Northeast Fisheries Science Center Reference Document 12-15

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W.J. Overholtz[1], E.T. Methrattra[4], F. Pranovi[5], W.T. Stockhausen[6]

[1]National Oceanic Atmospheric Administration, National Marine Fisheries Service,
Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA,
02543 USA

[2]Graduate School of Oceanography, University of Rhode Island,
South Ferry Road, Narragansett, RI 02882 USA

[3]Sea Research Foundation - Mystic Aquarium,55 Coogan Blvd., Mystic, CT 06355 USA

[4]Versar, Inc., Ecological Sciences and Applications, 9200 Rumsey Road, Columbia, MD 21045 USA

[5]Environmental Sciences, Informatics and Statistics Dept.,
Università Ca' Foscari, Castello 2737/b 30122, Venezia Italy

[6]National Oceanic Atmospheric Administration, National Marine Fisheries Service,
Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Seattle, WA 98115-6349 USA

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TABLE OF CONTENTS

Introduction 2
The Bread and Butter of Fisheries Ecology 3
  Estimating What Is Eaten: Diet Composition 3
  Estimating the Amount Eaten: Consumption 5
  Predator-Prey Interactions 8
Potential Competitive Interactions 11
  A Brief Primer on Competition 11
  Evaluating Competition 12
  Examples of Possible Competition from the NES LME 19
Symbiotic Background 19
  Examples of Positive Species Interactions in the NES LME 20
  Symbiosis Synthesis 23
Food Webs 24
  A Brief Primer on Food Webs 24
  Ecological Networks 27
Biodiversity, Ecosystem Resilience, and Stability 32
  Measures of Diversity 33
  Measures of Resiliency and Stability 33
  Examples from the NES LME 34
Summary and Conclusion 35
References Cited 39
Appendix 1. Contrasting Consumption Approaches: A Call for Parsimony 89
Appendix 2. An Analogy and General Rule? 92
Appendix 3. A brief history of food web theory 95

INTRODUCTION

Why are species interactions important? Further, why examine aggregated and community-level metrics? What practical information and resource management applications can we gain from knowing about these items? We'll revisit this question at the end of this work, but very simply the productivity of living marine resources (LMRs) is mitigated by their interactions with other species and the food webs within which they function. In fact, the realized production of LMRs, the production potential of LMRs, and the ability of LMR populations to recover from perturbations have all been shown to be strongly influenced by their interactions with other species (e.g., Estes et al. 1998, Jackson et al. 2001, Frank et al. 2005, 2007, Casini et al. 2008, Sandin et al. 2008, Baum and Worm 2009, Gamble and Link 2009, Essington 2010, Tyrrell et al. 2011).

Although the relative prominence among the triad of drivers known to influence LMR production (Link et al. 2010, Gaichas et al. 2012; Figure 1) varies under different conditions (Hunt and McKinnell 2006), the ecological effects driver (i.e. trophodynamics) can often be dominant. In many instances the effects of competition and predation can notably exceed the removals from fisheries (e.g., Hollowed et al. 2000b, Gamble and Link 2009, Tyrrell et al. 2011). Further, such interactions can have indirect and second-order affects as mediated via food-web dynamics. Clearly, the call to make community ecology (Mangel and Levin 2005) a basis for informing the management of LMRs specifically and more generally ecosystem-based management (EBM) has much merit. By its nature, a community-level focus is inherently much better positioned than a population-level focus to address issues of tradeoffs, interplay, and other connectivity dynamics as they affect LMRs, considerations that are increasingly important as we move towards EBM (e.g., Jennings and Kaiser 1998, NMFS 1999, Constable et al. 2000, Constable 2001, Link 2002a, 2010a, Garcia et al. 2003, Pikitch et al. 2004, Leslie and McLeod 2007).

Community ecology is comprised of many facets, with some facets quite distinct in marine communities compared to terrestrial, lotic, or lentic communities (Emery 1978, Steele 1985, 1991, Cohen 1994, Carr et al. 2003, Link et al. 2005). This distinction is important as much of theoretical community ecology has been developed in those non-marine systems, but such theories may or may not apply to marine communities at the scales which LMRs are distributed and managed. There are a plethora of issues that are important to consider in marine community ecology (MCE) as they can influence the dynamics of LMRs. Here we describe some of those issues influencing MCE, cognizant of the ecological theories for each topic.

We specifically describe common uses of MCE information in a marine LMR and EBM context. We do so by highlighting the type of species interaction, the information needed to evaluate it, and then examining a set of examples from the northeast shelf large marine ecosystem (NES LME) to elucidate those facets of MCE that are particularly useful in an LMR management context. Ultimately our use of MCE seeks to examine, prioritize, and quantify the interactions noted in Table 1 as they can influence the dynamics of LMRs and the systems they inhabit.

Beyond a singular focus on species interactions, MCE also warrants an examination of the biota in an ecosystem at a higher level of biological hierarchy. Various aggregate measures of marine communities have been proposed (Fulton et al. 2005, Link 2005, 2010b), as have a suite of synthetic and systemic metrics (Rice and Rochet 2005, Blanchard et al. 2010, Coll et al. 2010, Shin et al. 2010) to explore or infer properties related to diversity, stability, resilience, structure and functioning of a system. We also describe some of these synthetic or aggregated features that can characterize marine community ecology.

THE BREAD AND BUTTER OF FISHERIES ECOLOGY

In addition to measures of abundance, one of the key elements for studying and quantifying MCE is an examination of stomach contents. This information is vital to understanding the relationships among LMRs and represents what we view as the core information necessary to explore the sign, magnitude and impacts of species interactions. Here we build on our experience of maintaining a large food habits program (Link and Almeida 2000, Smith and Link 2010), focusing largely on what marine fishes eat, how much marine fishes need to eat, and how one would estimate those amounts. Certainly information is available for marine mammals, marine reptiles, seabirds, and invertebrates; we simply focused on fishes and a few selected invertebrates as they typically form the bulk of what is targeted as LMRs. Excellent primers on the topic are given by Hyslop (1980), Gerking (1994), Bowen (1996), and Cortés (1997). The emphasis is to identify key approaches and how to indentify key patterns for subsequent evaluation of predation, competition, shared resource use, and similar evaluations of species interactions.

Estimating What Is Eaten: Diet Composition

Why is knowing what fish eat important? It is difficult to determine the food web structure, and hence network properties, flows between network nodes, and resultant impacts, without some knowledge of who eats whom. That is, it is very difficult to evaluate the direction, magnitude and dynamics of species interactions without a reasonable knowledge of what constitutes the diets of key LMRs in a system.

Various information can be obtained from stomach content examination (Hyslop 1980, Bowen 1996, Cortés 1997) depending upon the question being addressed. An examination of stomach contents for the purpose of evaluating diet composition (D_{ij}) produces common data, usually of the form of frequency of occurrence (F_{ij}) and proportional fractions (P_{ij}) of the total diet. The latter can be estimated with respect to weight, number or volume of the prey (i.e. food) found in a predator's stomach. Each has merit under different situations and to address different questions, with the resultant output providing some sense as to the type of food being eaten. Of course the levels, number of categories, total amounts, and similar features are constrained by the sampling protocols, processing protocols, taxonomic resolution of the prey identification, and targeted objectives (e.g. Bowen 1996, Link and Almeida 2000, Smith and Link 2010). There are many ways to present and examine such resultant data.

The frequency of occurrence of F_{ij} can be calculated as

$$F_{ij} = \frac{n_{ij}}{N_j} \qquad \text{EQ 1}$$

where n_{ij} is the number of stomachs of predator j in which prey item i occurs, and N_j is the total number of predator j stomachs examined. The unweighted, simple mean diet composition ($P_{ij} = D_{ij}$) can be calculated as,

$$\bar{P}_{ij} = \frac{\sum_{k=1}^{N_j} w_{ijk}}{\sum_{k=1}^{N_j} w_{jk}} \qquad \text{EQ 2}$$

where k represents an individual fish, w_{ij} is the stomach weight of prey i in predator j, and

$$w_j = \sum_{k=1}^{N_j} \sum_{i=1}^{n_i} w_{ijk} \qquad \text{EQ 3}$$

is the total weight of all n_i prey species in predator j. A ratio of means may also be calculated (Malvestuto 1996),

$$\bar{P}_{ij} = \frac{\bar{w}_{ij}}{\bar{w}_j} \qquad \text{EQ 4}$$

inclusive or exclusive of empty stomachs, where the mean stomach weight of prey i in predator j is

$$\bar{w}_{ij} = \frac{\sum_{k=1}^{N_j} w_{ijk}}{N_j} \qquad \text{EQ 5}$$

and the mean stomach weight of predator j is

$$\bar{w}_j = \frac{\sum_{k=1}^{N_j} w_{jk}}{N_j} \qquad \text{EQ 6}$$

Although not emphasized here, these diet parameters can be estimated across several statistical groups or factors, including temporal factors such as decade, year (or year blocks), season, month, or time of day; spatial factors such as geographic region, stratum, or statistical area; abiotic factors such as depth, sediment type, wind speed and direction, current speed and direction, temperature, or salinity; and predator factors such as length, weight, age, condition factor, or sex. Weighted means can also be used to estimate mean weight of prey i in predator j for any such groupings, but we do not emphasize them here. These weighted means typically account for the fact that fish stomachs are often sampled as part of broader fish survey designs, thereby increasing statistical power and estimability of variance.

Variance estimators for each of these estimators can also be calculated, with caveats from normal, Poisson, negative binomial, gamma, lognormal, delta or similar statistical distributions (e.g., Pennington 1996, Tirasin and Jorgensen 1999). Here we principally report the simple arithmetic (unweighted, mean ratio, inclusive of empty stomachs; i.e., EQ 2 with statistical grouping across all factors) mean diet composition for example predators.

Examples of Fish Feeding from the NES LME

A simple examination of diet composition for an example benthivore, haddock (*Melanogrammus aeglefinus*), can reveal several features of interest (Figure 2). First, it is clear that this species eats a notable amount of echinoderms, a rather unusual prey item. Then, across multiple decades and with ontogeny, although the diets of haddock have exhibited minor shifts in diet (Figures 3, 4), they actually have remained rather consistent. Seasonal shifts in diet have been observed, with seemingly greater diversity in the spring, as have some shifts considering between Georges Bank and the Gulf of Maine regions of the NES LME (primarily amphipod versus ophiuroid prey; Figures 5, 6). In contrast the diet of an example planktivore, Atlantic herring (*Clupea harengus*; Figure 7), has exhibited some changes across multiple decades, particularly in the amount of euphasiids eaten, but less so than ontogenetic shifts in diet (eating some anchovies; Figures 8, 9). Seasonal and geographical shifts across various regions of the NES LME were also apparent for this predator (i.e. copepod versus euphausiid prey; Figures 10, 11), but the general feeding paradigm (largely planktivorous) did not fundamentally shift. Other examples are readily extant, but these two are representative of common benthivores and planktivores. Piscivores, shrimp-fish feeders, and other feeding guild examples are available in Smith and Link (2010) if of interest.

These patterns represent initial observations and have been used as context for addressing a suite of LMR questions, particularly the routine data request of "what does species X eat". Obviously further analyses for any individual fish (e.g. Garrison and Link 2000c, Link and Garrison 2002a, Link et al. 2002a, 2002b, 2007, Byron and Link 2010, Smith and Link 2010) or the fish community (e.g. Garrison and Link 2000a, 2000b, Link and Garrison 2002b) would need to be executed to further elaborate upon these initial patterns. Yet we provide these examples here to demonstrate the building blocks upon which other facets of MCE can be better evaluated.

Estimating the Amount Eaten: Consumption

Why is estimating fish consumption (how much fish eat) important? There are a plethora of multispecies and ecosystem models that hinge upon understanding how much fish consume. These models are increasingly being used in LMR management (e.g., Andersen and Ursin 1977, Bogstad et al. 1997, Tjelmeland and Bogstad 1998, Hollowed et al. 2000a, 2000b, Whipple et al. 2000, Constable 2001, Plagányi 2007, Townsend et al. 2008, Link 2010a, Link et al. 2011a). The models range from multispecies virtual population analysis, multispecies production models, energy budgets, to full system models (Plagányi 2007, Link et al. 2011). All require an understanding of how much food fish eat in order to incorporate energy flow into estimates of production as well as mortality from predation, regardless of how the model is structured. At the most basic level, values of consumption are required to initialize and validate these models. Additionally, many stock assessment models are expanding approaches to estimate other sources of mortality (especially predation mortality, M2; Hollowed et al. 2000b, Tyrrell et al. 2011) and consumptive demand of a stock or mammal population (Plagányi 2007, Link et al. 2011a). Central to estimating these other considerations of stock dynamics are estimates of fish consumption. As fisheries science and management continue to move towards ecosystem based fisheries management (EBFM; e.g. Jennings and Kaiser 1998, NMFS 1999, Constable et al. 2000, Constable 2001, Link 2002a, Garcia et al. 2003, Pikitch et al. 2004, Leslie and McLeod 2007, Link 2010a), the need to grasp the basic amount of food eaten by commercially valuable fish is paramount.

There are several methods whereby one can estimate fish consumption (Table 2). Although there are many (Appendix 1), we have primarily selected one approach, the gastric evacuation rate method (Eggers 1977, Elliott and Persson 1978). The point of noting these alternate approaches (Appendix 1) is to highlight the gradient of complexity of these models, identifying what parameters and data are needed. One can see (Table 2) the required data and parameters for each of these methods ranges from quite simple to highly complex. The first few are perhaps overly simplistic and may miss key factors that can affect consumption. Conversely, the latter two are perhaps overly complicated and may be unfeasible to parameterize more widely under local conditions (or else propagate parameters and associated biases from a more limited set). It is likely that the most parsimonious approach is the moderate one with some environmental realism but relatively minimal data and parameter requirements.

Given this recognition of parsimony, we typically use the evacuation rate method in the NES LME to estimate fish consumption. There has been copious experience using this approach to estimate fish consumption generally (e.g., Bromley 1991, dos Santos and Jobling 1988, 1991, 1992, 1995, Gerking 1994, Hansson et al. 1996, Jobling 1981, 1986, 1988, Jobling et al. 1994, Mehl and Sunnana 1991, Ponomarenko et al. 1978, Rindorf and Lewy 2004, Stefánsson and Pálsson 1997, Teschner et al. 2010, Teming and Andersen 1994, Temming and Herrmann 2003, Tyler 1970, Ursin et al. 1985, Waiwood and Majkowski 1984, Winger and Walsh 2001) and in the NES LME region (Durbin et al. 1983, Ursin et al. 1985, Pennington 1985, Overholtz et al. 1991, 2000, 2008, Tsou and Collie 2001a, 2001b, Link and Garrison 2002b, Link et al. 2002b, 2006, NEFSC 2007a, 2007b, Overholtz and Link 2007, Tyrrell et al. 2007, Link and Sosebee 2008, Link and Idoine 2009, Moustahfid et al. 2009a, 2009b, Deroba et al. 2010, DFO 2010, NEFSC 2010a, 2010b, 2011). Many of the properties associated with evacuation models have been debated and discussed (Hopkins 1966, Tyler 1970, Jobling 1981, 1986, Elliott 1979, Eggers 1979, Persson1986, Gerking 1994), with a general conclusion that whether the evacuation is exponential, surface area, or square root, the resultant consumption estimates are effectively comparable and given algebraic manipulations, are essentially mathematical variants of the same general approach (Persson 1986). Although multiple formulations of consumption have been proposed (e.g., dos Santos and Jobling 1988, Jobling 1986, 1988, Pennington 1985, Rindorf and Lewy 2004, Ursin et al. 1985), they effectively require the same kind of information and essentially seek to explore gut evacuation times, from which consumption rates are estimated. The main form of this approach is:

$$\frac{dS_i}{dt} = C_i e^S \qquad \text{EQ 7}$$

where S is stomach contents, t is time, C is consumption and where different assumptions about e yield subtly different formulae as noted above. In one of the more common forms, using the evacuation rate model to calculate consumption requires two variables and two to three parameters. The per capita consumption rate, C_i is calculated as:

$$C_i = 24 \cdot E_i \cdot \overline{S_i}^{\gamma} \qquad \text{EQ 8}$$

where 24 is the number of hours in a day and the evacuation rate E_i is:

$$E_i = \alpha e^{\beta T} \qquad \text{EQ 9}$$

and is formulated such that estimates of mean stomach contents (S_i) and ambient temperature (T) are the only data required. The parameters α and β are set as values that can be chosen from the literature (e.g., Durbin et al. 1983, Tsou and Collie 2001a, 2001b, Overholtz et al. 2000) or estimated experimentally (Bromley 1991, dos Santos and Jobling 1988, 1991, 1992, 1995, Jobling 1988, Temming and Anderson 1994, Temming and Herrmann 2003). The parameter γ is a shape function and is almost always set to 1 (Gerking 1994). The approach models evacuation (of stomach contents) rate by assuming non-linear evacuation, constant consumption, and that consumption equals what was evacuated. Appendix 2 explores the possibility of a general rule of thumb for at least one of these parameters.

Scaling Consumption

Once per capita consumption rates are estimated for each fish in a size class, temporal and/or spatial scheme *i*, those estimates can then be scaled up to an annual and stock wide basis, *C*:

$$C = 365 \cdot C_i \cdot N_i \qquad \text{EQ 10}$$

where N_i is the areal estimate of abundance for each fish in each size class, temporal and/or spatial scheme and 365 is the number of days in a year (which could also be ~180 if using half-years, ~ 90 if using quarters, etc.). This total consumption can be partitioned for the major prey items of each fish by multiplying it by the diet composition of each prey (D_{ij}, i.e., what fish eat, as noted above) to provide an estimate of particular prey removals.

Based upon the typical range of abundance estimates (10^3 to 10^{12} individuals) for most fish populations, estimates of abundance and changes in those estimates are likely going to dominate the scaling of total consumption by a broader range of magnitudes than the parameters and variables requisite for an evacuation method of estimating consumption. This is certainly true in marine ecosystems with highly abundant populations on the order of multiple billions of individuals. Even in lentic and lotic ecosystems with fish abundances on the order of hundreds to thousands of individuals, scaling by even just 2-3 orders of magnitude will dampen out much of the dynamics in the consumption parameters. Clearly any future work to estimate consumption will benefit from more refined abundance estimates. This is apt to be true for any consumption estimate methodology for a stock assessment, multispecies, or ecosystem model.

Examples of Consumption from the NES LME

We have chosen to loosely base the parameters, and certainly the variable estimates, off of common values calculated from our northwest Atlantic food habits database, a data set with over 550,000 fish stomachs (Link and Almeida 2000, Smith and Link 2010). These models have been developed for a wide range of groundfish, elasmobranch, and pelagic fish species (Link and Garrison 2002, NEFSC 2007b, Tyrrell et al. 2007, Link and Sosebee 2008, DFO 2010, NEFSC 2010a). Estimates for a few sets of stocks (e.g., the skate complex, NEFSC 2007b, Link and Sosebee 2008; spiny dogfish, *Squalus acanthias*, DFO 2010; Pollock, *Pollachius virens* and goosefish, *Lophius americanus,* NEFSC 2010a) have gone through a formal stock assessment model review. An example of which shows consumption by a set of skate species (Figure 12), consuming variably on the order of 5 to 100 thousand metric tons depending upon the species. This figure shows different sizes consuming different amounts of food, with the larger sizes, although less abundant, eating more food per capita than smaller fish. Estimates for some skate species were lower (e.g., Rosette skate, *Leucoraja garmani*), whereas others were notably higher (e.g. Little skate, *Leucoraja erinacea*), but these four species are representative examples (Link and Sosebee 2008). When one sums up consumption across all seven species of skate and then allocates that by diet composition to obtain the amount of prey removed, it is clear that as a complex skates are largely benthivorous (Figure 13). Over one hundred thousand metric tons of small crustaceans are consumed by skates in an average year. Skates can consume notable amounts of small pelagic forage fishes in an average year, but less than their consumption of the benthos.

One can readily imagine summing such calculations across a broader suite of predators for a focal prey species. These models have been developed predominately for forage stocks, including Atlantic herring, Atlantic mackerel (*Scomber scombrus*), longfin squid (*Loligo pealei*), butterfish (*Peprilus triacanthus*), several species of hakes, and Northern shrimp (*Pandalus borealis*) (NEFSC 2007a, 2007b, 2010b, 2011, Overholtz and Link 2007, Overholtz et al. 2008a, Link and Idoine 2009, Moustahfid et al. 2009a, 2009b, Deroba et al. 2010). Several of these models have been used as part of formal stock assessment reviews, usually to provide context and estimates of predation mortality (M2). An example across all northern shrimp predators shows that these fish can consume 40 to 60 thousand metrics of shrimp per year (Figure 14; Link and Idoine 2009). For context, previous shrimp biomass estimates were 2-5 times lower without this consideration of consumptive removals, implying a need to reevaluate assumptions of natural mortality (M) in the model.

Predator-Prey Interactions

Why would one want to consider predation? Very simply, the effect of predators has been shown to influence prey populations, and vice versa, as a cornerstone of ecological theory (sensu Lotka, Volterra, etc.) and as applied to marine communities (Bax 1991, 1998, Daan and Sissenwine 1991, Christiansen 1996, Hollowed et al. 2000b, Whipple et al. 2000, Tyrrell et al. 2011). Predation has been demonstrated to regulate both prey and predator populations, keep depressed prey populations in a predator pit, cause population fluctuations, and be of the same or greater magnitude than fisheries removals (Bax 1991, 1998, Gamble and Link 2009, Tyrrell et al. 2011).

Predation is the only interaction that results in opposite outcomes for the individuals involved (Table 1). As such, it warrants tracking as one of the key determinants of MCE dynamics in a system. Further, this species interaction is relatively easy to document compared to other species interactions (as noted above). Exploring predation is usually feasible, particularly documenting that it happened. Yet inferring how predation influences population and community dynamics, as well as these features that influence predation, requires further examination.

What Comprises Predation?

The diet of fishes represents a realization of feeding behavior and morphology (i.e., mouth shape, gape width, body shape, swimming ability, etc.). Within the constraints imposed by their morphology at any particular point in their life history, fishes feed opportunistically and eat what is most readily abundant at a particular time and place. Thus, there are key onotogentic (size), spatial, seasonal, habitat, and inter-annual features that influence the feeding of fishes. How one can delineate those key factors is increasingly feasible with large food habits data sets (e.g., Daan and Sissenwine 1991, Livingston et al. 1993, Link and Almeida 2000, Smith and Link 2010) and has shed insights into a range of LMR applications (e.g. predation, essential fish habitat, etc.; Reid et al. 1999, Link and Almeida 2000, Link et al. 2011a).

Predation has been decomposed into a sequence of major components (Holling 1959a, 1959b, O'Brien 1979, Link and Keen 1999). Generally, these components are detection (or encounter, which implies search), pursuit, attack (often combined with pursuit into the term ''reaction''), capture (or handling), and retention, ultimately ending in ingestion. The process of detection involves a fish's encountering, locating, and identifying a prey item. In pursuit, a fish alters swimming velocity and course to intercept the prey. An attack involves coordinating acceleration through the location of a prey item and either inhalation of a volume of water to bring the prey item toward the buccal cavity or mandibular contraction on the prey item. Capture occurs when a prey item (or significant portion thereof) enters the buccal cavity and mandibular manipulation keeps the prey item inside that cavity. Retention involves the movement of a prey item across the gill rakers toward the esophageal tract. At each step in the predation process, selectivity occurs.

There are a suite of terms associated with selectivity (Manly et al. 2010). Here we define selectivity (in the context of predators eating certain prey items from a suite of potential prey items) as the entire process associated with ''choosing'' (either actively or instinctively) among all possible prey, such that preferential utilization is exhibited by a predator. Electivity is a synonym for the entire process of selectivity. We define preference as the favored choice of a predator due to the morphological, physiological, ontogenetic, and environmental factors associated with both predator and prey. Prey suitability or prey choice are synonyms for prey preference. Prey utilization is the realized preference when preferences are coupled with an actual set of available prey (i.e., the ambient prey field), usually presented as diet composition. Ultimately then diet composition is a synonym for prey utilization.

The components of predation, which are realized in the selection of prey, which in turn are realized as observable diet, then represent the myriad of tradeoffs facing a predator when choosing to feed. The exogenous factors noted earlier, when coupled with endogenous factors (e.g. ontogeny, morphology, spawning status; e.g. Link and Burnett 2001), and the prey field itself thus influence what and how much fish eat. If one views these components and factors as driving the behavior behind the consumption in EQ 8, then clearly the bioenergetic constraints of predation by fishes can be so multi-determinant as to be effectively indeterminate (Gerking 1994). Such approaches have been used, however, to predict diets in the absence or limited presence of field sampling of stomachs (Link 2004), as well inform selectivity parameters in a plethora of models (as noted above; Plagányi 2007, Townsend et al. 2008). Some of these probabilistic approaches have also been used to parameterize predation terms in models and infer effects of predators on prey.

Other features influencing predation have been explored and explained via Optimal Foraging Theory, *sensu strictu* bioenergetic mass-balance constraints, predator pit theory, foraging arena theory, maximum alternate prey (prey switching) theory, and certainly many others. All seek to elucidate those features that determine how much and what predators eat. To be useful as an application in an LMR context, particularly to explore consumptive removals and estimate M2 (predation mortality; Hollowed et al. 2000b, Tyrrell et al. 2011), ultimately this information needs to be translated into the effects of one species onto another.

Modeling Predator-Prey Interactions

The classical Lotka-Volterra equations note that the change in abundance of prey N as

$$\frac{dN}{dt} = rN - \alpha NP \qquad \text{EQ 11}$$

and of predator *P* as

$$\frac{dP}{dt} = gNP - mP \qquad \text{EQ 12}$$

where *r* is the intrinsic rate of increase (growth) for the prey, α is the predation rate coefficient (aka interaction term), *g* is reproduction (or population growth) of predator per prey eaten, and *m* is predator mortality rate. This theory attempts to account for the mortality of predators on prey populations, as well as the positive effects of the prey for the predators. These linear approximations have been expanded to various functional responses (Holling 1959a, Moustahfid et al. 2010; e.g. See EQs B1.7-1.10 in Appendix 1) to account for the dynamic of predation (Hunsicker et al. 2011), particularly recognizing the potential for non-linear relationships among predator and prey responses. The cyclical dynamics of predator-prey population trajectories are well documented, as are the ability of chaotic dynamics to result from L-V interactions (Lotka 1925, 1932, Volterra 1926, Hunsicker et al. 2011). This simple relationship has driven much of the theory in community ecology and can have notable impacts on LMR populations.

The many considerations that modulate predation as noted above can be accommodated by various forms of the functional response, as well as estimating numerical and integrative responses (Hunsicker et al. 2011). Many of the models applied to LMRs use various forms of these equations to account for facets of predation (Hollowed et al. 2000a, Whipple et al. 2000, Plagányi 2007). Others have modified the L-V equations to account for other species interactions or have combined the logistic forms with Schaeffer modifications to simultaneously evaluation fishing mortality as well (e.g., Collie and DeLong 1999, Gamble and Link 2009; cf. EQ B1.7, B1.8).

Estimating the interaction strength (α) of predation directly has remained elusive. Typically this is a parameter that is fitted to a suite of time series data. Ultimately the key objective of all these efforts in an LMR context has been to account for predatory removals as they influence stocks of interest, as well as determining if there is sufficient food for many upper trophic level species of particular concern (e.g. protected species).

Often what happens is some form of consumption model (noted above) is applied, and the resulting consumptive removals of a prey species of interest are then modeled in a multispecies or extended stock assessment context (Link et al. 2011a). In practice for fisheries, this is treated as another source of removals akin to another "fleet," and may or may not use the Lotka-Volterra forms noted here, but typically uses some version of a functional response coupled with size and perhaps type selectivity in the feeding submodel of these population and community dynamics.

Examples from the NES LME

Tools have been developed to estimate interaction strengths from commonly available data and have been used to parameterize models which incorporate species interactions (Link et al. 2011b, R. Gamble pers. comm.). Additionally, both Collie and DeLong (1999) and Gamble and Link (2009) have made some recommendations for preliminarily setting the values of these coefficients as parameters in multispecies models, but then allowed them to remained fixed or allow the models statistically fit them. Methods to directly determine such parameters remain elusive.

Most of the efforts to evaluate predation in an LMR context in the NES LME have been to model the consumption of key species by including vectors or matrices in stock assessment models as other "fleets", and derive predation mortality (M2) values for tracking the magnitude of predation. For example, herring has been shown to exhibit higher M2 than fishing mortality (F), even despite variable levels of biomass (Figure 15; Overholtz et al. 2008). Several other examples are noted above in the discussion on consumption, all essentially confirming this same pattern for such forage fishes. In fact, several works have shown the natural mortality M is not constant over time, is not age invariant, and not fixed at 0.2 as is often assumed (reviewed in Tyrrell et al. 2011).

One key output of these approaches regarding predation as a relative source of mortality has been to track the consumption to landings or (catch; C:L) ratio. If consumptive removals relative to landings are approximately 1, and certainly if greater, then a rule of thumb is to treat predation mortality directly in the stock assessment models. An example for silver hake, *Merluccius bilinearis*, and red hake, *Urophycis chuss*, demonstrates the C:L ratio is usually greater than 1, often with a value of 2-5. In some instances consumption is 10-20 times higher than catches (Figure 16; NEFSC 2011). The implication is that predation is an important feature of these stock dynamics.

POTENTIAL COMPETITIVE INTERACTIONS

Why would one want to evaluate competition among LMRs? Seminal works have all noted the potential for competitive interactions to regulate population size, community structure, and ultimately influence or even limit the productivity of ecosystems (e.g., Lotka 1925, 1932, Volterra 1926, Gause 1934, Hardin 1960, Hairston et al. 1960). Including concepts such as the niche, competitive exclusion, resource partitioning, and interaction strength (among many others), several studies— focused on a diversity of species in a range of habitats and ecosystems (too numerous to quantify or review here; cf. Connell 1983, Schoener 1983, Sih et al. 1985, Ross 1986, Tilman 1990, Goldberg and Barton 1992, Gurevitch et al. 2000, Chase et al. 2002) — have been conducted to explore the many nuances of competition. Any treatment of species interactions in an MCE context requires an examination of competition.

A Brief Primer on Competition

This negative-negative interaction (Table 1) has the potential to limit the production of interacting LMRs. There is also the potential for competition to hinder the recovery of depleted stocks, or allow non-targeted stocks to outcompete their competitive dominants that are experiencing high fishing pressure. The salient point is that although difficult to measure, the theoretical potential for competition to notably alter the dynamics of LMRs and the MCE they comprise is high.

Given this theoretical potential, why is competition so hard to show for marine fishes, mammals, and bird communities? What is needed to show competition *might* exist? Essentially evidence is required that demonstrates that one species is negatively influencing another, not via predation, which is challenging in terrestrial ecosystems and even more challenging if not almost impossible in marine ecosystems.

Competition has generally been evaluated using experimental approaches (e.g., Paine 1966, 1971, 1976, Hall et al. 1970, Dayton et al. 1971, 1975, Zaret and Rand 1971, Werner and

Hall 1977, Lubchenco 1978, 1980, Larson 1980, Connell 1983, Schoener 1983, Sih et al. 1985, Mittelbach 1988, Tilman 1990, Goldberg and Barton 1992, Carr et al. 2002, Hixon and Jones 2005) or post-hoc evaluation of time series of species abundance and related statistical fitting of coupled population models (e.g., Schoener 1974b, 1985, Pimm 1978, 1985, Emlen 1980, Overholtz and Tyler 1985, Wootton 1997, Collie and DeLong 1999, Novak and Wootton 2008). These various approaches all have their strengths and weaknesses, and some combinations of these methods have been evaluated concurrently to demonstrate similar results across the methods (King and Pimm 1983, Berlow et al. 2004, Wooton and Emmerson 2005, Novak 2010). Yet unraveling the magnitude and specific determinants of competition has remained somewhat elusive. That is, it is hard to estimate competition in the field under natural conditions to the point where the effects are definitively attributable to competition and are defensible cognizant of prevailing theory.

Competition has been demonstrated quite readily in aquatic ecosystems (e.g., intertidal zones, coral reefs, freshwater lakes), with many of the key theories and tests having emerged from those studies (e.g., Connell 1961a, 1961b, Paine 1966, 1971, 1976, Dayton 1971, 1975, Hall et al. 1970, Zaret and Rand 1971, Menge and Menge 1974, Menge and Sutherland 1976, 1987, Werner 1977, Werner and Hall 1977, Lubchenco 1978, 1980, Menge et al. 1986). Collectively these works have significantly contributed to the development of competition theory. However, given the nature of such studies, the derived theory and hence thinking about competition has usually focused upon smaller, localized spatio-temporal scales and at the individual level for species that are strongly associated with particular habitats and that do not have large daily to annual ambits (Sih et al .1985, Auster 1988, Gurevitch et al. 2000, Carr et al. 2002, Chase et al. 2002, Hixon and Jones 2005, Lindholm et al. 2007).

Competition has been considered in a fisheries context before (e.g., Overholtz and Tyler 1985, Fogarty et al. 1991, Persson and Hansson 1998, Piet et al. 1999, Munday et al. 2001, Link et al. 2002b, Hixon and Jones 2005), but is not done so routinely and certainly not operationally (Link 2002a, 2010a). Competition has not been evaluated to the degree that other factors have been explored regarding their influence on commercially important fish populations or those communities in which they are embedded. This remains the case despite the observation that competition has the potential to rival the effects of fisheries removals or predation in magnitude (e.g., Bax 1991, Fogarty and Murawski 1998, Gamble and Link 2009; sensu Hairston et al. 1960). Although several studies have examined competition in fish communities that support major fisheries (e.g., Bax 1991, Christensen 1996, Collie and DeLong 1999, Gifford et al. 2009), doing so is required at the spatio-temporal scales at which fisheries operate and are managed (Auster 1988). These scales are very distinct from those at which most theory supporting and describing competition was derived. By nature, these scales effectively preclude experimental manipulations (unless considered in an adaptive management context; Walters 1986, Walters and Holling 1990) or a focus upon the response of individuals. As such, examination of competition at these scales for shelf fish communities would need to rely on information from broad-scale surveys and time series that are commonly extant in fisheries science.

Evaluating Competition

There are four requirements that must be fulfilled to demonstrate that competition between species is likely occurring: notable population impacts or responses of the interaction, spatio-temporal overlap, similarity of resource utilization, and limiting resources (as noted in Link et al. 2002b). Below we elaborate upon each point and then synthesize them into a quantitative protocol for determining if competition is probable, at least in a fisheries context. We provide examples for the NES LME for each step in evaluating competition.

Population Trajectories

For there to be significant ongoing competition, first one would need to observe opposite population trajectories for species suspected of being competitors, or at least trajectories where one species was notably reduced. Certainly inter-specific competition could be occurring among individuals, but if it did not translate to the population level then this would be irrelevant within a population and fisheries context. Additionally, competition could have occurred in the past, resulting in re-alignment along multidimensional niche space for these species in some form of a "dynamic equilibrium" (Lotka 1925, Volterra 1926, MacArthur 1970, DeAngelis and Waterhouse 1987), but that would not be expected to significantly alter current population trajectories reflective of the negative impacts of competition.

The data to evaluate this criterion could come from several standard sources common to fisheries science, including estimates of abundance or biomass from: surveys, tagging studies, or stock assessment outputs of at least ten years in length (Nicholson and Jennings 2004, Blanchard et al. 2010). These data are usually presented as composites for a stock, but if age or size structure were important that could also be considered if and as available. Evaluation would need to be pair-wise for any candidate species, but cognizant of other drivers affecting the community (Brown et al. 2001, Duplisea and Blanchard 2005) and likely done for multiple, possible candidate pairings.

There are several statistical methods to compare two (or more) time series (e.g., Bjornstad and Grenfell 2001, Zuur et al. 2007). Although we endorse them and certainly think they could inform the proposed evaluation, what ultimately is needed is a simple contrast between trajectories. Even a linear approximation of the slope of such time series, with suitable correction for auto-correlation (Bartlett 1946) if necessary, should be sufficient. Often the dynamics of populations are decidedly non-linear over a long time period, but the major, recent trends would be the primary data for evaluation. Certainly other factors, such as differential fishing mortality or differential response to changing environmental conditions, could be causing the observed patterns. That is why subsequent considerations would merit examination, but opposite population trajectories would need to be established as a first criterion to determine if competition might be occurring. Conversely, no distinction between population trajectories, especially if slopes were not significantly different, would indicate that the populations were not likely influenced by competition. Or if there are such interactions, some other driving factor was dominating the population dynamics such that competition would be masked. An example might be predator-mediated coexistence (Paine 1966, 1971, Hall et al. 1970, Dayton 1971, Caswell 1978), where the "predator" could be either other marine organisms or a fishing fleet that suppresses the competitive dominant, allowing the competitive inferior to maintain a population trajectory that effectively is not influenced by competition with the dominant. In such cases, the realized competition, even if potentially occurring, would not be of sufficient magnitude to drive the dynamics of the populations and would not warrant further examination, although continued monitoring and periodic re-examination of the population trajectories would be wise.

There are numerous examples of opposite trajectory patterns from the NES LME, and we strongly suspect from other ecosystems as well. Auster and Link (2009) and colleagues (Garrison and Link 2000a, 2000b, Link and Garrison 2002) have shown that within trophic guilds in this ecosystem, there is overall guild compensation such that biomass of most guilds remain stable, but individual species therein have changed dramatically. Contrasting functionally similar species, Link (2007) has previously documented that species such as skates and pleuronectids have also exhibited notable differences in population trajectories over time. As an example, benthivore echinoderm-feeding specialists all also exhibit opposite trajectories (Figure 17). One can readily observe quite distinct patterns from such commonly available survey data. Further, if one plots species abundance as cross-plots between possible competitors, one can elucidate probable competitive dominants whereby one species dominates along one axis or another, rather than being equally dispersed about the equality line. The example shown (Figure 18) indicates that haddock might be a competitive dominant relative to other echinoderm specialists, but less dominant with the more generalist benthivore little skate (Figure 18B). That is, in those instances where the pattern of cross-plotted abundances does not notably depart the line of equality, the species have similar abundance histories and thus may or may not be more susceptible to stronger competition, but certainly are neither competitive dominants nor inferiors.

Spatio-temporal Overlap

For species to compete, they need to be in the same place at the same time. We acknowledge that one could argue over the veracity of such a statement depending upon the specific type of competition being considered. Certainly direct or interference (aka scramble or contest) competition would require species to interact directly. Indirect or exploitation competition would not necessarily require species to spatio-temporally overlap. Yet that is from the classical view of competition between individuals. If scaled up to the level at which populations are distributed and at which fisheries operate and are managed, this implies that populations, even if competing via exploitative mechanisms, would need to use similar resources at these broader scales during the same general time and at the same general places, otherwise they would simply occupy different places and obtain the necessary resources elsewhere. The different places at this scale are much broader and hence lower spatio-temporal overlap would be indicated Taken as an integrated whole across an entire continental shelf, if species had high spatial overlap over long periods of time the potential for them to be using the same resources is high, irrespective of the mechanism operating at the individual level.

Further, one facet of niche space is simply place. Certainly there are differential responses in small scale fish distributions to variation in physical and biological habitats (e.g., Larson 1980, Carr et al. 2002, Auster et al. 2003a, 2003b, Hixon and Jones 2005, Lindholm et al. 2007), as well as associations with multiple environmental attributes across a range of scales. However if fish are repeatedly caught in the same survey tows, tows which can loosely be associated with various broad-scale habitat features such as temperature, light, depth, grain size substrate, major flow regimes, or frontal boundaries (e.g., Link and Demarest 2003, Methratta and Link 2006a, 2006b, 2007a, 2007b, Nye et al. 2009, 2011), the implication is that at these broad scales such fishes are generally utilizing the same physical spaces, even if individuals are exhibiting more nuanced distinctions in habitat usage at finer scales. Assessing spatio-temporal overlap among a suite of species pairings simply evaluates an amalgamated measure of the habitat features forming a part of a niche.

A simple measure of this would be one of the many forms of spatio-temporal overlap indices (Schoener 1970, Williamson 1993, Manly et al. 2010). These overlap estimates, usually on a scale from 0 to 1 or from 0 to ∞, indicate the degree to which a pair of species is co-occurring. These can be done at differing depth levels (Williamson 1993), but in the fisheries context are typically understood to be latitudinal and longitudinal coordinates of where the fishes were sampled via the sampling gear, usually trawl gear (Garrison 2000, 2001, Garrison et al. 2000b, 2002). These measures account for the differential abundance and distribution of fishes if executed using a statistically rigorous sampling design (e.g., Azarovitz 1981, NEFC 1988, Reid et al. 1999). Effectively one integrates the occurrence of species i in the presence of species j relative to the total, cumulative abundance of each, at each sampling location and as done across seasons, years, decades or whatever is an appropriate time frame. Here we present an example of one such index, the Williamson overlap index (SO_{ij}) as:

$$SO_{ij} = \frac{\Sigma_z (N_{iz} N_{jz}) m}{\Sigma_z (N_{iz}) \cdot \Sigma_z (N_{jz})} \qquad \text{EQ 13}$$

where z is a sample location (i.e., in this case a survey tow), m is the total number of samples, N_i is the abundance of species i, and N_j is the abundance of species j. If the index is equal to 1, then the degree of overlap is not different from the expectation where the species are uniformly distributed. A value <1 indicates less than expected overlap, while a value >1 indicates a greater than expected overlap, with the upper bound determined by the number of locations sampled.

The data required to calculate such spatio-temporal overlap indices are usually taken from fisheries independent surveys (although fisheries dependent surveys could also work). In most instances an individual trawl tow serves as a replicate over which the calculation is executed. This can be done for as many species pairings as are extant in the data.

There are some methods that use re-sampling techniques to determine “significance” of a given overlap value (Manly 1997, Garrison 2000, 2001). Although we support the role and importance of such statistical techniques, executing them is not always feasible and positive results usually end up supporting some general principles that have been derived empirically. A rule of thumb is that most overlap values, on a scale of 0 to 1, that are greater than 40% (1 on the Williamson scale) merit consideration, and effectively all values greater than 60% (2 on the Williamson scale) are significant (Ross 1986; L. Garrison pers. comm.). We endorse this simpler set of approximations in the context of determining the possibility that competition is occurring. If species exhibit high spatio-temporal overlap, then evaluating additional considerations of competition are warranted.

An example from the NES LME pelagic fish community shows that for most of the fish community, spatio-temporal overlap averages approximately 20-25% (Figure 19). For some selected species pairs, the overlap value is very high (i.e. > 70%; e.g., longfin squid, anchovies, *Anchoa*, round herring and shads, *Alosa*, with butterfish). For others the value of overlap is high enough (>40%) to warrant consideration (e.g., herring and mackerel). This implies that these stocks regularly occupy the same place and time. Clearly more nuanced evaluations at different spatial and temporal scales would be worth exploring, but here and as confirmed in other studies on the broader fish community (Garrison 2000, 2001, Garrison and Link 2000b, Garrison et al. 2000d, 2002, Link et al. 2002b, Link and Auster in press), the instances where spatio-temporal overlap is consistently high (i.e. 40-50%) are readily emergent.

Similarity of Resource Use

In addition to opposite population trajectories and high spatio-temporal overlap, for species to be significantly competing they must exhibit evidence of overlapping resource use. As species compete, they partition the use of niche space along multi-dimensional resource axes such that overlap of resource-use, and hence competition, is minimized. In so doing distinct guilds form with between-guild competition minimized and within guild competition then the basis for more focused resource partitioning (Root 1967, MacArthur 1970, Schoener 1974a). Ross (1986) has reviewed many of the features associated with resource partitioning for fishes. A key observation from that review is that for fishes, particularly as we have accounted for the habitat aspects of niches based on the spatio-temporal discussion above, resource overlap essentially becomes a discussion of food habits and dietary overlap.

Several studies of fishes, from wide variety of systems, demonstrate that high dietary overlap is indicative of shared resource use (reviewed in Ross 1986; e.g., Sala and Ballesteros 1997, Garrison and Link 2000a, 2000b, Colloca et al. 2010, Albouy et al. 2011). As such, high dietary overlap is suggestive that there is a high potential for inter-specific competition. Certainly shared resource use could be high and competition not a main factor, as in cases of a wide range of available prey in the prey field, a very productive set of prey, low densities of potential competitors, or fish that feed similarly but in different places. These caveats aside, generally when potential fish competitors feed on the same prey in the same approximate amounts, coupled with strong indicators from the prior two evaluation criteria noted above, the potential for competition is high.

Similar to spatial overlap, there are several means to measure resource overlap (e.g., Schoener 1970, Chesson 1978, Manly et al. 2010). These overlap estimates, usually on a scale from 0 to 1, indicate the degree to which a pair of species is sharing a resource. Here we present an example of one such index, the Schoener overlap index (O_{ij}) as:

$$O_{ij} = 1 - 0.5\left(\sum_{k} |p_{ik} - p_{jk}|\right) \qquad \text{EQ 14}$$

where p is the proportion of resource state k for predators i and j. Or stated in terms of fish diets, where p_{ik} = mean proportional diet composition of prey type k in predator i and p_{jk} = mean proportional diet composition of prey type k in predator j. When values are close to 0, there is minimal resource overlap; conversely, when values are close to 1 there is high resource overlap.

As with spatio-temporal overlap indices, there are several methods of re-sampling to determine “significance” of a given overlap value (Manly 1997, Garrison 2000, 2001). Again, executing them is not always feasible and a rule of thumb is that most overlap values on a scale of 0 to 1 that are greater than 40% merit consideration, and effectively all values greater than 60% are significant (Ross 1986; L. Garrison pers. comm). We again endorse this simpler set of approximations in the context of determining the possibility that competition may be occurring.

The data required to calculate this dietary overlap are based on common food habits (i.e., stomach contents) data. Fish stomach sampling, providing the percentage diet composition (by weight or volume or number, as is appropriate) of each prey k is needed. These diet compositions can then be integrated across all germane spatial, temporal, ontogenetic, and environmental factors to calculate an index of diet composition (D_{ij}) for any given predator j and prey item i. These would then represent the proportional uses (p) in EQ 25 (cf. EQ 2) for each competitor i-j pairing.

An example from the NES LME shows that for most of the demersal fish community, dietary overlap averages approximately 30-40% (Figure 20). For some selected species pairs, the overlap value is very high (i.e. > 80%; e.g., large-sized skates with each other, medium-sized hakes with each other, sculpins, *Myoxocephalus spp.*,-sea robins, *Prionotus spp.*,-black sea bass, *Centropristis striata*, or haddock-ocean pout, *Macrozoarces americanus*). These higher overlap pairings, with values > 60%, correspond to known feeding guilds (Garrison and Link 2000a, 2000b). For others the value of overlap is high enough to warrant consideration (35-50%). In this example that would include pairings of: silver hake and redfish, *Sebastes fasciatus*, goosefish and fourspot flounder, *Paralichthys oblongus*, haddock and American plaice, *Hippoglossoides platessoides*, and scup, *Stenotomus chrysops,* and black sea bass. All of these pairings would imply shared food resources as seen in the diet.

Evaluation of Resource Limitation

Of all the criteria for determining competition among fishes, evaluation of limiting resources remains the hardest to conclusively delineate. Proving that resources are in fact limiting in such an open environment at these scales is indeed truly daunting and in many cases, it simply may be infeasible to assess. In other instances, where food web models have evaluated feeding demands of fishes (e.g., Coll et al. 2006, 2008, Link et al. 2008, Gaichas et al. 2009, Link 2010b), the collective observation is that there does typically appear to be adequate food resources for fishes when the models include realistic assumptions that allow predators to switch to alternate prey if one prey population declines. In instances where the food is thought to be limiting, some of the key trophodynamic parameters in those models (e.g., consumption, production, ecotrophic efficiency) need to be only slightly adjusted to ensure that mass balance constraints are maintained. Thus it is unclear if marine systems, at the scale of large marine ecosystems (LMEs), consistently exhibit resource limitation.

It may be that any criterion for this consideration in the evaluation of competition is left as simply an assumption if the other three criteria are met. As that may not be satisfactory, we present a number of approaches which have the ability to provide crude/indirect evidence for resource limitation.

One indirect method is to examine the condition factor of fishes (K) with:

$$K = W \bullet 100\ L^{-3} \qquad \text{EQ 15}$$

where L is length (cm), W is weight (g), and 100 is a scalar depending upon units of measure (or can be 100000 if length is in mm; Fulton 1902, 1904), as averaged or integrated accordingly. Using this condition factor approach would be similar to the contrasting trajectories of population abundance. If two paired species exhibited opposite trends in K, then the potential for limiting resources would be identified. This evaluation criterion would be rather simple and reasonably straightforward as lengths and weights of fishes are routinely measured in fisheries surveys. As an even simpler proxy, one could examine the mean lengths of fishes for changes to observed growth, and by inference changes to resources that result in the observed growth. Estimating mean lengths tends to exhibit more dynamics than condition factor, but generally such values are still relatively stable about the long term mean. These two approaches are simple, but rarely provide evidence of resource limitation. If, however, remarkable dynamics are observed from these readily available data, then the probability for making a case for competition is heightened.

Another indirect approach would be to examine the percent body weight of fishes ($\%BW$) with:

$$\%BW = \frac{\bar{S}}{\bar{W}} \cdot 100 \qquad \text{EQ 16}$$

where S is mean stomach contents and W is mean weight, both in grams. Here the observed stomach contents and individual weight data commonly sampled on fisheries surveys provides an evaluation of the average amount of food consumed by a population relative to the average biomass—and inferred condition— of a population. As with abundance, condition factor, or mean length evaluations, if two paired species exhibited opposite trends in *%BW*, then the potential for limiting resources would be identified.

Alternatively, to address the general lack of information associated with this issue, we propose two additional options. One approach is that, where feasible, if surveys of all the potential prey in a prey field are extant, then the ratio of observed prey to the total, cumulative prey possible is calculated to evaluate whether food resources for a given species are in fact limited. This prey ratio (p') is:

$$p' = \frac{\Sigma_k B_{ik}}{\Sigma_k B_k} \qquad \text{EQ 17}$$

where B_{ik} is the biomass of all prey k found in predator i, and B_k is the biomass of all prey in the prey field that could be accessed by predator i and similar predators. Prior studies (Link and Auster in press) propose a threshold of 20%, below which a fish could be considered to have limiting prey. This threshold is based on the physiology of fishes needing to obtain more than a maintenance diet, the onset of early stages of starvation, and loss of reserve weight if food densities fall below about 20-25% of what is needed for basic metabolism (sensu Winberg 1956, FAO 1980). Although not definitive, this value represents a general threshold below which resources could be limiting and individual weight loss would likely occur (Winberg 1956).

As another alternative, a similar type of relationship could be quantified based on primary producers in an ecosystem. We propose the use of chlorophyll *a* values derived from satellite imagery as such measures are readily available for the vast majority of marine ecosystems at the scales under consideration. As a proxy for the base of the food web, this standing stock biomass ultimately limits all the magnitude of production at subsequently higher trophic levels. Here we propose the ratio of total biomass of the predator, multiplied by a consumption to biomass (*C/B*) ratio of 3 (approximately an average of all fishes from several sources; sensu Froese and Pauly 1994, Pauly and Christensen 1995, Greenstreet et al. 1997, Palomares and Pauly 1998, Link et al. 2006, Froese 2011), to the standing stock primary producer biomass of an ecosystem (converted to wet weight). The fish to producer ratio (p^*) is:

$$p^* = \frac{B_i \cdot 3}{chl\ a} \qquad \text{EQ 18}$$

where B_i is the biomass of species i, 3 is the *C/B* ratio (which could be input more precisely if known directly for the species under consideration), *chl a* is the chlorophyll *a* standing stock biomass (as converted to appropriate units, all for the same unit area at which B_i was estimated). Examples from the NES LME show that some species are well above a ratio of 1-1.5‰, whereas others are much lower than 0.5‰ (Figure 21). Here we would propose a threshold of 1.5‰, below which a fish could be considered to have limiting prey. This threshold is based on observations from a suite of empirical and food web modeling studies and although not definitive, represents a general threshold below which resources could be limiting (Coll et al. 2006, 2008, Link et al. 2008, Link 2010b). The theoretical basis for such a threshold is that for each trophic level (TL) from the basal TL, there is usually an order of magnitude lower biomass and productivity than primary producers. This largely considers transfer efficiencies of 15-20%, with fishes at TL 3 typically having such p^* ratios on the order of 10^{-3} to 10^{-4} (Link 2010b).

Collectively any one of these approaches should be measurable with extant data. The exception might be lack of time series data for the prey fields in the p' calculation. We propose these as more rigorous methods to ascertain whether resources might be limiting rather than simply making such an assumption. Of course, these would only need to be evaluated for individual fish species that have already been evaluated with the prior criteria noted above, in instances where competition is strongly suspected.

Examples of Possible Competition from the NES LME

From the examples we have presented while describing each of these steps to evaluate competition, a few examples will have emerged for the NES LME. For instance, it is clear that in the demersal fish community, there are a suite of benthivorous skates, gadids and pleuronectids that have high spatio-temporal and dietary overlaps, have had opposition population trajectories, and have the potential for some of those species to have some form of limiting resources. We are definitively not saying that such competition is occurring or proven amongst this suite of species. Rather, we are saying that should competition be more rigorously evaluated or attempted to be estimated, these taxa would be some of the first to consider as the potential for competition appears high among them.

Symbiosis: Mutualism, Commensalism, and Other Positive Species Interactions

Most discussions of species interactions infer negative influences among the species under consideration. Yet there are some species interactions that are mutually positive or positive for one species with no effect on the other (Table 1). So why are these positive interactions important to consider? Essentially because they describe some form of symbiotic relationships, without which the LMRs under consideration would not achieve their production potential, or in some cases even survive.

SYMBIOTIC BACKGROUND

Symbiosis is a close and potentially long term interaction between two species (Trujillo and Thurman 2011). Such interactions are an integral part of natural systems, helping to foster diversity (discussed below) and enabling organisms to survive in harsh or even extreme environments (Childress and Fisher 1992). Symbiotic relationships are found throughout the marine environment, with the highest occurrences in the tropics. The intensity or necessity of the interaction can vary widely between species pairs. For example, the well-known instances of parchment worms, *Chaetopterus*, and the *Polyonyx* crab or the clown fish and the sea anemones are obligate, species-specific interactions that are maintained for life. Both the *Polyonyx* crab and the clown fish depend on the living habitat created by their symbiotic host and are rarely found outside of it (Gray 1961, Fautin 1991). Remoras (Echeneidae), by contrast, associate with large marine organisms, but can switch between marine mammals, turtles and fish and are occasionally found on their own. Some species of remora have been observed in the NES LME (MacKenzie and Homans 1938; NEFSC unpubl. data).

Symbiotic relationships are typically broken into three categories (Trujillo and Thurman 2011; Table 1). An interaction in which both species benefit is called mutualism (e.g., zooxanthellae and coral, clownfish and sea anemone, vent worms and bacteria, etc.). An interaction in which one species benefits and the other species is not harmed is called commensalism (e.g., humpback whales, *Megaptera novaeangliae*, and barnacles) and interactions in which one species benefits and the other species is harmed is called parasitism (a sub category of predation, a specialized form of the negative-positive interaction; e.g., isopods on fish gills, whale lice on right whales). Parasites are an important part of the marine environment and can be a significant factor regulating populations, communities and ecosystems; however, given the specificity of that topic they will not be covered here as parasitology is a large discipline unto itself and beyond the scope of this chapter. Positive species interactions, as seen in these symbiotic relationships are common among marine organisms and a number have been documented for the NES LME.

Examples of Positive Species Interactions in the NES LME

Mutualism

Kelp beds are important habitat areas along the coastal NES LME and have varied in extent over the last few decades (Steneck et al. 2002). Sea urchins graze kelp, while urchins themselves have historically been kept in check by fish predators such as cod. With the decrease in fish predation, urchin populations increased, resulting in a reduction in kelp beds; and along with some other factors resulted in a new fishery for urchins (Vadas and Steneck 1995, Steneck et al. 2002). In this context, the mussel *Modiolus modiolus* is typically found proximal to kelp beds on New England's rocky coast. Those mussels, which settle higher off the bottom, can be overgrown by kelp, leading to being torn off by coastal storms due to increased surface area, whereby the storms remove both the kelp and mussel. Sea urchins graze the kelp on the outside of the mussels, keeping the mussel beds free from kelp and thus both limiting the lower depth range of the kelp beds and decreasing *Modiolus* mortality. In turn the mussel beds provide a three-dimensional habitat refugia for the urchins. Urchins in mussel beds were significantly less likely to be removed than urchins on urchin barrens when exposed to predation, fishing and storms (Witman 1987).

The sea anemone *Allantactis parasitica* is found on a high percentage of the predatory snail *Buccinum undatum* in deep water. The shell of the snail provides a hard substrate for the sea anemone to attach to, expanding the range of the sea anemone into mud habitat which would have been otherwise unavailable. The sea anemone in turn provides defense against predation as well as potential camouflage for the snail (Mercier and Hamel 2008).

The toad crab (*Hyas* sp.) and long nose spider crab (*Libinia dubia*) are decorator crabs found along the east coast of the United States. These crabs selectively choose and place invertebrates and algae on their carapace. The crabs provide a hard substrate and the potential for higher flow of nutrient-rich water to the invertebrates and algae. In turn the invertebrates and algae provide camouflage and defenses against predation (Hultgren and Stachowicz 2009).

Marine mammals and seabirds exhibit a facultative mutualistic relationship for locating and consuming prey (Pierotti 1988a). Small pelagic fish such as herring, sandlance, *Ammodytes dubius*, capelin, *Mallotus villosus*, and mackerel are important food items for predators, but have a patchy distribution in the ecosystem. Large whales such as humpbacks and minkes, *Balaenoptera acutorostrata*, drive small fish into tight aggregations on the surface through bubble netting and other, related feeding mechanisms. The large whales then lunge feed through the tightly packed school, often breaching the surface of the water. The dense aggregations provide a concentrated food resource for seabirds which can flock in large numbers to these aggregations. Pods of small cetaceans such as dolphins, porpoises and pilot whales are also known to drive fish schools into tight groups at the surface where they are preyed upon by both the marine mammals and seabirds (Evans 1982). While the seabirds utilize the concentrated fish schools, large flocks of birds may also serve to attract cetaceans to patchy prey. Researchers in the NES LME have repeatedly recorded a single bubble netting humpback being joined by multiple other humpbacks from some distances once a large flock of seabirds had congregated above the schooling fish (Pierotti 1988b). That study suggests that whales may follow large flocks of birds to fish schools. While both marine mammals and seabirds locate and consume fish in the absence of the other, the discovery of a fish school by one attracts the other. Seabirds such as gulls and kittiwakes can easily identify schools of fish from the air, but they are only able to feed on fish that are very close to the surface. Marine mammals can herd prey to the surface, but may utilize the presence of seabirds to locate the fish. Some seabirds such as auks (Alcidae*)*, however engage in pursuit diving and can swim well enough to drive schools of fish into tight aggregations on their own. Off the coast of Scotland, auks often initiate prey aggregation and are then joined by the surface feeding gulls and kittiwakes. The large flocks of these white birds in turn attract minke whales which can finish off the school of prey (Anderwald et al. 2011). It is unclear exactly how much the seabird – marine mammal interaction benefits these organisms, but in one example the diet of herring gulls in Witless Bay switched from intertidal organisms to pelagic fish and squid with the seasonal arrival of humpback and pilot whales (Perorti 1988b). Other top predators such as tuna are known to take advantage of prey aggregations created by dolphins (Clua and Grosvalet 2001). The tightly packed concentrations are almost always accompanied by seabirds.

Certain bivalves (sea scallops and oysters) have exhibited a mutualistic relationship with encrusting sponges. Sponges decrease predation on bivalves by providing camouflage and by decreasing the ability of predatory sea stars to open their shells. The sponge inhibits the tube feet from properly adhering to the shell and thus the sea stars cannot open the bivalves (Bloom 1975, Forrester 1979, Donovan et al. 2002, Heather et al. 2007). The bivalves provide a hard substrate for the sponge and increase the current flow around the sponge, both increasing the amount of food flowing past it and decreasing the amount of sediment that would cover it (Burns and Bingham 2002). Sponges also escape nudibranch predation while on scallops (Bloom 1975). Alternatively, barnacle encrustation increased predation on scallops by making it easier for sea stars to hold and open the scallops (Donovan et al. 2003, Heather et al. 2007).

Schooling is an important behavioral response in fish that confers many benefits. Fish typically school to avoid or escape predation, to increase feeding opportunities, to maximize spawning success, and to facilitate migration (Pitcher and Parrish 1993, Domenici and Batty 1997, Deblois and Rose 1996). In the NES LME the majority of small pelagic fish species school. For instance, herring, butterfish, menhaden, *Brevoortia tyrannus*, shad, and mackerel are all known to form large schools and are an important component of the food web. Some of these fish form mixed species schools which confer survival benefits to one or all of the species involved. Mixed species schools increase the total size of the school, potentially increasing its effectiveness, particularly in areas where one of the species is at low abundance (Keenlyside 1979). Cunner, *Tautogolabrus adspersus*, and juvenile cod, *Gadus morhua*, (15-20 cm TL) have been observed in mixed species schools nearshore (Auster 1984), where cunner were numerically dominant and segregated within the school nearest to substrate. When threatened, both cunner and cod fled together to seafloor shelter (rock crevices and amongst macroalgae), suggesting the occurrence in mixed species schools served a predator avoidance function. River herring (alewife, *Alosa pseudoharengus,* and blueback, *Alosa aestivalis*) are also known to school together (Neves 1981), as are butterfish and squid (Lange and Waring 1992). The exact relationships are not fully known, but in both cases they share similar predators and diets. Multi-species schools however may not be equally beneficial (and hence not entirely mutualistic) to the different species involved. Any given small pelagic species may school with other species as a matter of necessity, but the schooling-trap hypothesis suggests that the school will be guided by the numerically dominant species to its maximum benefit (Bakun and Cury 1999, Maes and Ollivier 2002). In addition to the species mix, the size structure of schooling individuals can influence the relative effectiveness for individuals in the school (Krause et al. 1996, 1998). The speed, direction, spawning events and food opportunities will be directed by the numerically dominant species and may not be optimal for the secondary species. For example, herring and sprat school together in European estuaries and exchange dominance roles over time (Maes and Ollivier 2002).

Mixed species groups of predators have been observed exhibiting coordinated behavior in search and pursuit of vagile prey (fish, shrimp and squid). For example, silver hake on the southern New England Shelf followed flounders and skates and preyed on shrimp disturbed by their swimming and foraging activities (Auster et al. 2003b). Facilitative mutualistic behaviors of predators are common in other LMEs and may be common in the NES LME as well, although direct observations are generally required and such work is limited due to depth and turbidity. For example, mixed species groups of midwater piscivores (e.g., amberjack, *Seriola sp.,* and blue runner, *Caranx crysos*) attack prey (e.g., YOY tomtate, *Haemulon aurolineatum*, and scads,) at sub-tropical reefs off the southeast US, driving prey toward the reef where demersal piscivores (e.g., black sea bass, scamp grouper, *Mycteroperca phenax*) attack dense aggregations of fleeing prey (Auster et al. 2009). Shark mackerel, *Grammatorcynus bicarinatus*, in the Coral Sea were observed using resting schools of other species as camouflage from which to approach and attack prey (Auster 2008).

Commensalism

The colonial tunicate *Didemnum* creates thick mats on Georges Bank and is considered the first invasive species to occupy deep water on the northeast shelf (Bullard et al 2007). The thick mats overgrow the invertebrates and pebble habitat that is often used by juvenile fish. Two species of polychaetes, *Nereis zonata* and *Harmothoe extenuate*, can grow in *Didemnum* and achieve sizes much larger than in areas without the tunicate. It has been suggested that the thick mats protect the worms from predation by fish and allow them to grow more rapidly (Lengyel et al. 2009). The colonial tunicate does not appear to derive any benefit.

Butterfish are summer residents of estuaries in the Southern New England-Mid Atlantic Bight region and feed on large numbers of the ctenophore *Mnemiopsis leidyi*. *Mnemiopsis* often carry a parasitic crustacean. Observations in the lab suggest that butterfish may selectively target the parasitic crustacean within the ctenophore (Oviatt and Kremer 1977). Some *Mnemiopsis* may be able to regenerate after the parasite is consumed.

Juvenile butterfish and harvestfish, *Peprilus alepidotus*, often congregate around the tentacles of sea nettles (jellyfish, *Chrysaora quinquecirrha*) and lion's manes to avoid predation from above and below. The butterfish do get stung by the nematocyst of the cnidarians, but are largely unaffected. As the fish grow they begin consuming the tentacles of the jellyfish and as adults consume the entire cnidarian (Mansueti 1963, Duffy 1988). This is loosely analogous to the clownfish-anemone example so commonly cited for commensalism, but has a significant shift with ontogeny.

Tilefish, *Lopholatilus chamaeleonticeps*, are a demersal species which live in self-dug burrows along the continental shelf. The burrows provide habitat and possible food items to a wide range of crustaceans and other fish. Lobsters, crabs and isopods are known to live in a commensal relationship with tilefish in their burrows (Able et al 1982; Grimes et al. 1986). Yellowfin bass, *Anthias nicholsi*, conger eels, *Conger oceanicus*, cusk (*Ophidiidae)*, redfish, hake and ocean pout have also been found in tilefish burrows (Grimes et al. 1986; Hood et al. 1988, Bowman 1986; Cooper et al. 1987). Some of the larger organisms may consume similar prey and compete with tilefish for food (Freeman and Turner 1977; Levy et al. 1988), but the overall effect is usually negligible to the tilefish.

Juvenile red hake have a commensal relationship with sea scallops, *Placopecten magellanicus*, along the east coast of the United States. The juveniles appear to take refuge in live sea scallop shells to avoid predation. It is unclear if there is any impact on the scallops (Wigley and Theroux 1971; Garman 1983), but none is suspected. Snailfish, *Libaris spp.*, are similarly often found in sea scallops (Brian Smith per. obs.).

Juvenile deep sea cusk eels, *Barathrites sp.*, on the New England sea mounts take refuge in the spines of pancake sea urchins, *Hygrosoma petersi* and *Phorosoma placenta*. The spines have been hypothesized to decrease predation on the juveniles and allow them to occupy areas away from permanent refuge structure (Moore and Auster 2009).

Symbiosis Synthesis

Symbiotic relationships are quite dependent on a variety of considerations. Yet the demographic implications for LMRs in the NES LME remain unknown. Clearly results from small-scale experimental studies have demonstrated enhanced survivorship and growth at the level of individuals that participate in group foraging (Bruno et al. 2003) but expanding to population and community scale responses remains a challenge. Further, there are few examples of approaches to quantify the extent of such behavioral interactions within a community or interacting trophic guilds. For example, simple descriptive statistics and comparisons between treatments have been used to compare rates of groups foraging across coral reef habitats, multivariate approaches have been used to describe the web of facilitative interactions between reef piscivores, and interaction strengths have been estimated in an interaction web based on functional roles of piscivores (Auster and Lindholm 2008). Such approaches are not widespread and have not been evaluated across ecosystems. Connecting behaviors, across ontogenetic stages, to survivorship, growth and reproduction will be needed to integrate the role of such interactions across LMR communities. Despite this concern over scaling, some common symbiosis patterns have emerged.

Butterfish utilize the tentacles of jellyfish, but the relationship changes depending on the size of the butterfish, the amount of prey available and the abundance of predators. The protection juvenile butterfish gain from jellyfish is important when butterfish predators are present, but when predators are absent or prey is limited butterfish consume parts of the jellyfish. The relationship changes from commensalism to predation as adult butterfish directly consume jellyfish. Environmental conditions can also have an important impact on the nature of symbiotic interactions. For example, zooxanthellae are obligate alga symbionts in coral that provide food for their host in return for nutrients and a safe structure. As the water quality changes (high temperatures, turbidity) the coral expel the zooxanthellae to the detriment of both (Wooldridge 2010). The coral may acquire new zooxanthellae better adapted to the current conditions or may remain bleached for some time. Like all aspects of the natural world the relationships are dynamic and vary depending on the conditions of the environment and the species involved (Hay et al. 2004; cf., Figure 1).

Symbiotic relationships are an important part of the marine environment. The interactions can benefit one or both species involved, but the relationships often link to much larger ecosystem processes (Hay et al. 2004). As noted above, seabirds, marine mammals and large predatory fish use one another to locate and consume patchy prey resources. The exact interactions are quite interesting (spy hoping by whales scanning for flocks of seabirds), but at a system level the interactions can result in an enormous transfer of energy between trophic levels. These large and highly migratory predators consume a huge mass of planktivorous fish and redistribute it throughout the system which could have important implications for future productivity. Like predation and competition, symbiotic relationships link individual species interactions with larger system dynamics (Hay et al. 2004).

FOOD WEBS

What are food webs and why are they important to consider in an LMR context? Why present yet another "horrendogram" of highly complex species interactions that on the surface poses no readily useful application of the information contained therein? Very simply, food webs are a road map of how biological communities interact. Without them, one is ill-suited to explore the issue of tradeoffs so necessary to implement EBM. Of all the possible species interactions noted (Table 1), but particularly predation and competition, the salient point is that none of them occur as simple, binary species pairings. Rather, they occur in the context of a myriad of such species and their interactions. If one has drastic changes to certain biota, say from excessive fishing pressure or a major environmental shift (the two external drivers in the triad; Figure 1), how will that trickle through and effect other species in an ecosystem? Elucidating possible competitors, secondary effects, alternate prey, or compensating guild-member dynamics all benefit from food web depictions. Without knowledge of a food web structure, even if rudimentary, attempting to quantify such impacts is near impossible.

A Brief Primer on Food Webs

A food web characterizes the flows of material and energy among groups of organisms within an ecological community that results when each organism consumes, or is consumed by, at least one other organism (Cohen et al. 1993). Principally, it depicts the network of consumer-resource interactions among the various groups (Winemiller and Polis 1996). The interactions depicted are binary in nature—whether groups interact through trophic relationships or not (Pimm 1982). Within a food web, organisms are grouped on the basis that consumption patterns are similar for organisms within the group and differ from organisms in other groups. While taxonomy provides one approach to this aggregation, the "trophic species" concept—the largest set of organisms with identical sets of predators and prey defines a group known as a trophic species (Cohen and Briand 1984, Cohen 1989)—is a widely-accepted convention that has been shown to reduce methodological biases (Cohen et al. 1990, Pimm et al. 1991, Martinez 1994), but is not without its critics (Schoener 1989, Polis 1991).

Pimm et al. (1991) distinguish among three types of empirical food webs: (1) source webs, (2) sink webs, and (3) community webs. Source webs trace trophic relationships from a single group of organisms (or set of groups) "upwards" through its predators, the predators on its predators, and so on. Sink webs trace the process in reverse, tracing trophic relationships from a single group of organisms "downwards" through the groups that it consumes, the groups that they in turn consume, etc. Community webs are defined as those that arise from picking a set of groups—without initial regard to interactive relations among the groups—and working out "who eats whom" (Pimm et al. 1991). In an alternative categorization, Winemiller and Polis (1996) distinguish among three types of food webs based upon their information content: (1) topological or descriptive webs, (2) flow or bioenergetic webs, and (3) interaction or functional webs. Topological webs are qualitative in nature; only the presence-absence of interactions between groups is indicated. Bioenergetic and interaction food webs are quantitative; the relative strengths of trophic interactions between groups are indicated. Bioenergetic webs quantify the transport through consumption of energy-matter among groups, while interaction webs depict the strength of links between groups in terms of their influence on the dynamics of community composition and structure. Most marine food webs are flow webs, with topologies retrospectively emergent and examined (Link et al. 2005).

Metrics for Topological Food Webs

The basis for much of the development of food web theory has been the comparison of empirical topological food webs from different communities (see, e.g., Pimm 1982, Lawton 1989, Cohen et al. 1990; see Appendix 3 for an expanded discussion on the history of food web theory). However, for all but the most species-poor communities, food webs exhibit complex interconnections among species, with speciose examples typically resemble plates of spaghetti (e.g. Link 2002b; Figure 22)—rendering direct graphical comparison among webs a fruitless task. To facilitate the inter-comparison of webs with regard to identifying general patterns from which general processes may be inferred, and specific applications derived for LMR contexts, a variety of descriptive metrics have been developed to reduce topological web complexity (e.g., Pimm et al. 1991, Bersier et al. 2002, Link et al. 2005; Table 3).

The number of species in a food web (*S*) is one of its fundamental properties. Several metrics that characterize the types of species composing a food web have been developed based on classifying species as consumers (*N*) or prey (*P*) and as top, intermediate, or basal (Briand and Cohen 1984, Bersier et al. 2002, Table 3). Top species are those that consume prey but are not consumed as prey, basal species are those that consume no prey but are consumed by other species and intermediate species are those that both consume prey and are consumed as prey (Pimm et al. 1991). The fraction of top (%*T*), intermediate (%*I*) and basal species (%*B*), as well as the ratio of prey to consumer species (*N:P*), have all been used as food web metrics (e.g., Briand and Cohen 1984, Sugihara et al. 1989, Cohen et al. 1990, Pimm et al. 1991, Havens 1992, Martinez 1994, Williams and Martinez 2000).

The pair of metrics known as generalization (*G*) and vulnerability (*V*) provide measures of the asymmetry between being a consumer and being prey. Generalization is defined as the mean number of prey species eaten per consumer species in a web (Schoener 1989, Table 3). Conversely, vulnerability is defined as the average number of consumer species per prey in a web (Schoener 1989, Table 3). Williams and Martinez (2000) defined normalized quantities based on generalization and vulnerability and introduced *sdG* and *sdV*, the standard deviations of normalized generality and normalized vulnerability respectively, as measures of variability that allow comparisons across webs of different size (Bersier et al. 2002).

The number of trophic links among species (*L*) in a food web is also one of its fundamental properties. Metrics that characterize the types of links involved in a food web have been defined based on the fraction of links involving top and intermediate species (*%T-I*), top and basal species (*%T-B*), only intermediate species (*%I-I*), and intermediate and basal species (*%I-B*) (Cohen and Briand 1984, Table 3).

However, *L* is not independent of *S*, as *S* determines the maximum number of possible trophic linkages among species. As such, *S* sets an upper bound on *L*. *S* thus functions as an overall scale for the food web. Linkage density and connectance are two metrics that attempt to capture the overall complexity of a food web by combining the number of species and number of links among species. The linkage density ($L_D=L/S$) is the mean number of links in which each species participates (Drossel and McKane 2003) while connectance (*C*) is defined as the ratio of realized links to potential links (Warren 1994) and represents the fraction of potential links for a web that are actually realized (Pimm et al. 1991) or, alternatively, the probability that any pair of species will interact (May 1972). Several slightly different definitions for connectance have been used (Warren 1994). The quantity $C_{dir} = L/S^2$ is referred to as "directed connectance"—S^2 is the total number of all potential trophic interactions (Martinez 1991, Warren 1994, Table 3). The quantities $C = L/[S(S\text{-}1)]$ and $C = 2L/[S(S\text{-}1)]$ are both referred to as "connectance" (Pimm et al. 1991, Warren 1994, Table 1). In both formulae, $S(S\text{-}1)$ is the number of possible trophic links in the web, ignoring cannibalism. The factor of 2 in the second formula arises because each link represents two interactions—consumer on prey and prey on consumer (Pimm et al. 1991). The latter formula is also consistent with the realized fraction of potential links in a web with *S* species that is "trophically-ordered" such that each species can (potentially) consume only species at lower trophic levels but no species at higher trophic levels and such that no cannibalism occurs (i.e., if the interaction matrix with consumer species in rows and prey species in columns were ordered by trophic level, then potential trophic interactions would be limited to the lower half-matrix below the diagonal).

The product $S \times C$, when coupled with an assessment of overall web interaction strength, either mean interaction strength (May 1973) or eigenvalues of the interaction matrices (Pimm 1982), can give an assessment of the overall mathematical stability for a system. It has been implied that if the square root of the product $S \times C$ multiplied by the mean interaction strength is less than unity, a system will be stable (May 1973). Given that constraint, Link (2002b) calculated a proxy for stability based upon the observed $S \times C$ values for the NES LME.

Several metrics based on characteristics of pathways through a food web along its trophic links have also been used to capture the complexity of food webs. These characteristics include the number and length of "maximal" food chains and the size and percentage of trophic cycles. Here, a food chain represents a distinct path within the food web from any species "downwards" along realized links to a basal species; a maximal food chain is defined as one that starts from a top predator (Pimm 1982, Cohen 1989, Bersier et al. 2002). A cycle is a directed sequence of links that start and end at the same species (Cohen 1989). The length of a cycle is the number of links contained in it: cannibalism represents a cycle of length one (A eats A), while "A eats B and B eats A" represents a cycle of length 2.

The number of maximal food chains (n_{mfc}) has been used as a food chain-based metric, as have the median (MED_{cl}), standard deviation (SD_{cl}) and maximum lengths (MAX_{cl}) of all maximal food chains, where the length of the food chain is equal to the number of links traversed (Bersier et al. 2002). However, defining maximal chain length is problematic when cycles are present in the web; similar metrics can be computed based on all chains that don't include cycles (Williams and Martinez 2000).

Metrics reflecting the degree of omnivory within a food web also utilize chain length information, but combine it with linkage topology. If one defines the trophic level for a given species as one plus the length of the longest food chain from a basal species up to the species of interest, then one can measure the degree of omnivory (*%O*). Omnivory is simply the proportion of species that consume prey from more than one trophic level (Bersier et al. 2002). A second related measure of omnivory is the mean of the standard deviations in chain lengths over all species (Goldwasser and Roughgarden 1993). A third is the ratio of the number of closed omnivorous links to the number of top species (Hall and Raffaelli 1991), where a closed omnivorous loop is a cycle starting from the consumer species that runs through at least two prey species that occupy different trophic levels (Bersier et al. 2002).

NES LME Food Web Example Metrics

The food web of the NES LME has been characterized (Link 2002b; Figure 22). The topological web itself has produced a suite of food web metrics that have informed and contextualized our understanding of how the biotic communities in the NES LME have changed over time. These metrics have not had direct application for LMR management in terms of biological reference points or thresholds, although it has contextually formed the basis for subsequent efforts that have. Further, this work has provided insights in an LMR management context for enhanced understanding of how the system is structured, how it could respond to perturbation, and how it could alter community dynamics. Future work exploring more specific details of these metric dynamics over both time and space would apt to be insightful given the notable perturbations this ecosystem has experienced (Link et al. 2011a, Fogarty and Murawski 1998). Summarizations suggest that generally the marine food webs are much more connected than terrestrial or freshwater counterparts (Table 4). This summary also suggests that generally interactions strengths in this food web are apt to be, on average, weaker than in other food webs (*S x C* in Table 4).

Also important to note is that depictions of the NES LME food web have served as the basis for construction of energy flow models, or more detailed "bioenergetic food webs" as noted above. These networks of biomass flows have been utilized in LMR management and are discussed further below. The key conclusion from NES LME topological web examination is that using the Lyapunov stability proxy, given bounds on average interaction strengths, the food web appears to be highly resilient and highly flexible in terms of general energy flows.

Ecological Networks

As noted above, ecological networks are a type of food web model, with particular emphasis not only on the topology (links between species or species groups; i.e., nodes in network parlance) but especially quantification of the flows between nodes. These are important as they allow one to explore the change in energy or biomass in response to various ecosystem perturbations.

Most network models retain some form of mass balance. The Ecopath with Ecosim (EwE) model has been widely used to describe aquatic systems and to explore the impacts of fishing on ecosystems (Christensen and Pauly 1992, 1993, Christensen et al. 2005). It is composed of a mass balance model (Ecopath; Polovina 1984, Pauly et al. 2000, Kavanagh et al. 2004, Christensen et al. 2005) from which temporal (Ecosim) and spatial (Ecospace) dynamic simulations can be developed (Walters et al. 1997). Mass balance (Ecopath) models have been developed for many regions across the NES LME: especially for the Gulf of Maine, Georges Bank, Southern New England and Middle Atlantic Bight ecosystems (Link et al. 2006, 2008, 2009). These ecosystems were similarly modeled using the Econetwrk software (Ulanowicz 2004, Dames and Christian, 2006), which functionally seeks to balance the network and energy budgets.

Data requirements for these models include estimates of biomass, production and consumption rates, diets and catch. These data requirements reemphasize the value of fish stomach sampling since a thorough understanding of trophic relationships is necessary to adequately construct and execute these models. Several diagnostics have been established to ensure that the input data, or proxies thereof, are reasonable and robust (Link 2010b), conforming to minimal standards for LMR application.

Cybernetics and Network Metrics

Ecological indices based on biomass ratios, trophic flows analysis, thermodynamic concepts, information theory and associated indicators are all obtainable from network analyses (Christensen and Walters 2004, Christensen et al. 2005, Cury and Christensen 2005, Link 2005). These can all address the relative prominence of any given node, the relative redundancy of the system, the amount of material flow and cycling through a set of connected biotic communities, and the structural resilience of a system to various perturbations.

First are a series of relatively simple production (*P*), biomass (*B*) and ratios thereof for several compartments of a network. These metrics not only provide a sense of the differences in structure between any set of ecosystems (e.g., Gaichas et al. 2009, Pranovi and Link 2009), but also serve as proxies for some of the key facets of ecosystem functioning (Link, 2005, 2010b). Ratios of fisheries catches to biological rates (production, respiration, consumption, and derived by values) also shed valuable insight into the relative impact and removal of fisheries to a food web. These have also served as useful diagnostics when initializing and balancing a network model (Link 2010b).

There is a plethora of network metrics output from many extant network analysis software packages (Christensen and Walters 2004, Christensen et al. 2005, Ulanowicz 2004). They can be categorized as follows.

There are metrics describing how energy flows through the system. Useful examples include the System Omnivory Index (a measurement of how the feeding interactions are distributed among trophic levels), Finn Cycling Index (a measure of the degree of energy re-utilization within a food web, representing the fraction of total flows of the system that is cycled), and the Lindeman pyramid (which measures the amount of biomass sequestered at each trophic level). To provide an indication of how efficiently energy flows within the food web, the average Transfer Efficiency, based on the values estimated for each passage from a given trophic level to the subsequent trophic levels can also be used.

There are metrics describing the system energy capacity, both in terms of potential and realized values. Examples include the informational network indices provided as output describing key cybernetic properties. Ascendency (*A*), taking into the account both the size of the ecosystem in terms of flows (total system throughput; *TST*) and their organization (information content), has been proposed to characterize the degree of development and maturity of an ecosystem (Ulanowicz 1986). Capacity (*C*) represents the upper limit of *A*. The Relative Ascendency measure (*A/C*) is the fraction of the potential level of organization that is actually realized (Ulanowicz 1986). It is hypothesized that high values of this index are related to low level of stress in the system and vice-versa. Hence disturbance activities, like eutrophication and fishing, are expected to produce a decrease in *A* (Wulff and Ulanowicz 1989). The complement to *A* is System Overhead (*O*), which represents the cost to an ecosystem for circulating matter (and energy) the way it does (Monaco and Ulanowicz 1997). Thus, overhead effectively represents the degrees of freedom a system has at its disposal to react to perturbations (Ulanowicz 1986). For the ranking of the different compartments in term of their contribution to overall system structure and functioning, Ulanowicz (1997) proposed estimating the relative Ascendency of each group. That is, Ascendency as a percentage of overhead is effectively a measure of resilience, ultimately measuring the distance from the potential complexity to the realized complexity.

There are metrics to describe the ecological role of each node in the web. A useful example to quantify the contribution of a particular species or group to the functioning of the entire network is the Mixed Trophic Impact (*MTI*). This index, quantifying the direct and indirect interactions between functional groups, allows one to estimate the global impact of each group on the other ones (Ulanowicz and Puccia 1990). The *MTI* analysis can be carried out by using two different approaches, according to Libralato et al. (2004). In the first approach, the *MTI* (here m_{ij} for all spp i+j), weighted by the inverse of the biomass of the impacted group (B_j),

$$aGI_i = \sum_j m_{i,j} \frac{1}{B_j} \qquad \text{EQ 19}$$

represents the absolute effect (absolute Global Impact – *aGI*) of the variation of a unit of impacting group and assesses the importance in terms of functioning of a unit of biomass of each.

In the second approach the *MTI* (m_{ij}), weighted by the impacting/impacted biomass ratio (B_i/B_j),

$$rGI_i = \sum_j m_{i,j} \frac{B_i}{B_j} \qquad \text{EQ 20}$$

represents a quantification of the effect on the ecosystem of a percentage variation of biomass of impacting group and assesses the relative effect of a variation of biomass of each compartment in relation to the present value (relative Global Impact – *rGI*).

Another metric closely related to the *MTI* is the keystoneness index (Libralato et al., 2006), which weights the role of a species or group relative to its biomass, allowing for identification of those groups that, even if characterised by a low biomass, play an important role in structuring and functioning of the ecosystem (Power et al., 1996). Keystoneness (KS_i) is based on the overall effect (ε_i) which is estimated from the *MTI* index (m_{ij}) as:

$$\varepsilon_i = \sqrt{\sum_{j=1}^{n} m_{ij}^2} \qquad \text{EQ 21}$$

The keystoneness (KS_i) of a functional group is thus calculated as:

$$KS_i = \log\left[\varepsilon_i(1 - p_i)\right] \qquad \text{EQ 22}$$

where p_i is the proportion of total system biomass made up by functional group *i*.

There are metrics describing the ecological effects of fishing activities. The Primary Production Required (*PPR*; Pauly and Christensen, 1995) index represents the estimate of the total amount of energy (expressed in terms of Primary Production and detritus equivalents) invested by the system to sustain a given biomass at a given trophic level. By applying it to a fishing activity, it allows the assessment of total energy required to sustain the catches and is obtained by back- calculating the flows for all pathways from the caught species down to lowest TL. To compare different ecosystems or different states of the same system, the index has to be normalized on the net Primary Production.

In order to assess the ecological role played by fishing activities in relation to the net energy export from the ecosystem, the L index (Libralato et al., 2008) has been also proposed. It is based on the assumption that the export of secondary production due to fisheries reduces the energy available for upper ecosystem levels, thus resulting in a loss of secondary production. The index takes into account both ecosystem properties (Primary Production and Transfer Efficiency) and fisheries features (Trophic Level of catches and Primary Production Required), quantifying effects of fishing at an ecosystem level. It is calculated as:

$$L = -\frac{PPR \cdot TE^{TLc-1}}{P_1 \cdot \ln TE} \qquad \text{EQ 23}$$

where *PPR* is again the Primary Production Required; *TE* is the Transfer Efficiency of the system; *TLc* is the mean Trophic Level of the catches; and P_1 is the Primary Production of the system. According to Libralato et al. (2008), it is possible to associate to each index value a probability of the ecosystem being sustainably fished and, by fixing the reference level for this probability, the index provides a basis for estimating, from an ecosystem point of view, the maximum allowable catches (Ecosystem-based Maximum Sustainable Catches – *EMSC*; for further details, see Libralato et al., 2008).

Admittedly, some of these network metrics are not immediately intuitive (e.g. Ascendancy), but upon further inspection they and others are rather insightful into the dynamics of a system. Furthermore, some have been proposed as possible LMR biological reference points, including simpler biomass ratio of network nodes (e.g. *B* ratios or pelagic to demersals; Link 2005) and the more nuanced perturbation indices (e.g. L-index, *EMSC*; Tudela 2005, Libralato et al. 2008, Coll et al. 2008).

Examples in the NES LME

Several network models have been developed in the NES LME as part of the EMAX (Energy Modeling and Analysis eXercise) efforts. These models have been used to further our understanding of ecosystem structure and functioning, explore hypotheses concerning ecosystem change, used as a basis for comparative studies (spatial and temporal), used to provide ecosystem indicators and used in various simulated perturbation experiments. Performance measures and metrics such as throughput, total flow, biomass ratios (e.g., pelagic fishes to zooplankton), and trophic reference points (i.e., marine mammal biomass to pelagic fish biomass ratios) have been tracked and compared with empirical information over the simulated time frame.

Focusing on one region, Southern New England (SNE), one can see that the relative contribution of biomass and production is dominated by invertebrates (Table 5), with benthos having a higher standing biomass and plankton have a higher productivity. This implies a relatively minimal contribution of overall flows to the network at upper trophic levels, including fishing. This implication is born out when examining a suite of network metrics, especially flow throughputs (Table 6) and the Lindeman pyramid (Table 7). This means that most energy is flowing and cycling through lower trophic levels, with almost half of it cycling through detrital pathways. This is not to imply that fisheries removals are not important, as they can alter the response of a network (Link et al. 2008, 2009, Pranovi and Link 2009), but that relative to overall production or internal consumption fisheries catches are a small fraction (Table 8).

When cumulative biomass was plotted against trophic level for all four regions of the NES LME, a distinct pattern emerged for the four regions (Figure 23). There is a major accumulation of biomass between trophic levels 2 and 3 in all the NES LME regions (Figure 23) resulting in a sigmoidal curve (Link et al. 2008). This increase is mostly from the megabenthos (e.g. surf clams, ocean quahogs, and sea scallops) that occur in these regions. Above trophic level 3, the cumulative biomass is relatively flat, although there is a small abrupt change between TL 3–4 for all the regions, except the Mid Atlantic Bight (MAB). Benthic biomass can readily stockpile in these ecosystems because of the high primary production and detrital recycling. In general, standing stocks of biomass for trophic levels above 3 are highest in the Gulf of Maine (GoM), Georges Bank (GB), intermediate in Southern New England (SNE), and lowest in the MAB (Figure 23). The greatest regional differences occur at TL1. It is noteworthy that MAB cumulative biomass at TL1 is lower than the other three regions and this relative difference propagates through to the higher trophic levels. Conversely GOM biomass at TL1 starts higher than the other three regions but tends to converge with levels present in GB and SNE at ~TL 3.7. Final cumulative biomass averages about 220 g m−2 for the GOM, GB, and SNE and is about 20 g m−2 lower for the MAB. These results partially explain why different fisheries have arisen in the different regions, targeting different stocks, and why the differential structuring of these networks have responded differently to fishing and environmental pressures over time.

We particularly note that results from these models have been used directly in a LMR management context (NEFSC 2008). The formal Groundfish Assessment Review Meeting (GARM III; NEFSC 2008) addressed two terms of reference germane to an ecosystem approach for the Gulf of Maine/Georges Bank fisheries: a) Determine the production potential of the fishery based on food chain processes and estimate the aggregate yield from the ecosystem; and b.) Comment on aggregate single stock yield projections in relation to overall ecosystem production, identifying potential inconsistencies between the two approaches.

The background behind these terms of reference involves the observation that relatively recent fisheries management decisions (1994-2005) for fish stocks in the US Northeast Shelf LME have resulted in resurgence among some of the depleted fish populations (NEFSC 2008). A topic of some concern among various stakeholders is whether the ecosystem can support these elevated levels of biomass (e.g., biomass level which would result in maximum sustainable yield, B_{MSY}) simultaneously for all the groundfish stocks, and more broadly, the entire fish community in the region. Analyses were completed for the Northeast LME to estimate the total system biomass, summed fisheries management target biomass, and compared results to other worldwide systems. Methods and analyses used data from either stock assessments or biomass-based approaches (Brodziak et al 1998; NEFSC 2008). Information on the biological reference points for groundfish, other demersals, and small pelagic components of the US Northeast Shelf

LME were summarized and compared to historical studies, recent energy budget analyses for the region and similar metrics for comparable worldwide temperate ocean systems.

Aggregate biological reference points (BRPs) were also estimated for important groups of groundfish, pelagic, and elasmobranch stocks on the NES LME with both the ecological network analyses and a surplus production modeling approaches (Prager 1994, Link et al. 2011a). The NES LME biomass targets for pelagic and demersal fishes are similar in scale to biomass estimates from previous studies of the region. Overall, this suite of models (NEFSC 2008) similarly suggest that the estimated maximum sustainable yield (MSY) level for all GARM species is lower than the sum of individual species MSY estimates and overall fishing mortality should be lower. If interactions among species are important, all species are unlikely to simultaneously be at B_{MSY}, which is supported by several lines of evidence and multiple approaches that all suggest that this constraint is real. It is precisely the evaluation of this sort of tradeoff that warrants the continued development of food web and network approaches.

BIODIVERSITY, ECOSYSTEM RESILIENCE, AND STABILITY

Biodiversity, simply stated, is the variety of life on earth. The term not only refers to diversity as described at the level of species but includes the diversity of genetic variation within species as well as the diversity of communities, habitats (landscapes), and ecosystems that influence the distribution and abundance of species and, in part, variation in the strength of species interactions. Species that are considered LMRs are components of the wider diversity of life within the NES LME region. Indeed the models discussed in the previous section illustrate and quantify such connectivity throughout. Resilience is the ability of a system to maintain ecosystem functions in the face of disturbance and thus resist perturbations or return to a prior state after a perturbation. Stability is the variability of a system level quantity such as total production about equilibrium (Holling 1973, Levin and Lubchenco 2008). Without knowing, or being able to know in any timely fashion, all of the species within an ecosystem, in practice one tends to default to depending on a level of resilience within functional guilds throughout the system, such that populations of multiple species can respond across a range of conditions and maintain function (Walker 1995).

Though there is some debate, numerous studies have found that communities with higher diversity are more resilient and more stable through time (e.g., MacArthur 1955, Doak et al 1998, Folke et al 2004, Loreau et al 2002, Hilborn et al 2003). The general paradigm is that higher diversity systems tend to have a lower level of individual species collapse, less variation in commercial catch and quicker recovery times from disturbances. Higher level system properties such as total biomass or productivity typically vary less over time and thus these systems can provide more consistent ecosystem services (Oksanen et al. 1981, Link 2005, NEFSC 2008, Auster and Link 2009).

Ecological theory suggests that higher level system properties are maintained due to compensation among species, i.e., the portfolio effect. Species compete for limited resources within their habitat and those that are the most successful become the numerically dominant taxa while those that are less successful are less abundant. These species typically exhibit negative covariance in abundance. The competitively dominant taxa may decline however due to changes in environmental conditions or fishing pressure, resulting in an increase in the previously competitively inferior species (Gonzalez and Loreau 2009). Negative covariance however is not a prerequisite for maintaining higher level system properties due statistically averaging of large numbers of species. Doak et al (1998) likened the statistical averaging of a diverse system to the portfolio effect in economics. The goal of a diversified “portfolio” is to offset a loss in any one asset by gains in other assets (Doak et al 1998, Figge 2004). Again it has been noted that the sum of the biomass of unrelated, independent species over time is less variable than the variability of the individual species and the variability of the sum decreases as the number of species increases. Species however are not independent, but model simulations indicate that positive relationships among species weakened such relationships, but did not entirely eliminate them. Negative relationships strengthened the relationship (Doak et al 1998). The individual species vary, but the variability is reduced at the higher level ecosystem processes such as total biomass (Doak et al 1998, Figge 2004, Gonzalez and Loreau 2009). Maintaining biodiversity thus provides functional redundancy among a number of species which dampens variation from large scale perturbations. Resiliency requires that there is great enough diversity at the stock, species or guild level to maintain the numerous ecosystem functions during perturbations. A loss of diversity has the potential to remove the redundancy in the system and cause large scale variations from year to year.

Measures of Diversity

Several indices are available for measuring the many facets of biological diversity (Table 9). These include but are not limited to species richness, a count of the total number of species; evenness, how individuals are distributed across the total number of species; measures that incorporate richness and evenness (e.g. Shannon Wiener, H’; Brillouin, HB); and the taxonomic-based metrics (taxonomic diversity, Δ; taxonomic distinctness, Δ* and Δ+). The Hill (1973) collection of diversity indices also includes alternate forms of species richness (N0), measures of evenness (N1), and the number of dominant species (N2). These metrics are variants of Shannon H’ and Simpson’s D, and cover the many considerations of diversity.

A notable caveat with many diversity indices is that they are highly sensitive to sampling effort, requiring an adequately controlled sampling or sub-sampling design to ensure unbiased data comparisons (Gotelli and Colwell 2001, Andrew et al. 2003, Kuo et al. 2010). In response, Warwick and Clarke (1995) proposed the three taxonomic-based diversity indices: Δ, Δ*, and Δ+ to assimilate the taxonomic relatedness of species in addition to their abundance with the exception of Δ+ (applied to presence/absence data). The mean values of these indices have been shown to be insensitive to sampling effort (see also Clarke and Warwick 1998). Δ is an extension to Simpson’s diversity index (D) incorporating taxonomic separation measured as the mean path length between two randomly chosen individuals under a taxonomic hierarchy (Jennings et al. 2001). Comparable to Δ, Δ* is solely a measure of taxonomic distinctness and does not consider species abundance, requiring randomly chosen individuals to be from different species.

All such diversity measures have their strengths and weaknesses, but for most evaluations of diversity some measure of presence (richness) and relative abundance are worth noting. Most use readily available information in a fisheries context and can track composite dynamics of a fish community.

Measures of Resiliency and Stability

Measuring abstract concepts such as resiliency and stability can be very challenging outside of controlled laboratory experiments. Large marine ecosystems are continuously being perturbed by changes to all aspects of the triad (Figure 1; environmental conditions and fishing in addition to trophodynamics), making it difficult to connect species responses with specific disturbances. Ives et al (2003) laid out some measures based on control theory. These methods require an estimate of the interaction matrix between species typically derived through some type of modeling process.

The maximum eigenvalue of the interaction matrix is a measure of the variance of the stationary distribution compared to the variance of the process error. Under steady state conditions a maximum eigenvalue less than one indicates that the system would return to its stationary distribution after a perturbation (following Pimm 1982). The lower the magnitude of the eigenvalues the more stable the system. The determinant of the interaction matrix is a measure of the rate at which a disturbed system would return to its equilibrium state. Again the lower the magnitude the quicker the system would return to its non perturbed state. The reactivity of the system measures the response of the system after a perturbation. A system which moves further away from equilibrium after a disturbance before moving towards equilibrium is considered less stable.

Also, apart from the Ives et al. (2003) framework, the May (1972, 1973) stability proxy (see food web metrics above; Table 3), which led to a criterion for community stability related to connectance ($b(SC)^{1/2}<1$, where b is mean interaction strength), has been used as a simpler way to examine stability and resilience. Under the assumption that mean interaction strength is independent of food web size, May's formula predicts that connectance should decline hyperbolically as the number of species increases. Based upon this observation, mean interaction strengths then determine how strongly or loosely connected the food web is, implying resilience to perturbation if below the given threshold.

In most studies however the stability of a system is typically measured as the variance of the higher level system process such as total biomass or the coefficient of variation. These values are often used to investigate the potential role of compensation in dampening perturbations (Ives et al. 2003). The variance ratio test compares the variance of the total (total biomass of the system, total biomass of a functional group) with the sum of the variances of the individual species within the total. A ratio of less than one suggests that species interactions dampen the variability of the individual species making the system more stable. Ratios of the coefficients of variations provide a similar analysis (Gonzalez and Loreau 2009). Given these observations, compensation is a well grounded theoretical concept, but has been very difficult to detect with field data (Houlahan et al 2007).

Examples from the NES LME

The groundfish community of the NES LME continental shelf has experienced declines in several diversity indices over time (Figure 24). Indeed, despite the fairly consistent number of species per tow (S tow^{-1}) over the time series (Azarovitz 1981; NEFC 1988; Reid et al. 1999), decreasing trends were seen with Δ and the Shannon H' index, suggesting reductions in species abundance and taxonomic relatedness (i.e. an overall narrower taxonomic hierarchy). Additionally, evenness diversity as measured by H' (ln (S)-1) has decreased since the early 1970s, indicating greater species dominance. This general decrease in diversity over time is noteworthy given the long history of fishing pressure, changes in community structure, and environmental factors considered for this region (Figure 1; see Boreman et al. 1997; Fogarty and Murawski 1998; Link et al. 2011a, Nye et al. 2009). In particular, high fishing pressure over the last few decades has led to declines in groundfish biomass and may have contributed to the decline in Shannon's diversity index. Yet partitioning out causality and variance among these drivers as it relates to diversity responses remains an important challenge.

Declines in diversity should lead to declines in functional redundancy and perhaps declines in system resilience. On Georges Bank fish biomass declined though the 1980s and 1990s and the variance ratio test for three broadly defined feeding guilds did not indicate compensation within the guilds (Gifford et al. 2009). The lack of compensation suggests that losses of some species within a feeding guild may not be offset by others and that external drivers were depleting entire feeding guilds. This study only examined a smaller subset of the fish community and may have missed key aspects of compensation that a broader species list would have captured. Compensation was indeed evident at the level of total fish biomass, indicating that there was enough functional redundancy in the system as a whole for compensation to dampen the impacts of the external drivers and imply some level of systemic resilience (Link et al. 2008, Gifford et al 2009).

Another study across the entire northeast shelf found strong compensatory dynamics within feeding guilds since the 1970s. The abundance of individual species within each feeding guild had changed over time, but the total number of individuals per tow had remained relatively constant in five of seven feeding guilds (Auster and Link 2009). Planktivores and shrimp eaters had increased in abundance from the 1970s to the 2000s, but the other groups did not exhibit significant changes in total numbers despite heavy fishing pressure and species replacements. There are serious concerns that large-scale depletions may fundamentally alter the function of the shelf ecosystem. In the NES LME, despite declines in species diversity it appears that functional diversity has been mostly preserved. Many high valued commercial species have declined, but through compensatory processes functionally similar species have replaced them to maintain the basic ecosystem functions of the NES LME food web (Auster and Link 2009).

Diversity has value as one of many indicators of ecosystem status. Perturbations typically decrease biomass, decrease diversity and increase the variability of fish abundance over time. Systems with high volatility do not produce a consistent set of ecosystem goods and services, plus they also tend to be more difficult to manage. Maintaining biodiversity has the potential to dampen some of the variability and produce a more consistent, stable set of ecosystem goods and services. It appears that the NES LME is mostly a resilient system, but consideration of these higher level metrics might better enable maintenance of such resilience and stability.

SUMMARY AND CONCLUSIONS

At the beginning of this document we asked why species interactions are important. In particular, we posed the question of what practical information LMR management applications can we gain from knowing about them? Returning to this question is critical if one is to usefully synthesize the broad array of MCE topics covered in this chapter. We propose to examine two example species to demonstrate the importance of ecological drivers as they can potentially impact the dynamics of LMR populations.

The first example is haddock. An astute reader will note that many examples throughout this document highlighted this taxon. Even before haddock eggs are spawned, they can face maternal influence mediated by oceanographic conditions and trophodynamic constraints from phytoplankton phenologies (Friedland et al. 2008). Once such eggs hatch into larvae, they face a plethora of factors that notably impact their survival (Walford 1938, Purcell et al. 1986, Werner et al. 1996, Garrison et al. 2000d, 2002,). Once such larvae settle to the ocean floor, they face a continued predation gauntlet from many piscivorous species (Lough et al. 1989, Smith and Link 2010; sensu Lindholm et al. 1999). They also need to obtain suitable juvenile habitat and suitable food for growth in the midst of intra- and interspecific competition (Lough et al. 1989, Frank et al. 2000; sensu Lindholm et al. 1999). As haddock mature and effectively grow out of the predation window they faced as juveniles, they are faced with additional challenges. They still face competition for benthic invertebrate food, and although specializing in echinoderm feeding, do need to minimize competition with ocean pout and American plaice, other echinoderm feeding specialists (Smith and Link 2010; Figures 17, 18, 20). Even competition with benthivorous skates is probably a consideration for this species (Figure 20; Smith and Link 2010). There is some evidence that haddock may be experiencing some form of competition, as growth and feeding have declined over the past several decades (Brodziak and Link 2008). Haddock can consume significant amounts of benthic invertebrates (Figures 2-6), which may be offset by commensalism among the benthic prey of haddock. In particular, it is thought that the invasive tunicate (Bullard et al. 2007, Lengyel et al. 2009) can provide localized areas of refugia for some haddock prey, ultimately altering observed haddock feeding (Smith 2009). Although primarily benthic in orientation, haddock can also influence the pelagia via consumption of herring eggs (Richardson et al. 2011) and presumably through similar egg predation can influence other species dynamics (D. Richardson, pers. comm.). The amount of energy flowing through haddock is relatively small compared to total throughputs for the system (Link et al. 2006, 2008), but in some cases haddock and associated groundfish can structure the food web towards a more "vertically-oriented" flow of energy (Link 1999; Table 4) compared to a more "horizontally-oriented" set of energy flows as seen in some regions. The utilization of recycled energy via detrital pathways is also high for haddock and similar benthivorous species (Link et al. 2006, 2008; Table 6), releasing system-level pressure on consumption of classical food chains of primary production. At times dominant numerically, haddock dynamics have not altered the diversity of the fish community too remarkably, with the exception of instances when there have been excessively strong year classes.

This relatively condensed story of haddock clearly demonstrates a plethora of issues that can influence haddock dynamics and that can be influenced by haddock. We hope the example illustrates that considering and managing this stock—and the stocks it interacts with—merits consideration of these facets of MCE, equally cognizant of the other two drivers in the triad (i.e., environmental, exploitation; Figure 1).

Another example is Atlantic herring. Before herring eggs hatch, they can be consumed by a suite of benthivorous fishes due to the demersal nature of herring spawning and egg deposition (e.g., Richardson et al. 2011; Smith and Link 2010). Once herring larvae hatch, they comprise food for a wide range of planktivorous fishes and other species (e.g., Purcell 1986, Fuiman and Gamble 1988). Herring larvae themselves are planktivorous (Blaxter 1965, Sherman and Honey 1971, Cohen and Lough 1983; Smith and Link 2010) and as such can compete with a plethora of other planktivores, including fishes, crustaceans, gelatinous zooplankton, and the larvae of other fishes. As herring mature, that degree of potential competition continues with all these other planktivorous taxa (Figures 9, 19). Additionally, herring can consume larvae of those species that upon achieving adulthood themselves eat herring, thus forming a case of the cultivation-depensation triangle (Walters and Kitchell 2001). Herring indeed serve as prey for a wide range of fish, bird, reptile and mammal predators in the NES LME (Overholtz and Link 2007, Overholtz et al. 2008, Link et al. 2009, Smith and Link 2010). In fact they and similar small pelagics compose the bulk of energy flowing through fishes in the NES LME food web (Link et al. 2008, 2009), representating arguably the key pathway of transferring lower trophic level production into a form suitable for consumption by upper trophic levels. Given their life history, herring are useful harbingers of environmental change, support a commercial fishery in their own right, and are one of the keystone species in the various regions of the NES LME (Link et al. 2008, 2009). Along with silver hake, this species has the highest linkage density in the NES LME food web (Link 1999, 2002b). The notable increases in herring abundance can affect measures of diversity for the NES LME. The functional redundancy of the small pelagic, planktivore guild has exhibited non-stationary patterns, implying greater dynamics and variance in at least this portion of the food web, with the attendant implications for system level resilience (Auster and Link 2009). In sum, knowledge of the dynamics of small pelagics in general and Atlantic herring in particular is critical for understanding the food web dynamics of the NES LME.

These two examples are illustrative of the potential applications of MCE-based knowledge for the NES LME. Amist this complexity of potential interactions how would one utilize or even prioritize this type of information to inform LMR management in the NES LME? That is, how does the example information presented here inform EBM? Recognizing that there are many useful solutions to the question posed, we posit six main suggestions to address this concern, emphasizing those steps that are feasible now under existing legislation and using extant data.

First, we assert that a system-level production cap needs to be and readily can be estimated for regions of the NES LME and that summed fisheries yields be routinely evaluated against it (NEFSC 2008, Link et al. 2008). This takes into account the plethora of issues associated with system level diversity, resilience, and production processes, cognizant of the limited amount of total production in any given area of the ocean (Link 2010a). Second and related, we propose similar estimations and evaluations of guild or functional group level quotas as is most germane to fisheries and market sectors (sensu Auster and Link 2009). This takes into account more specific flows in related, aggregate groups and capitalizes on the stability of functional redundancies often associated with them.

Third we propose that an evaluation of tradeoffs across biological groups, but particularly regarding threatened, endangered, or similarly protected species, be formally examined. This will account for the energetic demands of such groups with special status, aiming to mitigate some potential for competition (Link et al. 2008).

Fourth, for those stocks that are potentially forage fish and invertebrates, we strongly recommend assessing their stock status with some form of predation measures included. This accounts for the consumptive-supporting role these species have as keystones of energy flow in the system (Overholtz and Link 2007, Overholtz et al. 2008).

Fifth, for those stocks that are experiencing declines in growth or shifts in key population vital rates, as evinced via a suite of standard length and growth measures, we propose more formal evaluations of competitive interactions. This will address the need to accommodate, account for, and perhaps mitigate any competitive effects.

Finally, where there are commensal or mutualistic interactions noted, and where such positive interactions can be associated with particular places, we propose setting aside those areas for some form of closure or seasonal protection. This will ensure that any positive benefit of symbiosis has the chance to accrue to the populations and is not removed prior to its ability to result in a positive impact.

Certainly there are many more features we could have noted and certainly there are many other facets informed by MCE. Yet the few simple suggestions we posit here were provided as relatively straightforward ways in which MCE can inform LMR management (Mangel and Levin 2005) and help move towards the fuller implementation of EBM (Jennings and Kaiser 1998, NMFS 1999, Constable et al. 2000, Constable 2001, Link 2002a, 2010a ,Garcia et al. 2003, Pikitch et al. 2004, Leslie and McLeod 2007). We trust that the examples herein and the background provided to support each of the main facets of MCE help to demonstrate the utility, value and need for a broader consideration of these factors that influence LMR production. We trust that the proposed application of such MCE will be beneficial for the wise utilization and enhanced production of such resources.

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Table 1. Table of deleterious (-), no (0), or positive (+) influences of one population on another to note the broad categories of ecological interactions. Amensalism and neutralism are rare and thus are not treated in the text. Predation could also be parasitism or herbivory.

Effects of Species A on B / and B on A	-	0	+
-	-/- (Competition)	0/- (Amensalism)	-/+ (Predation)
0		0/0 (Neutralism)	0/+ (Commensalism)
+			+/+ (Mutualism)

Table 2. Types of methods to calculate consumption, noting the parameters and data required for each of the major approaches used to estimate fish consumption.

Approach	*Data Required*	*Parameters Required*	*Comments*
% Body Weight	body weight (*W*), stomach weight (*S*)		Mainly a diagnostic
Daily ration	stomach weight (S), number of hours to evacuate a stomach (n)		Mainly a diagnostic
Caudal Fin Aspect	height (*h*), surface area (*s*)		
C/B or Q/B	consumption (C), biomass (B)		Usually derived, not estimated directly
Gastric Evacuation	stomach contents (*S*), temperature (*T*)	α, β, estimated parameters or from Literature	
Functional Response	predator (*P*), prey (*N*), foraging times (*F*), prey k	search times (f), growth rates (r) of prey; capture rate (C), handling times (h) of prey k	
Bioenergetics	basal metabolic rates (M), growth (G), waste (W), production (P), reproduction (Repro), respiration (Resp), metabolic activity (MA), feces (F), urea (U)	specific dynamic action (SDA)	

Table 3. Common Food web metrics.

Metric	Description
S	No. of species
L	No. of trophic links
P	No. of predator species
N	No. of prey species
T	No. of top predators
I	No. of intermediate species
B	No. of basal species
$\%T = 100\ (T/S)$	% top predators
$\%I = 100\ [1-(B+T)/S]$	% intermediate species
$\%B = 100\ (B/S)$	% basal species
$N{:}P = N/P$	Ratio of prey to predators
L_{TI}	No. of links between top and intermediate species
L_{TB}	No. of links between top and basal species
L_{II}	No. of links between intermediate species
L_{IB}	No. of links between intermediate and basal species
$\%T\text{-}I = 100\ (L_{TI}/L)$	fraction of top to intermediate species links
$\%T\text{-}B = 100\ (L_{TB}/L)$	fraction of top to basal species links
$\%I\text{-}I = 100\ (L_{II}/L)$	fraction of intermediate to intermediate species links
$\%I\text{-}B = 100\ (L_{IB}/L)$	fraction of intermediate to basal species links
$C = \frac{L}{S\ (S-1)/2}$	Connectance
$C_{dir} = L/S^2$	Directed connectance
$L_D = L/S$	Linkage density
n_{mfc}	Number of maximal food chains
MED_{cl}	Median food chain length
SD_{cl}	Standard deviation of food chain length
MAX_{cl}	Maximum food chain length
$G = L/(I+B)$	Generality
$V = L/(T+I)$	Vulnerability
$S \times C$	Lyapunov stability proxy

Table 4. Major food web metrics from catalogues and more extensive webs, including the northeast shelf large marine ecosystem (NES LME). S=number of species, C=connectivity, SxC=Lyapunov stability proxy, Predator/Prey=the ratio of predators to prey, %Cycles=species that mutually prey on each other, % Cann.=cannibalistic species, L=number of links. Adapted from Link (2002).

Source	**S**	**C**	**SxC**	**Predator/Prey**	**% Cycles**	**% Cann.**	**L**	**Type of Ecosystem**
Catalogs (mean values)								
Cohen 1989, Cohen et al. 1990 (ECOWEB; extends Briand and Cohen 1987)	mean=17 range 3-48	27.3	4.6	1.18	<1%	<1%	31	Mixed
Schoenly et al. 1991	mean=24 range 3-90	19.2	4.6	0.64	<1%	<1%	53	Mixed, Mainly Terrestrial
Havens 1992	mean=38 range 10-74	21.1	8.0	-	-	-	148	Aquatic, Mainly lakes and ponds
Comprehensive Webs								
Sprules and Bowerman 1988	12	54.4	6.5	-	17%	25%	36	Aquatic- lake
Warren 1989	22	47.6	10.4	0.66	-	-	110	Aquatic- pond
Polis1991	30	66.4	9.0	0.90	53%	74%	409	Terrestrial- desert
Tavares-Cromar and Williams 1996	34	19.4	6.5	-	-	-	109	Aquatic- stream
Closs and Lake 1994	40	10.2	4.1	-	-	-	80	Aquatic- stream
Goldwasser and Roughgarden 1993	44	23.0	10.1	1.03	-	-	218	Terrestrial- tropical rain forest
Winemiller 1990	75	18.5	13.9	-	-	-	514	Aquatic- swamps, streams
Martinez et al. 1999	77	4.3	3.3	-	-	-	126	Terrestrial- grasslands
Hall and Raffaelli 1991	92	9.7	9.0	0.72	-	-	409	Estuary
Reagan et al. 1996	136	14.4	19.6	-	35%	in Cycles	1322	Terrestrial- tropical rain forest
Martinez 1991	182	14.4	26.2	1.14	-	-	2366	Aquatic- lakes
Link 2002	81	48.2	39.1	0.95	5%	31%	1562	Marine- Continental Shelf

Table 5. Relative contribution (%) of major compartments to Total Biomass and Total Production, and ratios between compartments for Southern New England. B = benthos, P = plankton, N = nekton, M = mammals. Adapted from Link and Pranovi 2009.

	Biomass	Production
Vertebrates	0.19	0.01
Invertebrates	0.81	0.99
invert/vert	4.22	84.25
P	0.35	0.97
B	0.48	0.03
N	0.16	0.002
M	0.001	1.91E-06
B/P	1.37	0.03
B/N	2.94	14.38
B/M	352.52	15220.31
N/P	0.47	0.002

Table 6. Summary statistics after mass balancing and network flow indices for Southern New England. Adapted from Pranovi and Link 2009 and Link et al. 2008.

Parameter	Units	SNE
Sum of all consumption	t/km²/year	8528.93
Sum of all exports	t/km²/year	812.82
Sum of all respiratory flows	t/km²/year	4038.61
Sum of all flows into detritus	t/km²/year	4782.62
Total system throughput	t/km²/year	18163
Sum of all production	t/km²/year	7132
Gross efficiency (catch/net p.p.)		0.0008
Calculated total net primary production (net p.p.)	t/km²/year	4850.902
Total primary production/total respiration		1.201
Net system production	t/km²/year	812.29
Total primary production/total biomass		27.24
Total biomass/total throughput		0.01
Total biomass (excluding detritus)	t/km²	178.10
Connectance Index		0.334
System Omnivory Index		0.303
Throughput cycled (excluding detritus)	t/km²/year	498.72
Predatory cycling index	% of throughput w/o detritus	5.80
Throughput cycled (including detritus)	t/km²/year	2577.27
Finn's cycling index	% of total throughput	14.19
Finn's mean path length		3.744
Finn's straight-through path length	without detritus	1.984
Finn's straight-through path length	with detritus	3.212
Ascendancy/Capacity (A/C)	(%)	18.9
Overhead/Capacity (O/C)	(%)	87.1

Table 7. Lindeman pyramid of flows in Southern New England (SNE); values are expressed as percentage of Total System Throughput (TST). Roman numerals represent trophic levels. Adapted from Pranovi and Link 2009 and Link et al. 2008.

	SNE
VI	0.014
V	0.129
IV	1.0
III	7
II	37
I	55

Table 8. Ratios between Total Catch and Production (P) or Consumption (Q) for the major targeted groups in Southern New England. B1 = commercial benthic species, N1 = pelagic commercial species; N2 = demersal commercial species. Adapted from Pranovi and Link 2009.

	Total Catch/P	Total Catch/Q
B1	0.03	0.01
N1	0.06	0.01
N2	0.14	0.07

Table 9. Indices of species biodiversity. Adapted from Jennings et al. (2001).

Index	**Formula**	**Measurement**
Species richness (S)	S	Number of species (S)
Margalef (D)	$(S-1)/\ln N$	Number of species (S) for given number of individuals (N)
Menhinick's (D)	$S/\sqrt{N}$	Number of species (S) for given number of individuals (N)
Shannon-Wiener (H')	$-\sum p_i \ln p_i$	Richness and equitability; p_i = proportion of species i abundance (n_i/N)
Evenness	H'/H_{max}, $H'/\ln S$, or $(\exp H')/S$	Evenness for H'
Brillouin (HB)	$(\ln N! - \sum \ln n_i)/N$	Richness and equitability; used to describe a known collection
Pielou Evenness (for HB)	HB/HB_{max}	Evenness for HB
Simpson's (D)	$\sum(n_i(n_I - 1)/N(N-1))$	Dominance; often expressed as 1-D or 1/D as D increases with decreasing diversity
Hill N_0	S	Number of species (S)
Hill N_1	$\exp H'$	Number of "abundant" species
Hill N_2	$1/D$	Number of dominant species; D is Simpson's Index
Taxanomic diversity (Δ)	$[\sum\sum_{i<j} \omega_{ij} x_i x_j]/[n(n-1)/2]$	Species diversity with taxonomic relatedness; x_i is the abundance of the ith species (s) observed, n is the total number of individuals in a sample ($\sum_i x_i$), and ω_{ij} weights the path length between variable definitions of species i and j linked in the taxonomy
Taxanomic distinctness (Δ^*)	$[\sum\sum_{i<j} \omega_{ij} x_i x_j]/[\sum\sum_{i<j} x_i x_j]$	Taxonmic distinctness without species diversity; see Δ for variable definitions
Taxanomic distinctness (Δ^+)	$[\sum\sum_{i<j} \omega_{ij}]/[s(s-1)/2]$	Taxonomic distinctness for presence/absence data; see Δ for variable definitions

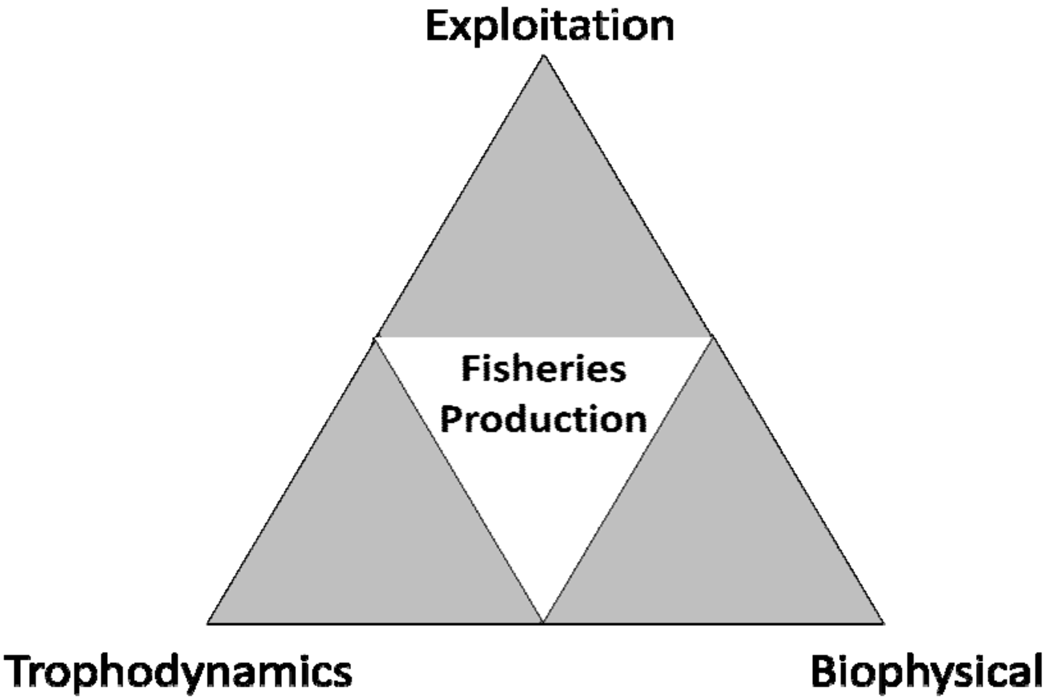


Figure 1. The triad of drivers influencing living marine resources (LMRs). Adapted from Link et al. 2011a.

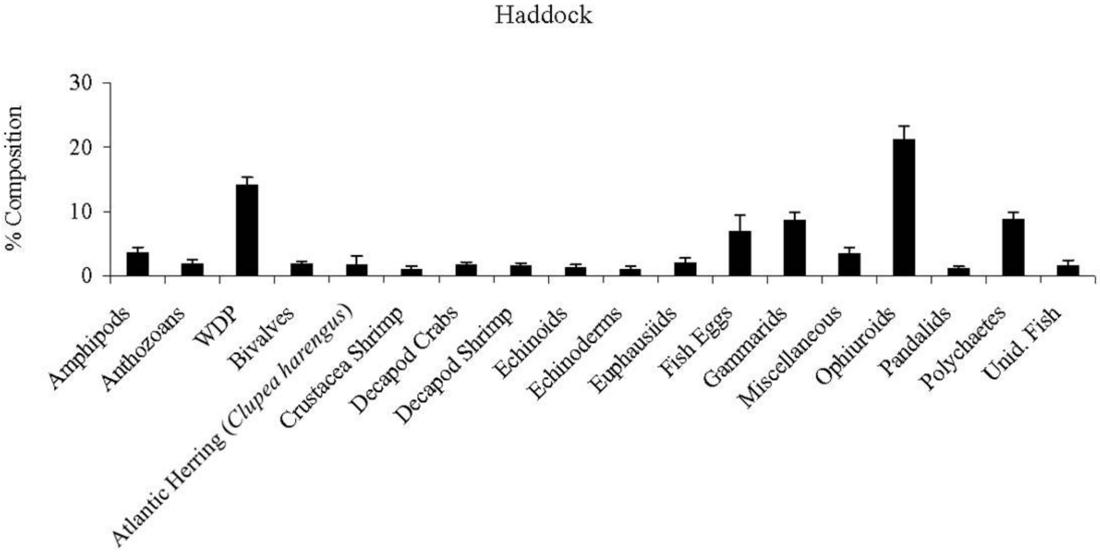


Figure 2. Diet composition of Haddock (*Melanogrammus aeglefinus*). WDP = well-digested prey; Unid. Fish = unidentified fish. Adapted from Smith and Link 2010.

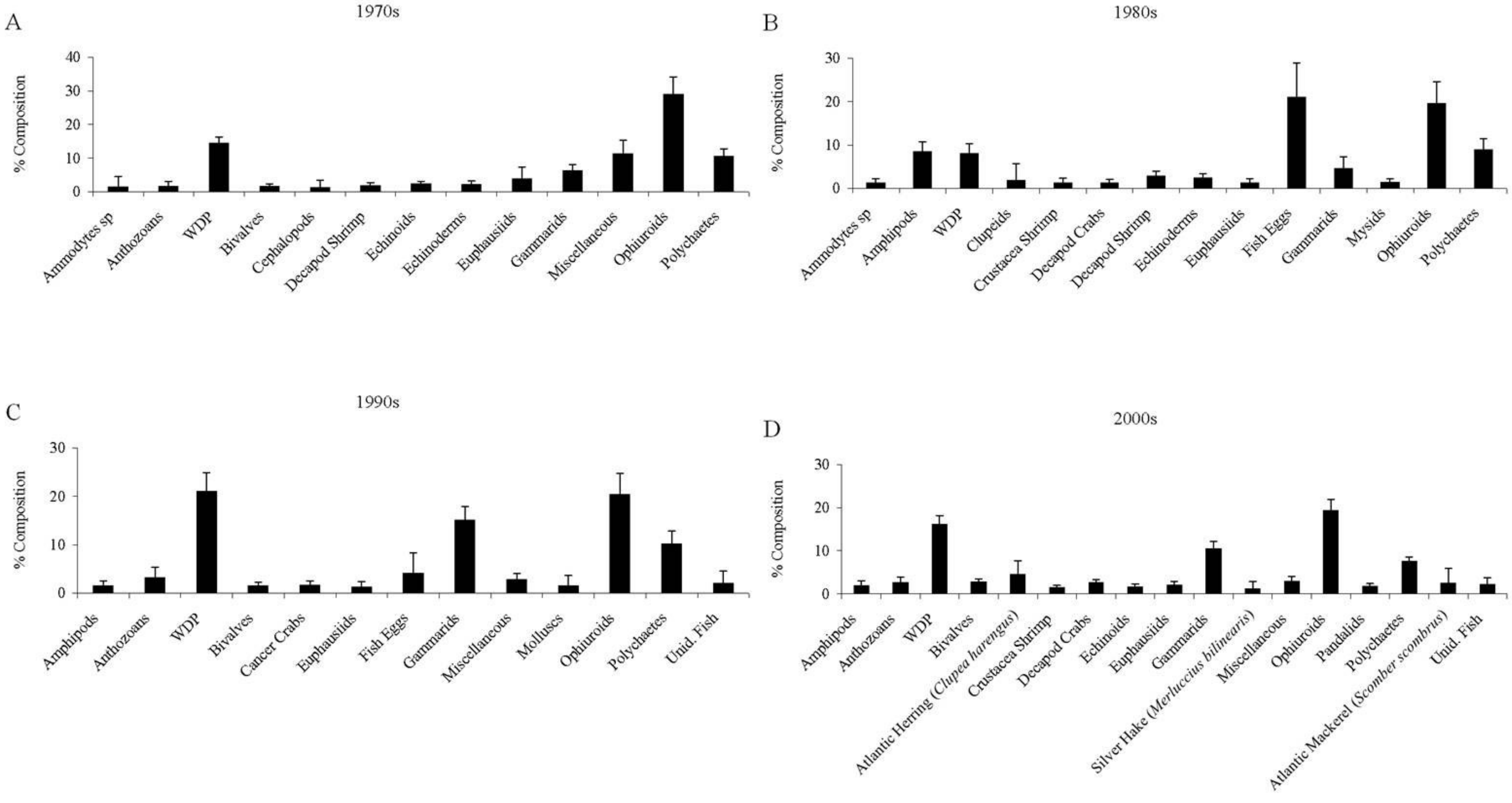


Figure 3. Diet composition of Haddock (*Melanogrammus aeglefinus*) over time. WDP = well-digested prey; Unid. Fish = unidentified fish. A-D, different decades. Adapted from Smith and Link 2010.

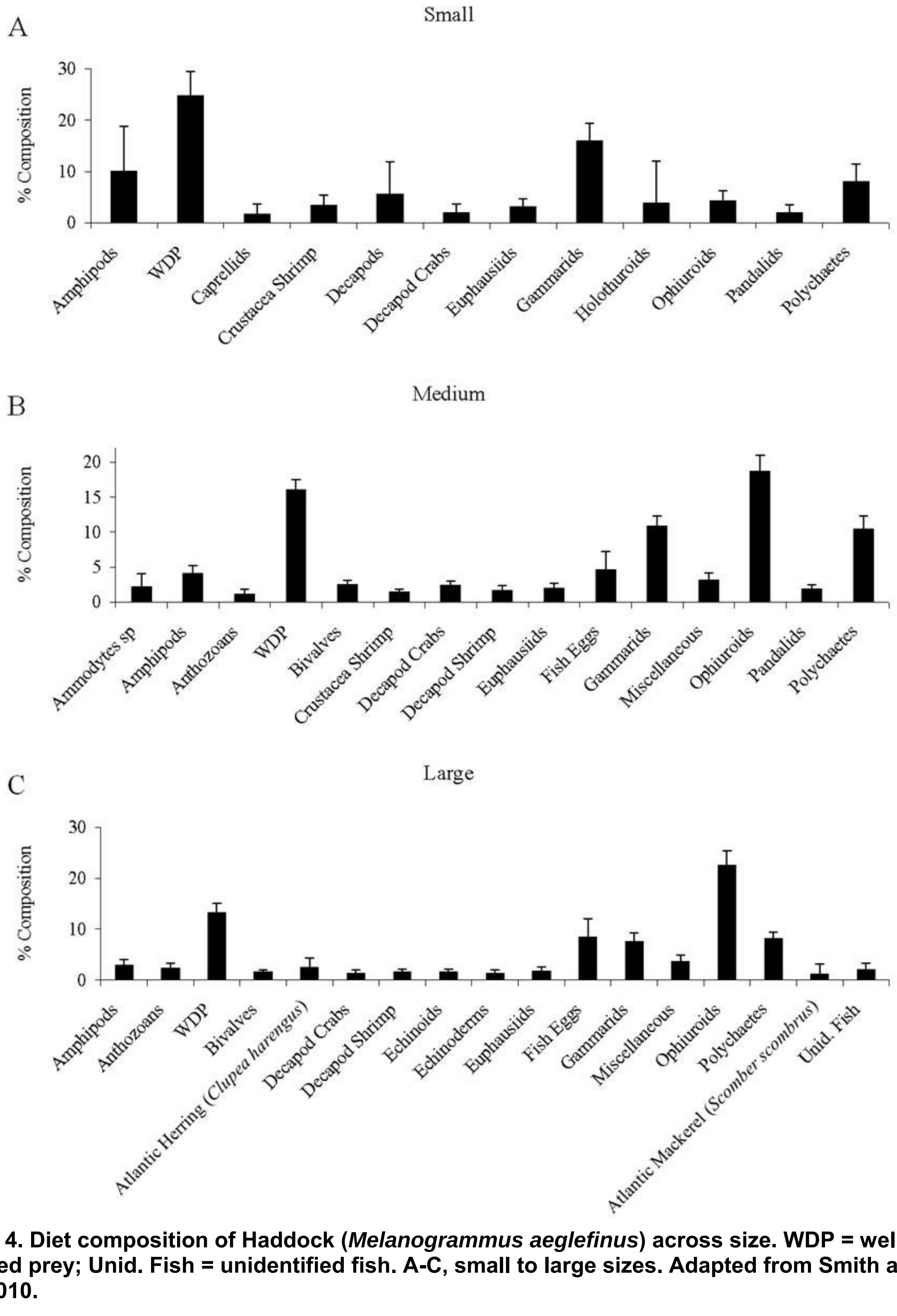
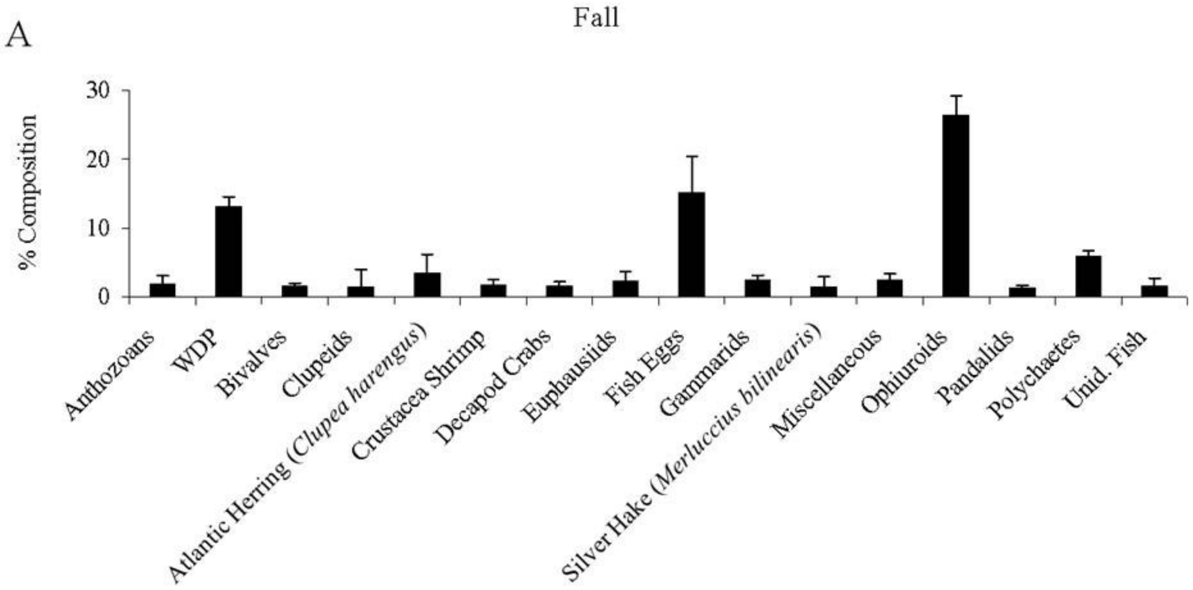
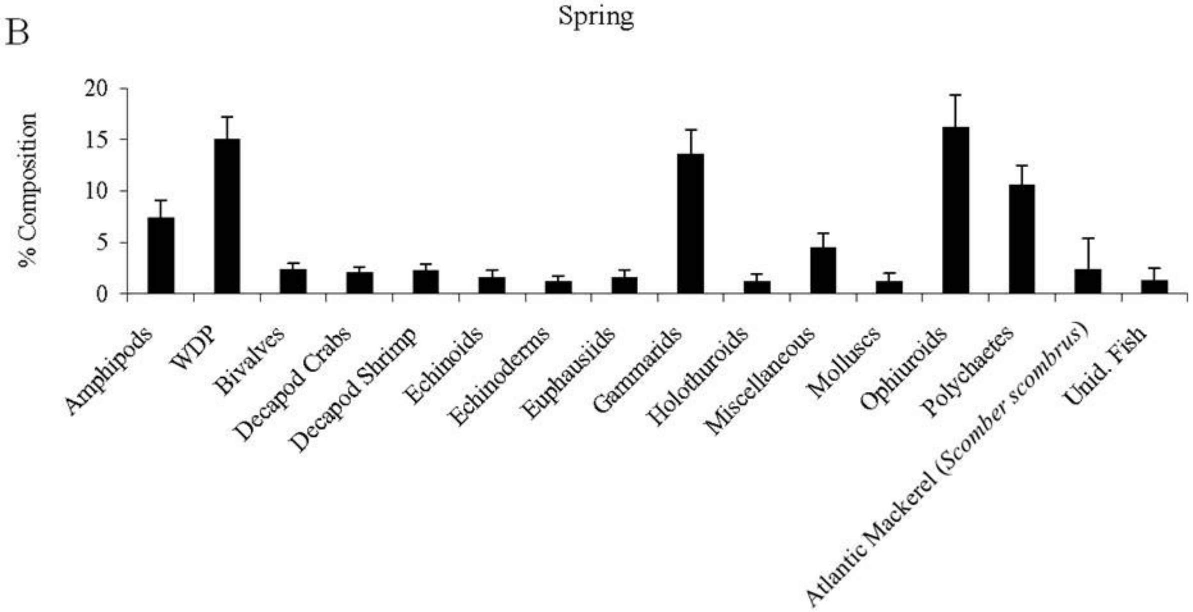


Figure 4. Diet composition of Haddock (*Melanogrammus aeglefinus*) across size. WDP = well-digested prey; Unid. Fish = unidentified fish. A-C, small to large sizes. Adapted from Smith and Link 2010.


A

Fall


B

Spring

Figure 5. Diet composition of Haddock (*Melanogrammus aeglefinus*) across seasons. WDP = well-digested prey; Unid. Fish = unidentified fish. A. Fall, B. Spring. Adapted from Smith and Link 2010.

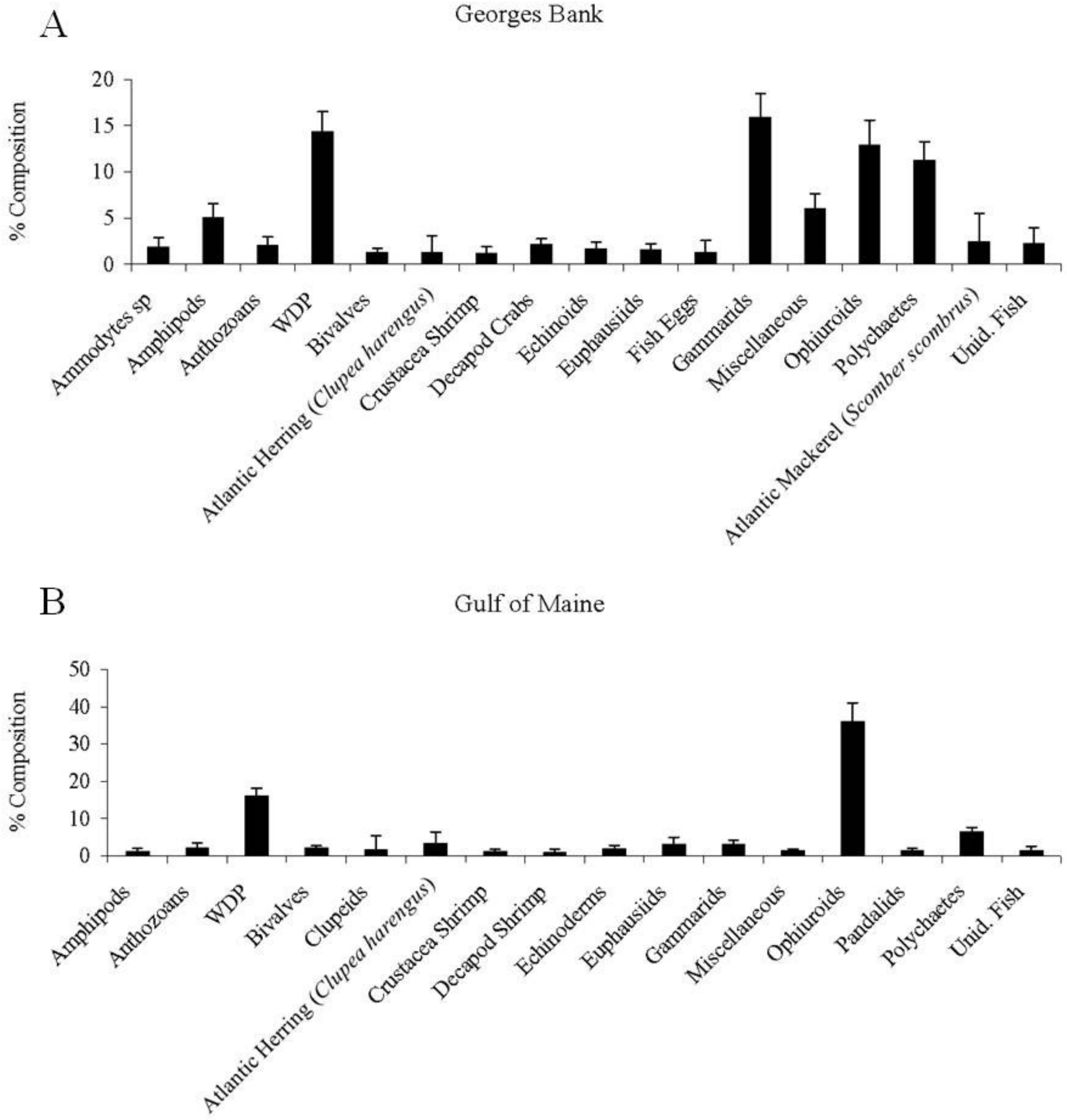


Figure 6. Diet composition of Haddock (*Melanogrammus aeglefinus*) across geographic regions. WDP = well-digested prey; Unid. Fish = unidentified fish. A. Georges Bank, B. Gulf of Maine. Adapted from Smith and Link 2010.

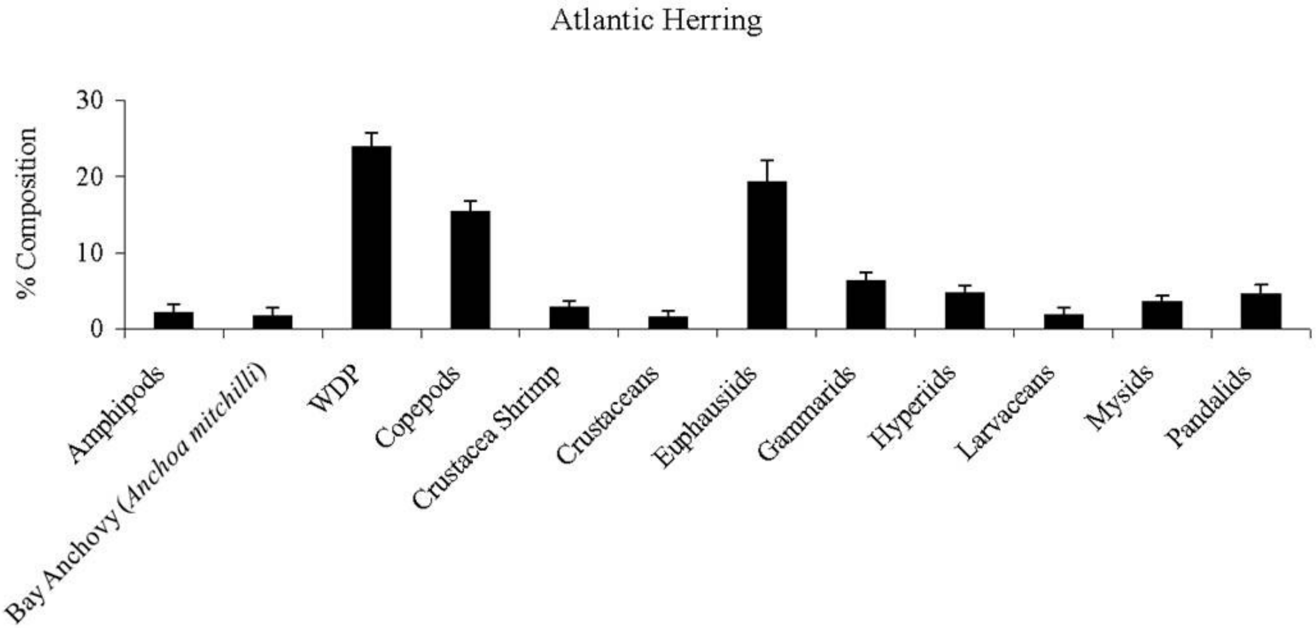


Figure 7. Diet composition of Atlantic herring (*Clupea harengus*). WDP = well-digested prey. Adapted from Smith and Link 2010.

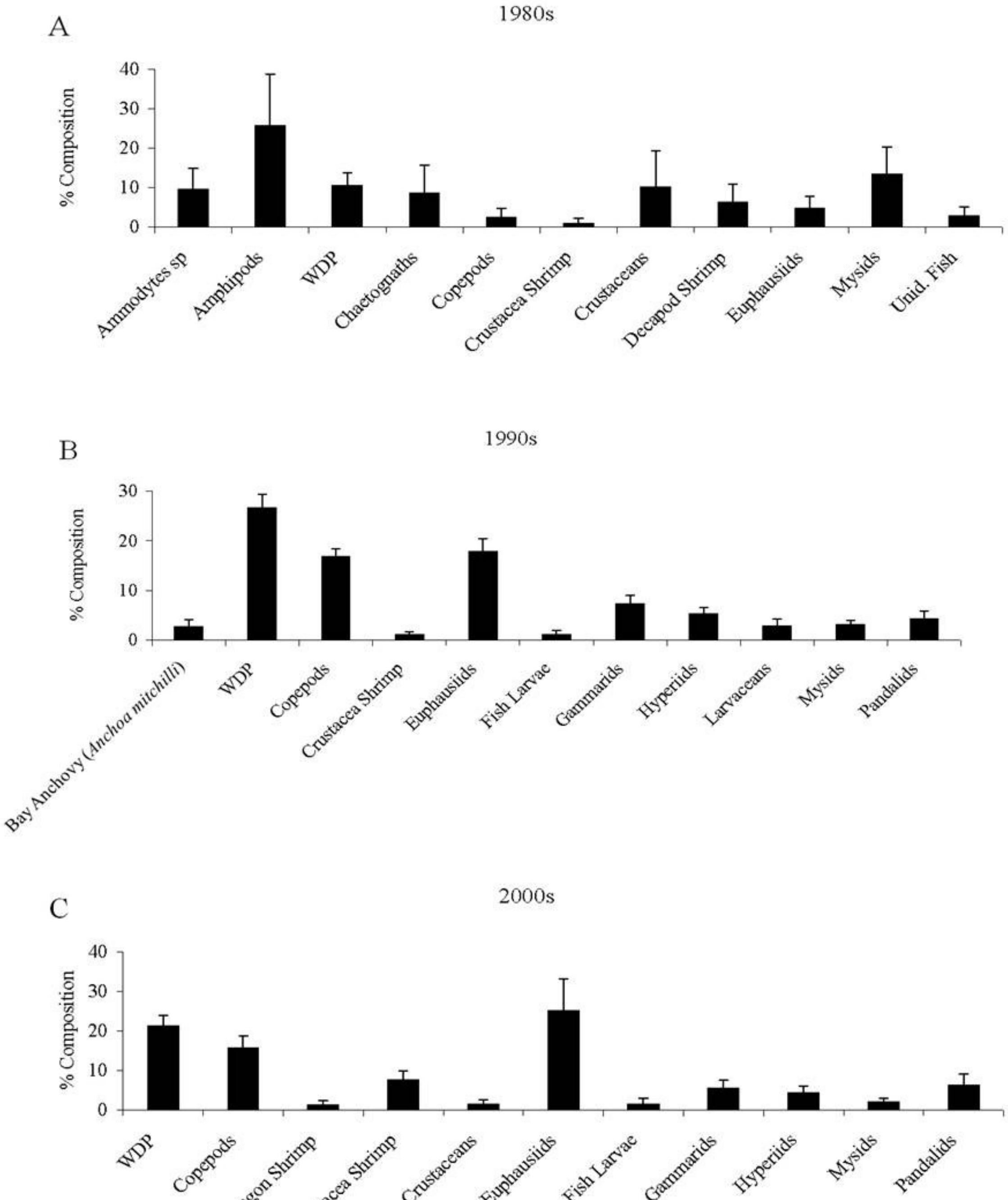


Figure 8. Diet composition of Atlantic herring (*Clupea harengus*) over time. WDP = well-digested prey. A-C, different decades. Adapted from Smith and Link 2010.

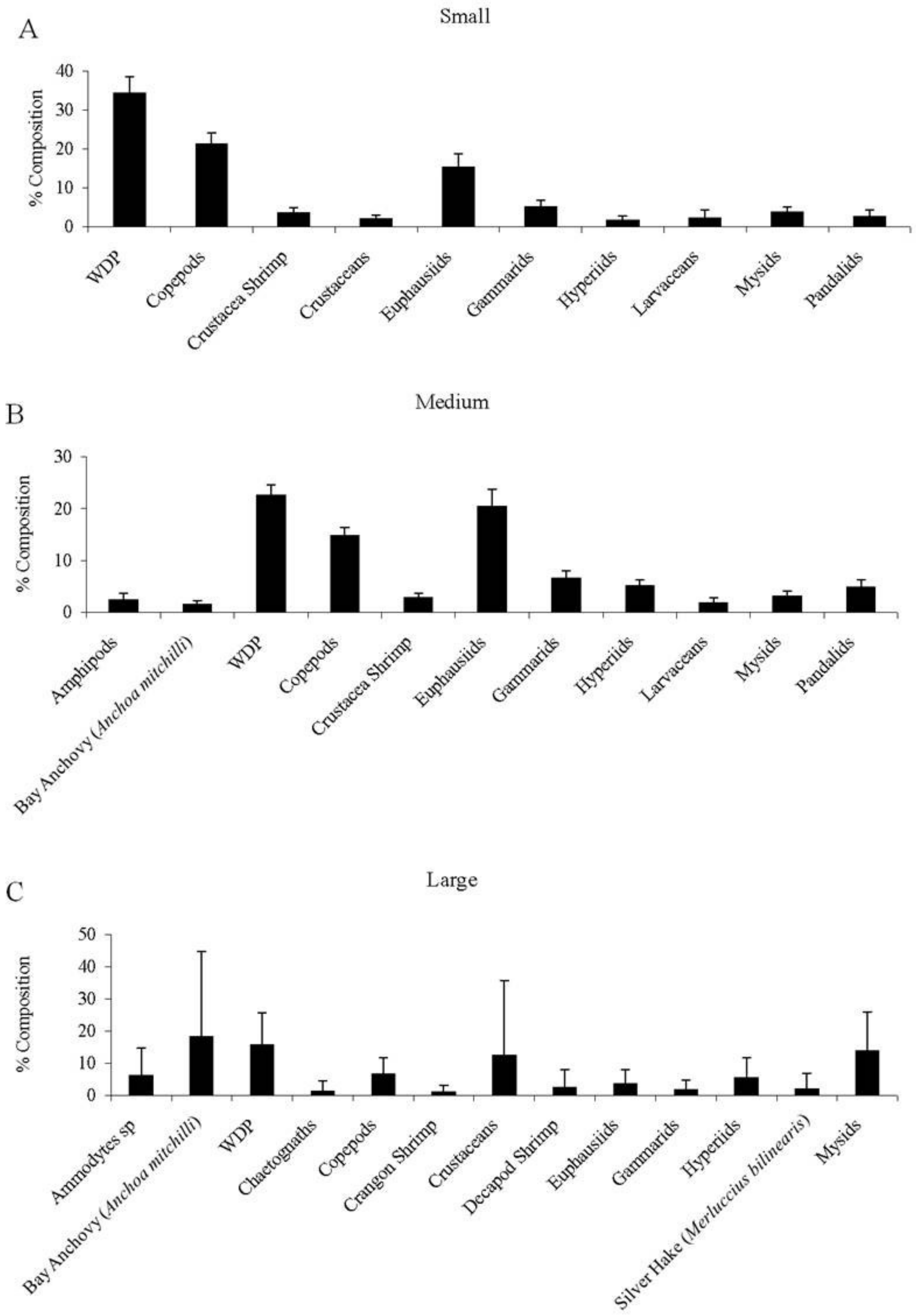


Figure 9. Diet composition of Atlantic herring (*Clupea harengus*) across size. WDP = well-digested prey. A-C, small to large sizes. Adapted from Smith and Link 2010.

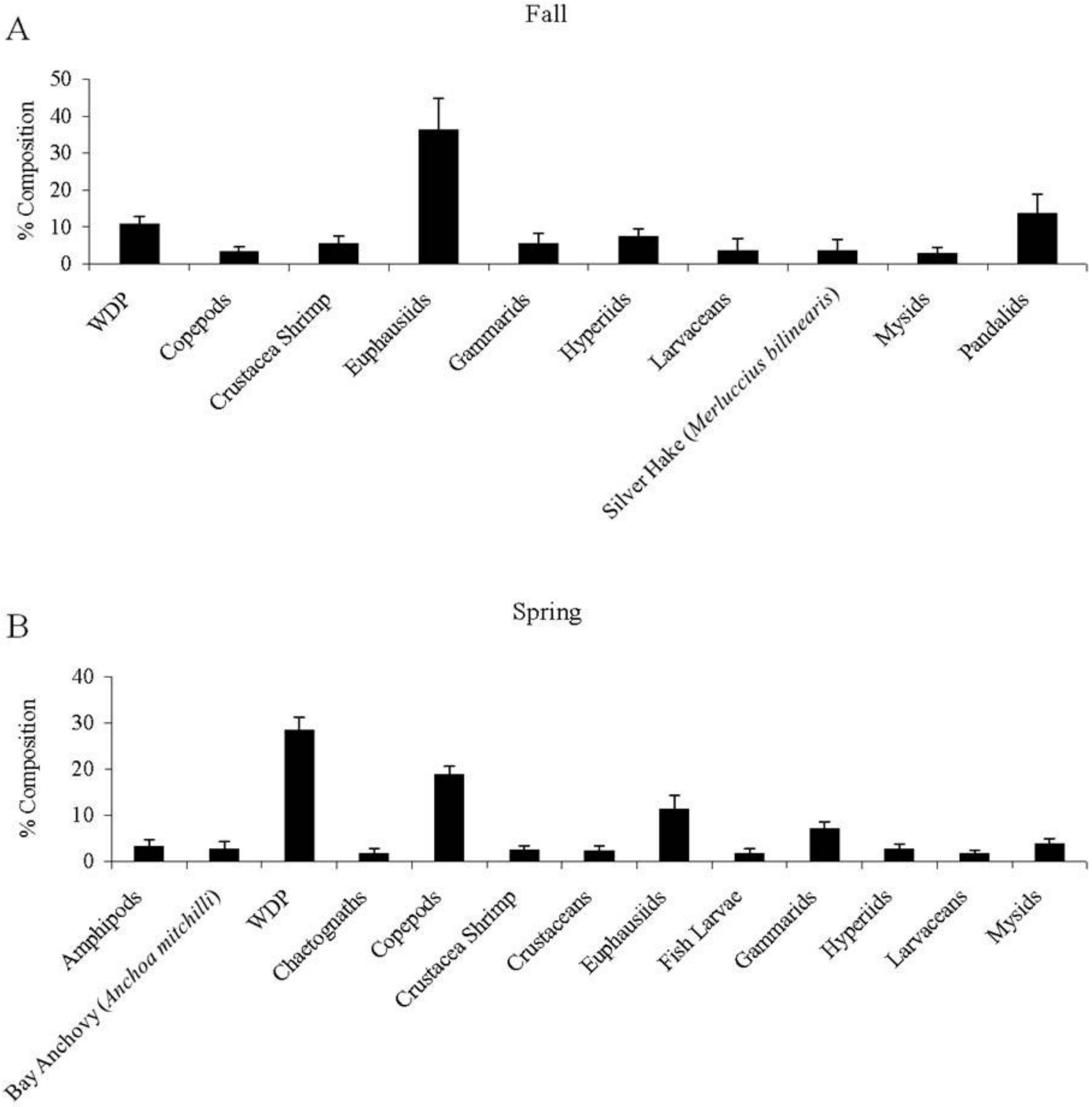


Figure 10. Diet composition of Atlantic herring (*Clupea harengus*) across seasons. WDP = well-digested prey. A. Fall, B. Spring. Adapted from Smith and Link 2010.

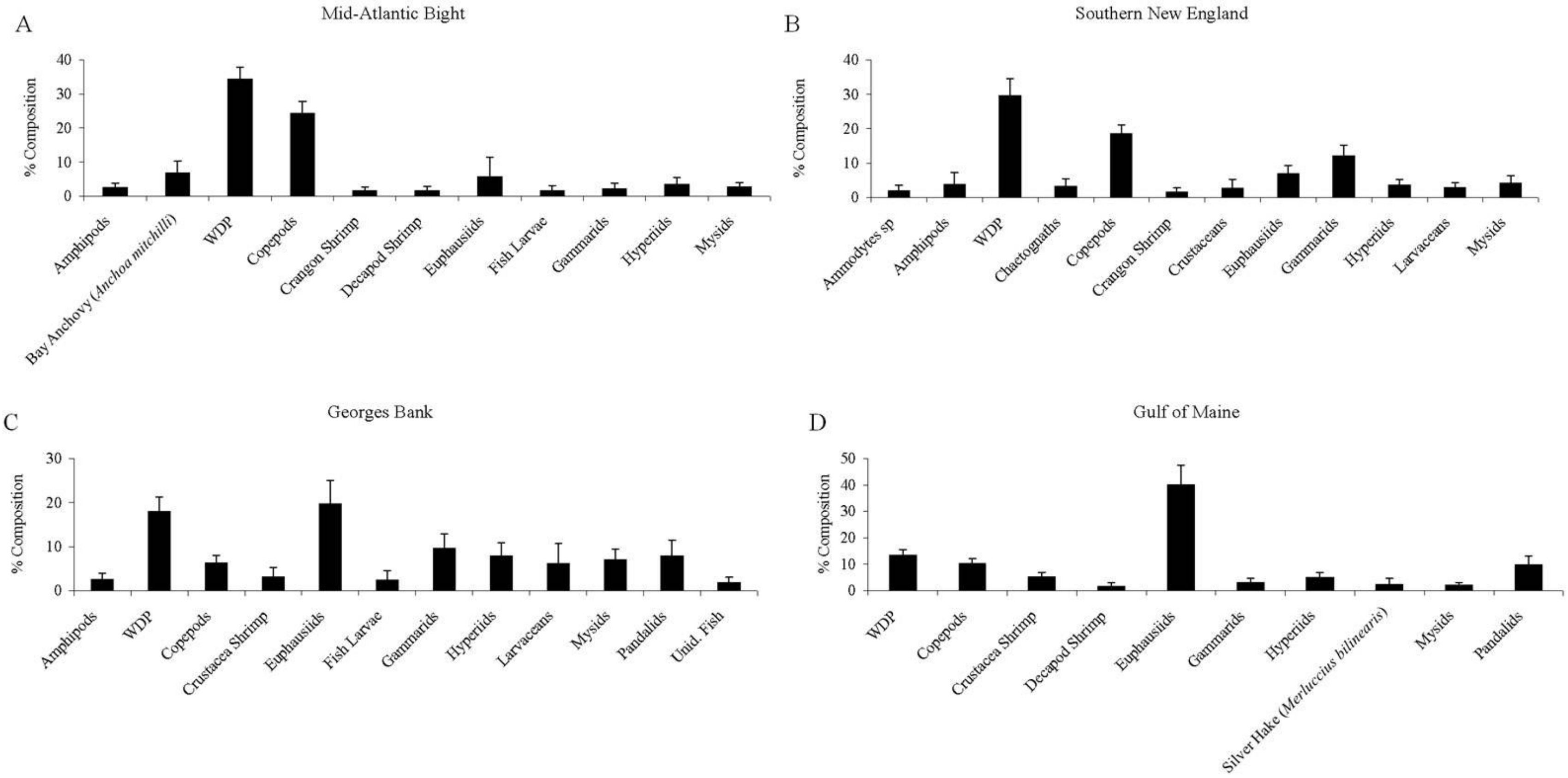


Figure 11. Diet composition of Atlantic herring (*Clupea harengus*) across geographic regions. WDP = well-digested prey. A-D, different geographic regions. Adapted from Smith and Link 2010.

Figure 12

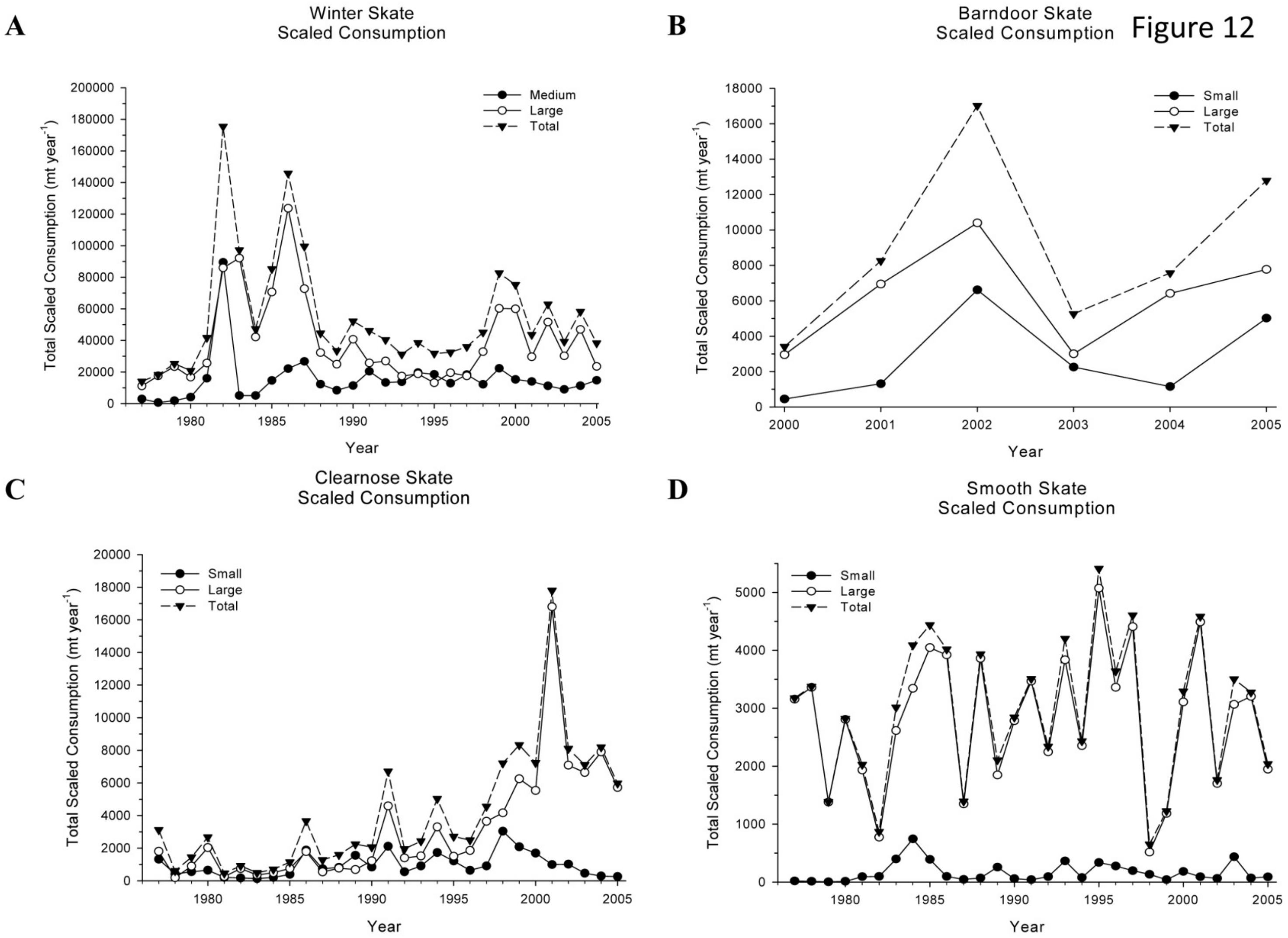


Figure 12. Example of consumption by a suite of skate species. A. Winter skate (*Leucoraja ocellata*). B. Barndoor skate (*Dipturus laevis*). C. Clearnose skate (*Raja eglanteria*). D. Smooth skate (*Malacoraja senta*). Adapted from Link and Sosebee 2008.

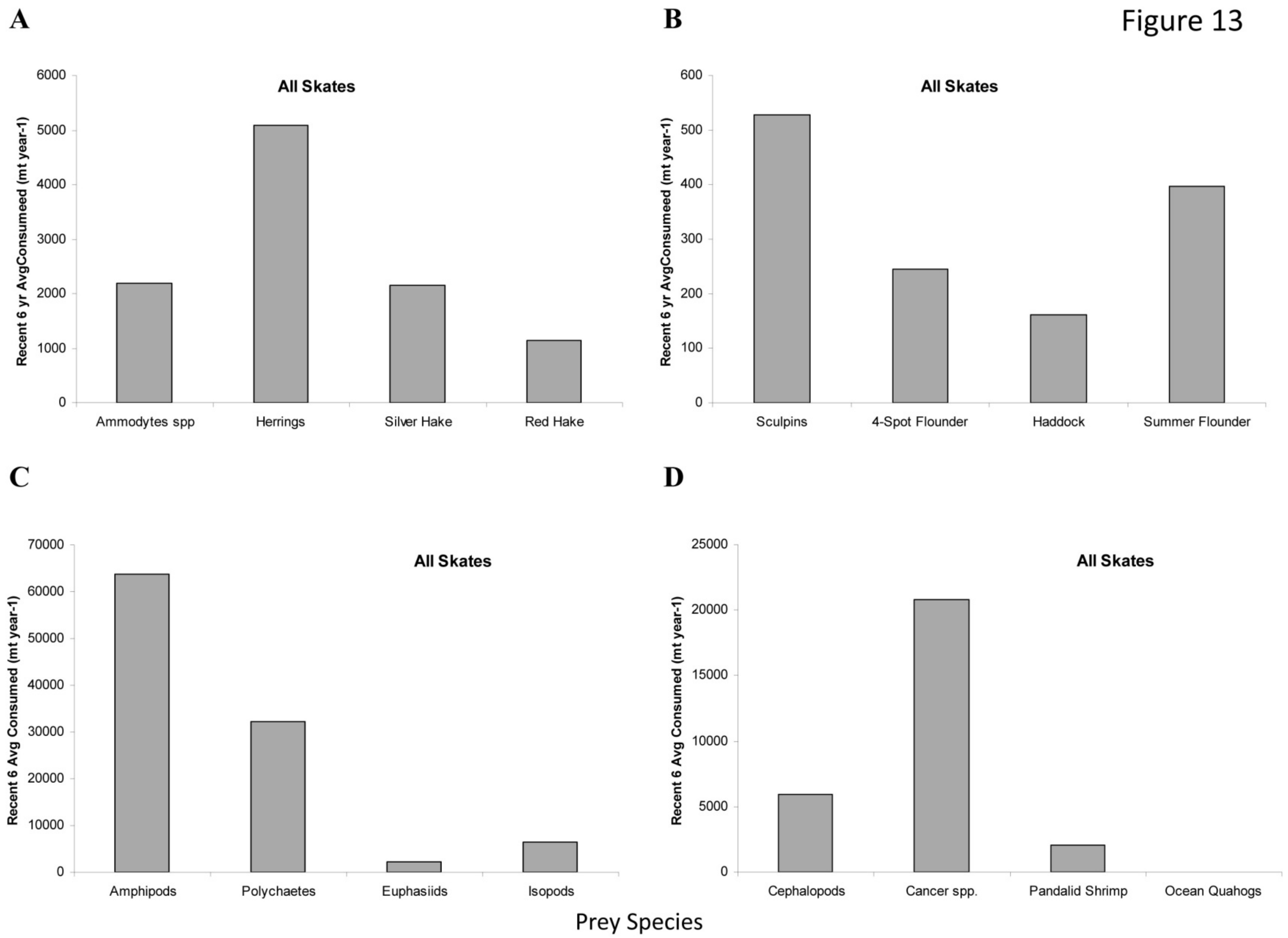


Figure 13. Average amount of particular prey items eaten by all seven main skate species during 2000-2005. A. Forage fishes. B. Other, demersal fishes. C. Small benthic invertebrates, crustaceans and polychaetes. D. Other, commercially important invertebrates. Adapted from Link and Sosebee 2008.

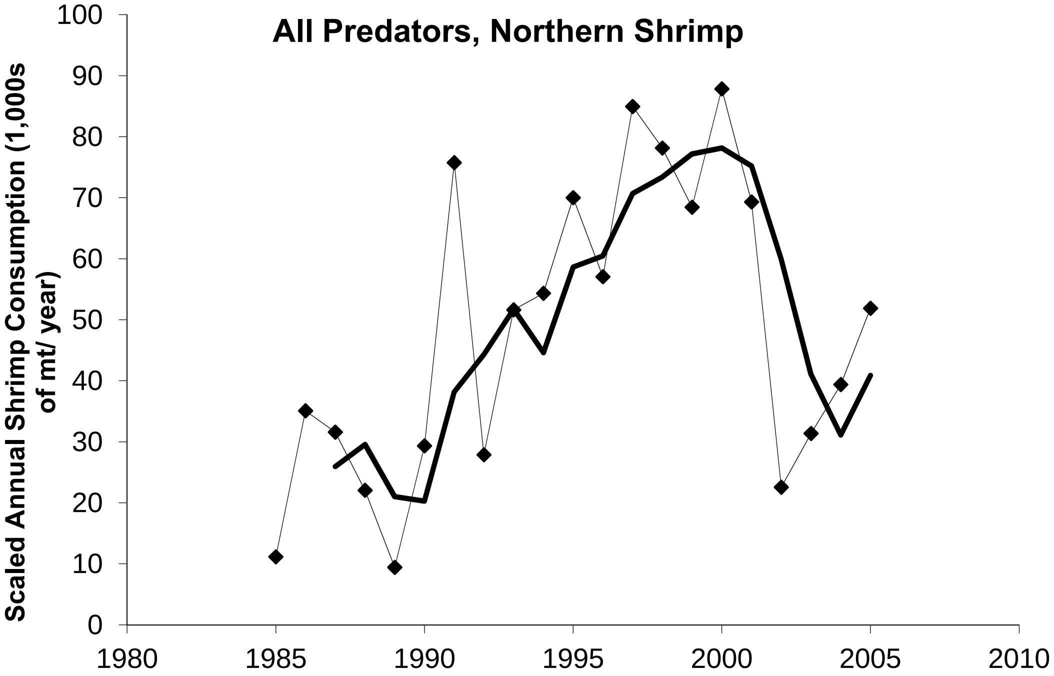


Figure 14. Total amount of pandalid shrimp consumed by a suite of 10 predators. Darker line is the 3 year moving average. Adapted from Link and Idoine 2009.

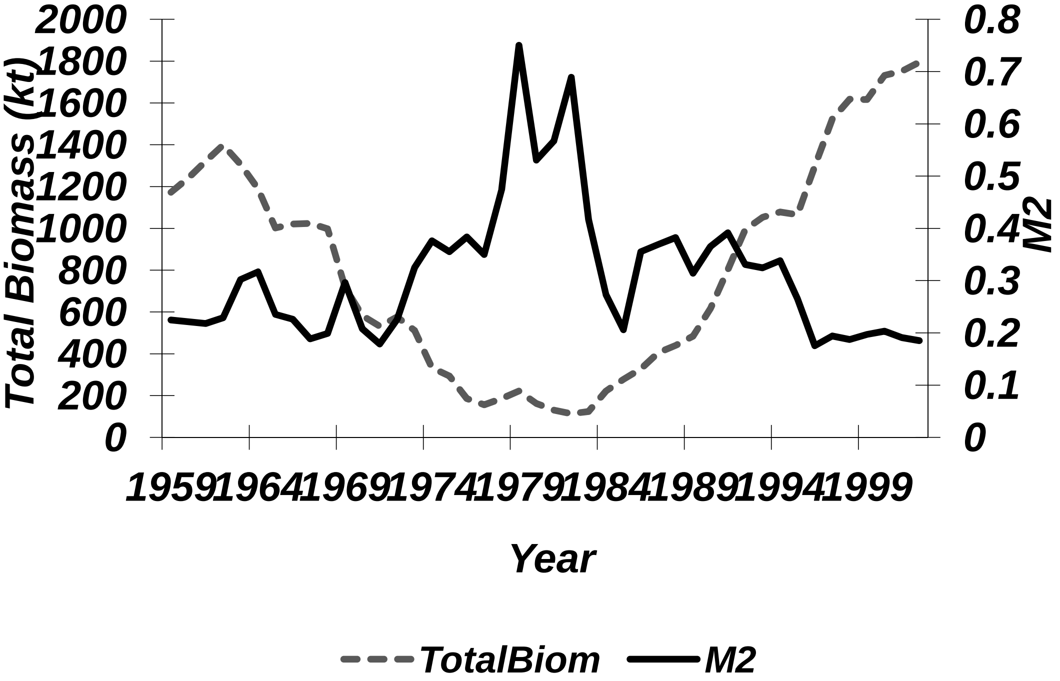


Figure 15. Predation mortality (M2) and biomass for Atlantic herring (*Clupea harengus*). Adapted from Overholtz et al. 2008.

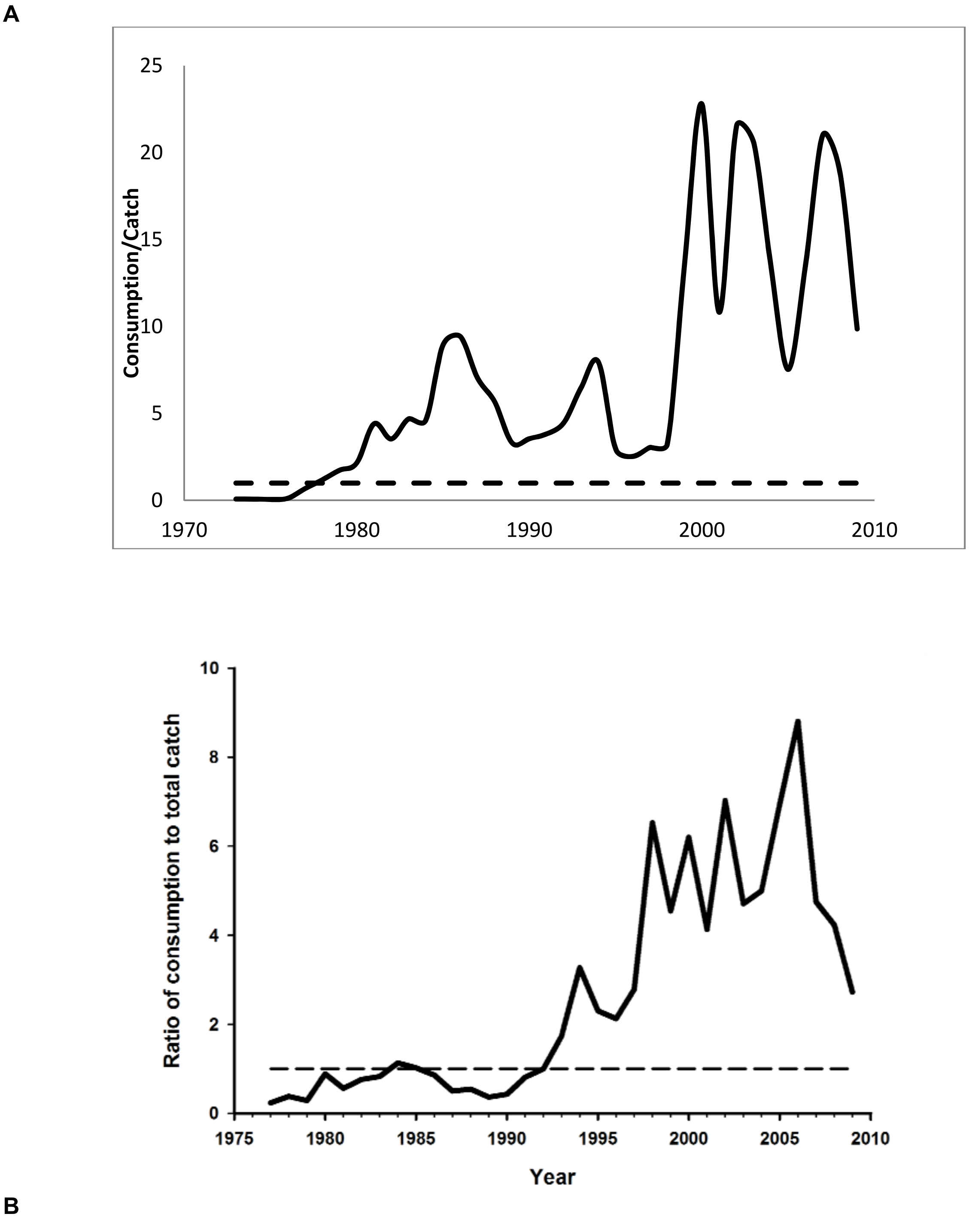
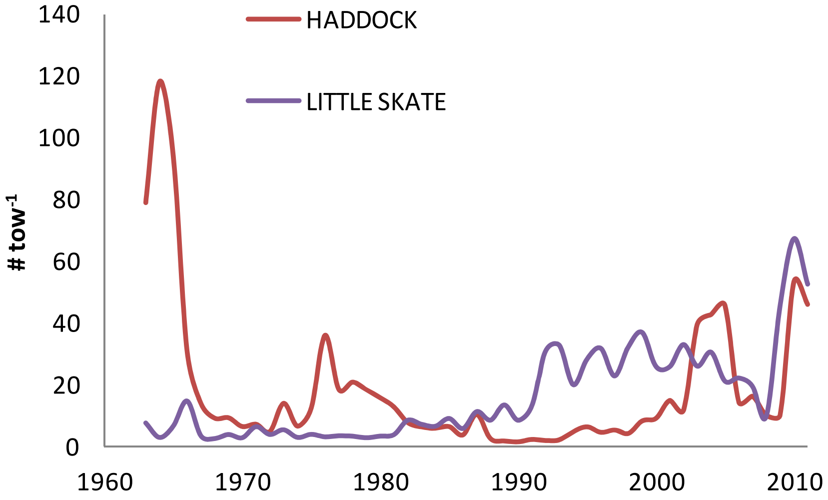


Figure 16. Consumption to landings ratios A. Silver hake (*Merluccius bilinearis*). B. Red hake (*Urophycis chuss*). Dashed line represents the 1:1 ratio. Adapted from NEFSC (2011).

A



B

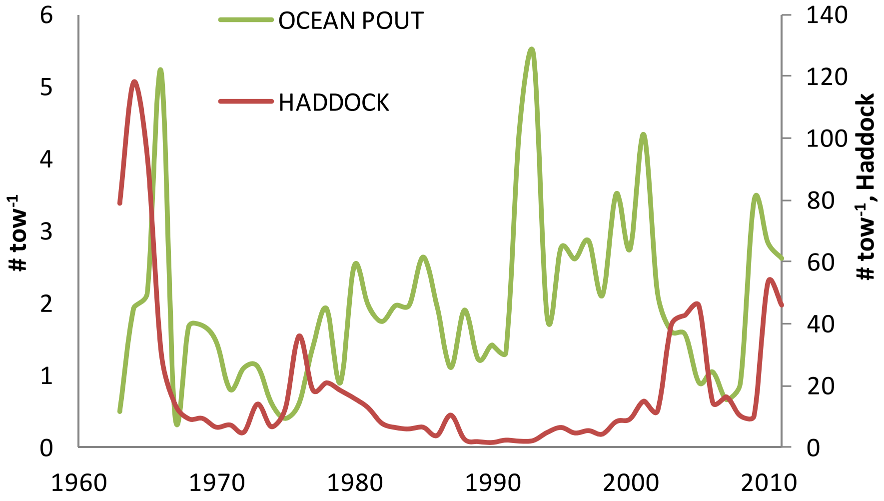


Figure 17. Population trajectories, from trawl survey indices of example species suspected of being competitors in the NES LME, particularly as benthivorous echinoderm feeding specialists. A. Haddock (*Melanogrammus aeglefinus*) and little skate (*Leucoraja erinacea)*. B. Haddock and ocean pout. Adapted from Link and Auster (in press).

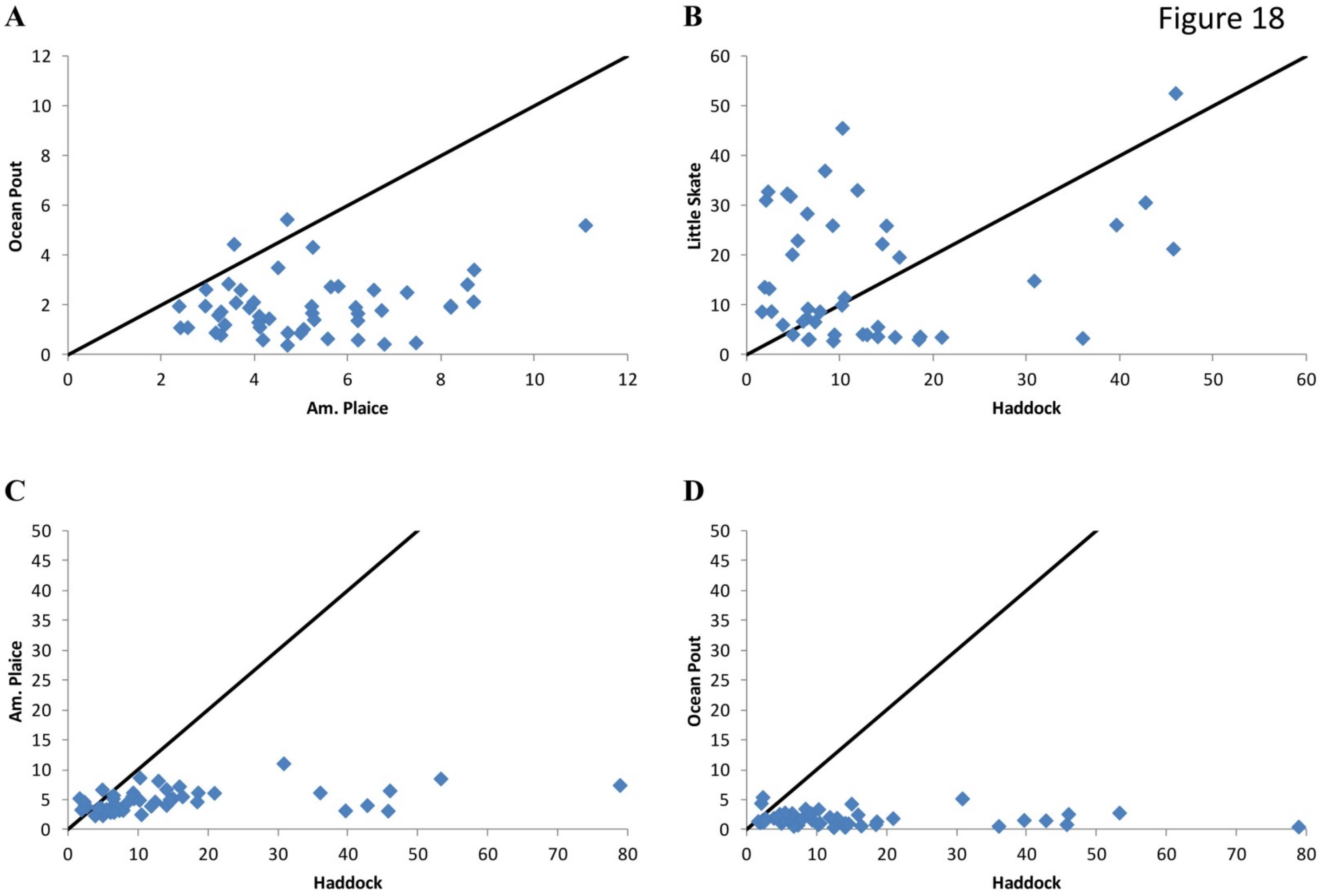


Figure 18

Figure 18. Biplots of species abundance for suspected pairs of competitiors. The black line is the equality (i.e., 1-to-1) line. A. Ocean pout (*Zoarces americanus*) and American plaice (*Hippoglossoides platessoides*). B. Little skate (*Leucoraja erinacea*) and haddock (*Melanogrammus aeglefinus*). C. American plaice and haddock. D. Ocean pout and haddock. Adapted from Link and Auster (in press).

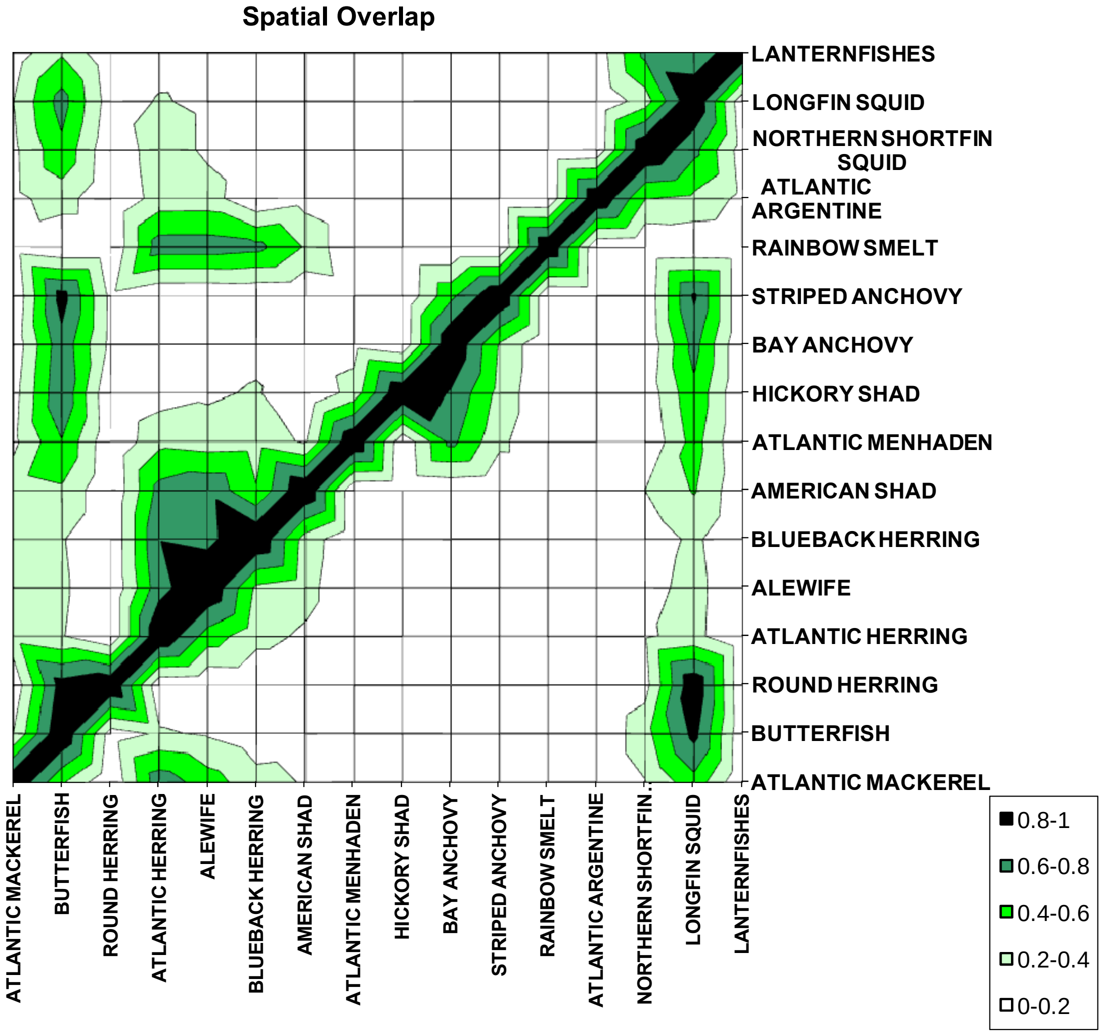


Figure 19. Plot of the matrix of spatial overlap index values for the small pelagic fish community from the northeast shelf large marine ecosystem (NES LME). Adapted from Link and Auster (in press).

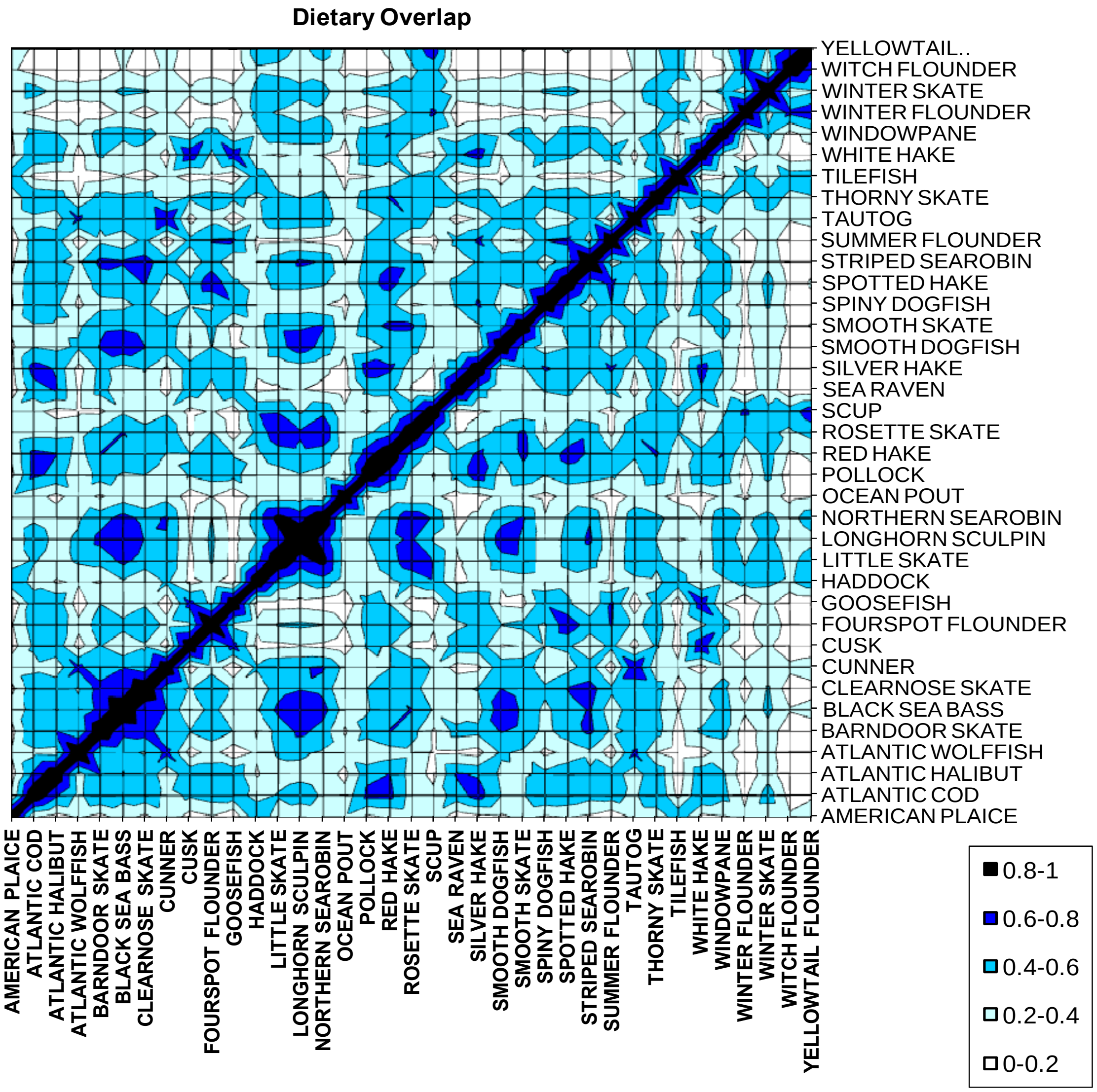


Figure 20. Plot of the matrix of dietary overlap index values for the demersal fish community from the northeast shelf large marine ecosystem (NES LME). Adapted from Link and Auster (in press).

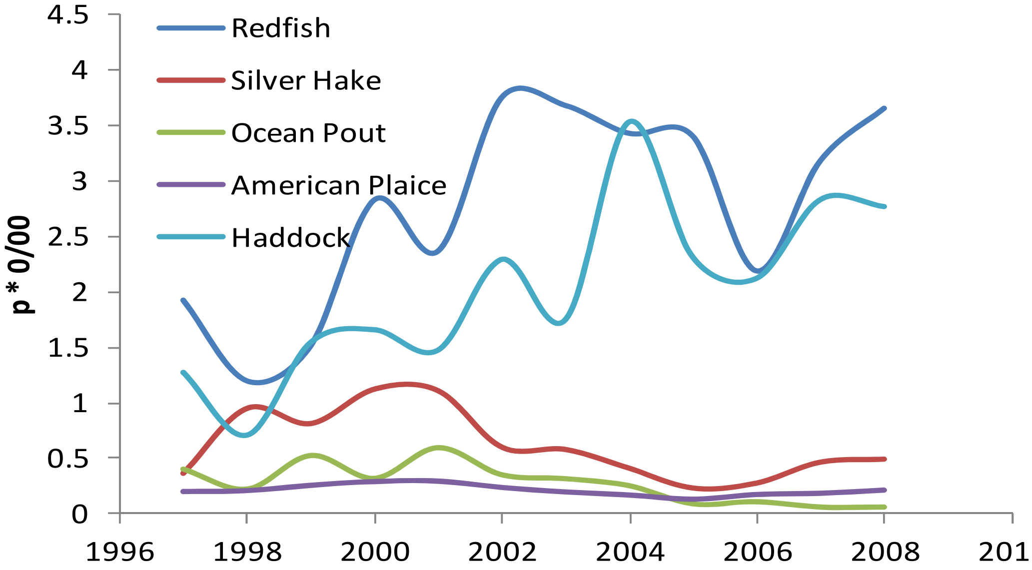


Figure 21. Fish to producer ratio (*p) for example benthivorous and shrimp-small fish feeding species. Adapted from Link and Auster (in press).**

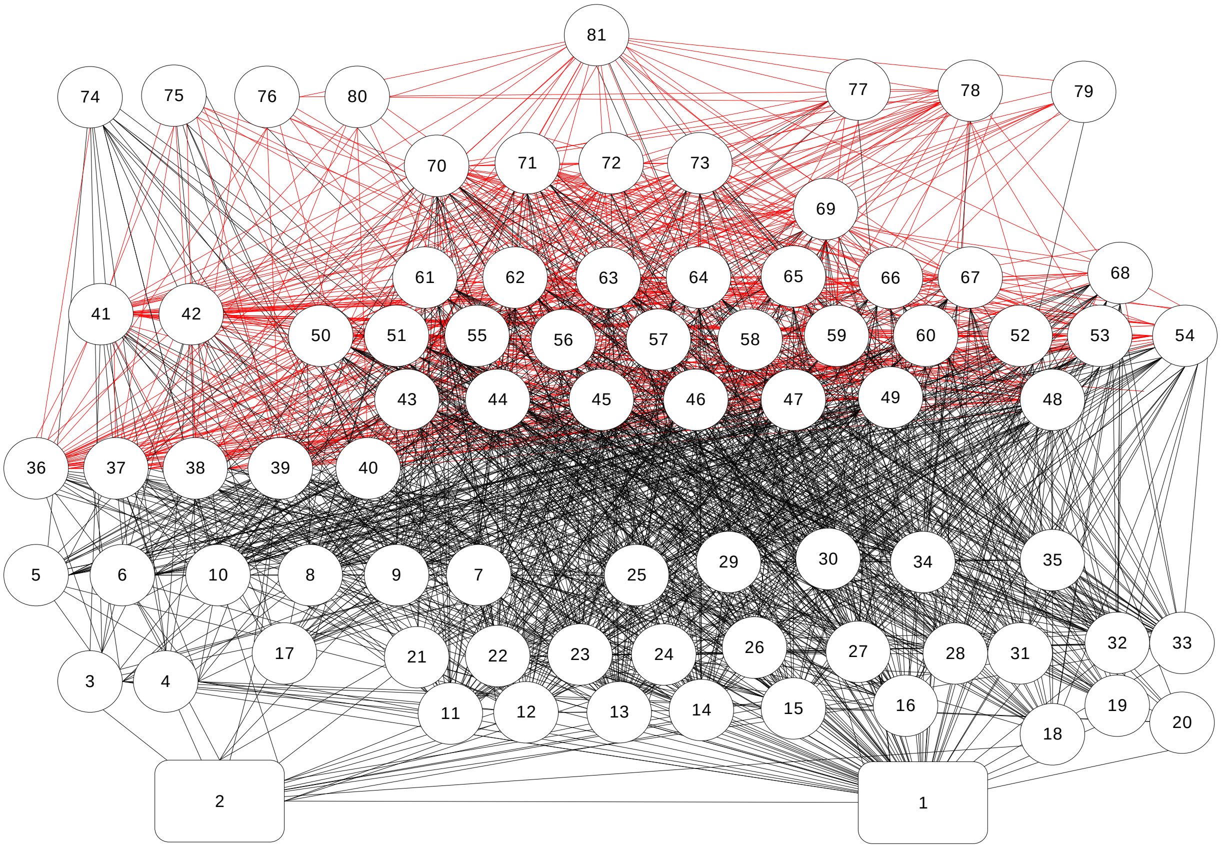


Figure 22. Food web of the northeast shelf large marine ecosystem (NES LME). Adapted from Link 2002.

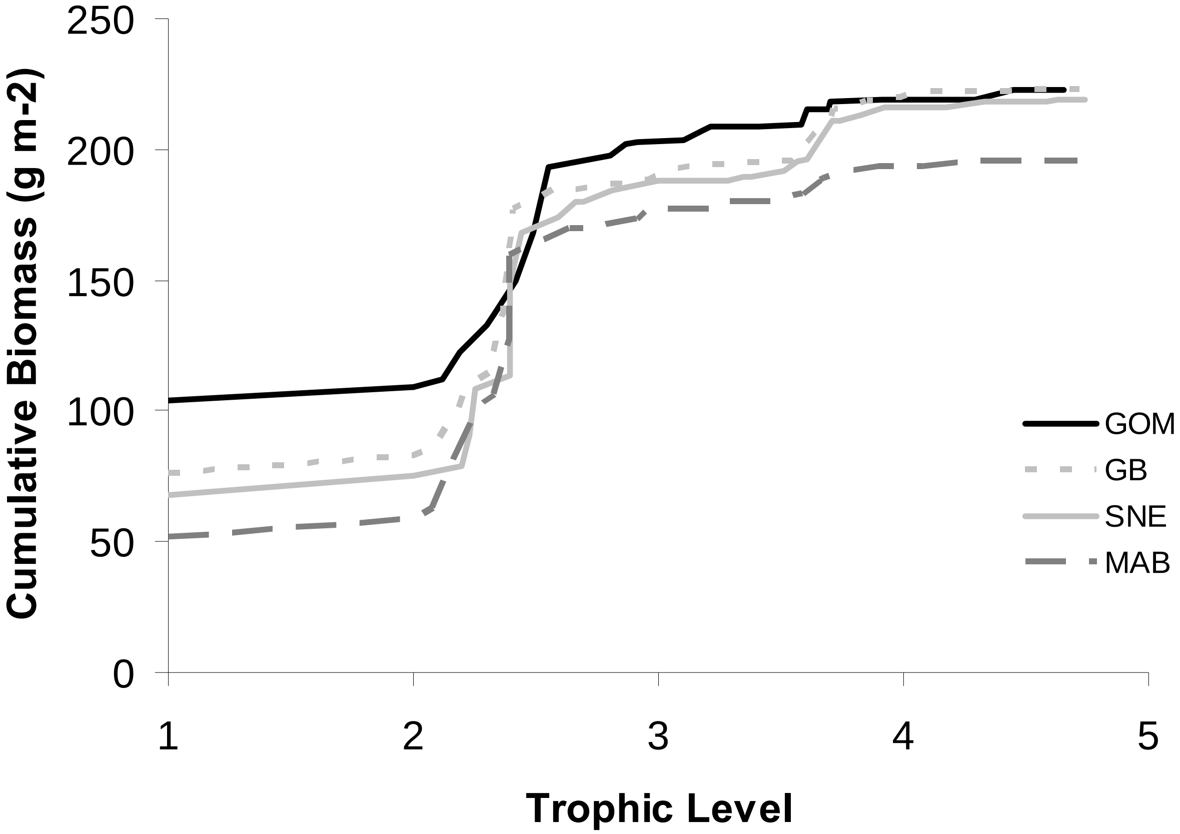


Figure 23. Cumulative biomass plotted against trophic level for the four regions. GOM=Gulf of Maine, GB=Georges Bank, SNE=Southern New England, MAB=Mid-Atlantic Bight. Adapted from Link et al. 2008.

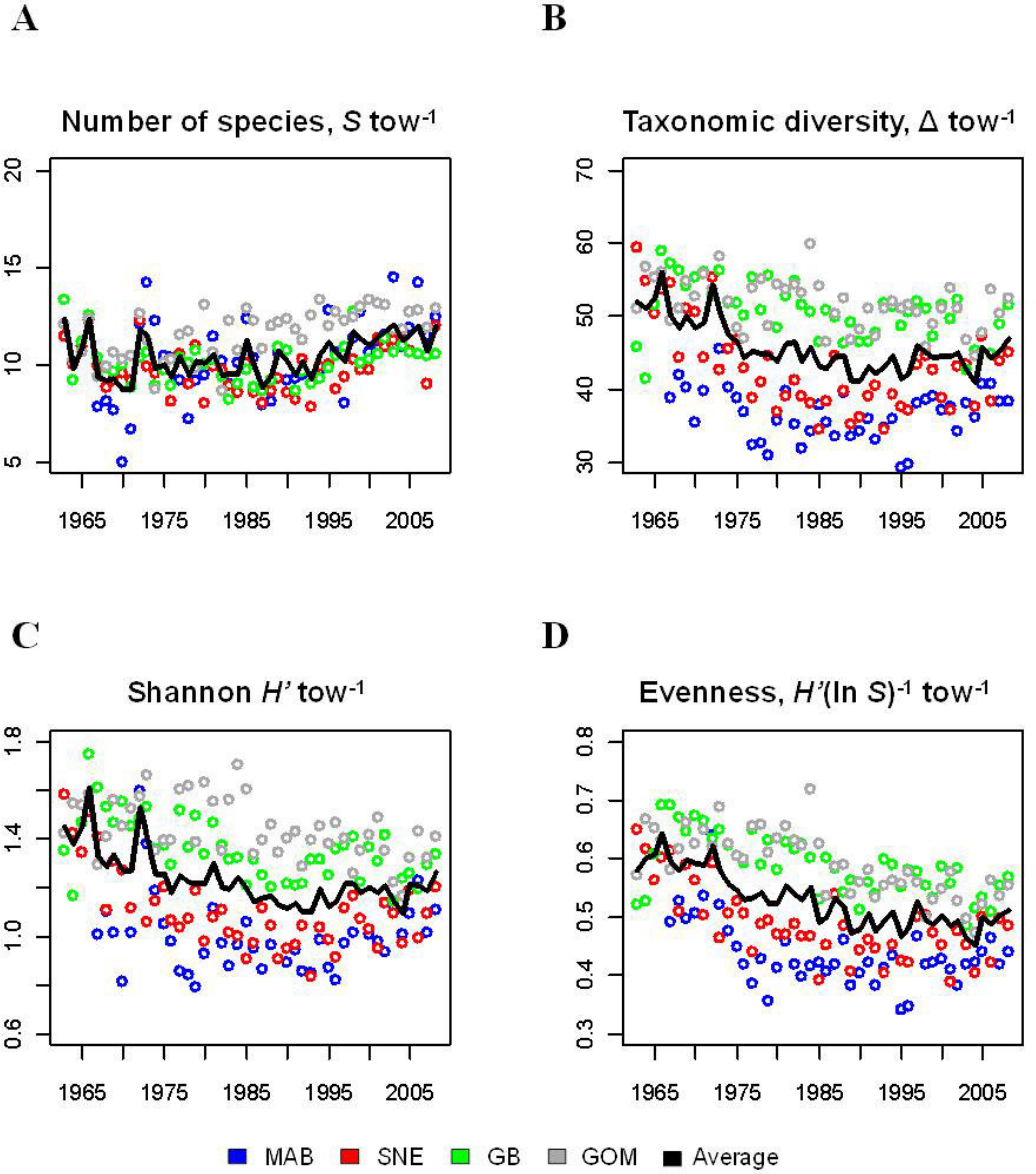


Figure 24. Average diversity index per tow by geographical region (1963-2008) for the groundfish community of the northeast shelf large marine ecosystem (NES LME). A. Species richness. B. Taxonomic diversity, Δ. C. Shannon Diversity, H'. D. Species evenness. For Δ, weighting scores were assumed to be equal for the eight taxonomic branch lengths considered: species, genus, subfamily, family, suborder, order, superorder, and class. MAB = Mid-Atlantic Bight; SNE = Southern New England; GB = Georges Bank; GOM = Gulf of Maine. Black lines represent average values across the four regions.

APPENDIX 1. CONTRASTING CONSUMPTION APPROACHES: A CALL FOR PARSIMONY

There are multiple approaches to estimating fish consumption, including: percent body weight (%BW), daily ration, consumption to biomass ratios (C/B or Q/B), caudal fin ratios, evacuation rate models, functional response models, and bioenergetics models.

The %BW method calculates the amount of food eaten per unit biomass per unit time, requiring body weight (*W*) and stomach weight (*S*):

$$\%BW = \frac{S}{W} \qquad \text{EQ B1.1}$$

This approach assumes what is found (on average) in stomachs represents population level consumption for any period of time. Data required are average body weight and stomach contents. This metric is more often a diagnostic back-calculated from other methods.

The daily ration approach is from Bajkov (1935) and similarly calculates the amount of food consumed (*C*) per capita per day, requiring stomach weight (S):

$$C = S \cdot (\frac{24}{n}) \qquad \text{EQ B1.2}$$

where *n* is the number of hours to evacuate a stomach. This approach assumes that what is found (on average) in stomachs is linearly evacuated. Data required are mean stomach contents. It too can be a diagnostic back-calculated from other methods.

The caudal fin-aspect ratio method (Palomares and Pauly 1989) assumes that body shape of fish roughly approximates a fish's activity and can be captured by the caudal fin. The aspect ratio of the caudal fin:

$$A = \frac{h^2}{s} \qquad \text{EQ B1.3}$$

uses the height (*h*) and surface area (*s*) of the fin and assumes that the aspect ratio is loosely related to consumption (or more specifically, Q/B or C/B ratios). This approach is admittedly best suited for tuna-like fishes.

The consumption to biomass (C/B or Q/B) ratios are basically literature values that are taken from consumption estimates, mostly 1940s and 1950s lab physiology studies (cf. references in Link et al. 2006). The caudal fin aspect ratio (general body plan; Palomares and Pauly 1989) or lab based evacuation/consumption study results are then reapplied to biomass estimates to come up with these ratio estimates. Values from similar species are often used as a proxy for species without direct measurements. This approach assumes constancy across a wide range of factors and produces unitless ratios applied to population level biomass, not abundance. This approach can also be a diagnostic back-calculated from other methods.

To estimate per capita consumption in a bit more specified manner, the gastric evacuation rate method is one approach (Eggers 1977, Elliott and Persson 1978). There are several approaches used for estimating consumption, but this approach was chosen as it was not overly simplistic (as compared to % body weight; Bajkov 1935) or overly complex (as compared to highly parameterized bioenergetics models; Kitchell et al. 1977). This approach is modified from Bajkov (1935) but explicitly accounts for temperature. Additionally, there has been copious experience using these models (e.g., Bromley 1991, dos Santos and Jobling 1988, 1991, 1992, 1995, Gerking 1994, Hansson et al. 1996, Jobling 1981, 1986, 1988, Jobling et al. 1994, Mehl and Sunnana 1991, Ponomarenko et al. 1978, Rindorf and Lewy 2004, Stefánsson and Pálsson 1997, Teschner et al. 2010, Teming and Andersen 1994, Temming and Herrmann 2003, Tyler 1970, Ursin et al. 1985, Waiwood and Majkowski 1984, Winger and Walsh 2001), particularly in the northeast shelf large marine ecosystem (NES LME) region (Durbin et al. 1983, Ursin et al. 1985, Pennington 1985, Overholtz et al. 1991, 2000, 2008, Tsou and Collie 2001a, 2001b, Link and Garrison 2002b, Link et al. 2002b, 2006, NEFSC 2007a, 2007b, 2010a, 2010b, 2011, Overholtz and Link 2007, Tyrrell et al. 2007, Link and Sosebee 2008, Link and Idoine 2009, Moustahfid et al. 2009a, 2009b, Deroba et al. 2010, DFO 2010). The main form is:

$$\frac{dS_i}{dt} = C_i e^S \qquad \text{EQ B1.4}$$

where different assumptions about e^S yield subtly different formulae. In one of the more common forms, using the evacuation rate model to calculate consumption requires two variables and two to three parameters. The per capita consumption rate, C_i is calculated as:

$$C_i = 24 \cdot E_i \cdot \overline{S_i}^{\gamma} \qquad \text{EQ B1.5}$$

where 24 is the number of hours in a day and the evacuation rate E_i is:

$$E_i = \alpha e^{\beta T} \qquad \text{EQ B1.6}$$

and is formulated such that estimates of mean stomach contents (S_i) and ambient temperature (T) are the only data required. The parameters α and β are set as values that can be chosen from the literature (e.g., Durbin et al. 1983, Tsou and Collie 2001a, 2001b, Overholtz 2000) or estimated experimentally (Bromley 1991, dos Santos and Jobling 1988, 1991, 1992, 1995, Jobling 1988, Temming and Anderson 1994, Temming and Herrmann 2003). The parameter γ is a shape function and is almost always set to 1 (Gerking 1994). The approach models evacuation (of stomach contents) rate by assuming non-linear evacuation, constant consumption, and that consumption equals what was evacuated.

Functional response models fit relationships between predator and prey populations (Holling 1959a, Yodzis 1994). This approach requires abundance of predator (P), prey (N_i), and alternate prey (N_k); foraging times (F), search times (f), and growth rates (r) of prey; capture rate (C) and handling times (h) of a particular prey k by a particular predator:

$$\frac{dN}{dT} = rN - FP \qquad \text{EQ B1.7}$$

or

$$\frac{dN}{dt} = rN \cdot (1 - \frac{N}{K}) - FP \qquad \text{EQ B1.8}$$

where,

$$F = \alpha N \qquad \text{EQ B1.9}$$

or

$$F = fF \cdot (\frac{C}{1 + \sum h_k C_k}) \qquad \text{EQ B1.10}$$

This approach assumes one of three standard “Types” of responses (I, II, or III; Holling 1959a, Moustahfid 2010), although other relationships have been described that explicitly address heterogeneity of predator and prey distributions (see Cosner et al. 1999) and variation in satiation effects (Jeschke et al. 2002). This approach generally assumes that predation rate depends upon prey and predator densities. Usually this method emphasizes a two species predator-prey pairing.

Bioenergetic models, aka the Wisconsin model (Kitchell et al. 1977; modified from Winberg 1956), model the full physiology of an (average) individual fish with a mass balance constraint. This approach requires detailed knowledge of basal metabolic rates (M), growth (G), and waste (W) to estimate consumption (C):

$$C = P + M + W \qquad \text{EQ B1.11}$$

where

$$P = G + Repro \qquad \text{EQ B1.12}$$

and

$$M = Resp + MA + SDA \qquad \text{EQ B1.13}$$

and

$$W = F + U \qquad \text{EQ B1.14}$$

with production (P) comprised of somatic growth (G) and reproduction (Repro, or gonad production), metabolism comprised of respiration (Resp), metabolic activity (MA, or active metabolism), and specific dynamic action (SDA, or the “cost” of digestion), and waste comprised of feces (F, or egestion) and urea (U, or excretion) needing to be measured, accounted for, or assumed.

The bioenergetics approach models the amount of food that is required to support other activities and is usually based on a laboratory experiment for estimates. The main assumption is that inputs equal outputs. Data required are probably the most extensive for any consumption estimating approach, often required detailed measurements of fish inhabiting respirometers.

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APPENDIX 2. AN ANALOGY AND GENERAL RULE?

There is a generally accepted power law for animal (mainly mammal) metabolic rates (Klieber 1947, Peters 1983). The law states that for any given sized animal, the relationship between metabolism and body size is a ¾ scaling:

$$M = aW^b \qquad \text{EQ B2.1}$$

where *a* varies by body shape, temperature, etc., but *b* is usually ~0.75.

There is also a general relationship for fish between fish weight and length (cf. Fulton 1902, 1904, von Bertlanffy 1957, Froese and Pauly 1994, Froese 2006, Froese 2011; e.g. Wigley et al. 2003). This relationship generally has weight as a function of length to the 3rd power:

$$W = aL^b \qquad \text{EQ B2.2}$$

where *a* varies widely based upon body shape, sex, maturity state, etc., but *b* is usually ~ 3.

We assert that for fish consumption, there may indeed exists a similar, general power law for gastric evacuation (as corrected for temperature). Recall that evacuation *E* is:

$$E_i = \alpha e^{\beta T} \qquad \text{EQ B2.3}$$

where α varies widely based upon body type, physiology, prey type, prey size, etc., but β is usually ~ 0.1. We note that simple sensitivity analyses inform this choice. Examining sensitivities to the various parameters and variables used in the gastric evacuation shows that for the scalar constant α, results appear to be realistic if constrained between 0.015 and 0.045, which corresponds to the previously reported range from the literature (Durbin et al. 1983, Tsou and Collie, 2001a, 2001b, Overholtz et al. 2000; Figures B2.1, B2.2). For the power parameter β, results appear to be robust around 0.11 (Figures B2.1, B2.2). The literature reports values of β with additional significant figures, which may not be necessary. It is probably reasonable to fix β at approximately 0.1. For both parameters, when within the normal range, the change in per capita consumption is minor, much less than one half an order of magnitude. These results demonstrate that within the range of fish field studies and modeling efforts, evacuation effectively functions as a tenth power.

Thus, similar to the ¾ power scaling law for mammal metabolism and 3rd power for fish weight-length relationships, there may exist a one-tenth power for fish evacuation based on average stomach contents. Theoretically, this tenth power law can be understood to be reflective of the maximal assimilation efficiency of material consumed, indicative of transfer efficiency across trophic levels, all realized as the rate and amount of food being digested, as modulated by temperature, not to exceed a power of approximately 1/10th due to inherent physiology of fishes. Certainly further exploration and verification of this hypothesis is warranted. But if validated, the tenth power of evacuation may ultimately end up serving as one of those useful approximations to facilitate much further extension of efforts while minimizing excessive need for copious laboratory studies.

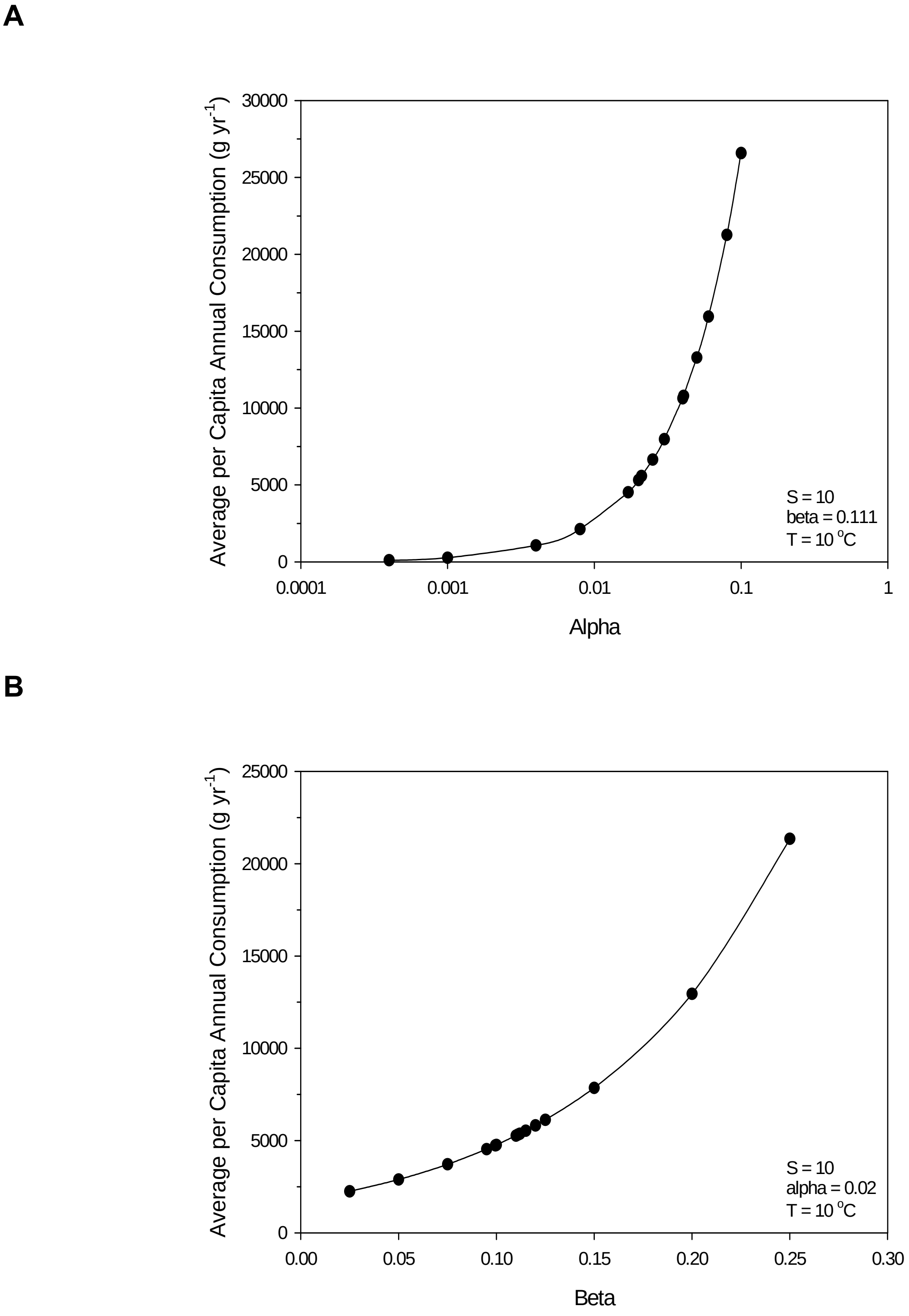

Figure B2.1. Sensitivity analysis of parameters in the gastric evacuation model. A. Evaluation of alpha. B. Evaluation of beta. Adapted from NEFSC 2007b.

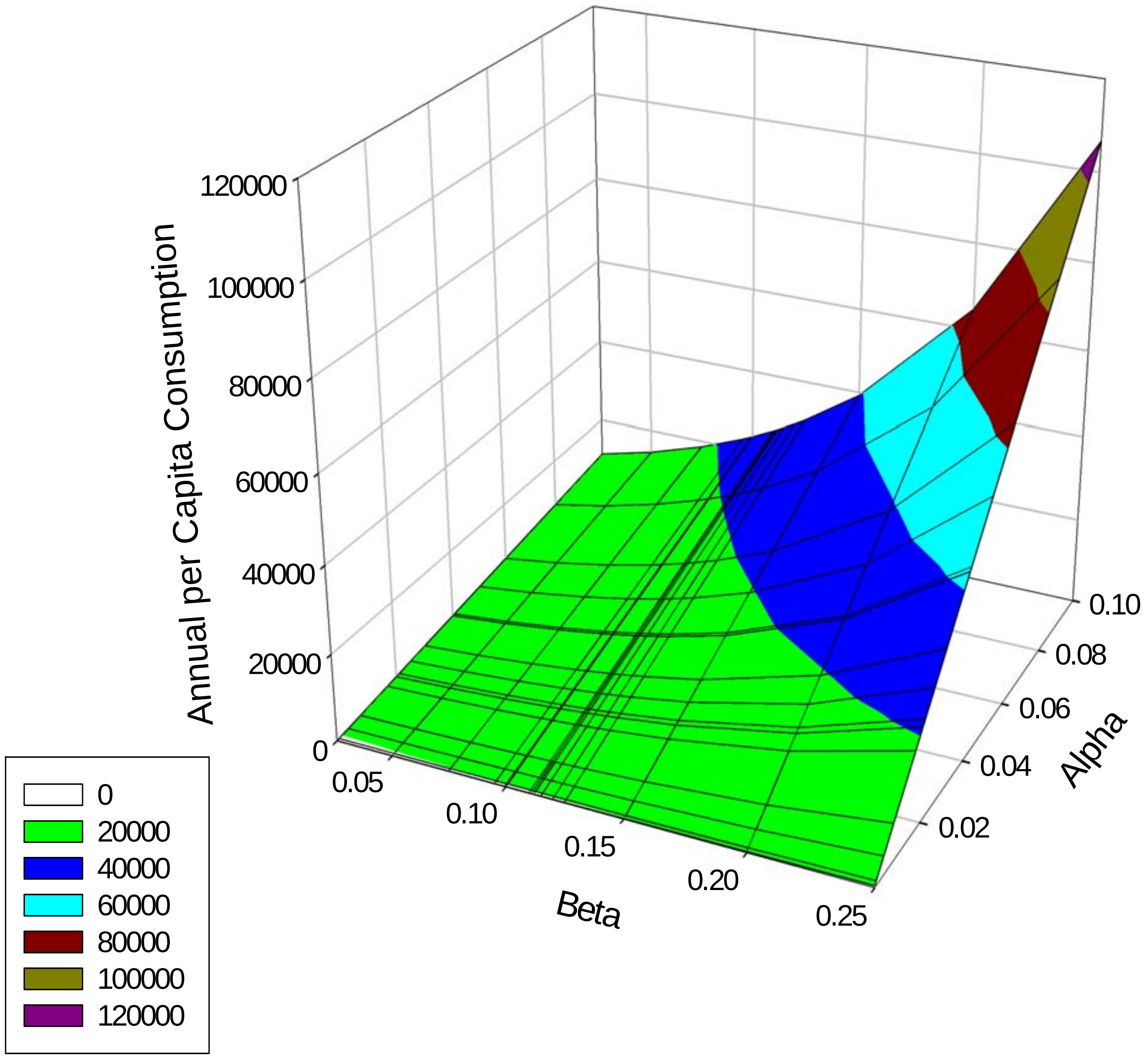

Figure B2.2. Paired sensitivity analysis of parameters and data inputs in the gastric evacuation model. Adapted from NEFSC 2007b.

APPENDIX 3. A BRIEF HISTORY OF FOOD WEB THEORY

The development of ecological theory concerning the patterns exhibited by food webs and the underlying processes they reflect can be divided into three temporal stanzas. Prior to 1970, "food web theory" was largely encapsulated in Elton's (1958) conceptual model that complexity engendered stability in ecological communities. Small webs evinced cyclic population fluctuations in both natural (high-latitude predator-prey populations) and model (two-species Lotka-Volterra models) systems. Furthermore, species-poor systems (e.g., agricultural plots) appeared to be more vulnerable to devastating pest outbreaks than highly speciose systems. Finally, increased food web complexity (i.e., links) led to rapid increases in the pathways available for energy to flow from basal to top species. The complexity-engenders-stability hypothesis enjoyed considerable support and approached the status of a mathematical theorem prior to theoretical attacks by May (1972, 1973) and others. Suffice it to say, we do not suspect that this stability-complexity debate is going to dampen any time soon, particularly regarding the determinants thereof (Paine 1988, Pimm et al. 1991, Haydon 1994, de Ruiter et al. 1995, McCann et al. 1998, Closs et al. 1999, Martinez 1992, 1994, Polis and Strong 1996, Dunne et al. 2002a, 2002b, 2004, Loreau et al. 2002, Berlow et al. 2004, 2009).

Subsequent to this initial stanza, May (1972, 1973), following up on computer simulation results by Gardner and Ashby (1970), developed a criterion for community stability related to connectance ($b(SC)^{1/2}<1$, where b is mean interaction strength) based on analysis of randomly-constructed webs. Under the assumption that mean interaction strength is independent of food web size, May's formula predicts that connectance should decline hyperbolically as the number of species increases. This prediction ushered in the second stanza of food web theory and led to numerous comparisons of catalogs of empirical food webs in attempts to test it (Briand and Cohen 1984; Cohen and Briand 1984; Sugihara et al. 1989; Cohen et al. 1990; Pimm et al. 1991; Havens 1992;). Other topological web metrics (see above) were introduced in these and associated studies to identify other potential patterns associated with food webs. By the end of the 1980s, food web theorists had developed a set of empirical relations based on these food web catalogs, some of which included 100+ webs (e.g.,). Cohen (1989) summarized several of these empirical relations as five "laws": (1) excluding cannibalism, cycles are rare, (2) food chains are short, (3) the proportions of top, intermediate and basal species (%T, %I, %B) are independent of web scale (the "species scaling law"), (4) the proportions of link types (%T-I, %T-B, %I-I, %I-B) are independent of web scale (the "link scaling law"), and (5) linkage density ($L_D = L/S$) is independent of web scale (the "link-species scaling law"). The last of these laws also encapsulates support for May's stability criterion as a constraint on trophic structure as it implies that connectance declines hyperbolically with increased species richness. In addition, Cohen (1978) found that the "niche overlap graph" of most webs was an "interval graph," that is, the overlaps of species' resource niches as revealed in food web diagrams could be collapsed onto a single dimension. Cohen (1989) also presented a model of community organization, the "cascade" model, that gave "remarkable quantitative agreement" between his empirical laws and the model's predictions based on a single parameter—the expected linkage density.

However, the edifice of empirical evidence supporting these relations has been seriously challenged on a number of grounds concerning the cataloged food webs. These include concerns that real species diversity was inadequately represented, species were poorly resolved and over-aggregated, actual links between species were under-represented, criteria for aggregation were inconsistent, ontological changes in diet were absent, cannibalism was ignored, and inconsistencies in sampling effort, spatiotemporal resolution and spatiotemporal aggregation giving rise to sampling artifacts could not be assessed (Paine 1988, Winemiller 1990, Hall and Raffaelli 1991, Kenny and Loehle 1991, Martinez 1991, Polis 1991, Goldwasser and Roughgarden 1997, Martinez et al. 1999). To some extent, these criticisms reflected the fact that few, if any, of the collected food webs had originally been developed with the intent of testing food web theory (Warren 1994).

The beginning of the third (and current) stanza in the development of food web theory around 1990 is marked by the crescendo in these criticisms and the development of the first webs designed to address them (e.g., Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991). In contrast to earlier webs, of which the structure of many resulted more from artistic convenience than from objective ecological criteria (Paine 1988), the procedures used to construct these new webs were objectively defined and well-documented. The new webs exhibited higher species diversity and topological complexity than typical older webs (Winemiller 1990: 4 tropical aquatic habitats, 58-104 species, 208-1243 links; Hall and Raffaelli 1991: temperate estuary, 92 species, 409 links; Martinez 1991: temperate lake, 93 trophic species [182 original taxa], ~1000 links; Polis 1991, desert community, ~3000 species). Topological properties associated with the new webs differed substantially from older webs: the average number of links per species was much higher in the new webs and food chains were much longer. Omnivory, cannibalism and looping were also more common than previously thought. In addition, it was shown that many food web properties were sensitive to the criteria used to aggregate species, as well as the level of aggregation, thus casting previous scale invariance laws (species, link, and link-species scaling laws) into question (Winemiller 1990, Martinez, 1991). Subsequently, using an analysis of the new webs, Martinez (1992) challenged the previously-observed hyperbolic scaling relation for connectance (Pimm 1982, Cohen and Newman 1988) and advanced the hypothesis of "constant connectance": that directed connectance is scale invariant. More recently, Williams and Martinez (2000) advanced an alternative to Cohen and Newman's (1988) cascade model, the model, thus completing the challenges to the empirical and theoretical edifice Cohen (1989) had outlined.

However, although the earlier results have been called into question by more recent analyses with new webs developed specifically to test hypotheses of food web theory, no clear consensus has emerged yet to replace the older (admittedly contentious even then) one. Simply put, food webs and their topological properties appear, at best, to be more complex than was previously hoped. However, this also means that the potential for significant additions to food web theory appears to be quite high.

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