate whether these drivers of food chain length are context-dependent. Finally, we test the predictions of our new theory using empirical data from lake and marine food webs.

2.3 A Mechanistic Theory for Food Chain Length

2.3.1 Towards a General Theory for Food Chain Length
Food chain length (FCL) has been the subject of extensive study and multiple hypotheses exist for what governs its natural variation, however, little theoretical framework exists for understanding the interconnectedness of these hypotheses (Post 2002). Here, we employ simple theoretical models integrating existing theory to highlight a more synthetic basis for FCL. Although the literature has frequently appealed to species richness as a driver of FCL (Cohen & Newman 1992, Holt 1996, Post et al. 2000), food web structure can also adapt to shifting environmental conditions such that even an unchanging assemblage of species may experience significant shifts in patterns of energy flow in a manner that alters FCL (e.g. Takimoto et al. 2012, Tunney et al. 2012). This latter aspect of FCL has been far less explored, and yet is likely often a fundamental aspect of changes in FCL. Below, we explore species richness-driven mechanisms for FCL and energy-driven mechanisms for FCL before then synthesizing the two related sets of mechanisms.

2.3.2 Species Richness and FCL Mechanisms
All else equal, it is often assumed that increasing species richness will be accompanied
by rising FCL, due to the addition of novel top predators or species insertions, which elongate pathways and thereby lengthen food chains. While the implicit assumption of species richness-driven FCL hypotheses is that species richness correlates positively with FCL, one can imagine cases where the addition of a species may, in fact, reduce FCL (e.g. Vander Zanden et al. 1999a, Doi et al. 2012). Theory for this aspect of FCL remains, to our knowledge, unexplored and further work is required. Nonetheless, that FCL correlates with species richness is a reasonable starting hypothesis.

While the species richness hypothesis has seldom been tested explicitly, existing hypotheses for correlates of FCL are easily tied to this mechanism. Specifically, both ecosystem size and resource availability often correlate strongly with species richness. By extension, species richness-driven theory predicts that increases in ecosystem size and productivity ought to, on average, beget increases in FCL. The Island Biogeography hypothesis (and Holt’s (1996) Sequential Trophic Dependency hypothesis) is arguably the most direct implementation of this general idea, as it posits that rises in species richness with ecosystem size should result in the addition of novel top predators and/or insertion of consumers at intermediate trophic levels, thereby lengthening food chains (Cohen & Newman 1992). Species richness-driven theory is also closely related to the Ecosystem Exploitation Hypothesis (Oksanen et al. 1981), which predicts that increasing resource availability allows the successive entrance of novel top predators.

2.3.3 An Energy-Driven Mechanism for Food Chain Length

With this in mind, we now turn to another aspect of FCL, the case where species richness is constant amid shifting food web topology (patterns of energy flow within food webs). Another suite of hypotheses posits a role of food web topology in mediating FCL. Predators should exert stronger top-down control on consumers with rising productivity (the Intraguild
Predation hypothesis; Holt & Polis 1997) and as ecosystem size declines below their foraging range (the Spatial Compression hypothesis; McCann et al. 2005). In both cases, consumer biomass is reduced, which in turn releases resource biomass. Omnivory among predators therefore becomes an energetically beneficial response to declining ecosystem size and rising productivity, and in turn leads to declining FCL across these gradients. In some sense, this aspect of FCL theory is related to the longstanding idea of ‘dynamical constraints’ (Pimm 2002); however, here we expand this idea beyond stability-driven changes to encompass ‘adaptive’ changes in food webs that alter FCL.

Energy availability has been less explored in the FCL literature although it underlies several existing hypotheses (e.g., Oksanen et al.’s (1981) Ecosystem Exploitation Hypothesis, Pimm & Lawton’s (1977) Dynamic Constraints Hypothesis). Here, we explore this theory beginning with the following familiar Lotka-Volterra food chain model with the addition of omnivory:

\[
\begin{align*}
\frac{dR}{dt} &= rR(1 - \frac{R}{K}) - a_{CR} CR - a_{PR} PR \\
\frac{dC}{dt} &= e_{CR} a_{CR} CR - m_C C - a_{PC} PC \\
\frac{dP}{dt} &= e_{PC} a_{PC} PC + e_{PR} a_{PR} PR - m_P P
\end{align*}
\]

(2.1)

where \( r \) is the growth rate of the resource (R), \( K \) is the carrying capacity of the resource, \( a_{CR} \) is the maximum consumption rates of the consumer (C) on the resource, \( a_{PC} \) and \( a_{PR} \) are the maximum consumption rates of the predator (P) on the consumer and resource, respectively, \( e_{CR} \), \( e_{PC} \) and \( e_{PR} \) are the conversion efficiencies of consumed biomass into new consumers and predators, and \( m_C \) and \( m_P \) are the consumer and predator mortality rates. If P consumes its prey as a linear function of prey density, then the degree of P’s omnivory (the ratio of P’s consumption of R relative to C) depends on the equilibrium sizes of R and C (i.e. the relative
availability of R and C to P).

The magnitude of vertical energy transfers (hereafter ‘energy flux’) through a food chain can be altered in 2 general ways: (i) changes in the resource’s carrying capacity (K), and (ii) changes in any of the parameters governing the rate of energy transfer between any consumer and resource (i.e. in Eq. 2.1, attack rate (a) or conversion efficiency (e)). Regardless of which method is employed, the theory that follows remains qualitatively the same. This simple realization allows us to generalize our FCL theory to simultaneously include productivity (using a surrogate, K) as well as any environmental or biological attribute (e.g., ecosystem size, discussed later) that might influence energy flux.

Following the approach of Rip & McCann (2011), we demonstrate that increasing energy flux through the food chain (i.e., increasing any a,e,K in Eqn. 2.1) gives rise to an increasingly top heavy biomass pyramid (Fig. 2.1a; extremely top heavy food webs have often been referred to as wasp-waisted pyramids) as increasing energy flow ultimately inflates P, which suppresses C and thereby allows R to increase. Such dramatic shifts in biomass have consequences when we allow the food chain to respond to the changing biomass structure via omnivory – the system effectively ‘adapts’ by modifying the relative amount of energy flow that goes to P from R (Fig. 2.1b), thereby changing FCL (Fig.2.1c). This occurs because P, which we have assumed consumes its prey as a linear function of prey density, increases the relative amount of R consumed relative to the amount of C consumed. Increasing energy flux therefore causes omnivory to arise passively among predators (Fig. 2.1b), shortening food chain length (Fig. 2.1c; McCann et al. 2005). For weak to moderate amounts of omnivory (McCann and Hastings 1997, Gellner and McCann 2012), this omnivorous response tends to be a stabilizing response to top-heavy biomass pyramid configurations (Fig. 2.1d). The strength of this omnivorous response will
increase if the top predator is allowed to behave (i.e. if P increases its preference for the more abundant resource R); such density dependent behavior, or switching, would exaggerate effects on food chain length. It is important to point out that this result is generally robust to additions of weak to moderate density dependence in C and P, and will persist as long as density dependence is not strong enough to prevent biomass build up (top-heaviness) in the biomass pyramid.

We have now shown that increases in productivity or energy flux in a given food chain, in the absence of species additions or deletions, can be generally expected to give rise to an increasingly top heavy biomass pyramid, which is accompanied by a change in the relative strength of different (i.e. omnivorous) energy pathways, which, in turn, drive a reduction in FCL. We now link this general theory to specific hypothesized drivers of FCL (ecosystem size, productivity, and dynamic constraints) proposed in the FCL literature.

2.3.4 The Relationship between Existing Hypotheses and Energy-Driven FCL Theory

Because reductions in ecosystem size (below the foraging scale of top predators) can increase the top-down pressure of predators on consumers (McCann et al. 2005, Van de Koppel et al. 2005, Tunney et al. 2012), the effect of declining ecosystem size on food chain length can be captured in our framework by increasing $a_{PC}$, the attack rate of predators on consumers. Similarly, the effect of rising ecosystem productivity on food chain length can be represented by increasing a surrogate for productivity ($K$, the carrying capacity of the basal resource).

Consequently, our framework predicts that for the case where species richness is constant, rising productivity and declining ecosystem size should both result in increasing energy flux and, therefore, increasingly top-heavy biomass pyramids. As such the R:C ratio is increased, which results in greater omnivory in P and, in turn, declining food chain length.

Notably, this simple theory speaks to the longstanding dynamical constraint hypothesis.
In its classic manifestation, this hypothesis argues that higher trophic levels are more likely to collapse, such that existing food chain length represents a leftover stable configuration. This hypothesis is closely related to the disturbance hypothesis, which argues that highly disturbed systems collapse to shorter FCL. Little evidence exists for the dynamic constraints hypothesis; however, it is worth pointing out that the above energy-driven FCL theory is a more subtle dynamic constraint hypothesis. While systems may indeed collapse due to instability, the above theory suggests that ecosystems also likely respond (through individual feeding) to looming instabilities by increasing foraging along different pathways (here, greater omnivory). Tunney et al. (2012) documented a specific case, theoretically and empirically, for a multi-channel lake food chain that works analogously to our simple general presentation here. We now use the above general theory to explore the context-dependent nature of ecosystem size and productivity as drivers of FCL.

2.3.5 The Context Dependency of FCL: Ecosystem Size or Productivity?

Finally, we consider the simultaneous effects of changing productivity and ecosystem size on biomass pyramid shape. Pursuant to the arguments above in section 2.3.4, we assume that declining ecosystem size increases the relative attack rate of mobile predators on their prey (i.e. increasing \( a_{PC} \)), and that productivity can be represented by \( K \). For simplicity, we use a consumer-resource framework to interpret the effects of ecosystem size (attack rate) and productivity (via the surrogate \( K \)) on food chain length. Specifically, we consider the 2-dimensional case of a predator (\( P \)) feeding on a consumer (\( C \)) (Fig. 2.2a). Note, the extension to the 3-dimensional version is simple (with either the Lotka-Volterra or Rosenzweig-MacArthur form) in that whenever the 2-dimensional framework predicts a high \( P:C \) ratio, this causes \( R \) to be released (i.e., when \( C \) is suppressed, \( R \) is released). As such, elevated \( P:C \) ratios imply low \( C:R \) ratios. Furthermore, as per Section 2.3.3, lower \( C:R \) ratios (i.e. Eltonian pyramids) give rise to
greater omnivory by P.

This simple theory predicts context-dependency in the response of food chain length to these environmental gradients. Figs. 2.2b and c show the results of increasing ecosystem size (i.e. decreasing attack rate, a_{PC}) on the biomass pyramid (i.e. P:C biomass ratio in Fig. 2.2b) and food chain length (Fig. 2.2c). For all levels of K, increasing ecosystem size reduces the biomass ratio of P:C (i.e. renders biomass pyramids more Eltonian (more pyramid-shaped; Fig. 2.2b). This reduction in P:C effectively cascades to increase the C:R ratio (recall Fig. 2.1). Thus, all else equal, increases in ecosystem size render C more abundant relative to R and reduce omnivory, in turn causing food chain length to rise with ecosystem size (Fig. 2.2c). Notably, food chain length in high-productivity systems is less influenced by ecosystem size, as these systems are already relatively top-heavy and omnivorous. Thus the strength of the effect of changing ecosystem size depends on productivity level – low-productivity systems are most dramatically impacted by increasing ecosystem size (i.e. lower a_{PC}).

We find a similar result for an experiment in which productivity (K) is varied (Figs. 2.2 d and e). Specifically, small ecosystems (which already have top-heavy biomass pyramids due to high attack rates) are less influenced by productivity than large ecosystems (Fig. 2.2d). Therefore changing productivity has a greater impact on food chain length in large than small ecosystems (Fig. 2.2e).

Collectively these results suggest that: (i) among low-productivity systems, ecosystem size is the dominant driver of food chain length, whereas (ii) among high-productivity systems, productivity should be the dominant driver. Additionally, (iii) among small ecosystems there should be little effect of productivity; instead ecosystem size should be the dominant driver of food chain length, and (iv) among large ecosystems, productivity should be the dominant driver.
of food chain length and there should be little effect of ecosystem size (Fig. 2.2b-e).

Notably, these predictions are robust to additions of bottom-up forcing (e.g. the addition of density dependence to predators). Doing so causes the predator isoclines in Fig. 2.2a to bend to the right, and the relative shift in P/C ratios with changing K and a_{PC} is conserved at all but very high levels of bottom-up forcing.

### 2.3.6 Summary

Collectively these arguments effectively argue for a context-dependent theory for FCL (Fig. 2.3). In effectively ‘large’ ecosystems (i.e. where a_{P} is low; Fig. 2.3a), FCL initially rises with increasing productivity due to bottom-up species richness-driven mechanisms, as depicted in Fig. 2.3a for very low productivity (sequential additions of novel predators or insertions of consumers at intermediate trophic levels; Oksanen et al. 1981, Holt 1996, Post 2002). Eventually, energy-driven food web mechanisms can begin to play a role when no additional predators or consumers are available to colonize the system, or when the system’s species pool is saturated. This threshold may also be driven by physiological “design constraints” (sensu Pimm 2002), which place upper limits on predator body size and speed, and by the benefits of dietary generalism, which both prevent the existence of long chains of specialized predators. At productivity levels above this threshold, rising energy flux causes food webs to become top heavy (i.e. elevated ratios of P : C biomass, and declining ratios of C : R biomass), which results in passive increases in omnivory among predators and, consequently, declining food chain length. Here, we show the outcome of increased omnivory. At very high levels of productivity, FCL may be mediated once again by species richness-driven mechanisms, i) as omnivory becomes strong (i.e. strong intraguild predation, whereby predators eventually extirpate IG-prey at high productivity), ii) as environmental conditions related to high productivity render systems inhospitable (e.g. anoxia), or iii) as the rising dominance of inedible producers or consumers
(Leibold 1996) renders increases in energy unavailable for transfer to higher-order consumers.

In effectively ‘small’ ecosystems (i.e. where \( a_p \) is high; Fig. 2.3b), FCL again initially rises with increasing productivity due to species richness-driven mechanisms. However, due to stronger top-down interactions in small systems (i.e. stronger \( a_p \); Fig. 2.2a), the threshold at which food web mechanisms begin to influence FCL occurs at a lower level of productivity, and food chain length declines more rapidly with further increases in productivity than in ‘large’ ecosystems.

2.4 Empirical Methods

2.4.1 Food Web Data

Food chain length data for lake systems were derived from the database of Vander Zanden & Fetzer (2007), who used \( ^{15}\text{N} / ^{14}\text{N} \) stable isotope data to calculate maximum trophic position among all species present in a food web. We modified their database as follows: i) in lakes with food web manipulation (e.g. top predator addition) we used pre-manipulation values of maximum food chain length; ii) we did not use food webs when there was evidence that a top predator was present > 6 months of the year) but not included in the food web (e.g. seals in Lake Baikal); and iii) we removed multiple instances of the same sampling location and instead used only first instance listed. We did not use their data for marine bounded systems owing to difficulties in finding reliable productivity data.

Food web topology, omnivory, and food chain length data for marine bounded systems were from the database of carefully selected ecosystem network (EcoPath) models assembled for Ch.1 (Appendix 1 and Table A.1)). For network models, food chain length was the maximum trophic position of all functional groups present in the food web. As discussed in Appendix A1, within food webs, trophic positions calculated using network models and \( ^{15}\text{N} / ^{14}\text{N} \) stable
isotopes are strongly correlated, indicating that estimates of trophic position from network models are reasonably accurate. Both stable isotope data and network food web models represented trophic interactions averaged over annual time scales. Food webs included birds and marine mammals. Groups present < 6 months of the year (e.g. migratory species) were removed from models prior to analysis because transient species are subsidized by production derived from outside focal ecosystems. In cases where some higher order consumers appeared to be excluded from the food web model, the predator group was omitted from biomass pyramid analyses and the system was excluded from analyses of food chain length, but remaining data from the ecosystem were included in analyses of C : R biomass ratios and omnivory.

2.4.2 Evaluating support for the Species Richness Mechanism for Food Chain Length

To evaluate the species richness mechanism for food chain length, we evaluated the relationship between food chain length and fish species richness. We used fish to represent ecosystem species richness because fish are more likely than other phyla to be well-studied and accurately identified. Estimates of fish species richness were derived from food web source publications or literature whose stated purpose included the enumeration of fish species richness. When possible, estimates were cross-referenced using several sources, and where discrepancies existed we used the largest estimate found. For marine systems, some species richness estimates represented long time periods (e.g. total fish species observed in assessment trawls over 30 years). The use of long-term species richness data renders estimates less susceptible to problems of under-sampling. However, because food web models and stable isotope data represent finite time periods, long-term estimates may over-estimate species richness for food webs with high temporal species turnover (e.g the Baltic and North Seas). Several species lists grouped fish from rare or cryptic families, or when species identification was problematic. In these cases we assumed that a family included three species. We cannot assess the quality of these data using
species accumulation curves (Gotelli & Colwell 2001); nevertheless the data show the expected positive relationship with ecosystem size in lakes ($\rho << 0.001$, $R^2 = 0.60$, F-value = 80.08, n = 56) but not in marine bounded systems. Moreover, our predictions involve qualitative patterns evaluated at a logarithmic scale, rendering the result less susceptible to moderate inaccuracies in species richness.

2.4.3 Evaluating predictions for the Energy Flux theory for Food Chain Length

Ecosystem volume was estimated for lakes and marine bounded systems as a hyperbolic sinusoid ($0.43 \times \text{area} \times \text{maximum depth}$, after Post et al. 2000), or as area $\times$ mean depth when maximum depth was not known. Marine systems were considered bounded if their connection to adjoining water bodies represented $< 20\%$ of the total ecosystem perimeter (e.g. embayments, coastal lagoons, and atolls with narrow openings to open ocean systems).

For lakes, where phytoplankton represent the largest contribution to primary productivity and where phosphorus availability is the dominant driver of phytoplankton production (Wetzel 2001), ecosystem productivity was estimated using Total Phosphorus concentration (TP; derived from source publications or from a Web of Science search for data collected during the food web sampling period). For marine bounded systems, where productivity is derived from phytoplankton, but with important contributions from benthic macrophytes, epiphytic, epibenthic producers, we used total primary production ($t \; \text{WW} \; / \; \text{km}^2 \; / \; \text{yr}$) to represent ecosystem productivity.

We evaluated predictions for biomass pyramid shape and omnivory (i.e. Fig. 2.2b & d) in marine bounded systems only (we lacked biomass pyramid and diet data for lakes), and predictions for food chain length (i.e. Fig. 2.2c & e) in both marine bounded and lake systems.

Among our marine bounded food webs, ecosystem volume ranged from $4 \times 10^{-2}$ to $4.2 \times 10^4 \; \text{km}^3$, representing an extensive gradient of ecosystem size. However, total primary productivity...
production ranged from 300 – 9100 t WW / km² / yr (~ 30 to 910 g C / m² / yr), with most food webs having high productivity 1000 – 9100 t WW / km² / yr (~ 100 – 910 g C / m² / yr). Under these conditions, our theory shows that top-heaviness and omnivory should be positively related to productivity, and unrelated or weakly related to ecosystem size (Fig. 2.2, and Section 2.3.5). By extension, food chain length should be negatively related to productivity and unrelated or weakly related to ecosystem size (Fig. 2.2b-e). Predictions for biomass pyramid shape were evaluated using log ratios of C : R and P : C biomass. Our basal resource group consisted of all autotrophs. Our consumer group consisted of all consumers with trophic position 2-2.5 (i.e. primary consumers), and our predator group consisted of all consumers with trophic position > 2.5 (top predators and mesopredators were grouped because both groups consumed primary consumers). Because fish species composition was not constant across our productivity and ecosystem size gradients, it was not possible to evaluate the diet of a single fish species across these gradients. Instead, predictions for omnivory were evaluated using an aggregate group of fish with common length 33-40cm (which equates to a foraging range of ~100 – 110 km, using the regression for fish from Fig.1 in McCann et al. 2005). Fish common lengths were taken from fishbase.org. For each food web, the diets of all fish falling within this length category were tabulated and omnivory was calculated as the weighted average (according to fish biomass) of the fraction of consumer diets comprised of basal resources (autotrophs and detritus).

Lakes were classified as oligo-, meso-, or eutrophic after Carlson (1977; i.e. Oligotrophic: TP < 10 ug/L, Mesotrophic: TP 10 – 24 ug / L, Eutrophic: TP > 24 ug / L). Oligo- and mesotrophic lakes were pooled for analyses because they showed similar responses to environmental gradients. Lakes with volume < 0.1 km³ were classified as small and those with volume > 0.1 km³ were classified as large. For this analysis, we use only lakes for which both
volume and productivity are known.

Hypotheses were evaluated using the `lm()`, `AIC()`, and `logLik()` functions for linear regression and Akaike’s Information Criterion in R (R Core Development Team 2011).

### 2.5 Empirical Results

Food chain length was not related to fish species richness in marine systems (Fig. 2.4a). In lakes, when data were pooled across all levels of productivity and ecosystem size, there was no correlation between food chain length and fish species richness (Fig. 2.4b). However, among oligo- and mesotrophic lakes, where our theory predicts that food chain length should be driven by ecosystem size, food chain length was positively related to fish species richness (Fig. 2.4b). This correlation was likely due to the positive effect of ecosystem size on species richness, rather than an effect of richness per se. This logic is supported by a likelihood ratio test, which demonstrated that a model with fish species richness and ecosystem size did not fit the data better than a model with only ecosystem size (D-statistic = 0.122).

Productivity and ecosystem volume were negatively correlated among lake systems ($r = -0.39$, $p = 0.006$, $n = 47$) but not among marine bounded systems ($p = 0.85$; although the correlation was marginally significant in systems with high productivity: $r = -0.72$, $p = 0.066$, $n = 7$). Within categories of small and large lakes, and low and high productivity lakes, productivity and ecosystem size were not correlated.

In marine bounded systems, our results matched most of the predictions of our theory for systems at high productivity (i.e. that productivity should be the dominant driver of food chain length; Fig. 2.2d & e). Biomass pyramids became more top-heavy with rising productivity – the log ratio of $P/C$ rose while the log ratio of $C/R$ declined across the productivity gradient (Fig. 2.5a). Across the ecosystem size gradient, only the log ratio of $C/R$ was significantly related to
ecosystem size (Fig. 2.5b). There was a positive and significant relationship between fish
omnivory and total primary production (Fig. 2.5c), but not ecosystem size (Fig. 2.5d). There was
no relationship between food chain length and total primary productivity, except in systems with
very high productivity (Fig. 2.5e). Food chain length was positively related to ecosystem size
(Fig. 2.5f). Because productivity and ecosystem size were negatively correlated in systems with
high productivity ($\rho = 0.066$), among high productivity systems food chain length cannot be
ascribed to a unique driver. However, among high-productivity systems, Akaike’s Information
Criterion indicated that the relationship between food chain length and productivity was better
than that with ecosystem size ($\Delta$AIC = 3.99). Moreover, that the food web topology – omnivory
mechanism was supported across the productivity gradient (Figs. 2.5 a & c) but not across the
ecosystem size gradient (Figs. 2.5b & d) suggests that the FCL – ecosystem size pattern was
driven by the marginal correlation between productivity and ecosystem size in high-productivity
systems. Regardless of which environmental driver was most important, the overall result for
marine bounded systems is that biomass pyramid shape, omnivory, and food chain length were
driven by the magnitude of vertical energy flux.

In lakes, our results also matched the predictions of the Energy Flux theory for the
context-dependent nature of food chain length. In oligotrophic and mesotrophic lakes, food
chain length was positively related to ecosystem size (Fig. 2.6a) and was not related to
productivity (Fig. 2.6b). In eutrophic lakes, food chain length was not related to ecosystem size
(Fig. 2.6a) and was negatively related to productivity (Fig. 2.6b). Among small lakes, food chain
length was not related to productivity (Fig. 2.6c), however, in contrast to predictions, food chain
length was not related to ecosystem size either (Fig. 2.6d). Among large lakes, food chain length
was negatively related to productivity (Fig. 2.6c) and showed no relationship with ecosystem
2.6 Discussion

It is not surprising that a species richness-driven mechanism for food chain length is not supported in lake or marine ecosystems. Most ecosystems in natural settings are likely not in early successional states, and, moreover, have likely been altered by anthropogenic influence. This result does not indicate that the species richness mechanism is always unimportant, but rather that it is likely more important in young ecosystems and those with extremely low productivity, where colonization and extinction are the dominant processes mediating species richness. It is notable that evidence for a species richness-based positive relationship between productivity and food chain length (i.e. the EEH) derives largely from simple experimental systems (e.g. Kaunzinger & Morin 1998, Jenkins et al. 1992) and from natural settings with low or limiting productivity (e.g. geologically young oligotrophic lakes: Vander Zanden et al. 1999b; note that these data were not included in our analysis of lakes because total phosphorus data were not available; oligotrophic Scandinavian lakes: Persson et al. 1992; arctic tundra: Oksanen et al. 1981, Aunapuu et al. 2008), although a recent meta-analysis (Takimoto & Post 2013) reported strong positive effects of productivity on food chain length in what were likely highly productive systems (Everglades wetlands, neotropical rivers).

Instead, we documented significant effects of an adaptive behavioural mechanism (omnivory) on food chain length. A longstanding paradigm underlying our conception of ecosystem response to environmental change invokes species richness as the dominant mediator of ecosystem response. However, food web topology is increasingly recognized as an important mediator of ecosystem responses, at least over some ranges of environmental gradients (McCann et al. 2005, McCann 2007, Tunney et al. 2012, Salt 2013), and adaptive trophic behaviour is
known to enhance food web stability (Kondoh 2003, Rooney et al. 2006, Valdovinos et al. 2010). Omnivory provides one such adaptive and stabilizing mechanism (McCann & Hastings 1997, Vandermeer 2006, McCann 2012, Gellner & McCann 2012), by muting strong, unstable interactions (e.g. high $a_{PC}$) and strengthening others (e.g. $a_{CR}$; McCann 2012). The widespread prevalence of omnivory in natural settings (Thompson et al. 2007) suggests that this strategy may be important at a global scale.

The longstanding Dynamic Instability hypothesis (Pimm & Lawton 1977) suggests that long food chains do not exist because they are dynamically unstable (due to the diminishing stabilizing influence of bottom-up controlled basal resources on top predators when food chains are long). Sterner et al. (1997) documented flaws in the logic underlying this theory; nevertheless, the Dynamic Instability hypothesis has remained a central organizing idea in the food chain length literature. Our results provide a mechanistic explanation for this hypothesis, suggesting that long chains, which might otherwise result from species richness-driven mechanisms under conditions of high vertical energy flux (i.e. high energy availability in productive and small ecosystems), do not exist because omnivory occurs as a passive and stabilizing response to top-heavy biomass pyramids. As ecosystems move along environmental gradients of productivity and ecosystem size that promote top-heaviness, omnivory first exerts a stabilizing effect on unstable top-heavy biomass pyramids, followed by collapse at extreme ends of these gradients when the predator extirpates the consumer (a manifestation of Rosenzweig’s (1971) Paradox of Enrichment and Pimm & Lawton’s (1977) Dynamic Instability hypotheses).

We further show that environmental drivers of topologically-driven changes in FCL are context-dependent. Ecosystem size drives food chain length in small systems where spatial compression is strongest, and in low to intermediate productivity systems where effects of
productivity are weakest. Conversely, productivity drives food chain length in large systems, where the constraints of spatial compression are alleviated, and in highly productive systems. This context-dependency explains why various studies have reported different outcomes for tests of drivers of food chain length. Studies which found no relationship between food chain length and productivity, but a positive relationship with ecosystem size, were evaluated in low to intermediate productivity systems (e.g. Post et al. 2000 used a few oligotrophic and mostly mesotrophic lakes), where we show that food chain length is driven by ecosystem size with little effect of productivity. The preponderance of published supporting evidence for a role of ecosystem size, but not productivity, may be due to the use of relatively small study systems, where our theory predicts that ecosystem size should be more important. That food chain length is set by a suite of context-dependent drivers was first suggested by Post (2002) and later by Takimoto et al. 2012, who showed that when IGP is strong (in our framework, when biomass pyramids are wasp-waisted), food chain length is shorter than when IGP is weak (i.e. when biomass pyramids are Eltonian, in our framework).

We evaluate our theory in aquatic systems only. We may be more likely to find support for our top-down-driven theory in aquatic systems (where food webs are often characterized by traits rendering them susceptible to top-down control; for example strong size-structuring, relative lack of inedible producers and consumers, which all result in greater vertical energy flow; Shurin et al. 2006, De Bruyn et al. 2007) than in terrestrial systems (which are often characterized by factors promoting bottom-up control). However, although our theory arises from a top-down driven mechanism, it is robust to all but the strongest levels of bottom-up forcing.

To isolate the effect of environmental gradients on food chain length from confounding
effects of top predator identity and community composition, an ideal test of these hypotheses would maintain a constant regional species pool across environmental gradients. Instead, the large ranges of ecosystem size and productivity required to evaluate our framework (i.e. to have ‘complete’ gradients of ecosystem size and productivity) in natural field settings necessarily involved compositional turnover in the regional species pool, because maintaining a constant species pool can be achieved only over a small environmental gradients.

In conclusion, we provide the first demonstration that, in contrast to predictions of classical hypotheses, the effects of ecosystem size and productivity on food chain length are independent of species richness in natural settings. We show instead that food chain length arises from a behavioural (omnivory) mechanism, the context-dependent nature of which is readily predicted by simple consumer-resource models. We demonstrate that rising productivity drives declining food chain length at high productivity, and that declining ecosystem size should drive declining food chain length in small systems. As such, our theory and results reconcile a large literature of seemingly inconsistent results. Notably, two primary agents of anthropogenic change are pushing ecosystems towards small ecosystems (via habitat fragmentation) and highly productive ecosystems (via eutrophication), the very settings where omnivory and eventually ‘omnivorous collapse’ are predicted to have the greatest impact on food chain length. As such, our theory and results provide tractable predictions for the impacts of these 2 stressors on food chain length.

2.7 References


Sabo, J.L., Finlay, J.C., Kennedy, T. & Post, D.M. (2010). The role of discharge variation in


2.8 Figures

Fig. 2.1. Equilibrium results from Eqn. 2.1 for the effect of increases in any a, e, or K on a) biomass pyramid shape (i.e. biomass ratios of P : C, and C : R), b) the degree to which P is omnivorous, c) food chain length, and d) stability (for systems with and without omnivory), for the following parameters: \( r = 2.0 \), \( k = 3.0 \), \( a_{CR} = 1.1 \), \( a_{PC} = 0.7 \), \( a_{PR} = 0.2 \), \( e_{CR} = 1.0 \), \( e_{PC} = 1.0 \), \( e_{PR} = 1.0 \), \( m_C = 0.7 \), \( m_P = 0.7 \).
Fig. 2.2. The simultaneous effects of increasing ecosystem productivity (i.e. increasing $K$) and decreasing ecosystem size (i.e. increasing $a_{PC}$) on biomass pyramid shape, omnivory, and food chain length. a) Isoclines of a 2-level Lotka-Volterra model demonstrate equilibrium predator and consumer biomass under simultaneous changes in ecosystem productivity and size. At very low productivity, only the consumer is present. Panels b & c show the effect of ecosystem size, at various levels of productivity, on the degree of top-heaviness (i.e. the ratio of equilibrium predator and consumer biomass), resultant omnivory, and consequent food chain length. Panels c & d show the same for the effect of productivity at various levels of ecosystem size. As demonstrated earlier in this section (Fig. 1b), top-heavy food webs (i.e. with elevated predator : consumer biomass ratios) promote greater omnivory. Panels (b) and (d) demonstrate that i) productivity should have little effect on food chain length in small systems, but a large effect in large systems, and ii) ecosystem size should have a large effect on food chain length in low productivity systems, but little effect in high productivity systems.
Fig. 2.3. Summary of the context-dependent nature of food chain length across gradients of increasing energy availability predicted by a simple Lotka-Volterra model a) in effectively ‘large’ ecosystems (i.e. where $a_{PC}$ is weak), and b) in effectively ‘small’ ecosystems (i.e. where $a_{PC}$ is strong).
Fig. 2.4. The relationship between food chain length and fish species richness in a) marine bounded systems and b) lakes. The relationship is significant in oligo- and mesotrophic lakes (dotted line; \( p = 0.045, R^2 = 0.14, F\)-value = 4.434, \( n = 29 \)).
Fig. 2.5. The relationships between environmental gradients mediating energy flux and biomass pyramid shape, fish omnivory, and food chain length for marine bounded systems. a) The relationship between total primary production and the log ratio of consumer : resource biomass (solid line; $p = 0.077$, $R^2 = 0.34$, F-value = 4.128, $n = 10$) and the log ratio of predator : consumer biomass (dotted line; $p = 0.018$, $R^2 = 0.572$, F-value = 9.343, $n = 9$). b) The relationship between ecosystem size and the log ratio of consumer : resource biomass (solid line; $p = 0.032$, $R^2 = 0.458$, F-value = 6.747, $n = 10$), and the log ratio of predator : consumer biomass showed no significant change ($p = 0.376$, $n = 9$). c) The relationship between total primary production and omnivory among fish 33-40cm ($p = 0.025$, $R^2 = 0.594$, F-value = 8.788, $n = 8$). d) The relationship between ecosystem size and omnivory among fish 33-40cm ($p = 0.71$, $n = 8$). The relationship between food chain length and e) total primary production (all systems: no relationship; for systems with very high productivity: $p = 0.011$, $R^2 = 0.76$, F-value = 15.67, $n = 7$), and f) ecosystem volume for marine bounded systems (for all system: $p = 0.013$, $R^2 = 0.61$, F-value = 10.79, $n = 9$).
Fig. 2.6. The relationships between lake food chain length and environmental gradients mediating energy flux.  a) Food chain length is related to ecosystem volume in oligo- and mesotrophic lakes (dotted line; p = 0.00002, R^2 = 0.52, F-value = 27.11, n = 27), but not in eutrophic lakes (solid line shown for demonstrative purposes; p = 0.52, n = 23).  b) Food chain length is related to total phosphorus in eutrophic (solid line; p = 0.012, R^2 = 0.266, F-value = 7.62, n = 23) but not oligo- and mesotrophic lakes (dotted line shown for demonstrative purposes; p = 0.56, n = 27).  c) Food chain length is related to total phosphorus in large (solid line; p = 0.017, R^2 = 0.255, F-value = 6.84, n = 22) but not small lakes (dotted line shown for demonstrative purposes; p = 0.68, n = 28).  d) Food chain length is not related to ecosystem volume in either small (p = 0.35, n = 28) or large lakes (p = 0.28, n = 22).
Chapter 3. Seagrass Benthic Community Response to Eutrophication is characterized by Rising Dominance of an Inedible Consumer

3.1 Abstract
Community modules provide strong, generalizable predictions for the effects of productivity on food web structure. Among these, the diamond module (DM; predation on competing prey) predicts the compositional turnover from edible to less edible consumers with rising productivity, mediated by a shift from competition to predation as drivers of community structure. These predictions have been rarely evaluated in natural settings, where consumers are often dietary generalists and where eutrophication often shifts the relative dominance of basal resources and the energy channels they support, thereby altering prey availability and shifting constraints on putative community modules. Here we evaluate whether the diamond module predicts benthic community compositional response to eutrophication in seagrass systems where diamond module consumers couple into alternative energy pathways. Benthic communities were dominated by edible consumers (polychaetes) at oligotrophic sites, and a less edible consumer (the mud brittle star *Ophiophragmus filograneus*) rose in dominance with eutrophication. We show evidence that compositional turnover was facilitated by energy inputs to the focal diamond module from alternative energy channels – i) subsidies to the DM-predator (young-of-year fish) from the alternative epiphytic algae channel likely facilitated suppression of polychaete biomass, in turn promoting compositional turnover to less edible brittle stars, and ii) turnover was likely further accelerated when inedible consumers coupled into another alternative resource (phytoplankton). Finally, eutrophication facilitated a more rapid shift to predation-structured communities in systems with greater overall resource availability but similar predation pressure. These results highlight the role of alternative energy channels in determining how community modules manifest in natural settings and demonstrate that community modules, when combined
with knowledge of natural history, can provide a mechanistic framework to predict effects of eutrophication.

3.2 Introduction
Community response to productivity has long interested ecologists and remains a question of contemporary importance given current patterns of anthropogenic change (Cloern 2001, Smith 2003, Rabalais et al. 2009). In the last 30 years ecologists have developed strong predictions for how community modules (simple units of 3-4 species interacting as predators, prey, and competitors, and which comprise the building blocks of food webs; e.g. food chain, diamond module, intraguild predation; Holt 1997) respond to changing productivity. Among these, the diamond module (predation on competing prey) predicts community compositional turnover from edible to less edible taxa across productivity gradients, arising from a shift in the relative importance of competition and predation (Leibold 1989, 1996, Holt 1997).

Although the diamond module response to rising productivity is well supported in theoretical and simple laboratory experimental systems (e.g. Leibold 1989, Holt et al. 1994, Abrams & Walters 1996, Chase 1999, Rip et al. 2010) it has been rarely evaluated in natural settings (e.g. Chase et al. 2000, Chase 2003, Vasseur et al. 2005, Klausmeier & Litchman 2012) despite its potential to provide a synthetic predictive framework for ecosystem response to environmental change. Community module predictions assume that modules remain compartmentalized across productivity gradients (i.e. that modules retain their shape – that interactions are stronger within modules than with groups external to modules; Holt 1997). However, in natural settings productivity gradients often shift the relative dominance of basal resources, and, by extension, the relative importance of the energy channels they support (e.g. shift from macrophytic to epiphytic and planktonic primary producers in increasingly productive ecosystems; Scheffer et al. 1993, Hemminga & Duarte 2000, Cloern 2001). Because higher-order
consumers are often dietary generalists, shifts in energy channel importance (i.e. shifts in the relative availability of prey within and external to community modules) may cause modules to lose their compartmentalization, in turn modifying responses to productivity from community module predictions (e.g. Novak 2013, and see next section). In the case of the diamond module, the predicted response (compositional turnover) may be accelerated or attenuated, depending on where subsidies from alternative energy channels enter the module. The degree to which predation-mediated compositional turnover is realized in natural settings may be further modified by cross-ecosystem differences in overall energy availability in basal resource pools as top-down control prevents edible consumers from responding to greater energy availability, thereby allowing inedible consumers, especially those in communities with greater overall energy availability, greater access to shared resources.

Here we posit a conceptual model for how subsidies from alternative energy channels influence the response of a focal diamond module to productivity in natural settings. We evaluate these predictions in benthic communities of shallow seagrass systems situated across a gradient of anthropogenic eutrophication, where nutrient loading drives strong shifts in the relative importance of energy channels (Hemminga & Duarte 2000, Cloern 2001). Specifically, we evaluate whether benthic communities are dominated by an edible consumer (polychaetes) in oligotrophic systems, and by a less edible consumer (the mud brittle star, *Ophiophragmus filograneus*) in eutrophic systems. We assess consumer diets to evaluate whether there is evidence that alternative energy channels play a role in mediating compositional turnover. Finally, we compare compositional turnover between 2 seagrass ecosystem types with contrasting availability of the shared resource (sediment organic matter, SOM) but similar levels of predator abundance.
3.3 Diamond modules in natural settings

The diamond module is a common motif in natural settings (Milo et al. 2002, Bascompte & Melian 2005) organized around a generalist predator that differentially consumes intermediate consumers with a range of edibilities (Fig. 1a). At low ecosystem productivity, where a shared resource (DM-resource) is limiting and where a generalist predator (DM-predator) is present at low abundance, communities consist exclusively of superior resource exploiters (DM-edible consumers). Because these groups often employ ‘fast’ growth strategies (often associated with minimal investment in defense strategies; Agrawal et al. 1999), they are, in general, readily edible to potential predators. Rising ecosystem productivity augments both DM-resource biomass (allowing novel consumers to colonize) and DM-predator biomass. The resultant increased predation pressure, which is necessarily focused on the DM-edible consumer, holds this consumer in check, thereby facilitating a shift in community dominance to better-defended groups (DM-inedible consumer), eventually extirpating the DM-Edible consumer at high ecosystem productivity.

Although the diamond motif is common, the generalist nature of higher-order consumers and the well-documented shift in energy channel importance over ecosystem productivity gradients, suggest that the module is unlikely to remain compartmentalized with rising ecosystem productivity in natural settings. Instead, the DM-generalist predator likely often couples into alternative energy channels (e.g. Novak 2013), and intermediate DM-consumers may also be fueled by these alternative pathways. Thus, from an empirical perspective, tests of the diamond module theory require an extended version of the simple focal module to a more complex, but empirically realistic, module.

The degree to which the diamond module prediction (compositional turnover with rising productivity) is realized in natural settings depends on food web topology (i.e. where subsidies
from alternative energy channels enter the focal diamond module). **When subsidies enter at the DM-predator, (Fig. 1b), compositional turnover will generally be accelerated.** This occurs because subsidies cause predator density to increase with ecosystem productivity (as long as the predator can consume from the alternative energy channel with reasonable efficiency), holding the DM-Edible consumer approximately in check (DM-Edible consumer biomass may show moderate increases or declines under different assumptions), thereby facilitating a shift to dominance by the DM-Inedible consumer. Alternatively, compositional turnover may be attenuated, or even reversed, if i) the generalist (DM-)predator switches its diet away from the focal diamond module (i.e. the DM-Edible consumer) to consume primarily from an alternative energy channel, relieving predation pressure on the DM-Edible consumer and thereby allowing increases in ecosystem productivity to drive increases in the DM-Edible consumer, or ii) an alternative energy channel is more successful in taking up rising ecosystem productivity than the focal diamond module, but is of sufficiently poor quality accessibility that it cannot fuel increases in generalist (DM-) predator biomass.

**When alternative channel subsidies enter instead at the DM-Edible consumer (Fig. 1c), compositional turnover is again accelerated,** as rising DM-Edible consumer biomass is consumed by the DM-predator, thereby facilitating compositional turnover to the DM-Inedible consumer (unless resources in the alternative energy channel are of sufficiently poor quality or accessibility to prevent increases in DM-Edible consumer biomass). **When alternative channel subsidies enter at the DM-Inedible consumer (Fig. 1d), compositional turnover is again accelerated.** This phenomenon may be due entirely to bottom-up forcing, if the DM-Inedible consumer is subsidized by a donor-controlled alternative resource (e.g. high phytoplankton biomass driven by anthropogenic nutrient inputs) or if subsidies cause the DM-Inedible
consumer to increase at a rate that allows it to suppress the DM-resource. Alternatively, if the DM-Inedible cannot suppress the DM-resource (e.g. if the DM-resource is donor-controlled), then increases in the DM-predator may play a role in mediating compositional turnover to the DM-Inedible consumer.

Overall, with few exceptions, the addition of realistic dietary generalism and alternative energy channels to a focal diamond module readily facilitates acceleration of community compositional turnover to less edible consumers with rising productivity. Further, the degree to which turnover is due to the predator (i.e. top-down forcing) correlates with the degree to which the predator rises with ecosystem productivity.

In what follows, we consider a focal diamond module in benthic communities of shallow seagrass systems across a productivity gradient and follow the fate of subsidies entering the module from alternative energy channels. Similar to diamond module predictions, we find that rising ecosystem productivity yields an increase in the generalist DM-predator, and an increase in the DM-Inedible consumer relative to the DM-Edible consumer. Diet analyses suggest that subsidies from alternative energy channels likely accelerate this outcome.

3.4 Methods

3.4.1 Study System

In oligotrophic seagrass communities, the primary basal resource is detritus (sediment organic matter; SOM). Seagrasses, although dense, are rarely consumed and instead fuel food webs by providing detrital inputs to SOM (Cebrian 1999). With rising nutrient loading epiphytic algae become an increasingly important resource, while phytoplankton may also increase. The resultant water column shading and epiphytic algal overgrowth are thought to contribute to seagrass decline. SOM generally increases with eutrophication as well, likely due to greater
inputs of senescent planktonic and epiphytic algae (Hemminga & Duarte 2000, Cloern 2001).

We evaluate a putative extended diamond module in the benthic fauna, where community biomass is dominated by polychaetes (‘DM-Edible consumer) and by the amphiurid mud brittle star (O. filograneus; ‘DM-Inedible consumer’). Both consume SOM – polychaetes can be detritivorous or omnivorous (consuming detritivorous meiofauna or polychaetes), while O. filograneus is a generalist primary consumer, consuming detritus but with the ability to suspension feed as well (Woodley 1975, J.M. Lawrence, Department of Integrative Biology, University of South Florida, pers. comm.). Both can be consumed by small generalist predators dominant in our study system (young-of-year pinfish Lagodon rhomboides in Halodule meadows and young-of-year pinfish and pigfish Orthopristis chrysoptera in Thalassia meadows; ‘DM-Predator’), although O. filograneus is less edible by virtue of its poor nutritional quality (due to an extensive calcium carbonate internal skeleton) and predation refugia (due to its large body size and burrowing behaviour, leaving only its arms exposed to sub-lethal predation (Stancyk 1974, Woodley 1975, Stoner 1980). Young-of-year pinfish and pigfish can also consume mesograzers (amphipods and Hippolyte shrimp) and primary producers in the epiphytic algae channel (Stoner 1980, Heck et al. 2000). Thus in this extended diamond module, the DM-Predator and DM-Inedible consumer can couple into alternative energy channels.

Across a eutrophication gradient, we evaluate biomass in the focal diamond module: i) the DM-resource (SOM), ii) the DM-edible consumer (polychaetes), iii) the DM-inedible consumer (mud brittle star), and iv) density of the shared predator, and biomass in an alternative energy channel: v) an alternative basal resource (epiphytic algae) and vi) epifaunal mesograzers (amphipods (mostly Cymadusa compta) and broken-back shrimp Hippolyte spp.)). We then evaluate vii) diets of the DM-Predator and DM-Inedible consumer, and finally viii) the degree of
compositional turnover across the eutrophication gradient (the fraction of total benthic community biomass represented by brittle stars).

We compare the degree of compositional turnover between 2 seagrass ecosystem types with contrasting availability of the shared resource (SOM) but similar levels of predation: i) mixed *Thalassia testudinum* / *Syringodium filiforme* meadows, where seagrass detrital inputs to SOM are low because open vegetation canopies facilitate export of floating seagrass detritus; consequently, SOM is low and edible / less edible consumers likely compete for SOM, and ii) *Halodule wrightii* meadows, where seagrass detrital inputs to SOM are high because dense canopies of narrow *Halodule* blades facilitate retention of seagrass detritus; consequently, SOM is present at greater levels and competition for SOM is likely less important than it is in *Thalassia* systems. Under similar levels of predator abundance (and, presumably, similar predation pressure on edible consumers), systems with greater availability of the shared resource (i.e. *Halodule* systems) should experience relatively greater energy flows to inedible consumers, as predation pressure prevents edible consumers from taking up the shared resource and thereby allowing inedible consumers greater access instead. It follows that *Halodule* systems should have lower edible consumer biomass and more rapid compositional turnover to the inedible consumer – that is, for a given level of the eutrophication gradient, *Halodule* systems should have lower polychaete biomass and should be dominated by brittle stars to a greater degree than *Thalassia* systems. We do not contrast module compartmentalization between system types, because we evaluated predator diets in *Halodule* systems only.

3.4.2 Field Collections
We sampled 6 *Halodule* and 3 mixed *Thalassia* / *Syringodium* meadows situated in the lee of barrier islands on Florida’s central Gulf coast (Fig. 3.2), representing a gradient of anthropogenic eutrophication in each system type. Sites were sampled in May and June of 2010.
and 2012. Sites were 1.0 – 1.5 m depth and 10 – 50 m from shore.

Sediment organic matter (SOM) was collected from surface sediments (5 cm depth) and assessed for organic matter content (Sed. % OM) following standard methods (Short & Coles 2001). Water column particulate organic matter (POM) was assessed (2012 only) from unfiltered whole water collected 25 cm below the surface and at least 50 cm above the seagrass canopy, following standard laboratory procedures (Short & Coles 2001). Seagrass blades were collected from 4 quadrats (25 x 25 cm; 625 cm$^2$) placed at 10 m intervals along a 60 m transect. Live blades were separated from detrital tissue, dried at 60°C for 48 hours, and weighed to the nearest 0.1 mg.

To assess epiphyte cover approximately 20 live Halodule or 10 live Thalassia blades were subsampled from each quadrat. These were gently rinsed and scraped of epiphytes, dried at 60°C for 48 hours, and weighed to the nearest 0.1 mg.

Benthic fauna were collected from 4 cores (10 cm diameter; 78.5 cm$^2$) placed at 10 m intervals along the transect and sampled to 20 cm depth. Brittle stars were collected from 4 cores placed at 10 m intervals along the transect during 2010 sampling and from 12 cores placed at 5 m intervals during 2012 sampling. Samples were gently sieved on-site using 500 um mesh fabric and frozen until lab analysis. Brittle star arms were examined for evidence of regeneration (evidence of fish predation; Clements et al. 1994). Only omnivorous and detritivorous polychaetes are included in the ‘polychaete’ category because strictly carnivorous species (i.e. Diopatra cuprea) do not consume the shared resource (SOM). “Other” taxa identified in samples were Cyathura carinata and Idotea isopods, juvenile crabs < 5 mm, banded dwarf hermit crabs Pagurus annulipes, hermit sipunculans Phascolion strombus, small omnivorous snails (e.g. Nassarius vibex, Bulla, Modulus), and small deposit-feeding snails (e.g. Cerithium muscarum, Bittiolum). Epifaunal mesograzers were collected from hauls of 6 sweep nets (30 x 25 cm,
500um mesh) pulled rapidly through the seagrass canopy across a distance of 1.8m (swept area 5580 cm$^2$), at 10m intervals on the transect. All fauna were dried at 60°C for 48 hours and weighed to the nearest 0.01mg.

Predators (young-of-year pinfish and young-of-year pigfish) were collected using baitfish traps (33 x 36 x 61 cm; 1.3cm mesh) which collected individuals with total length 6-11cm. Predator abundance was estimated as catch per unit effort (CUE; individuals collected per hour soak time on incoming or high tides). Juvenile pinfish exhibit marked ontogenetic omnivory, consuming primarily copepods and amphipods at lengths < 3.5cm, epifaunal crustaceans (amphipods, small shrimp), polychaetes, and plant matter at lengths 4-9cm, and exclusively plant matter at lengths > 9cm (Stoner 1980). We restricted dietary (isotopic) analysis of pinfish to individuals 6-8cm total length, over which range pinfish diets are relatively similar (Stoner 1980).

3.4.3 Stable Isotope Analysis
Epiphytic algae and benthic faunal tissues were dried, homogenized, treated with 3.7% HCl to remove carbonates, dried at 60°C for 72 hours, and homogenized again. 5-10 individuals were combined for each polychaete sample, while brittle stars were analyzed individually. Sediments were suspended in deionized water, heavy particulates (sand) allowed to settle, and the resulting suspension was decanted onto pre-combusted Whatman GF/F glass fiber filters (0.7um pore diameter), following the procedure of Tewfik et al. (2005). Filters with SOM and POM were treated with 3.7% HCl for 30 minutes, rinsed with deionized water, and gently scraped of organic matter, which was then dried at 60°C for 72 hours and homogenized. Dorsal muscle was excised from pinfish collected from *Halodule* systems, dried at 60°C for 72 hours, and homogenized.

Dried homogenized tissue was weighed and packed into tin capsules for isotopic analysis.
by the University of New Hampshire (UNH, Durham, NH, USA) Stable Isotope Laboratory and by Isotope Tracer Technologies Inc. (IT²; Waterloo, ON, Canada). Replicate samples analyzed at UNH had precision ± 0.21‰ (δ¹³C; n = 12) and ± 0.12‰ (δ¹⁵N; n = 12). Replicate samples analyzed at IT² had precision ± 0.16‰ (δ¹³C; n = 4) and ± 0.43‰ (δ¹⁵N; n = 3). For replicate samples analyzed at both labs, IT² values for δ¹³C were lighter (i.e. more negative) than those reported by UNH (difference = 0.46‰ ± 0.17; n = 4), and IT² values for δ¹⁵N were heavier (i.e. more positive) than those reported by UNH (0.08‰ ± 0.13; n = 2). Because the between-lab difference in measured δ¹³C was greater than precision of δ¹³C estimates within each lab, δ¹³C values reported by IT² were corrected by +0.46 to facilitate comparisons with UNH data. The between-lab difference in measured δ¹⁵N did not exceed lab precision estimates for δ¹⁵N, therefore δ¹⁵N was not corrected between labs. Because HCl can have non-uniform effects on δ¹⁵N, 2 – 3 unacidified replicates of tissues treated with HCl were used to estimate the effect of acidification on δ¹⁵N values. δ¹⁵N values were corrected for acidification when its effect was greater than the precision of δ¹⁵N estimates (Table 3.1).

### 3.4.4 Statistics

Marine plant and primary consumer δ¹⁵N reflect anthropogenic wastewater inputs to coastal ecosystems (McClelland et al. 1997, Cole et al. 2004, Tewfik et al. 2007). We used δ¹⁵N values of epiphytic algae to identify a gradient of eutrophication. These values were correlated with δ¹⁵N values of several primary consumers at our sites (e.g. the gastropod grazer *Cerithium muscarum*; r = 0.84, p = 0.038 at 6 sites where data were available). For sites sampled in 2010, δ¹⁵N values reported for epiphytic algae are δ¹⁵N values corrected for acidification, using correction coefficients listed in Table 3.1. For sites sampled in 2012, δ¹⁵N values are from unacidified samples. In the absence of δ¹⁵N estimates for epiphytic algae at Anclote Key, known to be the most oligotrophic among our *Halodule* sites based on human occupancy (zero) and long
term chlorophyll a data (data available at wateratlas.usf.edu, Station ID = St. Joseph Sound W1), epiphytic algae δ¹⁵N was assigned a value (δ¹⁵N = 0.3) half that of the next most oligotrophic site (δ¹⁵N = 0.6).

Analysis of covariance models were used to evaluate effects of eutrophication (i.e. δ¹⁵N of epiphytic algae), and between-system (i.e. Halodule vs. Thalassia) differences therein, on a) environmental conditions surrounding the focal diamond module (i) DM-resource availability (logit-transformed Sed % OM) and quality (C/N ratio), ii) availability of resources in an alternative energy channel, i.e. epiphytic algae cover and epifaunal mesograzer biomass, iii) DM-predator density (CUE), iv) the degree to which the DM-Predator couples into the alternative epiphytic algae channel, and v) the degree to which the DM-Inedible Consumer couples into the alternative phytoplankton channel), and b) the degree of compositional turnover across the eutrophication gradient (i.e. the proportion of total benthic community biomass represented by brittle stars (arcsin sqrt)). Interactions between eutrophication level (log δ¹⁵N of epiphytic algae) and system type (Halodule or Thalassia) were insignificant for all dependent variables except epiphytic algae cover. Therefore an ANCOVA model with an interaction term was used to evaluate effects of eutrophication and system type on epiphytic algae cover (i.e. Epiphytic algae cover = log δ¹⁵N Epiphytic Algae + System Type + log δ¹⁵N Epiphytic Algae*System Type + ε), and ANCOVA models without interaction terms (i.e. Dependent Variable = log δ¹⁵N Epiphytic Algae + System Type + ε) were used to evaluate effects of eutrophication and system type on remaining dependent variables. Because brittle star diets were dramatically different between sampling years at Halodule sites, I evaluated whether brittle star biomass and community dominance also differed between sampling years using an ANCOVA model (Dependent Variable = log δ¹⁵N Epiphytic Algae + Year + ε; interaction terms were not significant).
Diets of the DM-Predator (in *Halodule*) and DM-Inedible consumer (in *Halodule* and *Thalassia*) were evaluated using a stable isotope approach at several sites representative of the eutrophication gradient. Consumer diets were estimated using Bayesian mixing models with the siar 4.2 package in R (Parnell et al. 2010, R Core Development Team 2011, Parnell & Jackson 2013) using no priors. Mixing models were constrained to potential prey items identified from natural history knowledge of brittle star diets (i.e. SOM and POM; Woodley 1975, J.M. Lawrence, Department of Integrative Biology, University of South Florida, pers. comm.) and from pinfish dietary items identified by Stoner (1980). Pinfish δ¹³C values were corrected for lipid content following Post et al. (2007). For sites sampled in 2012, POM δ¹³C was measured directly. For sites sampled in 2010, a universal δ¹³C value for particulate organic matter (POM) was back-calculated from the mean of δ¹³C values of several bivalves (*Parvilucina nassula, Anadara ovalis, Crassostrea virginica*; muscle tissue) collected at 4 sites across the eutrophication gradient, assuming a trophic enrichment factor of +0.8 ‰ (Vander Zanden & Rasmussen 2001). Variation in bivalve δ¹³C was low among sites and species (mean - 25.2‰, SD 0.5‰) and δ¹³C did not vary with eutrophication level. Published data suggest that filter-feeder δ¹³C does not vary across a large eutrophication gradient (e.g. Tewfik et al. 2005; Δ = 0.1‰ between marine coastal oligotrophic and hypereutrophic sites). Moreover, variation in δ¹³C is low among different size fractions of marine coastal POM (Moncrieff & Sullivan 2001), suggesting that interspecific variation in bivalve δ¹³C is also low. Brittle star diets were determined using only δ¹³C values, because i) acidification had inconsistent effects on brittle star δ¹⁵N, rendering corrections for acidification not possible, and ii) the mud brittle star is known to be a strict primary consumer (Woodley 1975, J.M. Lawrence, Department of Integrative Biology, University of South Florida, pers. comm.).
3.5 Results

3.5.1 Eutrophication Gradient

$\delta^{15}$N values for epiphytic algae established eutrophication gradients in *Halodule* and *Thalassia* systems (Fig. 3.3). The large range of $\delta^{15}$N values (0.3 – 4.2‰ ($\Delta = 3.9‰$) in *Halodule* meadows, 0.9 – 4.9‰ ($\Delta = 4.0‰$) in *Thalassia* meadows; recall that $\delta^{15}$N is a multiplicative scale) compares favourably with ranges of epiphyte $\delta^{15}$N across known large gradients in eutrophication (e.g. epiphyte $\delta^{15}$N = 0.6 – 4.4‰ ($\Delta^{15}$N = 3.8‰) for 0 – 1110 humans / km$^2$ with raw sewage entering the latter; Tewfik et al. 2005) and suggests that we sampled a broad eutrophication gradient.

3.5.2 The Focal Diamond Module

DM-resource quantity (Sed %OM; Fig. 3.4a) declined from oligotrophic to mesotrophic systems, likely reflecting declining detrital seagrass inputs (214 g dw live seagrass / m$^2$, 70 g dw seagrass detritus / m$^2$ at the most oligotrophic *Halodule* site (Anclote Key), contrasted with 96 g dw live seagrass / m$^2$, 11 g dw seagrass detritus / m$^2$ at a mesotrophic *Halodule* site (Sarasota)), and increased from mesotrophic to eutrophic systems ($p = 0.001$, $F_{1,4} = 64.08$), likely reflecting rising inputs of alternative basal resources (phytoplankton, epiphytic algae; Tewfik et al. 2005). Sed % OM was greater in *Halodule* than *Thalassia* systems ($p = 0.037$, $F_{1,7} = 6.58$). Conversely, quality of the DM-resource improved (i.e. declining C/N ratio) from oligotrophic to mesotrophic sites, likely due to declining detrital seagrass inputs as described above, and subsequently declined (i.e. rising C/N ratio) in *Halodule* systems from mesotrophic to eutrophic sites, although a trend was not clear in *Thalassia* systems (Fig. 3.4b).

DM-Edible consumer (polychaetes) biomass rose with eutrophication ($p = 0.044$, $F_{1,7} = 5.99$; Fig. 3.4c) and was greater in *Thalassia* than *Halodule* systems ($p = 0.028$, $F_{1,7} = 7.67$). Although the interaction between eutrophication and system type was not significant, polychaete
biomass appeared to rise with eutrophication in *Halodule* systems, but decline in *Thalassia* systems. DM-Inedible consumer (brittle star) biomass rose with eutrophication \( (p = 0.027, F_{1,7} = 7.73; \text{Fig. 3.4d}) \) and was greater in *Halodule* than *Thalassia* meadows \( (p = 0.014, F_{1,7} = 10.61) \).

DM-Predator CUE rose across the eutrophication gradient \( (p = 0.027, F_{1,5} = 9.62; \text{Fig. 3.4e}) \) and did not differ between *Halodule* and *Thalassia* systems \( (p = 0.76, F_{1,5} = 0.10) \).

### 3.5.3 Alternative energy channels

An alternative resource, epiphytic algae cover \( (\text{g dry weight (dw) / g dw seagrass}) \), increased with eutrophication \( (p = 0.001, F_{1,7} = 27.87; \text{Fig. 3.5a}) \) and was greater in *Thalassia* than *Halodule* meadows \( (p = 0.005, F_{1,7} = 16.77) \). Conversely, areal biomass of epiphytic algae \( (\text{g dw / m}^2) \) showed a declining, although insignificant, trend with eutrophication, reflecting declining seagrass areal biomass and was greater in *Thalassia* than *Halodule* systems \( (p = 0.006, F_{1,7} = 14.65; \text{Fig. 3.5a, inset}) \).

Epiphytic algal mesograzer biomass (amphipods and *Hippolyte* shrimp) showed a unimodal relationship with eutrophication, likely reflecting intraguild predation (unpubl. data) and did not differ between *Halodule* and *Thalassia* systems \( (p = 0.31, F_{1,6} = 1.21, \text{Fig. 3.5b}) \).

Water column particulate organic matter (POM; collected only in 2012) showed no trend across the eutrophication gradient.

### 3.5.4 Generalist consumer coupling into alternative energy channels

Pinfish collected from *Halodule* systems derived approximately 50% of their diet from the DM-edible consumer (polychaetes) and the remaining 50% from consumers and resources in the alternative epiphytic algae channel at all levels of eutrophication \( (\text{Fig. 3.6a}) \). Arm regeneration scars were observed only at the most eutrophic *Halodule* site (Walsingham Bridge; observed in 22% of individuals collected whole), suggesting that predation on brittle stars was
low or nonexistent across the eutrophication gradient, and low when brittle star density was high. At sites sampled in 2010, diet mixing models indicated that brittle stars derived an increasing proportion of their diet from phytoplankton with increasing eutrophication; conversely, in 2012, brittle stars diets consisted of only SOM, regardless of eutrophication level (Fig. 3.6b).

### 3.5.3 Compositional Turnover

Polychaetes and brittle stars were the dominant members of benthic communities, except at the eutrophic Thalassia site (Fig. 3.7, and see below), and compositional turnover manifested with eutrophication in both Halodule and Thalassia systems. The most oligotrophic sites were dominated by the DM-edible consumer (polychaetes) with the DM-Inedible consumer (brittle stars) absent (in Halodule) or nearly absent (in Thalassia), and dominance of the DM-Inedible consumer rose with eutrophication ($p = 0.038, F_{1,7} = 6.54$; Fig. 3.7). At the most eutrophic Thalassia site (Sanibel Island), benthic infaunal biomass was not dominated by the DM-inedible consumer, but instead by another filter feeder (Cross-barred venus *Chione cancellata*; ~30mm length) sufficiently large to escape predation by young-of-year fish. Collectively, suspension-feeder (brittle star and venus) biomass accounted for $77\%$ of benthic faunal biomass at Sanibel. We did not consider *Chione* when evaluating the SOM-polychaete-brittle star-YOY fish diamond module because *Chione* were unlikely to have accessed the DM-resource (low SOM and POM at Sanibel suggested low sediment resuspension).

In Halodule systems, turnover was consistently greater in 2010, when the DM-inedible consumer coupled into an alternative resource (phytoplankton; Fig. 3.6b) than for a comparable level of eutrophication in 2012. However the difference was not significant ($p = 0.18, F_{1,4} = 2.57$), likely due to insufficient statistical power (power = 0.55). Notably, DM-Inedible consumer biomass was significantly greater in Halodule systems in 2010 than in 2012 ($p = 0.019, F_{1,4} =$
14.61), while DM-Edible consumer biomass did not differ between sampling years ($p = 0.95, F_{1,4} = 0.003$).

Turnover was accelerated (i.e. occurred at lower levels of eutrophication) in *Halodule* systems relative to *Thalassia* systems ($p = 0.003, F_{1,7} = 18.86$), despite similar levels of predator abundance in both system types.

### 3.6 Discussion

The nonlinear responses in quantity and quality of the DM-resource indicate that compositional turnover was not attributable to the focal diamond module alone. Instead, our overall result (Fig. 3.8) is consistent with predictions for an extended diamond module, in which subsidies from alternative energy channels to the DM-predator and DM-Inedible consumer accelerate compositional turnover. In the most oligotrophic *Halodule* system only polychaetes were present (Fig. 3.6), despite high availability of the DM-resource (Fig. 3.4a), likely because low-quality sediments of seagrass origin facilitated colonization by competitively superior polychaetes. From oligotrophic to mesotrophic systems, rising DM-Predator density (fueled by subsidies from the epiphytic algae energy channel; Figs. 3.5, 3.6) likely suppressed polychaete biomass to a sufficient degree (note that although polychaete biomass rose with eutrophication, the rise was likely less than it would have been in the absence of the DM-predator) that the DM-Inedible consumer was able to colonize, despite declining sediment quantity. Entry of the DM-Inedible consumer may have been facilitated in part by improved sediment quality (declining C/N, Fig. 3.4b, likely owing to declining detrital seagrass inputs) as well. From mesotrophic to eutrophic systems, compositional turnover to the DM-Inedible consumer was associated with rising DM-resource quantity (sediment % organic matter) and rising density of the DM-Predator.
In *Halodule*, that DM-Inedible consumer dominance rose despite declining sediment quality, ostensibly favouring the competitively superior DM-Edible consumer, suggests that rising DM-predator density (subsidized by the epiphytic algae channel) was more important than rising DM-resource quantity (sediment % organic matter) in mediating compositional turnover.

We found evidence that compositional turnover may have been additionally facilitated by subsidies to the DM-Inedible consumer from another alternative energy channel (phytoplankton). Among *Halodule* systems sampled in 2010 brittle stars derived most of their diet from phytoplankton, with the remainder of their diets comprised of SOM (Fig. 3.6b). Brittle star biomass (as well as community dominance, although the difference was not significant) was greater in 2010 than in 2012, when brittle stars did not couple into phytoplankton. A causative relationship between brittle star diet and biomass in 2010 is supported by documentation of increased somatic growth in brittle stars with greater phytoplankton availability (Skold & Gunnarsson 1996, Nilsson 1999). A similar phenomenon occurred in *Thalassia* systems, where the combined biomass of taxa capable of accessing phytoplankton (brittle stars and bivalves, the latter inedible to young-of-year fish by virtue of large body size (30mm)), comprised 77% of benthic community biomass (Fig. 3.7).

Eutrophication facilitated a more rapid shift to predation-structured communities in systems with greater overall resource availability but similar predation pressure. Compositional turnover arose more rapidly in *Halodule* systems, where overall availability of the shared resource (SOM) was greater, than in *Thalassia* systems – for a given level of eutrophication, inedible consumers comprised a greater fraction of benthic community biomass in *Halodule* than *Thalassia* systems (e.g. Belleair Beach (*Halodule*) vs Cayo Costa (*Thalassia*), which had similar levels of eutrophication; Fig. 3.7). These results echo an underlying narrative of this thesis, that
food web structure is increasingly mediated by top-down forces with rising energy availability.

Rising dominance of less edible consumer capable of coupling into alternative energy channels may be a common, generalizable signature of community response to eutrophication and other agents of global change, with larger implications for overall food web structure. Eutrophication often manifests as a shift in autotroph dominance, from slow-growing benthic macrophytes to fast-growing epiphytic and planktonic algae which are able to access donor-controlled allochthonous nutrient inputs (Cloern 2001). It follows that defended (inedible) consumers capable of coupling into these alternative, donor-controlled energy channels should be able to accumulate high biomass in eutrophic systems in a donor-controlled manner. The ecological literature has accumulated several examples of this phenomenon, each replicated at large scales. Australia’s Great Barrier Reef has experienced large population growth of the inedible crown-of-thorns starfish, thought to be attributable, in part, to anthropogenic phytoplankton blooms which improve larval & juvenile survival (Brodie et al. 2005). In the Caribbean Sea and other locales, eutrophic seagrass sites are characterized by high densities of urchins capable of harvesting the energy of senescing phytoplankton blooms when the latter are incorporated into sediments (Tewfik et al. 2005, 2007, review: Eklof et al. 2008); however, the phenomenon may also be attributable to harvest of urchin predators (Estes et al. 1998, Eklof et al. 2008). Jellyfish blooms have been attributed to multiple natural and anthropogenic phenomena, including eutrophication (reviews: Purcell et al. 2007, Richardson et al. 2009). Finally, widespread rising dominance of suspension and deposit-feeding brittle stars (*Amphiura filiformis*) in the North Sea has been attributed to rising availability of phytoplankton associated with eutrophication, with minor roles attributed to declines of flatfish predators (Pearson et al. 1985, Buchanan & Moore 1986, Rosenberg et al. 1987, Josefson et al. 1993). This phenomenon
may have important consequences for communities beyond community composition. Because inedible consumers are capable of sequestering energy in a form that is inaccessible to predators, they may, in turn, be capable of attenuating trophic cascades otherwise predicted to arise across productivity gradients (i.e. the Ecosystem Exploitation Hypothesis; Oksanen et al. 1981). This phenomenon has been documented in simple laboratory (van der Stap 2007) and more complex natural settings (Chase 2003).

In conclusion, we have showed that eutrophication promoted the rising importance of predation in structuring benthic community composition and that this phenomenon was likely facilitated by subsidies to generalist consumers in the diamond module, from alternative energy channels which rose in importance with eutrophication. We also show that communities with greater availability of a shared resource experience more rapid compositional turnover, despite similar predator densities, echoing an underlying theme of this thesis, that greater energy availability facilitates greater importance of top-down forces in mediating food web structure. Although community modules may not map directly to realized effects of rising productivity in natural systems (e.g. Novak 2013), we demonstrate that community module predictions can indeed provide a useful conceptual framework on which knowledge of natural history can be added to accurately predict the outcome of rising productivity. Understanding whether and how community modules, the building blocks of food webs, manifest and interact with other structures in the larger food webs in which they are embedded will contribute to a highly synthetic framework for how complex natural systems respond to productivity as a whole.

3.7 References


Fig. 3.1. Predicted outcomes of rising productivity in a focal diamond module when a) consumers do not couple into alternative energy channels, and when subsidies from alternative energy channels enter the focal diamond module at b) the DM-predator, c) the DM-Edible consumer, and d) the DM-Inedible consumer.
Fig. 3.2. Locations of *Halodule* (yellow) and *Thalassia* (blue) meadows sampled.
Fig. 3.3. $\delta^{15}$N values of epiphytic algae indicate gradients of increasing eutrophication (from left to right) in *Halodule* and *Thalassia* systems. Error bars indicate standard error. Numbers in parentheses indicate sample size (the number of replicate $\delta^{15}$N values). See text for explanation of value for Anclote Key.
Fig. 3.4. The relationship between eutrophication and biomass of members of the focal diamond module in *Halodule* and *Thalassia* systems: a) DM-resource quantity (sediment % organic matter. Analyses were performed using logit-transformed data; untransformed data are shown here for ease of interpretation), b) DM-resource quality (sediment stoichiometry), c) the DM-Edible consumer (polychaetes), d) the DM-Inedible consumer (mud brittle star), e) DM-predator density (CUE).
Fig. 3.5. The relationship between eutrophication and biomass of member of the alternative epiphytic algae energy channel: a) the alternative basal resource (epiphyte cover on seagrass; note different scales of axes for Halodule and Thalassia systems; inset: the relationship between eutrophication and epiphyte areal biomass \((\text{g dw epiphytic algae / m}^2)\); b) prey in the alternative epiphytic algal channel (mesograzers; (amphipods and Hippolyte shrimp).
Fig. 3.6. The relationship between eutrophication and coupling of diamond module consumers into alternative energy channels. a) The degree to which the DM-Predator (pinfish) in selected *Halodule* systems coupled into the alternative epiphytic algae channel. B) The degree to which the DM-Inedible consumer (mud brittle star) coupled into the alternative phytoplankton channel.
Fig. 3.7. Benthic community composition. Sites are presented in order of increasing eutrophication. Asterisks indicate *Halodule* sites sampled in 2010; the remainder were sampled in 2012. N.B. statistical analyses for compositional turnover were performed using arcsin-sqrt proportional data; untransformed data are shown here for ease of interpretation.
Fig. 3.8. Conceptual representation of seagrass community structure across the eutrophication gradient in *Halodule* systems sampled in 2010. Circle size represents relative biomass; arrow widths represent % dietary contributions. Brown arrows represent the diamond module based on SOM; green arrows represent the epiphytic algae alternative energy channel; blue arrows represent the phytoplankton alternative energy channel. For *Halodule* sites sampled in 2012, there was a smaller increase in brittle star biomass with increasing degree of eutrophication, and brittle stars did not couple into phytoplankton.
Table 3.1. Mean (SD) effect of 3.7% HCl on epiphytic algae $\delta^{15}$N. *Asterisk indicates tissue for which $\delta^{15}$N estimates were corrected for acidification (i.e. where effects of acidification were greater than the precision of $\delta^{15}$N estimates).

<table>
<thead>
<tr>
<th>Tissue</th>
<th>$\Delta^{15}$N (SD)</th>
<th>n</th>
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</thead>
<tbody>
<tr>
<td>Epiphytic algae (2010)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>from <em>Halodule</em></td>
<td>-0.26 (0.01)*</td>
<td>2</td>
</tr>
<tr>
<td>from <em>Thalassia</em></td>
<td>-1.08 (0.05)*</td>
<td>2</td>
</tr>
<tr>
<td>SOM</td>
<td>+0.47 (0.01)*</td>
<td>2</td>
</tr>
<tr>
<td>Polychaetes</td>
<td>+0.22 (0.2)</td>
<td>3</td>
</tr>
<tr>
<td>Brittle Stars</td>
<td>NA (inconsistent effect)</td>
<td>6</td>
</tr>
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</table>
Epilogue

The conclusions of this thesis are three-fold. First, food web responses to rising productivity are non-linear. Rising productivity does not simply cascade up and down linear grazing channels. Instead, at the scale of large, whole food webs, I show that rising productivity is redirected to bottom-up controlled detritus channels as primary producers become less edible, subsidizing generalist predators, which in turn exert top-down control on herbivores in an apparent trophic cascade. A similar phenomenon occurs in food webs at a sub-ecosystem scale, where an alternative energy channel which arises with rising productivity subsidizes a generalist predator, which in turn facilitates community compositional turnover from edible to less edible consumers. Again at the scale of large, whole food webs, rising energy availability likely first increases food chain length and then causes food chain length to decline (whether due to the effect of productivity or ecosystem size on energy flux) as rising energy flux creates top-heavy biomass pyramids, favouring omnivory and subsequently causing food chain length to decline. These results stand in contrast to predictions of the classical hypothesis for top-down control (EEH). Importantly, the Productivity / Top-down Principle (PTP; that top-down control is a fundamental response of communities to rising productivity, and that top-down control becomes stronger with rising productivity), as it is informed by community module theory, suggests that assumptions underlying the EEH (i.e. strong consumer-resource interactions, linearity and singularity of food chains, rarity of omnivory, and lengthening of food chains with rising productivity) are accurate only over ranges of low productivity: a) before consumer-mediated defenses cause the diversion of energy from vertical trophic transfer, rendering bottom-up control more important and/or diverting energy into growing detritus channels, b) when energy inputs are limiting to vertical diversity (i.e. food chain length), and c) before top-down control
becomes sufficiently strong that omnivory becomes beneficial among top predators. It is notable that the EEH was proposed based on empirical observations from low-productivity (arctic tundra) ecosystems (Oksanen et al. 1981), and that much of its supporting evidence is derived from tests carried out in simple laboratory (e.g. Kaunzinger & Morin 1998, Kneitel & Miller 2002) or low productivity systems (e.g. boreal lakes; Persson et al. 1992, Vander Zanden et al. 1999, Jeppesen et al. 2000).

The second conclusion of this thesis is that seemingly contradictory results for effects of productivity on food web structure may not be contradictory after all. Instead, they may be equally predicted by mechanistic, context-dependent theories. In the first chapter I show that classical theory for top-down control of grazing channels (HSS, EEH), long plagued by the question of plant inedibility, is in fact explained in part by declining plant edibility with rising productivity. In the second chapter I show that conflicting results for the effect of productivity and ecosystem size on food chain length are in fact explained by a simple mechanistic, energy-driven theory for food chain length, which predicts that ecosystem size is the most important driver of food chain length at low productivity, while productivity is the most important driver in large or eutrophic ecosystems.

The third conclusion of this thesis is that the structural diversity of food webs (i.e. McCann’s (2007) biostructure concept) is an important mediator of community response to productivity. A long-standing focus of productivity research has revolved around the relationship between productivity and species richness, and the implications thereof for ecosystem stability. I posit that it is equally important to consider biostructural diversity, in its capacity to buffer ecosystems against the productivity-driven collapse predicted by the Paradox of Enrichment (Rosenzweig 1971). Although this thesis did not evaluate stability, it is notable that the structures
I identify that arise with productivity – growing detritus pools and bottom-up controlled detritus channels (Ch. 1), omnivory (Ch. 2), inedible resources and consumers (Ch. 1, 3), parallel energy channels (Ch. 1, 3) – have been associated with greater stability (DeAngelis 1992, McCann & Hastings 1997, Moore et al. 2004, Rooney et al. 2006, Vandermmer 2006, Gellner & McCann 2012).

These results have important ramifications, not only for our understanding and management of eutrophication, a significant contemporary threat to ecosystems at a global scale (Vitousek et al. 1997, Cloern 2001, Rabalais et al. 2009), but also for our understanding of cumulative effects of anthropogenic stressors.

In 175 years ecology has developed many predictions, often contradictory, for the effects of productivity on the structure and function of ecological communities (e.g. Borer & Gruner 2009). Evidence exists to support many of these theories, and evidence to support one theory often seems to discount the importance, or even constitute refutation, of another. This approach runs the risk of throwing out the proverbial baby with the bathwater – in divesting ourselves of ostensibly inaccurate hypotheses, we risk neglecting important information. Moving forward, the challenge to ecologists must surely be to elucidate the underlying mechanisms that link seemingly contradictory ideas.

References


Applications, 7, 737-750.
Appendix 1. Descriptions and Selection Criteria for Marine Food Webs derived from Network Models

Marine food web models were assembled using an EcoPath framework except for the Chesapeake Bay mesohaline ecosystem. Ecopath models (Christensen & Walters 2004) use the principle of energetic mass balance to describe food web structure: \( P_i = M2_i + M0_i + Y_i + E_i + BA_i \), where \( Y_i \) is harvest (if applicable), \( E_i \) is the net migration rate (if applicable), and \( BA_i \) is the biomass accumulation rate (used if group i’s biomass is not at equilibrium for the reference period). \( P_i \) is the production of functional group i, calculated as \( B_i \cdot (P/B)_i \), where \( B_i \) is biomass and \( (P/B)_i \) is the biomass-specific production rate. \( M2_i \) is predation, calculated as

\[
\sum_{j} B_j \cdot (Q/B)_j \cdot DC_{ji}
\]

where \((Q/B)_j\) is the biomass-specific consumption rate of predator \( j \), and \( DC_{ji} \) is the fraction of predator \( j \)’s diet that is derived from prey \( i \). \( M0_i \) is mortality not attributed to predation, calculated as \( P_i \cdot (1 - EE_i) \). \( EE_i \) is the ecotrophic efficiency (the fraction of functional group \( i \)’s production used in the system), calculated as \( Y_i + E_i + BA_i + (B_i \cdot M2_i) / P_i \).

A system of linear equations representing all \( i \) functional groups in a food web is solved iteratively and any missing parameters are estimated, generally by using knowledge of local natural history to vary \( B_i \) and \( DC_{ji} \) until \( EE_i \leq 1 \) for each functional group. A second equation balances energy flows within each functional group: \( Q_i = P_i + R_i + Q_i \cdot (1 - AE_i) \), where \( Q_i \), \( R_i \), and \( AE_i \) are the consumption rate, respiration rate, and assimilation efficiency of functional group \( i \).

Essington (2007) demonstrated that Ecopath model performance (precision of output biomass estimates) is most sensitive to accurate input biomass, and is robust to user variation in model balancing and errors (up to 25% CV) in dietary habits, with errors arising when groups are over-aggregated. As such we retained food web models for analysis if at least 60% of biomass data were derived from local estimates (i.e. biomass data were not derived from similar
ecosystems external to the focal system, nor left to be estimated by the Ecopath algorithm). Furthermore, we only used models for which autotroph primary production and biomass were derived from local and independent estimates, for which most primary consumer (zooplankton and detritivorous benthic invertebrate) biomass data were also local estimates, and for which ≥ 40% of consumer diets were derived from local estimates. We set the diet information criteria to a lower threshold because some groups for which diets are not often assessed locally can nevertheless be assigned to a grazing or detritus energy channel (e.g. sedentary polychaetes), or may be known only at a global scale owing to species rarity (e.g. cetaceans). Food web models were assessed for completeness by performing internet and scientific literature searches for natural history accounts of each ecosystem.

Of > 120 food webs evaluated, these criteria yielded 18 marine food webs which were retained for analysis (Table A1: list of food webs & summary statistics). For most food webs >80% of biomass data were derived from local estimates. Although using food webs constructed of primarily local data does not safeguard against inaccuracies in these data, most of the food webs we use are from well-studied ecosystems and were constructed by local experts familiar with their natural history. Furthermore, statistical comparisons of trophic positions calculated using Ecopath and ratios of $^{15}\text{N} / ^{14}\text{N}$ stable isotopes indicate that EcoPath models constitute accurate representations of food web structure ($r = 0.69 - 0.99$, with most coefficients > 0.85; notably some of these food webs, including that with the weakest correlation coefficient, did not meet our selection criteria; Kline & Pauly 1998, Mathisen & Sands 1999, Hagy 2002, Dame & Christian 2008, Nilsen et al. 2008, Milessi et al. 2009, Navarro et al. 2011). As such, we believe that the selected food web models constitute reasonable approximations of these ecosystems.

Some webs included a bacteria compartment while others omitted this group.
Furthermore some webs considered microbial loop groups (e.g. flagellates, ciliates, rotifers) to be distinct functional groups while others considered these to be part of general zooplankton groups. To correct for these between-study differences in functional group resolution we set bacteria trophic level to 1 and flagellate, ciliate, and rotifer trophic level to 2, and used these values to recalculate trophic positions for the rest of the food web ($TP_j = 1 + \sum_i^n DC_{ji} \cdot TP_i$ where $DC_{ji} =$ the fraction of predator j’s diet that is derived from prey i and $TP_i =$ the trophic position of prey i).

For the Chesapeake Bay food web we added meiofauna to the diets of the polychaete *Nereis succinea* (50%), blue crab (5%), spot (5%), croaker (5%), and hogchoker (10%) to reflect results of Hagy (2002). All models were constructed for an annual time period. The food webs had 15 – 55 functional groups. Most food web models included birds and marine mammals. Transient species present < 6 months of the year (e.g. migratory whales, birds, tunas) were removed from the models prior to analysis. Following this correction all food webs had food chain length ≥ 3.5. Biomass and primary production were converted to tonnes wet weight (t WW) / km$^2$ and t WW / km$^2$ / yr where necessary, using conversions noted in the source publications for each food web. When these were not mentioned we used conversions of 13.3 g WW / g C for autotrophs and detritus (the mean of published conversion factors for aquatic producers; 10 and 16.7 g WW / g C), 10 g WW / g C for heterotrophs, and 20 g WW / g C for meiofauna (Opitz 1996 and references therein).

**References**


<table>
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<tr>
<th>No.</th>
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<th>Reference</th>
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<th>% Consumer Biomass from local estimates</th>
<th>% Diet Data from local estimates</th>
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<td>Fundy / West Scotian Shelf (NAFO Division 4X)</td>
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<td>86</td>
<td>73</td>
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<td>Coll et al. 2007</td>
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<td>29% + 25% from similar nearby fjord**</td>
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<td>17*</td>
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<td>Villanueva 2004, Villanueva et al. 2006</td>
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<td>Wolff et al. 1996</td>
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<td>95</td>
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</table>

* models for bounded systems used in Ch. 2
** model does not meet selection criteria but is included because trophic position data match well with stable isotope data (Nilsen et al. 2008)
*** authors state that “most of these data were based on biological and ecological studies made in [the] system.”
References (with corresponding food web no.)


