

## THE CHALLENGES OF EVALUATING COMPETITION AMONG MARINE FISHES: WHO CARES, WHEN DOES IT MATTER, AND WHAT CAN ONE DO ABOUT IT?

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### ABSTRACT

Among species interactions, competition is obviously more nuanced to investigate than predation. Certainly there have been copious, seminal works on competition in marine and freshwater ecosystems, most often on research executed at smaller ecological scales such as rocky intertidal zones, coral reefs, or littoral zones, and often involving experimental manipulation. Such studies have typically emphasized organisms with relatively high site fidelity, and all have focused primarily at the individual level. Here we springboard from those studies to explore competition among marine fishes at broader spatiotemporal scales, scales at which fish populations are distributed, scales at which their associated fisheries operate and are managed, and as observed under ambient (i.e., nonexperimental) system dynamics. Inferring that competition *might* be occurring among marine fishes requires four conditions: opposite population trajectories, high spatiotemporal overlap, high dietary overlap, and some indication of resource limitation. We used those criteria to examine cases of species pairings from the Northeast United States Large Marine Ecosystem to ascertain if there are broadly applicable rules of thumb to determine when competition might be a significant consideration. We assert that such rules exist, and where competition is strongly suspected, we provide an empirically based method of calculating first-order, model-free interaction terms that can scope the potential magnitude of competitive effects. We do so very much cognizant of several caveats and theoretical considerations; but our main premise is that estimating and evaluating competition for marine fishes from extant, commonly available data is feasible, is highly germane, and has many valuable applications for multispecies and ecosystem models as we move toward ecosystem-based fisheries management.

Evaluating the processes that interact to determine the relative abundance of species is arguably the central tenet of ecology (Elton 1927, Hutchinson 1959). In particular, interspecific competition has long been of significant interest, having had a prominent place in ecological studies. Seminal works have all noted the potential for competitive interactions to regulate population size and community structure, ultimately to influence or even limit the productivity of ecosystems (see e.g., Lotka 1925, 1932, Volterra 1926, Gause 1934, Hardin 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 diversity of habitats and ecosystems (too numerous to list 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.

Competition has generally been evaluated through experimental approaches (see 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 (see e.g., Schoener 1974b, 1985, Pimm 1978, 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, Wootton and Emmerson 2005, Novak 2010). Yet unraveling the magnitude and specific determinants of competition has remained elusive. That is, estimating competition in the field under natural conditions, to the point where the effects are definitively attributable to competition and are defensible, while cognizant of prevailing theory, remains difficult.

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,b, Paine 1966, 1971, 1976, Hall et al. 1970, Dayton 1971, 1975, 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 have usually focused on smaller, localized spatiotemporal 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).

Marine fishes are diverse and widespread across the continental shelves of the global ocean. Many exhibit significant, broad-scale movement patterns and have facultative but not usually obligate habitat associations. Although understanding the dynamics of unexploited populations and communities of shelf fishes is of fundamental scientific interest regarding the role of species interactions, many species are the direct targets of fisheries. Several studies have implied that competition might structure fish communities, particularly after perturbations from fishing activities (e.g., Fogarty et al. 1991, Fogarty and Murawski 1998, Jennings and Kaiser 1998, Persson and Hansson 1998, Hollowed et al. 2000a,b). As such, it is recognized that the assessment and management of the species supporting fisheries ought to account for species interactions (Link 2002, 2010a).

Competition has been considered in a fisheries context before (see e.g., Overholtz and Tyler 1985, Fogarty et al. 1991, Piet et al. 1999, Munday et al. 2001, Link et al. 2002, Hixon and Jones 2005), but is not done so routinely and certainly not operationally (Link 2002, 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 (see e.g., Bax 1991, Fogarty and Murawski 1998, Gamble and Link 2009). 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), studies are needed that address the problem at the spatiotemporal scales at which fisheries operate and are managed (Auster 1988). Competition among fishes in a fisheries context should

therefore be evaluated at the large physiographic scales at which populations respond (Cook and Auster 2005), such as significant portions of continental shelves and slopes, if not even Large Marine Ecosystems (LMEs, Sherman 1991). These scales are much larger than 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) or a focus on the responses 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 competitive interactions at these spatiotemporal scales will require a theoretically robust and readily usable approach to determine if competition is indeed occurring, and, if it is, a coupled protocol for estimating its effects. This is especially germane in a fisheries context given the numerous recent calls to consider ecosystem-based fisheries management (e.g., Link 2002, 2010a, Pikitch et al. 2004, Leslie and McLeod 2007). The primary issue is to establish an approach that can be used to infer strongly that competition is important if it is suspected to exist. Then, if competitive interactions are indeed indicated on the basis of these fundamental criteria, an approach is needed for estimating competition coefficients from readily available data. Here we present a proposed protocol for exploring, evaluating, and quantifying both aspects [determination (i.e., existence) and estimation (i.e., magnitude)] of competition for shelf fish communities in a fisheries context. We use the Northeast US Large Marine Ecosystem (NEUS LME) as an example (a list of species from the NEUS LME is given in Appendix 1).

#### EVALUATION PROTOCOL

There are four requirements that must be fulfilled to demonstrate competition between species is likely occurring (as noted by Link et al. 2002): opposite population trajectories (notable population responses), high spatiotemporal overlap, high dietary overlap (i.e., similarity of resource utilization), and some indication of resource limitation. These criteria to infer whether competition may be occurring all reflect the same theses of earlier studies on competition; namely that species must be in the same time and place for competition to occur, their niches must overlap along multiple dimensions for what could be finite resources, and the populations must be observably affected. Below we elaborate upon each point and then synthesize them into a quantitative protocol for determining whether competition is probable, at least in a fisheries context.

**OPPOSITE 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 in which one species was notably reduced. Certainly interspecific competition could be occurring among individuals, but if not reflected at the population level, then this would be irrelevant for a population and fisheries context. Additionally, competition could have occurred in the past, resulting in realignment 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 realignment 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 in fisheries science, including estimates of abundance or biomass from surveys, tagging studies, or stock assessment outputs. Typically these are presented as at least annual estimates of stock abundance but could be noted seasonally or multiannually depending upon the available data. These data are usually presented as composites for a stock, but if age or size structure were important, they could also be considered if and as available. Clearly time-series duration would have to be sufficient for this evaluation; we recommend at least 10 yrs (Nicholson and Jennings 2004, Blanchard et al. 2010). Evaluation would have 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.

Several statistical methods can be used to compare two (or more) time series (see e.g., Bjornstad and Grenfell 2001, Zuur et al. 2007). Although we endorse them and certainly think they could inform the proposed evaluation, what is ultimately needed is a simple contrast between trajectories. Even a linear approximation of the slopes of such time series, with suitable correction for autocorrelation (Bartlett 1946) if necessary, should be sufficient. Often the dynamics of populations are decidedly nonlinear over a long period, but the major, recent trends would be the primary data for evaluation. Although we stop short of recommending a purely “eye-ball” approach, essentially a classical “X” pattern formed by the trajectories of two populations plotted together over time, it would be a strong indication of likely competition. 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 this one would need to be met 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. Alternatively, if there are such interactions, some other driving factor might so dominate the population dynamics as to mask competition. 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 effectively uninfluenced 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 in the NEUS LME (Fig. 1) and, we strongly suspect, in other ecosystems as well. We (Auster and Link 2009) and colleagues (Garrison and Link 2000a,b, 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. Examples from the NEUS LME show that piscivores (Fig. 1A–D) often have similar trends but much lower magnitudes relative to one another, but some even exhibit quite opposite trajectories (Fig. 1C). Benthivorous echinoderm-feeding specialists often exhibit opposite

trajectories (Fig. 1E–H), as do mesopelagics (Fig. 1I), benthivorous scavengers and crab-feeding specialists (Fig. 1J–L), and small pelagic, shrimp-feeding fishes and squids (Fig. 1M–N). One can readily observe quite distinct patterns from such commonly available survey data. Further, if species abundances of possible competitors are plotted against one another, probable competitive dominants can be identified (Fig. 2A, C, D, H, K, L) in cases where one species dominates along one axis or another rather than being equally dispersed about the equality line. In those instances where the pattern of cross-plotted abundances matches the line of equality (Fig. 2B, E, F, G, I, J), 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.

**SPATIOTEMPORAL OVERLAP.**—Generally speaking, for species to compete, they must be in the same place at the same time. Certainly direct or interference (aka scramble or contest) competition requires species to interact directly. Indirect or exploitation competition would not necessarily require species to spatiotemporally overlap. Yet that is from the classical view of competition between individuals. At the scale at which populations are distributed and fisheries operate and are managed, even exploitation competition would require use of similar resources during the same general time and at the same general places; otherwise the species would simply occupy different places and obtain the necessary resources elsewhere. Species with high spatial overlap, integrated over the entire continental shelf, over long periods are likely to be using the same resources, irrespective of the mechanism operating at the individual level.

Further, one facet of niche space is simply place. Certainly small-scale fish distributions respond differently to variation in physical and biological habitats (see e.g., Larson 1980, Carr et al. 2002, Auster et al. 2003, Hixon and Jones 2005, Lindholm et al. 2007) and are associated with multiple environmental attributes across a range of scales, but at the core of defining habitat are geospatial coordinates. Although, at the scales discussed here, oceanic features of habitat tend to be homogenized (and even more so in the pelagic realm), occupation of different habitats by these types of fishes does indeed imply differences in broad-scale habitat requirements, usage, and thus niches. For instance, if fishes are repeatedly caught in the same survey tows, tows that can loosely be associated with various broad-scale habitat features such as temperature, light, depth, finer-grained substrates, major flow regimes, or frontal boundaries (e.g., Link and Demarest 2003, Methratta and Link 2006a,b, 2007a,b, Nye et al. 2009, 2011), the implication is that, at these broad scales, such fishes are generally using the same physical spaces, even if individuals are exhibiting more nuanced distinctions in habitat usage at finer scales. Assessing spatiotemporal 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 indices of spatiotemporal overlap (Schoener 1970, Williamson 1993, Manly et al. 2010). These overlap estimates, usually on a scale from 0 to 1 or from 0 to  $\infty$ , indicate the degree to which a pair of species is co-occurring. They 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 caught in the sampling gear, usually trawl gear (Garrison 2000, 2001, Garrison et al. 2000, 2002). These measures account for

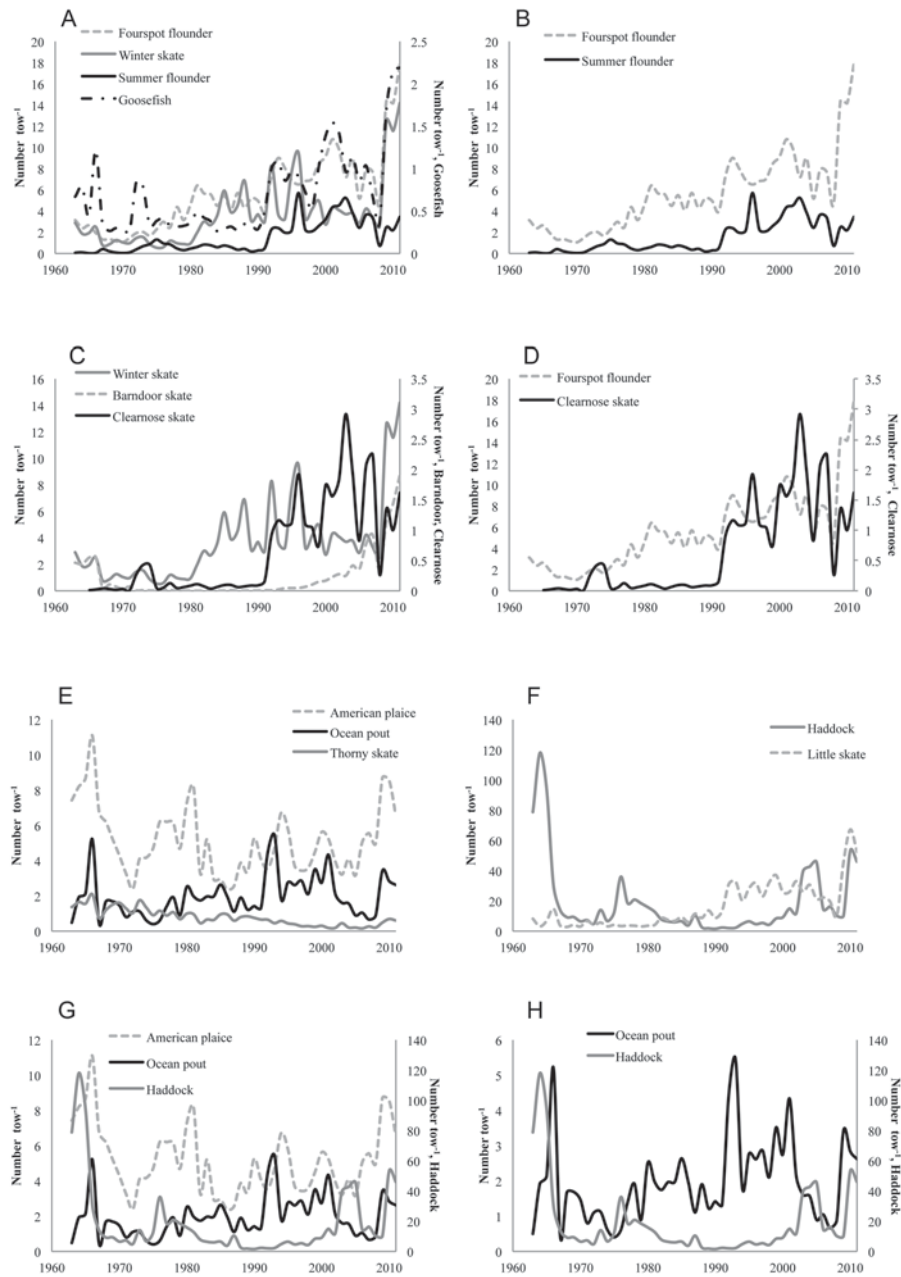


Figure 1. Population trajectories, from trawl-survey indices of example species suspected of being competitors in the Northeast United States Large Marine Ecosystem. (A) Four species of piscivores. (B) A pair of piscivores. (C) Three species of skates. (D) A piscivorous flatfish and an omnivorous skate. (E) Three benthivores. (F) Two common benthivores, a major gadid (haddock), and a skate. (G) Three species of echinoderm-feeding specialists. (H) A pair of echinoderm feeders. (Opposite page) (I) Three species of mesopelagics or small pelagics (butterfish). (J) A pair of benthivorous, scavenger-crab feeding fishes. (K) Three species of crab-feeding benthivores. (L) A pair of crab-feeding benthivores. (M) A pair of shrimp-small fish feeders. (N) A pair of small pelagics.



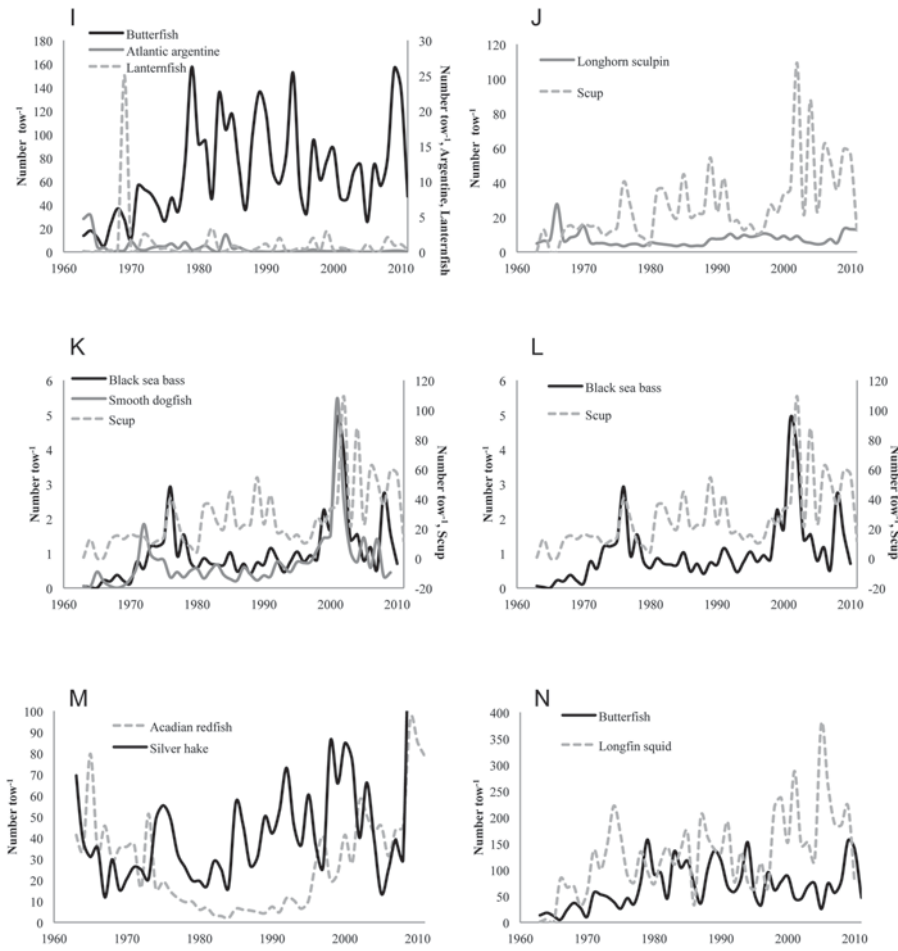


Figure 1. Continued.

the differential abundance and distributions of fishes if executed according to a statistically rigorous sampling design (see e.g., Azarovitz 1981, NEFSC 1988). Effectively the occurrence of species  $i$  in the presence of species  $j$  is integrated 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:

$$SO_{ij} = \frac{\sum_z (N_{iz} N_{jz}) m}{\sum_z (N_{iz}) \cdot \sum_z (N_{jz})} \quad (\text{Eq. 1})$$

where  $z$  is a sample location (in this case a 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 does not differ from the expectation that the species are uniformly distributed. A value  $<1$  indicates less than expected overlap, and a

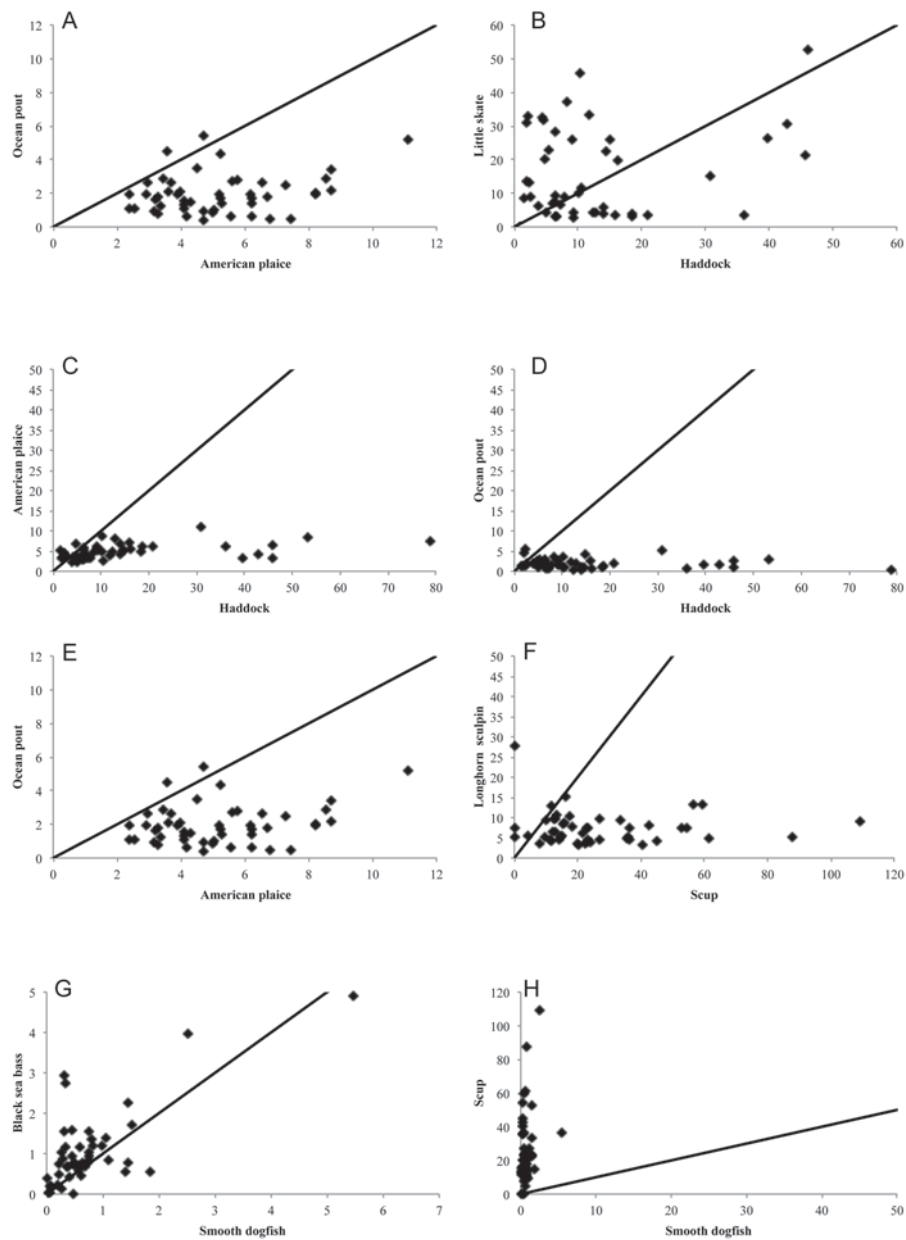


Figure 2. Biplots of species abundances for suspected pairs of competitors. All units are in number tow<sup>-1</sup>. The black line is the equality (i.e., 1-to-1) line. (A) Echinoderm-feeding specialists. (B) Benthivores. (C) Echinoderm-feeding specialists. (D) Echinoderm-feeding specialists. (E) Shrimp-small fish feeders. (F) Benthic scavengers. (G) Crab-feeding benthivores (H) Crab-feeding benthivores. (Opposite page) (I) Piscivores. (J) Piscivores. (K) Piscivores. (L) Piscivores.



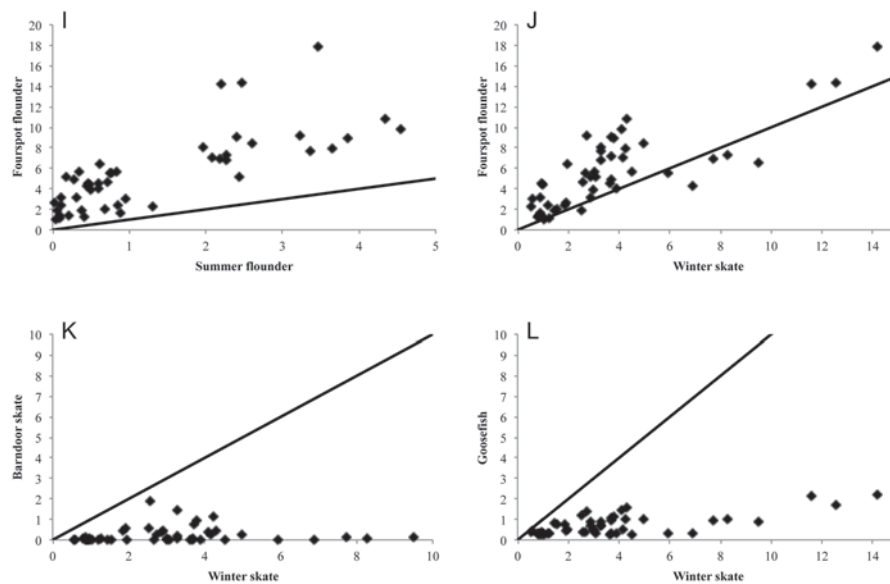


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value  $>1$  indicates a greater than expected overlap; the upper bound is determined by the number of locations sampled.

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

Some methods use resampling techniques to determine “significance” of a given overlap value (Manly 1997, Garrison 2000, 2001). Although we acknowledge the role and importance of such statistical techniques, they are 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  $>40\%$  (1 on the Williamson scale) merit consideration, and effectively all values  $>60\%$  (2 on the Williamson scale) are significant (Ross 1986; Garrison, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL, pers comm). We endorse this simpler set of approximations in the context of determining that competition might be occurring. If species exhibit high spatiotemporal overlap, then evaluating additional considerations of competition is warranted.

An example from the NEUS LME shows that, for most of the fish community, spatiotemporal overlap averages approximately 25%–30% (Fig. 3). For some selected species pairs, the overlap is very high ( $>70\%$ ), for both demersals (Fig. 3A; e.g., silver hake, spiny dogfish, or summer flounder with several species) and pelagics (Fig. 3B; e.g., longfin squid, anchovies, round herring, and shads with butterfish). For others the value of overlap is high enough ( $>40\%$ ) to warrant consideration; examples are pairings of various piscivores (e.g., fourspot and summer flounder), benthivores (e.g.,

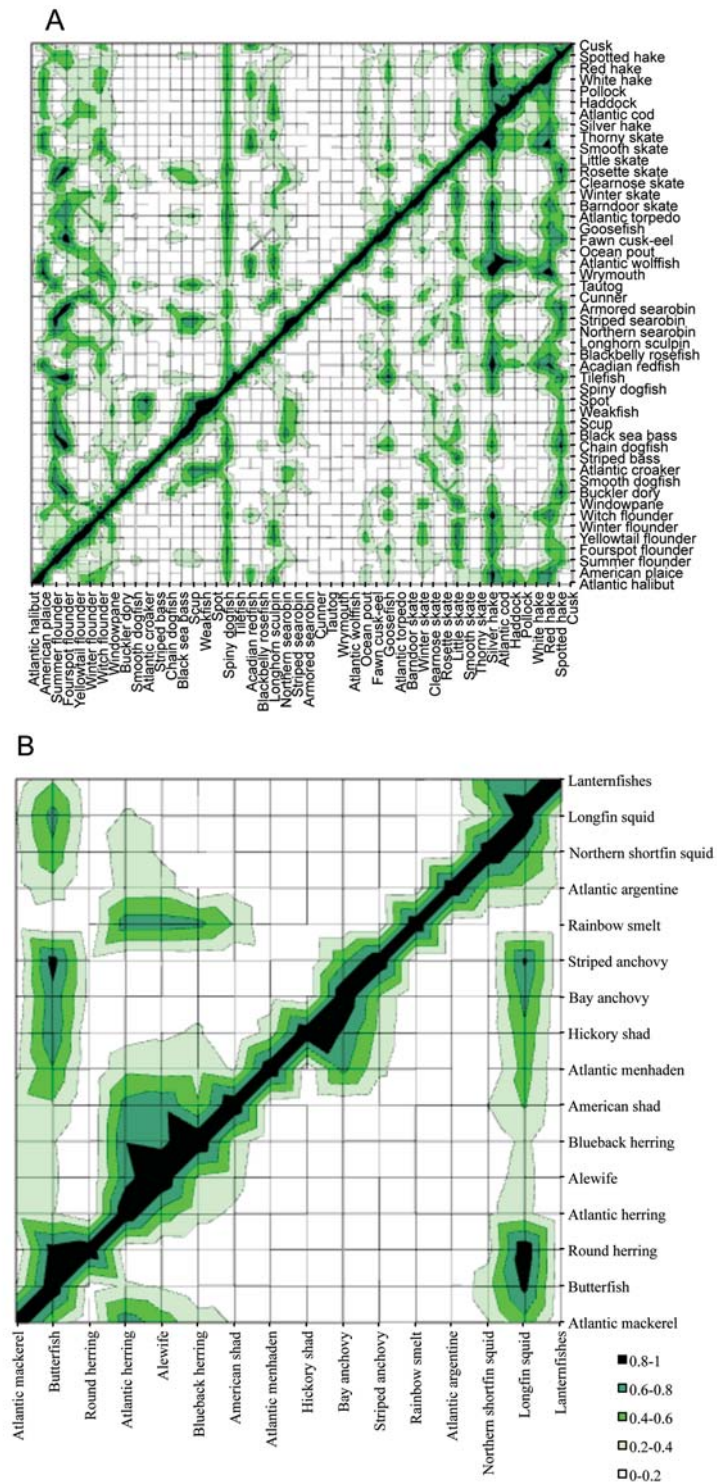


Figure 3. Plot of the matrix of spatial-overlap indices for the fish community from the Northeast United States Large Marine Ecosystem. (A) Demersal species. (B) Pelagic species.

haddock and American plaice, scup and black sea bass), small pelagics (e.g., herring and mackerel), and shrimp feeders (e.g., silver hake and redfish).

**SIMILARITY OF RESOURCE USE.**—Species significantly competing must exhibit, in addition to opposite population trajectories and high spatiotemporal overlap, evidence of overlapping resource use. As species compete, they partition the use of niche space along multidimensional resource axes such that overlap of resource use, and hence competition, is minimized. As a result, distinct guilds form; between-guild competition is minimized and competition within guilds becomes the basis for finer resource partitioning (Root 1967, MacArthur 1970, Schoener 1974a). Ross (1986) has reviewed many of the features associated with resource partitioning by fishes and made the key observation that, for fishes, particularly once habitat aspects of niches based on spatiotemporal overlap have been accounted for, the discussion of resource overlap becomes essentially that of food habits and dietary overlap.

Several studies of fishes from a wide variety of systems demonstrate that high dietary overlap indicates shared resource use (reviewed by Ross 1986; see also Sala and Ballesteros 1997, Garrison and Link 2000a,b, Colloca et al. 2010, Albouy et al. 2011) and therefore high potential for interspecific competition. Certainly species could share resources without competing strongly—for example, if a wide range of prey are available, if the prey species are very productive, if densities of potential competitors are low, or if the potential competitors feed similarly but in different places. When potential fish competitors feed on the same prey in approximately the same amounts, coupled with strong indicators from the prior two evaluation criteria noted above, the potential for competition is high.

Resource overlap, like spatial overlap, can be measured in several ways (see e.g., Schoener 1970, Chesson 1978, Manly et al. 2010). These overlap indices, usually on a scale from 0 to 1, indicate the degree to which a pair of species share a resource. An example is the Schoener overlap index ( $O_{ij}$ ):

$$O_{ij} = 1 - 0.5 \left( \sum_k |p_{ik} - p_{jk}| \right) \quad (\text{Eq. 2})$$

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  $j$ . Values close to 0 indicate minimal resource overlap; values close to 1 indicate high resource overlap.

Again, several methods of resampling can determine the “significance” of a given overlap value (Manly 1997, Garrison 2000, 2001), but again, they are not always feasible, and a rule of thumb is that most overlap values >40% merit consideration, and effectively all values >60% are significant (Ross 1986; Garrison, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL, pers comm). We again endorse this simpler set of approximations when the goal is simply to determine that competition might be occurring.

The information required to calculate this dietary overlap are based on common food-habit (i.e., stomach-content) data. Fish stomach sampling can provide the percentage diet composition (by weight or volume or number, as appropriate) of each prey  $k$ . These diet data can then be integrated across all germane spatial, temporal, ontogenetic, and environmental factors to calculate an index of diet composition

( $D_{ik}$ ) for any given predator  $i$  and prey item  $k$ . These diet compositions would then represent the proportional uses ( $p$ ) in Equation 2 for each competitor  $i$ - $j$  pairing.

An example from the NEUS LME shows that, for most of the fish community, dietary overlap averages approximately 30%–40% (Fig. 4). For some selected species pairs, the overlap is very high (>80%) in demersals (Fig. 4A; e.g., large skates with each other, several medium-sized hakes with each other, sculpins-sea robins-black sea bass) and pelagics (Fig. 4B; e.g., river herrings, squids, herring-mackerel). These higher-overlap pairings (with values >60%) correspond to known feeding guilds (Garrison and Link 2000a,b). For others, the value of overlap is high enough (35%–40%) to warrant consideration; for instance, silver hake and redfish, goosefish and fourspot flounder, and scup and black sea bass.

#### 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 truly daunting, and in many cases, it may simply be infeasible. In other instances, where food-web models have been used to evaluate feeding demands of fishes (see e.g., Coll et al. 2006, 2008, Link et al. 2008, Gaichas et al. 2009, Link 2010b), food resources for fishes have typically appeared to be adequate, because if one prey population declines, predators can switch to alternate prey. Where food is thought to be limiting, some of the key parameters in those models (e.g., EE, C/B, P/B) need to be only slightly adjusted to ensure that mass-balance constraints are maintained. Whether marine systems, at the scale of LMEs, consistently exhibit resource limitation therefore remains unclear.

One possibility would be simply to assume resource limitation if the other three criteria are met. As that assumption may not be satisfactory, other approaches could be implemented.

An indirect method would be to examine the condition factor of fishes ( $K$ ):

$$K = W \cdot 100L^{-3} \quad (\text{Eq. 3})$$

where  $L$  is length (cm),  $W$  is weight (g), and 100 is a scalar depending on units of measure (or can be 100,000 if length is in mm; Fulton 1902, 1904), as averaged or integrated accordingly. Using this condition-factor approach is similar to using the contrasting trajectories of population abundance. If two paired species exhibited opposite trends in  $K$ , then the potential for limiting resources would be implied. Implementation of this criterion should be reasonably simple and straightforward, as lengths and weights of fishes are routinely measured in fisheries surveys. Similarly, one could examine mean lengths of fishes as an even simpler proxy for changes to observed growth and, by inference, changes to the resources needed to realize that observed growth. Because condition factor is a function of the inverse of length cubed, its dynamics tend to be more stable over time (Fig. 5), and major shifts are rarely seen (two examples of such shifts are butterfish, Fig. 5A, and American plaice, Fig. 5C). Mean lengths tend to exhibit more dynamics than condition factor but are generally still relatively stable about the long-term mean (Fig. 6). These two approaches may not be the most promising ways to determine whether resources are limiting for



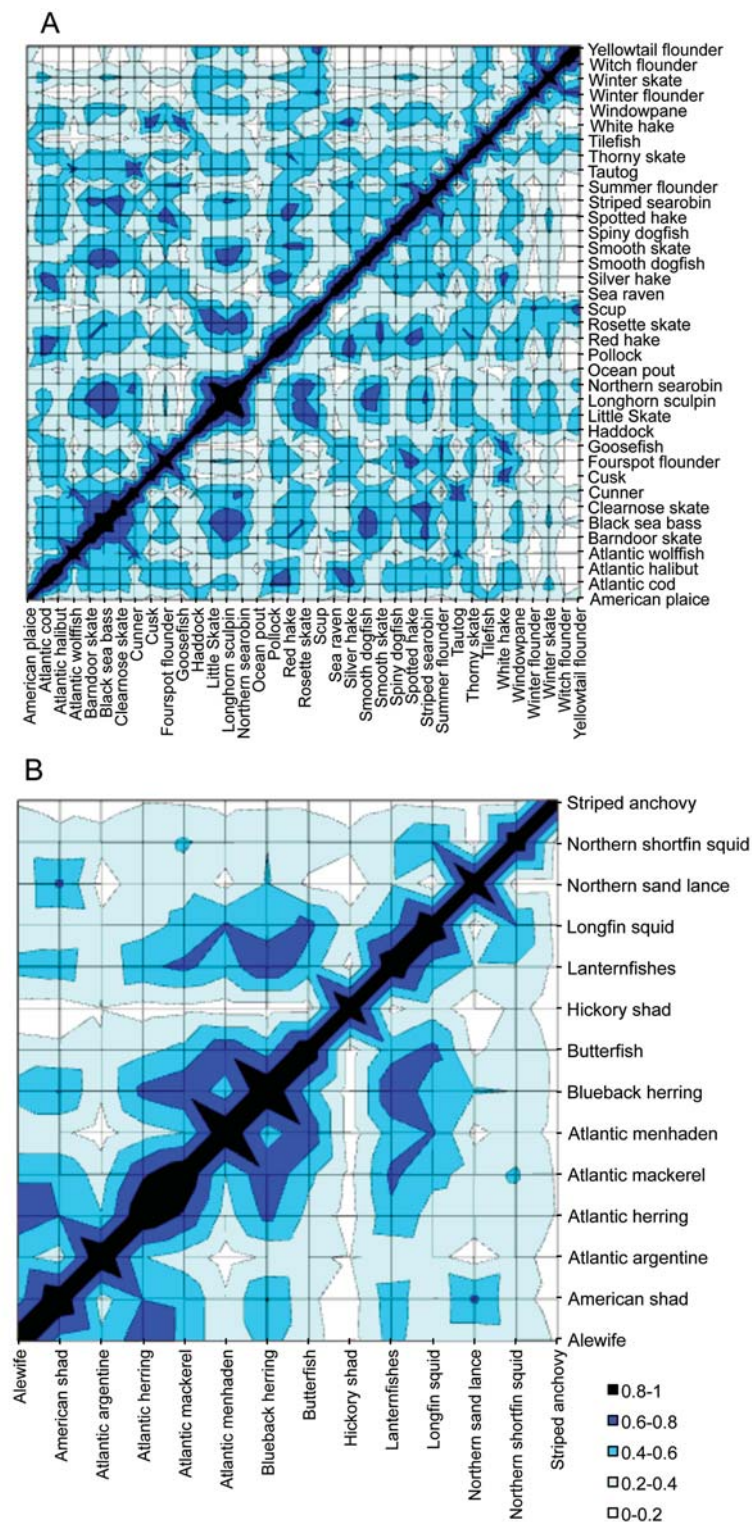


Figure 4. Plot of the matrix of dietary-overlap indices for the fish community from the Northeast United States Large Marine Ecosystem. (A) Demersal species. (B) Pelagic species.

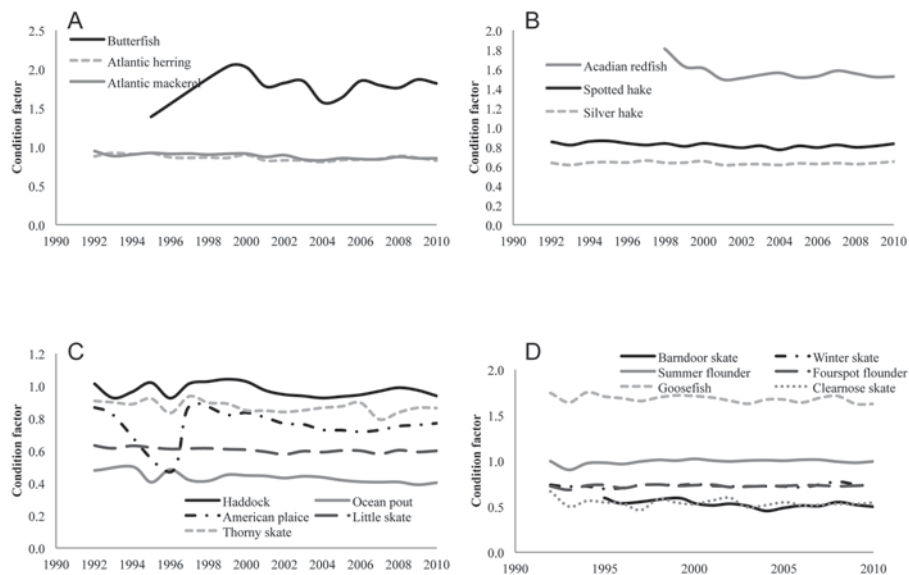


Figure 5. Time series of condition factor (ratio of weight to length) for example species from the Northeast United States Large Marine Ecosystem. (A) Small pelagics. (B) Shrimp-small fish feeders. (C) Benthivores. (D) Piscivores.

fishes, but if remarkable dynamics are observed from these readily available data, then the probability of making a case for competition is increased.

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

$$\%BW = \frac{\bar{S}}{\bar{W}} \cdot 100 \quad (\text{Eq. 4})$$

where  $\bar{S}$  is mean stomach contents and  $\bar{W}$  is mean weight, both in grams. Here the observed stomach-content and individual-weight data commonly sampled on fisheries surveys provide a measure of the ratio 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, opposite trends in %BW for two paired species would indicate the potential for limiting resources. Examples from the NEUS LME show that values across species are readily notable, but trajectories may be more dynamic than that of either condition factor or mean length (Fig. 7). For example, smooth dogfish and longhorn sculpin (Fig. 7A) or ocean pout and American plaice (Fig. 7C) may have different %BW trajectories over time, implying possible changes to their resource availability and usage.

Alternatively, to address the general lack of information associated with this issue, we propose two additional options. One is, if surveys of all the potential prey in a prey field are available, to calculate the ratio of the biomass of prey found in predator stomachs to the total cumulative prey biomass possible. This would additionally evaluate whether food resources for a given species are in fact limited. This prey ratio ( $p'$ ) is:



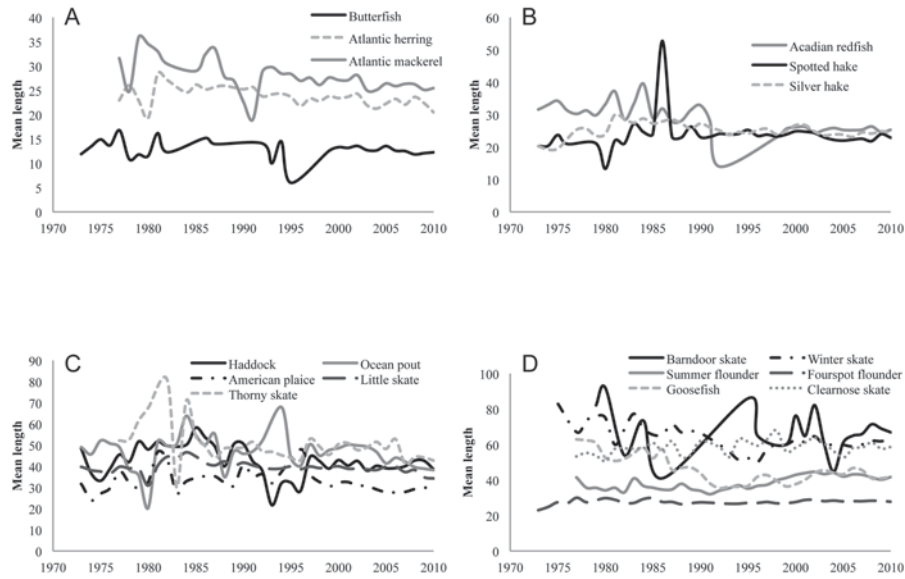


Figure 6. Time series of mean length for example species from the Northeast United States Large Marine Ecosystem. (A) Small pelagics. (B) Shrimp-small fish feeders. (C) Benthivores. (D) Piscivores.

$$p' = \frac{\sum_k B_{ik}}{\sum_k B_k} \quad (\text{Eq. 5})$$

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 to which predator  $i$  and similar predators have access. Examples from the NEUS LME demonstrate that some piscivorous predators (e.g., goosefish) have wide access to the fish prey field, whereas others (e.g., winter skate, fourspot flounder) do not (Fig. 8A). We would propose a threshold of 20%, below which a fish could be considered to have limited prey. This threshold is based on physiological data showing that fishes show early signs 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).

Another alternative, for use if data to calculate  $p'$  are not available, is to calculate a similar type of ratio based on the system's primary producers. Chlorophyll  $a$  values derived from satellite imagery 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 production at higher trophic levels. 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:

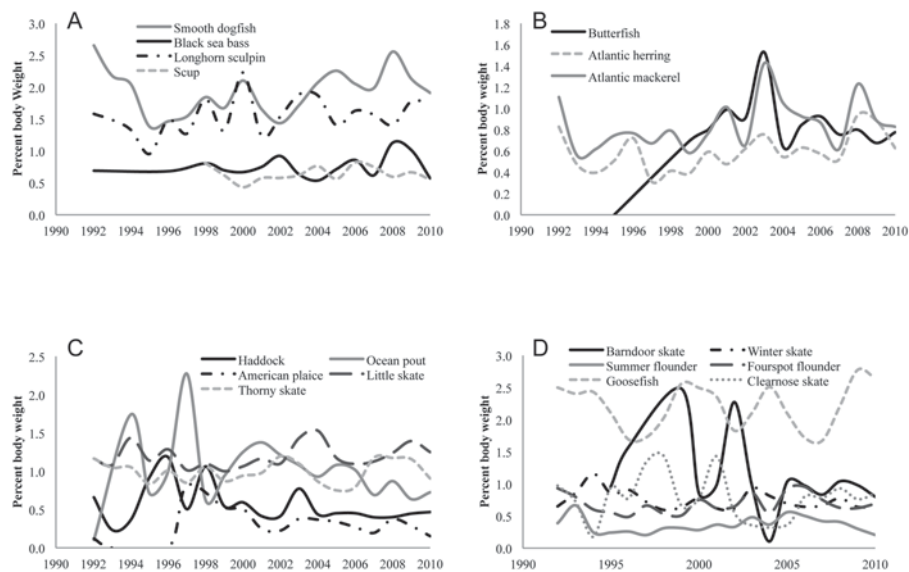


Figure 7. Time series of percent body weight (percentage of fish body weight made up by stomach contents) for example species from the Northeast United States Large Marine Ecosystem. (A) Benthic crab feeders. (B) Small pelagics. (C) Benthivores. (D) Piscivores.

$$p^* = \frac{B_i \cdot 3}{\text{chl } a} \quad (\text{Eq. 6})$$

where  $B_i$  is the biomass of species  $i$ , 3 is the  $C/B$  ratio (which could be adjusted if actually known for the species under consideration),  $\text{chl } a$  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 NEUS LME show that some species are well above a ratio of 1‰, whereas others are much lower than 0.5‰ (Fig. 8B). On the basis of observations from a suite of empirical and food-web modeling studies (Coll et al. 2006, 2008, Link et al. 2008, Link 2010b), we would propose a threshold of 1.5‰, below which a fish could be considered to have limited prey. The theoretical basis for such a threshold is that biomass of each trophic level from the basal one tends to be an order of magnitude lower than the preceding one, as a result of transfer efficiencies of only 15%–20% across trophic levels; fishes at trophic level 3 typically have  $p^*$  ratios on the order of  $10^{-3}$  to  $10^{-4}$  (Link 2010b).

Any one of these five approaches should be feasible with available data, although time-series data for the prey fields in the  $p'$  calculation might be lacking. We propose these as methods to ascertain whether resources might be limiting more rigorous than simply assuming that they are. Of course, they would only need to be applied for individual fish species that had already been deemed to meet the first three criteria, that is, in instances where competition was strongly suspected.

**SYNTHESIS.**—This suite of competition criteria is summarized in Table 1. Our aim here was to establish a protocol that provides a pragmatic, feasible, empirically based, theoretically supported, and relatively rapid means to determine whether competition among fishes merits further consideration. The rules of thumb we suggest (and those from the literature, e.g., Ross 1986, Coll et al. 2008, Link 2010b) for deciding

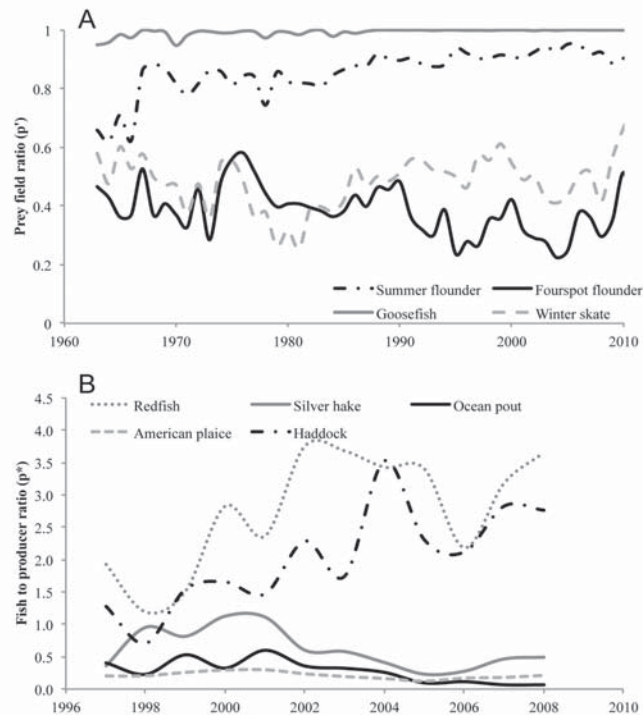


Figure 8. Prey-field ratio (ratio of prey found in predator stomach to total prey available) for example piscivores. (A) The prey-field ratio estimates were for the fish prey field only. (B) Fish to producer ratio (units of fish mass produced per units of primary production, %) for example benthivorous and shrimp-small fish feeding species.

what outcomes merit further consideration provide a simplified approach that affords operational fisheries and ecology practitioners a tool to readily determine whether or not competition warrants further evaluation. Certainly these levels could, and should, be explored in a plethora of simulations, sensitivity analyses, advanced statistics, and so forth, but here we chose to propose this more ad hoc, pragmatic approach, which is based on literature values, empirical evidence from the NEUS LME, and recognition that evaluating a situation often requires adaptation and synthesis of previous research. We do not mean to ignore caveats and the need for further exploration of this protocol; we simply wanted to establish a set of criteria (or at least make a first attempt to do so) for determining whether the magnitude of competition should be explored further.

We also tried to keep this proposed protocol firmly based on data that are commonly available in a fisheries science context. The debate over measuring competition aside (see below), what we propose is an evaluation of whether competition cannot be ruled out, as distinct from measuring it or even proving definitively that it is occurring.

If the criteria we propose are met, and competition is indeed suspected, then the need to calculate interaction terms arises. These terms can be used as important parameters in a wide range of extended stock-assessment, multispecies, food-web, and full-system models (Hollowed et al. 2000a, Townsend et al. 2008). The question

Table 1. Proposed steps to evaluate whether competition might be occurring among pairs of fish species. If these criteria are met, then one would likely need to begin to estimate the magnitude of competition coefficients or interaction terms. Condition factor, ratio of weight to length; percent body weight, percentage of fish body weight made up by stomach contents; prey-field ratio, ratio of prey found in predator stomach to total prey available; fish-to-producer ratio, units of fish mass produced per units of primary production (%).

Evaluation criterion	Value or pattern indicating possible competition
Opposite population trajectories	Population trends of possible competitive pairings exhibiting classical "X" pattern or at least reduced in one member of the pair.
High spatiotemporal overlap	On scale of 0 to 1, value of >60%, "yes"; value of >40%, to be evaluated and considered further. On scale of 0 to $\infty$ , value of >2, "yes"; value of >1, to be evaluated and considered further.
High overlap in resource use	On scale of 0 to 1, value of diet overlap >60%, "yes"; value of >40%, to be evaluated and considered further.
Possibility of limiting resources	From condition factor, mean length, or percent body weight: trends of possible competitive pair exhibiting classical "X" pattern or at least lower-than-expected values in one member of the pair. From prey-field ratio, value <20%. From fish-to-producer ratio, value <1.5%. Else assume that resources are limiting.

becomes: if competition has been rigorously evaluated and deemed highly probable, how would one attempt to measure it?

#### COEFFICIENT ESTIMATION PROTOCOL

An entertaining debate during the mid-1980s addressed the question of whether or not interaction coefficients were obtainable (Rosenzweig et al. 1984, 1985, Pimm 1985, Schoener 1985). The ultimate objective was, and remains, to estimate such coefficients without having to resort to various experimental perturbations (see e.g., Shenbrot and Krasnov 2002). This "holy grail" debate highlighted the two main ways to estimate interaction coefficients (classically denoted as  $\alpha$ 's, but more specific to competition,  $\beta$ 's): through some form of a ratio-overlap method (MacArthur and Levins 1967, Schoener 1974b) or through some form of statistical fitting to "census" data (Pimm 1978, Schoener 1974b, 1985, Emlen 1980). Various methods of estimating this factor have been proposed, but have suffered from one or more limitations: (1) they were linked to data that were highly interpretable to the scale of observation, (2) they were linked to contentious assumptions about the underlying Lotka-Volterra equations or resource-use curves, (3) they were too simplistic and lacked full mechanistic detail, (4) the heterogeneity of the environment in which competition was occurring obviated any "average" niche condition for competition, or (5) they yielded inconsistent results when similar or comparable methods were applied to the same data and situation (Abrams 1975, Rosenzweig et al. 1984, 1985). Development of a model-free, mechanistically supportable, scale-constrained, and scale-appropriate estimate of such interaction coefficients could perhaps provide some insight for the theory of ecology and also for practical use in fisheries management.

Here we detail our attempt to develop an approach to calculate such  $\beta$ 's. By establishing these model-free interaction-strength estimates, we are not tied to a specific functional form and rather aim to “back out” the coefficients using first principles based on known mechanisms and requirements for competition.

What we propose is based on readily available information, neither modeled nor experimental, that can be used to estimate these interaction coefficients. Moreover, most of the information required to calculate such coefficients would have largely already been obtained for the competition-evaluation portion of the protocols we noted above. This approach, although not without caveats, represents one method of moving the scientific debate (and application of its resultant information) forward in addressing this important topic.

**THE RATIO-PRODUCT METHOD.**—The ratio-product method we propose makes use of known facets of competition among fishes. It is also dimensionless and model-free, so it can be applied in whatever functional forms are used to assess the effects of competition among pairs of populations. Effectively, these coefficients are intended to link the effects of one population's abundance on another.

The ratio-product method estimates a competition interaction coefficient,  $\beta$ , to quantify the effects of species  $j$  on species  $i$  as:

$$\beta_{ij} = \frac{O_{ij} \cdot SO_{ij}}{AE_i} \cdot \frac{P_j / B_j}{P_i / B_i} \cdot \frac{L_{\infty,i}}{L_{o,i}} \quad (\text{Eq. 7})$$

where  $O_{ij}$  is the maximum observed dietary overlap between competitors  $i$  and  $j$ ,  $SO_{ij}$  is the maximal observed spatial overlap between species  $i$  and  $j$ ,  $AE_i$  is the assimilation efficiency of species  $i$ , the  $P/B$ s are the production-to-biomass ratios of each species,  $L_{\infty,i}$  is the maximum length for species  $i$ , and  $L_{o,i}$  is the observed average length for species  $i$ . The overlap indices capture the known energy-input and space-usage aspects of fish niches. Both have been described above but would have to be normalized to a 0–1 scale here. The  $O_{ij}$ 's in particular capture the essence of the various forms of  $p_{ik}$ 's noted in prior works (MacArthur and Levins 1967, Schoener 1970, 1974b). Maximum observed values are chosen here because they capture the strongest potential for competition rather than the variation that can occur interannually.

The assimilation efficiencies account for the difference between what fishes consume and what is converted into novel fish tissue. Here and for the most part, the  $AE_i$ 's range between 60% and 90% and here are assumed to be approximately 85% (Link et al. 2006; see FishBase, cited in Froese and Pauly 1994, Froese 2011). The  $O_{ij}$ 's are divided by these  $AE_i$ 's to account for the proportion of the resource actually being used (i.e., the diets,  $D_{ik}$ ; cf. Eq. 2). The  $P/B$ s are included because most  $C/B$ s (which could also be included to reflect consumption rates), at least for teleosts, do not differ widely within a nominal range, whereas similar species, especially even congeners, can differ widely in  $P/B$  (Froese and Pauly 1994, Link et al. 2006, 2008, Froese 2011). If species differed notably in  $C/B$ s, those ratios could be considered here as well. Further, the  $P/B$ s of competitor  $j$  given here either discount, if  $j$  is the competitive dominant, or effectively enhance, if it is the competitive inferior, the potential production of species  $i$ , so as to ultimately reflect the effect of species  $j$  on species  $i$ . These factors effectively capture the relative growth potentials between the

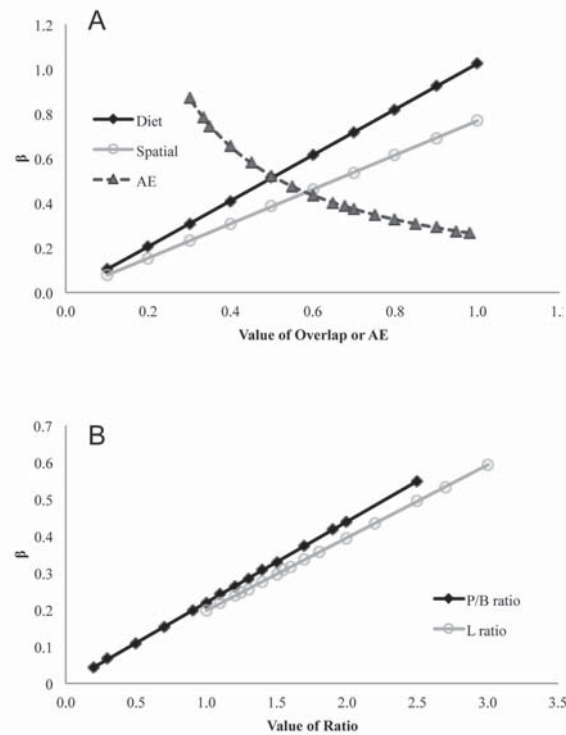


Figure 9. (A) Changes in  $\beta_{ij}$  as a function of changes to  $O_{ij}$ ,  $SO_{ij}$ , and  $AE_i$ . (B) Changes in  $\beta_{ij}$  as a function of changes to  $P_i/B_i/P_j/B_j$  and changes to  $L_{\infty,i}/L_{o,i}$ . All variables as defined in Table 2.

two potentially competing populations and could readily be included as the intrinsic rate of increase,  $r$ , if it is available, but  $r$ 's tend not to be easily measurable.

Finally, we considered including condition factors ( $K$ ) as noted in the evaluation protocol above, but we include length instead because it exhibits less intraannual variability than weight and because  $K$  is significantly modulated when divided by length cubed (Eq. 3). We chose  $L_{\infty}$  for species  $i$  as an indicator of the maximal growth potential; it is determined from standard von Bertalanffy (1934, 1957) growth curves with readily obtainable fish lengths and is then discounted by the average observed lengths of species  $i$  during the spatiotemporal extent of the study. This length ratio reflects the realized potential for competition to be affecting the population. The ratio could also be that of observed to maximum possible weight, but the latter is often harder to determine for fishes, given the nuances of life histories. Effectively this ratio captures the relative amount of realized to potential growth for an affected population.

How to combine these factors has previously been explored in many prior studies (see e.g., MacArthur and Levins 1967, Schoener 1974b, 1985, Pimm 1985, Rosenzweig et al. 1985, Wootton 1997, Berlow et al. 2004, 2009, Wootton and Emerson 2005, Novak and Wootton 2008, Novak 2010). Our ultimate choice was a cross-product of ratios that capture what we assert are the essential facets of competition among fishes. The information needed to calculate these factors in the ratio-product method are readily available for the vast majority of fisheries contexts. The main properties



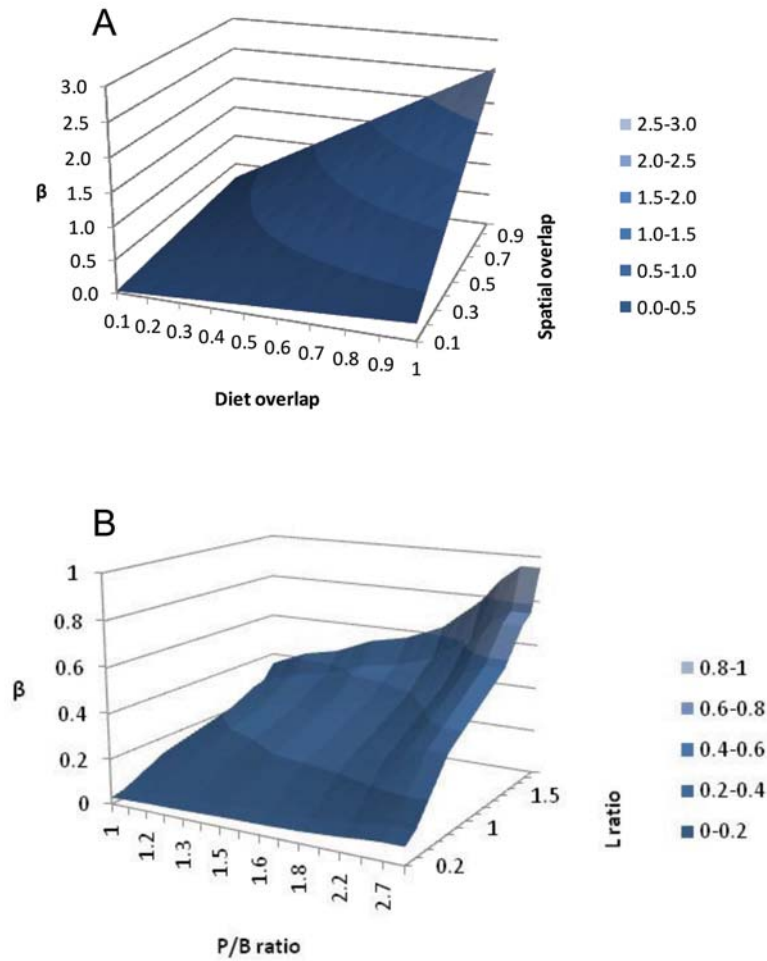


Figure 10. Surface plots: (A) Changes in  $\beta_{ij}$  as a function of changes to  $O_{ij}$  and  $SO_{ij}$ . (B) changes in  $\beta_{ij}$  as a function of changes to  $P_i/B_i/P_j/B_j$  and  $L_{\infty,i}/L_{\infty,j}$ . All variables as defined in Table 2.

of this cross-product certainly should be explored in more detail, perhaps through simulations over the ranges and forms of its inputs. A preliminary sensitivity analysis showed that the two overlap values influence  $\beta$  linearly, and in combination they reinforce one another (Figs. 9A, 10A). The  $P/B$  and length ratios similarly influence  $\beta$  linearly (Fig. 9B), but in combination show a rougher surface as a result of the differential influences of each factor, though still to a lesser extent than the overlap indices (Fig. 10B). The  $AE$  exhibits a curvilinear decay as it increases (Fig. 9A). The  $AE$  observation is important in that, as efficiency increases, the potential for competition declines, implying that species with efficient physiologies are less subject to the effects of competition. Of all these factors, diet overlap seems to have the largest effect on  $\beta$  (Figs. 9, 10).

We readily acknowledge that this formulation could and perhaps should be modified to include other inputs, omit or replace what has been proposed, or explore different ways to combine these features. Yet we propose this ratio-product method as a

first step toward resurrecting competition theory—perhaps as another step in search of the “holy grail”—and for a fisheries context that desperately needs at least an attempt to begin quantifying competition for operational uses.

**EXAMPLE CALCULATIONS.**—Examples from hypothetical situations show one of four main patterns (Table 2). First is that competitive dominants with high spatial overlap (j1) do not need high dietary overlap to produce higher coefficient values. Even the most competitively dominant (j2) would have, if not in the same place as species *i*, a lower coefficient than another species with higher overlap (i.e., j1). Second, competitive inferiors with high spatial overlaps (j4) have much lower coefficient values than the competitive dominants. Third, the same is true for competitive inferiors with high diet overlaps (j3). Finally, the two overlap indices and  $P/B$  appear to trade off, such that a high value of one could be offset by lower values of the other. The sensitivity analyses described above (Figs. 9, 10) support this observation as well.

Examples based on the NEUS LME fish community show a range of potential competition levels (Table 3). These species pairings were selected as described above; key piscivores (fourspot and summer flounders), crab-feeding benthivores (scup and black sea bass), echinoderm-feeding specialists (American plaice, ocean pout, had-dock), and shrimp-small fish feeders (redfish, silver hake) were examined as illustrative cases and for proof of concept. Most of these example  $\beta$ 's ranged from 0.3 to 1, though a few values were more extreme; these central values are comparable in magnitude to prior estimates of such interaction coefficients (sensu Novak 2010; see e.g., Wootton 1997, Berlow et al. 2004, 2009, Wootton and Emerson 2005, Novak and Wootton 2008). Values much larger than 3 or smaller than 0.001 (cf. Wootton 1997) would have raised doubts about the reasonableness of the approach, both from comparison to those other studies and from first principles.

As in the hypothetical example (Table 2), the resultant  $\beta$ 's reflected the combined influence from a range of factors, all of which influencing the estimates of these interaction terms. Interestingly, the  $\beta$ 's within a species pairing were never equal, and although some were comparable, they clearly indicated competitive dominants and inferiors. For example, the potential competitive effect of summer flounder on fourspot flounder is less than vice versa; the same is also clearly true for effects of redfish on silver hake. These results indicate that competition can be estimated regardless of the results of the evaluation protocol but are apt to be strongest with  $\beta$ 's > 0.8. Estimates of  $\beta$ 's greater than 0.8 resulted from high spatial and dietary overlaps, notable distinctions between the  $P/B$  values, and an observed length much lower

Table 2. Example competition-interaction coefficients as calculated for hypothetical situations by the ratio-product method.  $O_{ij}$  is the dietary overlap between species *i* and *j*;  $SO_{ij}$  is the spatiotemporal overlap between species *i* and *j*;  $AE_i$  is the assimilation efficiency of species *i*;  $P_i/B_i$  and  $P_j/B_j$  are the production-to-biomass ratios of species *i* and *j*, respectively;  $L_{\infty,i}$  is the maximum length for species *i*;  $L_{o,i}$  is the average observed length for species *i*; and  $\beta_{ij}$  is the competition-interaction coefficient.

Species	$O_{ij}$	$SO_{ij}$	$AE_i$	$P_i/B_i$	$P_j/B_j$	$L_{\infty,i}$	$L_{o,i}$	$\beta_{ij}$
i			0.85	0.5	—	70	45	
j1	0.4	0.8	—	—	0.7	—	—	0.820
j2	0.6	0.3	—	—	0.9	—	—	0.593
j3	0.7	0.4	—	—	0.4	—	—	0.410
j4	0.3	0.6	—	—	0.3	—	—	0.198

Table 3. Examples of competition-interaction coefficients for species pairings from the Northeast US Large Marine Ecosystem as calculated by the ratio-product method, showing the effect of the first species on the second in each pair.  $O_{ij}$  is the dietary overlap between species  $i$  and  $j$ ;  $SO_{ij}$  is the spatio-temporal overlap between species  $i$  and  $j$ ;  $AE_i$  is the assimilation efficiency of species  $i$ ;  $P_i/B_i$  and  $P_j/B_j$  are the production to biomass ratios of species  $i$  and  $j$ , respectively;  $L_{\infty,i}$  is the maximum length for species  $i$ ;  $L_{o,i}$  is the average observed length for species  $i$ ; and  $\beta_{ij}$  is the competition interaction coefficient.

Species	$O_{ij}$	$SO_{ij}$	$AE_i$	$P_i/B_i$	$P_j/B_j$	$L_{\infty,i}$	$L_{o,i}$	$\beta_{ij}$
Summer flounder on fourspot flounder	0.608	0.485			0.5			0.5157
			0.85	0.6		49	27.46	
Foursplot flounder on summer flounder	0.608	0.502			0.6			0.8182
			0.85	0.5		75	39.50	
Scup on black sea bass	0.362	0.639			0.5			0.6634
			0.85	0.5		62	25.46	
Black sea bass on scup	0.362	0.505			0.5			0.5357
			0.85	0.5		38	15.25	
Ocean pout on haddock	0.282	0.386			0.5			0.1922
			0.85	0.7		88	41.84	
Haddock on ocean pout	0.282	0.389			0.7			0.3883
			0.85	0.5		98	45.56	
American plaice on haddock	0.561	0.509			0.5			0.5046
			0.85	0.7		88	41.84	
Haddock on American plaice	0.561	0.498			0.7			1.0745
			0.85	0.5		70	29.96	
Silver hake on Acadian redfish	0.431	0.928			0.6			1.0073
			0.85	0.5		48	26.90	
Acadian redfish on silver hake	0.431	0.249			0.5			0.3166
			0.85	0.6		76	25.30	

than  $L_{\infty}$ . These instances also showed the clearest distinctions in abundance trends (Fig. 1A, B, G, H, M), clear competitive dominants (Fig. 2C, D, I), strongest observed dynamics in condition factor (Fig. 5B, C), mean length (Fig. 6B–D), and percent body weight (Fig. 7C, D), also corresponding to some of the lower  $p^*$  values (Fig. 8B). That is, where competition was most strongly suspected, the estimation protocol confirmed the suspicions by producing higher values of the interaction coefficients. We assert that, as a proof of concept, the proposed protocol initially seems to result in reasonable, logically consistent outcomes.

## DISCUSSION

The protocol we have described here for determining whether competition is likely to exist between fish species at the scale of continental shelves, and if it is, for calculating competition interaction terms is the first attempt to carry out both facets of this task in a broader ecosystem-based-management context. The dual nature of the approach should not be overlooked; too often only one facet is examined. The rules of thumb proposed here extend previously proposed protocols (see e.g., MacArthur and Levins 1967, Schoener 1974b, 1985, Pimm 1985, Ross 1986) by providing a first attempt to quantify the process. Our results show a promising way forward, making use of data already commonly collected during fisheries surveys to incorporate

another class of species interactions into population assessments and predictions, ultimately for use in fisheries management (Link 2002, 2010a). Although our approach uses ecological patterns that are consistent with theories and observations of competition, we note that technically it does not overtly or definitively prove that competition is, or is not, occurring. However, the interaction terms derived from this approach, when used in any number of population, multispecies, and ecosystem models, will directly account for competition that heretofore had been ignored.

The multiple caveats associated with assumptions about competition derived by our approach must be made clear and potentially addressed. These include a diversity of current and past competitive interactions that may be difficult for this larger-scale approach to detect, including competitive exclusion (Hardin 1960); the “ghost of competition past” (Connell 1980), i.e., cases where competition in the evolutionary past acted as a selective force and led to resource partitioning that minimizes competition in the present time; guild-level competition, where a complex web of competitive interactions are distributed among species within a guild but masked more broadly; and sample-scale issues that could mask the scope of competitive interactions at localized scales or the scale of individuals (especially passive, scramble, and interference competition). Additionally, the full range of considerations regarding multidimensional niche development and resource partitioning (see e.g., Root 1967, MacArthur 1970, Schoener 1974a) remain germane. We acknowledge these caveats and that the approach we describe here is constrained by and suited to the scale of LMEs.

If competition is not suspected to occur, then what? Of course, competition may in fact not be occurring. Alternatively, a mismatch between the spatiotemporal scales at which observations are made and that at which competition operates at particular times and places might mask the existence of such competition. Scaling therefore certainly merits further consideration. We also recognize that competition may be important at the local and individual level; although, as evaluated here, it would not be an important driver at the scale at which populations are assessed and fisheries operate. Variation in competitive interactions across the distribution of a species, effects of variation in local abundance of potential competitors, and scaling of the effects of competition across life-history stages (Hollowed et al. 2000b) can minimize the population-level responses of competition. Conversely, important competition at smaller scales could indeed influence broader-scale, population-level observations. If so, we hope the approach we propose here will detect such effects. Scaling up from individual- to population-level phenomena is an important test for ramping up ecological concepts to relevant population scales and operationalizing ecological concepts for use in a management context. We acknowledge this persistent challenge in ecology (Tilman 1990, Walters and Holling 1990, Fahse et al. 1998), but we also assert that continuing to infer, without evaluation, that local, individual phenomena are automatically translated to broad-scale, population-level responses should be discouraged.

Other factors may be in play that are associated with or amplify the caveats listed above, masking competition at the scale of our observations: ontogenetic variation in distribution (Methratta and Link 2007a,b), trophic-guild membership and associated masking (Garrison and Link 2000a,b), environmental variation in carrying capacity and hence the resource base (Hairston et al. 1960, Oksanen et al. 1981, Pauly and Christensen 1995), facilitation by a third species on a competitive pair (Hay et al.

2004), or the reduction by predation pressure of the effects of competitive dominants (i.e., predator-mediated coexistence, Caswell 1978; see e.g., Paine 1966, 1971, Hall et al. 1970, Dayton 1971). The specific effects of fisheries, where humans serve the role of predator, should particularly be considered in regard to its role in regulating the abundance of competitors (Fogarty and Murawski 1998, Jennings and Kaiser 1998, Link 2002, 2010a, Link et al. 2002).

Despite all these caveats, we assert that the ability to evaluate and estimate competition from already existing information is valuable and sorely needed. We have demonstrated a method of doing so that is pragmatic, easy to apply and that builds on developed theory and readily available data. Where species interactions are suspected, incorporating them can have distinct effects on population estimates and resulting outputs used to manage fisheries resources (Hollowed et al. 2000a, Link 2010a, Tyrrell et al. 2011). The inability to explore cursorily the magnitude of such species interactions can lead to risk-prone management advice; even evaluating the possibility that competition exists is an important step forward in a fisheries context. Estimating the potential magnitude of such interactions and including them in models that estimate population trajectories is a significant step toward better management of fisheries resources. The protocols we propose can and should be widely and readily tested from the perspectives of both theoretical ecology and applied fisheries.

Revisiting the “holy grail” debate (Rosenzweig et al. 1984, 1985, Pimm 1985, Schoener 1985) is intriguing. Our protocol is not the “grail” nor is it perfect—we readily admit that it may need some level of tweaking—yet a continuation of the search for a means to calculate  $\beta$ 's from empirical data definitely seems warranted. We do not claim that estimating interaction coefficients proves or disproves that competition is occurring or that such estimations singularly serve as theoretical advances. Rather, we note that, in many fisheries-related instances, competition has been noted as or suspected of being important (Overholtz and Tyler 1985, Bax 1991, Fogarty et al. 1991, Christensen 1996, Fogarty and Murawski 1998, Jennings and Kaiser 1998, Persson and Hansson 1998, Collie and DeLong 1999, Piet et al. 1999, Hollowed et al. 2000a,b, Munday et al. 2001, Link et al. 2002, Hixon and Jones 2005, Gifford et al. 2009), and here we provide a pragmatic protocol for attempting to assess competition in a quantitative, theoretically defensible, feasible manner. Even Sir Galahad had to take some initial and intermediate steps in his quest for the holy grail, and we posit that the approach we present serves as yet one more step in the quest to unlock the mysteries of competition.

Our goal here was to demonstrate the potential value of a merger among different, underutilized approaches—from individual-based to population scales and from fundamental ecology to applied fisheries. Certainly the intellectual realms of basic ecology and fisheries interests remain divided in many respects, and developments in the two disciplines often remain separated. Although greater integration has occurred especially over the last decade, we note that fisheries data afford an opportunity to test some existing and emerging ecological theories and the opportunity to use those results to inform real-world management issues. Extending general ecological principles to other contexts and situations is important and valuable. Here we highlight the need to do so for other types of LMEs (e.g., boreal, tropical; nonshelf) beyond those used in our examples. In addition, extending these principles into operational approaches is important for other types of aquatic ecosystems (e.g., estuaries, lakes, large rivers). Further extensions of this approach could also be considered

for nonaquatic ecosystems and for terrestrial species. The key consideration would be to develop protocols for evaluating and estimating competition on the basis of readily available data for the broader scales at which economically important populations operate and are managed, without the need for having to resort to experiments or similar approaches geared to smaller scales and individuals.

Heretofore, competition among fishes at the scale of an LME has been suggested, suspected, or simulated, but attempts to evaluate, examine, or quantify it have been rare. The approach and underlying theoretical context that we describe herein is intended to produce some progress toward addressing such species interactions. The necessity of addressing competition, and other forms of species interactions, will only continue to increase in importance as we move toward ecosystem-based fisheries management (Pikitch et al. 2004, Leslie and McLeod 2007, Link 2010a). What we propose herein is one more step in that direction.

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#### LITERATURE CITED

- Abrams P. 1975. Limiting similarity and the form of the competition coefficient. *Theor Popul Biol.* 8:356–375. [http://dx.doi.org/10.1016/0040-5809\(75\)90052-0](http://dx.doi.org/10.1016/0040-5809(75)90052-0)
- Albouy C, Guilhaumon F, Villéger S, Mouchet M, Mercier L, Culioli JM, Tomasini JA, Le Loc'h F, Mouillot D. 2011. Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology. *Mar Ecol Prog Ser.* 436:17–28. <http://dx.doi.org/10.3354/meps09240>
- Auster PJ. 1988. A review of the present state of understanding of marine fish communities. *J Northw Atl Fish Sci.* 8:67–75.
- Auster PJ, Lindholm J, Valentine PC. 2003. Variation in habitat use by juvenile Acadian redfish, *Sebastes fasciatus*. *Environ Biol Fish.* 68:381–389. <http://dx.doi.org/10.1023/B:EBFI.0000005751.30906.d5>
- Auster PJ, Link JS. 2009. Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. *Mar Ecol Prog Ser.* 382:163–172. <http://dx.doi.org/10.3354/meps07962>
- Azarovitz TR. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. *Can Spec Publ Fish Aquat Sci.* 58:62–67.
- Bartlett MS. 1946. On the theoretical specification and sampling properties of autocorrelated time-series. *J R Stat Soc Suppl.* 8:27–41.



- Bax NJ. 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. *ICES Mar Sci Symp.* 193:217–224.
- Berlow EL, Dunne JA, Martinez ND, Stark PB, Williams RJ, Brose U. 2009. Simple prediction of interaction strengths in complex food webs. *Proc Natl Acad Sci USA.* 106:187–191. PMID:19114659. PMCID:2629248. <http://dx.doi.org/10.1073/pnas.0806823106>
- Berlow EL, Neutel A-M, Cohen JE, De Ruiter PC, Ebenman B, Emmerson M, Fox JW, Jansen VAA, Jones JL, Kokkoris GD, et al. 2004. Interaction strengths in food webs: issues and opportunities. *J Anim Ecol.* 73:585–598. <http://dx.doi.org/10.1111/j.0021-8790.2004.00833.x>
- Bjornstad ON, Grenfell BT. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. *Science.* 293:638–643. PMID:11474099. <http://dx.doi.org/10.1126/science.1062226>
- Blanchard JL, Coll M, Cotter J, Link J, Trenkel V, Vergnon R, Yemane D, Shin Y-J. 2010. Trend analysis of indicators: a comparison of recent changes in the status of marine ecosystems around the world. *ICES J Mar Sci.* 67:732–744. <http://dx.doi.org/10.1093/icesjms/fsp282>
- Brown JH, Whitman TG, Morgan Ernest SK, Gehring CA. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science.* 293:643–650. PMID:11474100. <http://dx.doi.org/10.1126/science.293.5530.643>
- Carr MH, Anderson TW, Hixon MA. 2002. Biodiversity, population regulation, and the stability of coral reef fish communities. *Proc Natl Acad Sci USA.* 99:11,241–11,245. PMID:12177430. PMCID:123240. <http://dx.doi.org/10.1073/pnas.162653499>
- Caswell H. 1978. Predator-mediated coexistence: a non-equilibrium model. *Am Nat.* 112:127–154. <http://dx.doi.org/10.1086/283257>
- Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ. 2002. The interaction between predation and competition: a review and synthesis. *Ecol Lett.* 5:302–315. <http://dx.doi.org/10.1046/j.1461-0248.2002.00315.x>
- Chesson J. 1978. Measuring preference in selective predation. *Ecology.* 59:211–215. <http://dx.doi.org/10.2307/1936364>
- Christensen V. 1996. Managing fisheries involving predator prey species. *Rev Fish Biol Fish.* 6:417–442. <http://dx.doi.org/10.1007/BF00164324>
- Coll M, Libralato S, Tudela S, Palomera I, Pranovi F. 2008. Ecosystem overfishing in the ocean. *PLoS One.* 3:e3881. PMID:19066624. PMCID:2587707. <http://dx.doi.org/10.1371/journal.pone.0003881>
- Coll M, Palomera I, Tudela S, Sarda F. 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, northwestern Mediterranean. *J Mar Syst.* 59:63–96. <http://dx.doi.org/10.1016/j.jmarsys.2005.09.001>
- Collie JS, DeLong AK. 1999. Multispecies interactions in the Georges Bank fish community. *In: Ecosystem approaches for fisheries management.* AK-SG-99-01. Alaska Sea Grant College Program. p. 187–210.
- Colloca F, Carpentieri P, Balestri E, Ardizzone G. 2010. Food resource partitioning in a Mediterranean demersal fish assemblage: the effect of body size and niche width. *Mar Biol.* 157:565–574. <http://dx.doi.org/10.1007/s00227-009-1342-7>
- Connell JH. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology.* 42:710–723. <http://dx.doi.org/10.2307/1933500>
- Connell JH. 1961b. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol Monogr.* 31:61–104. <http://dx.doi.org/10.2307/1950746>
- Connell JH. 1980. Diversity and coevolution of competitors, or the ghost of competition past. *Oikos.* 35:131–138. <http://dx.doi.org/10.2307/3544421>
- Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat.* 122:661–696. <http://dx.doi.org/10.1086/284165>

- Cook RR, Auster PJ. 2005. Use of simulated annealing for identifying essential fish habitat in a multi-species context. *Conserv Biol.* 19:876–886. <http://dx.doi.org/10.1111/j.1523-1739.2005.00613.x>
- Dayton PK. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr.* 41:351–89. <http://dx.doi.org/10.2307/1948498>
- Dayton PK. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol Monogr.* 45:137–159. <http://dx.doi.org/10.2307/1942404>
- DeAngelis DL, Waterhouse JC. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecol Monogr.* 57:1–21. <http://dx.doi.org/10.2307/1942636>
- Duplisea DE, Blanchard F. 2005. Relating species and community dynamics in a heavily exploited marine fish community. *Ecosystems.* 8:899–910. <http://dx.doi.org/10.1007/s10021-005-0011-z>
- Elton CS. 1927. *Animal ecology*. London: Sidgwick and Jackson.
- Emlen JM. 1980. Field estimation of competition intensity. *Theor Popul Biol.* 19:275–287. [http://dx.doi.org/10.1016/0040-5809\(81\)90022-8](http://dx.doi.org/10.1016/0040-5809(81)90022-8)
- FAO (Food and Agriculture Organization of the United Nations). 1980. Aquaculture development and coordination programme. Fish feed technology: nutritional bioenergetics in fish. ADCP/REP/80/11.
- Fahse L, Wissel C, Grimm V. 1998. Reconciling classical and individual-based approaches in theoretical population ecology: a protocol for extracting population parameters from individual-based models. *Am Nat.* 152:838–852.
- Fogarty MJ, Murawski SA. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol Appl.* 8:S6–S22.
- Fogarty MJ, Cohen EB, Michaels WL, Morse WW. 1991. Predation and the regulation of sand lance populations: an exploratory analysis. *ICES Mar Sci Symp.* 193:120–124.
- Froese R. 2011. The science in FishBase. *In*: Christensen V, Maclean J, editors. *Ecosystem approaches to fisheries: a global perspective*. Cambridge, UK: Cambridge University Press. p. 47–54.
- Froese R, Pauly D. 1994. FishBase as a tool for comparing the life history patterns of flatfish. *Netherlands J Sea Res.* 32:235–239. [http://dx.doi.org/10.1016/0077-7579\(94\)90001-9](http://dx.doi.org/10.1016/0077-7579(94)90001-9)
- Fulton TW. 1902. The rate of growth of fishes. 20th annual report of the Fishery Board of Scotland. 1902:326–446.
- Fulton TW. 1904. The rate of growth of fishes. 22nd annual report of the Fishery Board of Scotland. 1904:141–241.
- Gaichas S, Skaret G, Falk-Petersen J, Link JS, Overholtz W, Megrey BA, Gjoesaeter H, Stockhausen W, Dommasnes A, Aydin K. 2009. A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. *Prog Oceanogr.* 81:47–62. <http://dx.doi.org/10.1016/j.pocean.2009.04.005>
- Gamble RJ, Link JS. 2009. Analyzing the tradeoffs among ecological and fishing effects on an example fish community: a multispecies (fisheries) production model. *Ecol Model.* 220:2570–2582. <http://dx.doi.org/10.1016/j.ecolmodel.2009.06.022>
- Garrison LP. 2000. Spatial and dietary overlap in the Georges Bank groundfish community. *Can J Fish Aquat Sci.* 57:1679–1691. <http://dx.doi.org/10.1139/f00-117>
- Garrison LP. 2001. Spatial patterns in species composition in the northeast United States continental shelf fish community during 1966–1999. Spatial processes and management of fish populations. *Proceedings of the 17th Lowell Wakefield Fisheries Symposium*. AK-SG-01-02:513–537. Fairbanks: University of Alaska Sea Grant.
- Garrison LP, Link JS. 2000a. Dietary guild structure of the fish community in the Northeast United States Continental Shelf Ecosystem. *Mar Ecol Prog Ser.* 202:231–240. <http://dx.doi.org/10.3354/meps202231>

- Garrison LP, Link JS. 2000b. Fishing effects on spatial distribution and trophic guild structure in the Georges Bank fish community. *ICES J Mar Sci.* 57:723–730. <http://dx.doi.org/10.1006/jmsc.2000.0713>
- Garrison LP, Michaels W, Link JS, Fogarty MJ. 2000. Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem: I. Spatial overlap associated with hydrographic features. *Can J Fish Aquat Sci.* 57:2455–2469. <http://dx.doi.org/10.1139/f00-229>
- Garrison LP, Michaels W, Link JS, Fogarty MJ. 2002. Spatial distribution and overlap between ichthyoplankton and pelagic fish and squids on the southern flank of Georges Bank. *Fish Oceanogr.* 11:267–285. <http://dx.doi.org/10.1046/j.1365-2419.2002.00205.x>
- Gause GF. 1934. *The struggle for existence*. Baltimore: Williams and Wilkins. Reprinted 1964, New York: Hafner.
- Gifford DJ, Collie JS, Steele JH. 2009. Functional diversity in a marine fish community. *ICES J Mar Sci.* 66:791–796. <http://dx.doi.org/10.1093/icesjms/fsp076>
- Goldberg DE, Barton AM. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am Nat.* 139:771–801. <http://dx.doi.org/10.1086/285357>
- Greenstreet SPR, Bryant AD, Broekhuizen N, Hall SJ, Heath MR. 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES J Mar Sci.* 54:243–266. <http://dx.doi.org/10.1006/jmsc.1996.0183>
- Gurevitch J, Morrison JA, Hedges LV. 2000. The interaction between competition and predation: a metaanalysis of field experiments. *Am Nat.* 155:435–453. PMID:10753073. <http://dx.doi.org/10.1086/303337>
- Hairston NG, Smith FE, Slobodkin LB. 1960. Community structure, population control, and competition. *Am Nat.* 94:421–425. <http://dx.doi.org/10.1086/282146>
- Hall DJ, Cooper WE, Werner EE. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol Oceanogr.* 15:839–928. <http://dx.doi.org/10.4319/lo.1970.15.6.0839>
- Hardin G. 1960. The competitive exclusion principle. *Science.* 131:1291–1297. PMID:14399717. <http://dx.doi.org/10.1126/science.131.3409.1292>
- Hay ME, Parker JD, Burkepile D, Caudill CC, Wilson AE, Hallinan ZP, Chequer AD. 2004. Mutualisms and aquatic community structure: the enemy of my enemy is my friend. *Ann Rev Ecol Evol Syst.* 35:175–197. <http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132357>
- Hixon MA, Jones GJ. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology.* 86:2847–2859. <http://dx.doi.org/10.1890/04-1455>
- Hollowed AB, Bax N, Beamish R, Collie J, Fogarty M, Livingston P, Pope J, Rice JC. 2000a. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES J Mar Sci.* 57:707–719. <http://dx.doi.org/10.1006/jmsc.2000.0734>
- Hollowed AB, Ianelli JN, Livingston PA. 2000b. Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock. *ICES J Mar Sci.* 57:279–293. <http://dx.doi.org/10.1006/jmsc.1999.0637>
- Hutchinson GE. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am Nat.* 93:145–159. <http://dx.doi.org/10.1086/282070>
- Jennings S, Kaiser MJ. 1998. The effects of fishing on marine ecosystems. *Adv Mar Biol.* 34:201–352. [http://dx.doi.org/10.1016/S0065-2881\(08\)60212-6](http://dx.doi.org/10.1016/S0065-2881(08)60212-6)
- King AW, Pimm SL. 1983. Diversity and stability: a reconciliation of theoretical and empirical results. *Am Nat.* 122:229–239. <http://dx.doi.org/10.1086/284132>
- Larson RJ. 1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. *Ecol Monogr.* 50:221–239. <http://dx.doi.org/10.2307/1942480>
- Leslie HM, McLeod KL. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Front Ecol Environ.* 5:540–548. <http://dx.doi.org/10.1890/060093>

- Lindholm J, Auster PJ, Knight A. 2007. Site fidelity and movement of Atlantic cod *Gadus morhua* at deep boulder reefs in the western Gulf of Maine. *Mar Ecol Prog Ser.* 342:239–247. <http://dx.doi.org/10.3354/meps342239>
- Link JS. 2002. Ecological considerations in fisheries management: when does it matter? *Fisheries.* 27:10–17. [http://dx.doi.org/10.1577/1548-8446\(2002\)027<0010:ECIFM>2.0.CO;2](http://dx.doi.org/10.1577/1548-8446(2002)027<0010:ECIFM>2.0.CO;2)
- Link JS. 2007. Under-appreciated species in ecology: “ugly fish” in the northwest Atlantic Ocean. *Ecol Appl.* 17:2037–2060. PMID:17974340. <http://dx.doi.org/10.1890/06-1154.1>
- Link JS. 2010a. *Ecosystem-based fisheries management: confronting tradeoffs.* Cambridge, UK: Cambridge University Press.
- Link JS. 2010b. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. *Ecol Model.* 221:1582–1593. <http://dx.doi.org/10.1016/j.ecolmodel.2010.03.012>
- Link JS, Demarest C. 2003. Trawl hangs, baby fish, and closed areas: a win-win scenario. *ICES J Mar Sci.* 60:930–938. [http://dx.doi.org/10.1016/S1054-3139\(03\)00131-0](http://dx.doi.org/10.1016/S1054-3139(03)00131-0)
- Link JS, Garrison LP. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. *Fish Res.* 55:71–86. [http://dx.doi.org/10.1016/S0165-7836\(01\)00300-9](http://dx.doi.org/10.1016/S0165-7836(01)00300-9)
- Link JS, Garrison LP, Almeida FP. 2002. Interactions between elasmobranchs and groundfish species (Gadidae and Pleuronectidae) on the northeast US shelf. I: evaluating predation. *N Am J Fish Manag.* 22:550–562. [http://dx.doi.org/10.1577/1548-8675\(2002\)022<0550:EIBEAG>2.0.CO;2](http://dx.doi.org/10.1577/1548-8675(2002)022<0550:EIBEAG>2.0.CO;2)
- Link JS, Griswold CA, Methratta EM, Gunnard J. 2006. Documentation for the Energy Modeling and Analysis Exercise (EMAX). Northeast Fisheries Science Center Reference Document, 06-15.
- Link J, Overholtz W, O'Reilly J, Green J, Dow D, Palka D, Legault C, Vitaliano J, Guida V, Fogarty M, et al. 2008. The northeast US continental shelf Energy Modeling and Analysis Exercise (EMAX): ecological network model development and ecosystem metrics. *J Mar Syst.* 74:453–474. <http://dx.doi.org/10.1016/j.jmarsys.2008.03.007>
- Lotka AJ. 1925. *Elements of physical biology.* Baltimore: Williams and Wilkins.
- Lotka AJ. 1932. The growth of mixed populations, two species competing for a common food supply. *J Wash Acad Sci.* 22:461–469.
- Lubchenco J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am Nat.* 112:23–39. <http://dx.doi.org/10.1086/283250>
- Lubchenco J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology.* 61:333–344. <http://dx.doi.org/10.2307/1935192>
- MacArthur RH. 1970. Species packing and competitive equilibrium among many species. *Theor Popul Biol.* 1:1–11. [http://dx.doi.org/10.1016/0040-5809\(70\)90039-0](http://dx.doi.org/10.1016/0040-5809(70)90039-0)
- MacArthur R, Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am Nat.* 101:377–385. <http://dx.doi.org/10.1086/282505>
- Manly BFJ. 1997. *Randomization, bootstrap, and Monte Carlo methods in biology.* London: Chapman and Hall.
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2010. *Resource selection by animals: statistical design and analysis for field studies.* 2nd ed. Dordrecht: Kluwer.
- Menge BA, Lubchenco J, Gaines SD, Ashkenas LR. 1986. A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web. *Oecologia.* 71:75–89. <http://dx.doi.org/10.1007/BF00377324>
- Menge JL, Menge BA. 1974. Role of resource allocation, aggression, and spatial heterogeneity in coexistence of two competing intertidal starfish. *Ecol Monogr.* 44:189–209. <http://dx.doi.org/10.2307/1942311>

- Menge BA, Sutherland JP. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am Nat.* 110:351–369. <http://dx.doi.org/10.1086/283073>
- Menge BA, Sutherland JP. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat.* 130:730–757. <http://dx.doi.org/10.1086/284741>
- Methratta ET, Link JS. 2006a. Seasonal variation in groundfish habitat associations in the Gulf of Maine-Georges Bank region. *Mar Ecol Prog Ser.* 326:245–256. <http://dx.doi.org/10.3354/meps326245>
- Methratta E, Link J. 2006b. Associations between surficial sediments and groundfish distributions in the Gulf of Maine-Georges Bank ecosystem. *N Am J Fish Manage.* 26:473–489. <http://dx.doi.org/10.1577/M05-041.1>
- Methratta ET, Link JS. 2007a. Ontogenetic variation in habitat associations for four groundfish species in the Gulf of Maine-Georges Bank ecosystem. *Mar Ecol Prog Ser.* 338:169–181. <http://dx.doi.org/10.3354/meps338169>
- Methratta ET, Link JS. 2007b. Ontogenetic variation in habitat associations for four flatfish species in the Gulf of Maine-Georges Bank ecosystem. *J Fish Biol.* 70:1669–1688. <http://dx.doi.org/10.1111/j.1095-8649.2007.01428.x>
- Mittelbach GG. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology.* 69:614–623. <http://dx.doi.org/10.2307/1941010>
- Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology.* 82:2177–2189. [http://dx.doi.org/10.1890/0012-9658\(2001\)082\[2177:ICACIA\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[2177:ICACIA]2.0.CO;2)
- NEFSC (Northeast Fisheries Science Center). 1988. An evaluation of the bottom trawl survey program of the Northeast Fisheries Science Center. NOAA Tech. Memo. NMFS-F/NEC-52.
- Nicholson MD, Jennings S. 2004. Testing candidate indicators to support ecosystem-based management: the power of monitoring surveys to detect temporal trends in fish community metrics. *ICES J Mar Sci.* 61:35–42. <http://dx.doi.org/10.1016/j.icesjms.2003.09.004>
- Novak M. 2010. Estimating interaction strengths in nature: experimental support for an observational approach. *Ecology.* 91:2394–2405. PMID:20836461. <http://dx.doi.org/10.1890/09-0275.1>
- Novak M, Wootton JT. 2008. Estimating nonlinear interaction strengths: an observation-based method for species-rich food webs. *Ecology.* 89:2083–2089. PMID:18724718. <http://dx.doi.org/10.1890/08-0033.1>
- Nye JA, Joyce TM, Kwon Y-O, Link JS. 2011. Silver hake tracks changes in northwest Atlantic circulation. *Nat Commun.* 2:412. PMID:21811241. <http://dx.doi.org/10.1038/ncomms1420>
- Nye JA, Link JS, Hare JA, Overholtz WJ. 2009. Changing spatial distribution of fish stocks in relation to climate and population size within the northeast United States continental shelf. *Mar Ecol Prog Ser.* 393:111–129. <http://dx.doi.org/10.3354/meps08220>
- Oksanen L, Fretwell SD, Arruda J, Niemela P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am Nat.* 118:240–261. <http://dx.doi.org/10.1086/283817>
- Overholtz WJ, Tyler AV. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. *Fish Bull US.* 83:507–520.
- Paine RT. 1966. Food web complexity and species diversity. *Am Nat.* 100:65–75. <http://dx.doi.org/10.1086/282400>
- Paine RT. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology.* 52:1096–1106. <http://dx.doi.org/10.2307/1933819>
- Paine RT. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology.* 57:858–873. <http://dx.doi.org/10.2307/1941053>
- Palomares MLD, Pauly D. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Mar Freshwat Res.* 49:447–453. <http://dx.doi.org/10.1071/MF98015>



- Pauly D, Christensen V. 1995. Primary production required to sustain global fisheries. *Nature*. 374:255–257. <http://dx.doi.org/10.1038/374255a0>
- Persson A, Hansson LA. 1998. Diet shift in fish following competitive release. *Can J Fish Aquat Sci*. 56:70–78. <http://dx.doi.org/10.1139/f98-141>
- Piet GJ, Pet JS, Guruge WAHP, Vijverberg J, Van Densen WLT. 1999. Resource partitioning along three niche dimensions in a size-structured tropical fish assemblage. *Can J Fish Aquat Sci*. 56:1241–1254. <http://dx.doi.org/10.1139/cjfas-56-7-1241>
- Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, et al. 2004. Ecosystem-based fishery management. *Science*. 305:346–347. PMID:15256658. <http://dx.doi.org/10.1126/science.1098222>
- Pimm SL. 1978. An experimental approach to the effects of predictability on community structure. *Am Zool*. 18:797–808.
- Pimm SL. 1985. Estimating competition coefficients from census data. *Oecologia*. 67:588–590. <http://dx.doi.org/10.1007/BF00790031>
- Root RB. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol Monogr*. 37:317–350. <http://dx.doi.org/10.2307/1942327>
- Rosenzweig ML, Abramsky Z, Brand S. 1984. Estimating species interactions in heterogeneous environments. *Oikos*. 43:329–340. <http://dx.doi.org/10.2307/3544150>
- Rosenzweig ML, Abramsky Z, Kotier B, Mitchell W. 1985. Can interaction coefficients be determined from census data? *Oecologia*. 66:194–198.
- Ross ST. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia*. 1986:352–368. <http://dx.doi.org/10.2307/1444996>
- Sala E, Ballesteros E. 1997. Partitioning of space and food resources by three fish of the genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. *Mar Ecol Prog Ser*. 152:273–283. <http://dx.doi.org/10.3354/meps152273>
- Schoener TW. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*. 51:408–418. <http://dx.doi.org/10.2307/1935376>
- Schoener TW. 1974a. Resource partitioning in ecological communities. *Science*. 185:27–39. PMID:17779277. <http://dx.doi.org/10.1126/science.185.4145.27>
- Schoener TW. 1974b. Some methods for calculating competition coefficients from resource–utilization spectra. *Am Nat*. 108:332–340. <http://dx.doi.org/10.1086/282911>
- Schoener TW. 1983. Field experiments on interspecific competition. *Am Nat*. 122:240–285. <http://dx.doi.org/10.1086/284133>
- Schoener TW. 1985. On the degree of consistency expected when different methods are used to estimate competition coefficients from census data. *Oecologia*. 67:591–592. <http://dx.doi.org/10.1007/BF00790032>
- Shenbrot G, Krasnov B. 2002. Can interaction coefficients be determined from census data? Testing two estimation methods with Negev desert rodents. *Oikos*. 99:47–58. <http://dx.doi.org/10.1034/j.1600-0706.2002.990105.x>
- Sherman K. 1991. The large marine ecosystem concept: research and management strategy for living marine resources. *Ecol Appl*. 1:349–360. <http://dx.doi.org/10.2307/1941896>
- Sih AP, Crowley P, McPeck M, Petranka J, Strohmeier K. 1985. Predation, competition, and prey communities: a review of field experiments. *Ann Rev Ecol Syst*. 16:269–311. <http://dx.doi.org/10.1146/annurev.es.16.110185.001413>
- Tilman D. 1990. Constraints and tradeoffs: towards a predictive theory of competition and succession. *Oikos*. 58: 3–15. <http://dx.doi.org/10.2307/3565355>
- Townsend HM, Link JS, Osgood KE, Gedamke T, Watters GM, Polovina JJ, Levin PS, Cyr N, Aydin KY, editors. 2008. Report of the NEMoW (National Ecosystem Modeling Workshop). NOAA Technical Memorandum NMFS-F/SPO-87.
- Tyrrell MC, Link JS, Moustahfid H. 2011. The importance of including predation in some fish population models: implications for biological reference points. *Fish Res*. 108:1–8. <http://dx.doi.org/10.1016/j.fishres.2010.12.025>



- Volterra V. 1926. Fluctuations in the abundance of a species considered mathematically. *Nature*. 118:558–560. <http://dx.doi.org/10.1038/118558a0>
- von Bertalanffy L. 1934. Untersuchungen über die Gesetzmäßigkeit des Wachstums. I. Allgemeine Grundlagen der Theorie; mathematische und physiologische Gesetzmäßigkeiten des Wachstums bei Wassertieren. *Arch Entwicklungsmech*. 131:613–652 (translated into English).
- von Bertalanffy L. 1957. Quantitative laws in metabolism and growth. *Q Rev Biol*. 32:217–231. PMID:13485376. <http://dx.doi.org/10.1086/401873>
- Walters C. 1986. *Adaptive management of renewable resources*. Caldwell, NJ: Blackburn Press.
- Walters CJ, Holling CS. 1990. Large-scale management experiments and learning by doing. *Ecology*. 71:2060–2068. <http://dx.doi.org/10.2307/1938620>
- Werner EE. 1977. Species packing and niche complementarity in three sunfishes. *Am Nat*. 111:553–578. <http://dx.doi.org/10.1086/283184>
- Werner EE, Hall DJ. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology*. 58:869–876. <http://dx.doi.org/10.2307/1936222>
- Williamson CE. 1993. Linking predation risk models with behavioral mechanisms: identifying population bottlenecks. *Ecology*. 74:320–331. <http://dx.doi.org/10.2307/1939295>
- Winberg GG. 1956. Rate of metabolism and food requirements of fishes. *Fish Res Board Can Transl Serv*. 194.
- Wootton JT. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecol Monogr*. 67:45–64. [http://dx.doi.org/10.1890/0012-9615\(1997\)067\[0045:EATOPC\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(1997)067[0045:EATOPC]2.0.CO;2)
- Wootton JT, Emmerson M. 2005. Measurement of interaction strength in nature. *Ann Rev Ecol Evol Syst*. 36:419–444. <http://dx.doi.org/10.1146/annurev.ecolsys.36.091704.175535>
- Zaret TM, Rand AS. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology*. 52:336–342. <http://dx.doi.org/10.2307/1934593>
- Zuur AF, Ieno EN, Smith GM. 2007. *Analyzing ecological data*. New York: Springer.

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Appendix 1. Common and scientific names of species examined for our study. Species emphasized in the text as potential competitive pairs are marked with asterisks.

Common name	Scientific name
Acadian redfish*	<i>Sebastes fasciatus</i> Storer, 1854
Alewife	<i>Alosa pseudoharengus</i> (Wilson, 1811)
American plaice*	<i>Hippoglossoides platessoides</i> (Fabricius, 1780)
American shad	<i>Alosa sapidissima</i> (Wilson, 1811)
Armored searobin	<i>Peristedion miniatum</i> Goode, 1880
Atlantic argentine	<i>Argentina silus</i> (Ascanius, 1775)
Atlantic cod	<i>Gadus morhua</i> Linnaeus, 1758
Atlantic croaker	<i>Micropogonias undulatus</i> (Linnaeus, 1766)
Atlantic halibut	<i>Hippoglossus hippoglossus</i> (Linnaeus, 1758)
Atlantic herring	<i>Clupea harengus</i> Linnaeus 1758
Atlantic mackerel	<i>Scomber scombrus</i> Linnaeus, 1758
Atlantic menhaden	<i>Brevoortia tyrannus</i> (Latrobe, 1802)
Atlantic torpedo	<i>Torpedo nobiliana</i> Bonaparte, 1835
Atlantic wolffish	<i>Anarhichas lupus</i> Linnaeus, 1758
Barndoor skate	<i>Raja laevis</i> Mitchill, 1818
Bay anchovy	<i>Anchoa mitchilli</i> (Valenciennes, 1848)
Black sea bass*	<i>Centropristis striata</i> (Linnaeus, 1758)
Blackbelly rosefish	<i>Helicolenus dactylopterus</i> (Delaroche, 1809)
Blueback herring	<i>Alosa aestivalis</i> (Mitchill, 1814)
Buckler dory	<i>Zenopsis conchifera</i> (Lowe, 1852)
Butterfish	<i>Peprilus triacanthus</i> (Peck, 1804)
Chain dogfish	<i>Scyliorhinus retifer</i> (Garman, 1881)
Clearnose skate	<i>Raja eglanteria</i> Bosc, 1800
Cunner	<i>Tautoglabrus adspersus</i> (Walbaum, 1792)
Cusk	<i>Brosme brosme</i> (Ascanius, 1772)
Fawn cusk-eel	<i>Lepophidium profundorum</i> (Gill, 1863)
Fourspot flounder*	<i>Hippoglossina oblonga</i> (Mitchill, 1815)
Goosefish	<i>Lophius americanus</i> Valenciennes in Cuvier and Valenciennes, 1837
Haddock*	<i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)
Hickory shad	<i>Alosa mediocris</i> (Mitchill, 1814)
Lanternfishes	Myctophidae
Little skate	<i>Raja erinacea</i> Mitchill, 1825
Longfin squid	<i>Loligo pealeii</i> Lesueur, 1821
Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i> (Mitchill, 1814)
Northern searobin	<i>Prionotus carolinus</i> (Linnaeus, 1771)
Northern shortfin squid	<i>Illex illecebrosus</i> (Lesueur, 1821)
Ocean pout*	<i>Zoarces americanus</i> (Bloch and Schneider, 1801)
Pollock	<i>Pollachius virens</i> (Linnaeus, 1758)
Rainbow smelt	<i>Osmerus mordax</i> (Mitchill, 1814)
Red hake	<i>Urophycis chuss</i> (Walbaum, 1792)
Rosette skate	<i>Raja garmani</i> Whitley, 1939
Round herring	<i>Etrumeus teres</i> (DeKay, 1842)
Scup*	<i>Stenotomus chrysops</i> (Linnaeus, 1766)
Silver hake*	<i>Merluccius bilinearis</i> (Mitchill, 1814)
Smooth dogfish	<i>Mustelus canis</i> (Mitchill, 1815)
Smooth skate	<i>Raja senta</i> Garman, 1885

## Appendix 1. Continued.

Common name	Scientific name
Spiny dogfish	<i>Squalus acanthias</i> Linnaeus, 1758
Spot	<i>Leiostomus xanthurus</i> Lacépède, 1802
Spotted hake	<i>Urophycis regia</i> (Walbaum, 1792)
Striped anchovy	<i>Anchoa hepsetus</i> (Linnaeus, 1758)
Striped bass	<i>Morone saxatilis</i> (Walbaum, 1792)
Striped searobin	<i>Prionotus evolans</i> (Linnaeus, 1766)
Summer flounder*	<i>Paralichthys dentatus</i> (Linnaeus, 1766)
Tautog	<i>Tautoga onitis</i> (Linnaeus, 1758)
Thorny skate	<i>Raja radiata</i> Donovan, 1808
Tilefish	<i>Lopholatilus chamaeleonticeps</i> Goode and Bean, 1879
Weakfish	<i>Cynoscion regalis</i> (Bloch and Schneider, 1801)
White hake	<i>Urophycis tenuis</i> (Mitchill, 1814)
Windowpane	<i>Scophthalmus aquosus</i> (Mitchill, 1815)
Winter flounder	<i>Pseudopleuronectes americanus</i> (Walbaum, 1792)
Winter skate	<i>Raja ocellata</i> Mitchill, 1815
Witch flounder	<i>Glyptocephalus cynoglossus</i> (Linnaeus, 1758)
Wrymouth	<i>Cryptacanthodes maculatus</i> Storer, 1839
Yellowtail flounder	<i>Limanda ferruginea</i> (Storer, 1839)