Patterns of variability in predation on marine fish

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**Abstract**

**People have considered some things for a long time. There is one thing about these things that we don’t know about. Here we took some things and did some things to them to learn more about the things we don’t know about. We found some things that were interesting. These things have broad implications for lots of other things.**

**Keywords: things**

**Ok, but really:** The relative importance of how predator consumption shapes population, community, and ecosystem scale processes is still an active area of study in ecology. In general, it is thought that predation is a more important structuring force in simple food webs with fewer and stronger trophic connections, and is less important in large complex ecosystems such as those found off continental shelves. When there are many predator populations, increases in one can be compensated for with declines in another, resulting in a relatively constant rate of predation mortality overall. The two hypothesized mechanisms for this are statistical averaging, where populations vary independently of one another, and compensatory dynamics, where populations vary asynchronously. We utilized a comparative database of biomasses of (mainly) commercial fish species across 11 large marine ecosystems and paired it with mass-balance food web models of each system to ask two main questions. First, how diverse are sources of predation in large marine ecosystems, and second, how do species within predator assemblages vary with another, and do these patterns result in a dampening of variability of the assemblage at large. We found that the predator assemblages were only moderately diverse; approximately one-third of the assemblages we studied had a single predator accounting for over half of all predation. We did find evidence that, in general, more diverse predator assemblages are more temporally stable due to independently fluctuating predator populations. However, we also saw ecosystems with non-independent predator assemblages, both synchronous and asynchronous. Assemblages that are either synchronous or that have low diversity have a greater potential to vary dramatically and result in large-scale changes throughout the social-ecological system. Therefore, quantifying and understanding this potential is important in order to target systems where precautionary management of predators might be particularly important.

**Keywords:** things

**Introduction**

It has long been acknowledged that trophic processes have the potential to drive changes in the abundances of populations, which has important implications for management of exploited ecosystems. Ecosystem and predator-prey models driven from the top down by predation tend to have dynamics that are more non-linear, harder to understand, and less predictable (Pace *et al.*, 1999). Therefore, when and if exploited ecosystems are dominated by top down control, they can be difficult to manage due to their increased susceptibility to dramatic community shifts and less predictable responses to perturbations, whether anthropogenic or environmental (Estes *et al.*, 2011). Importantly, the strength of predation control and trophic cascades is remarkably variable among systems, even within a system type (Shurin *et al.*, 2002). Therefore, understanding what drives the population- and community-scale consequences of consumption is a key question in ecology.

The influence of predation likely depends, in part, on community structure and dynamics. Ecologists often predict that species in complex, diverse food webs with many weak trophic linkages are buffered from top-down down control and community-wide trophic cascades because of compensatory responses of predators (Strong, 1992). This is because species are subject to a diverse assemblage of predators whose temporal dynamics are not synchronized, so prey experience a relatively constant rate of predation even if a single predator undergoes a large reduction in abundance (Power, 1992; Polis and Strong, 1996). Under this view, changes in a single predator population are unlikely to cascade through the food web and result in species cascades, and the diversity of predator populations prevents community cascades from occurring (Polis, 1999). However, diversity does not necessarily render dramatic community cascades impossible if exploitation or any other driver suddenly depletes the entire guild of predators at once (Baum and Worm, 2009).

There are two possible explanations for why more diverse predator guilds should be more temporally stable. First, compensatory dynamics occur in diverse assemblages of similar species that have complementary responses to the environment, resulting in asynchronous populations (Gonzalez and Loreau, 2009). The idea of compensatory dynamics hypothesizes that species within communities have evolved to maximize the niche space utilized, so that one population compensate for changes in another (Tilman, 1996). Second, the statistical averaging hypothesis puts forth that the stabilization occurs because populations simply vary in a statistically independent manner, and so the standard deviation of their sum is less than the sum of their standard deviations; this is the same statistical mechanism that causes the standard error of the mean to decrease with increasing sample size (Doak *et al.*, 1998). Either mechanism can dampen the importance of predation in driving population fluctuations of prey, and thus increase stability, in more diverse ecosystems.

Empirical evidence in large marine ecosystems for compensatory dynamics and the negative effect of diversity on the strength of predator control is mixed. The dominance of bottom-up control in marine systems, as measured between adjacent trophic levels, has been found to be correlated with higher predator diversity (Frank *et al.*, 2006; Boyce *et al.*, 2015), though simple correlations between predators and prey that are frequently used in such studies can be poor metrics (Pershing *et al.*, 2015). Work across system types on trophic cascades (i.e., separated by two trophic levels) has found no relationship between species richness at any trophic level and the strength of top-down control (Borer *et al.*, 2005). Actual examination of the possible mechanisms for a relationship between diversity and trophic control, either functional complementarity or statistical averaging, has generally been difficult to assess in large marine ecosystems because of data requirements and slow rates of population turnover (Naeem, 2006). Lindegren *et al.* (2016) found evidence supporting the hypothesis of functional complementarity in several trophic guilds, including predators, in the Southern California Current, but there is still a need to take a comparative cross-system examination (Link *et al.*, 2012) that explicitly explores the mechanisms by which predator diversity could decrease top-down regulation.

To understand linkages between predator diversity and top-down regulation, we first must develop meaningful time series of predation intensity that account for the different roles each species plays. To date, metrics of predation have generally taken one of two fairly simple approaches that both benefit from being easy to compute and understand, but also have key weaknesses. The first method is to sum the abundances of all piscivorous species (e.g., Frank *et al.*, 2005; Lucey *et al.*, 2012; Lindegren *et al.*, 2016). This approach acknowledges that species are predated upon by a diverse assemblage of consumers, allowing the potential to test hypotheses about connections between predator diversity and top-down control. However, it ignores the fact that some predators are relatively minor consumers (i.e., comprise a small amount of predation mortality) while others might be more important, either due to different consumption rates, diets, or habitat overlap. The second approach is to take a single species that is thought to be particularly important and track only its abundance (e.g., Worm and Myers, 2003; Holsman *et al.*, 2012; Minto and Worm, 2012). This acknowledges the outsize importance of key predator species, but ignores secondary predators that may still consume significant prey biomass. Most importantly it prevents any examination of functional complementarity or diversity-stability relationships because there is only one predator population. Therefore, new metrics are needed to bridge the divide between these two endpoints.

In this study, we take a unique comparative database of multispecies abundances across large marine ecosystems in North America and Europe to ask how diverse marine predator assemblages are, and to establish a mechanism by which increased predator diversity could promote bottom-up control and community stability. We combine these abundance data with information on diet and consumption compiled in mass-balance food web models for each system to better quantify predator assemblages from the perspective of different prey populations. We then 1) quantify whether and in what cases predation tends to come from many different consumers versus a smaller number of key species, and 2) examine the relationship between predator diversity and synchrony within the predator assemblages. Predator assemblages can vary asynchronously (consistent with compensatory dynamics), independently (consistent with statistical averaging), or synchronously (Fig. 1). Predator assemblages that are more synchronous display more temporal variability that is not dampened by increased predator diversity; systems with such predator assemblages should be more susceptible to predator control. We explore whether those three modes of variation are associated with diversity of the predator assemblage, or if one mode is dominant across systems.

**Methods**

We combined published static food web models (Christensen and Pauly, 1992) with abundance information from surveys and stock assessments across large marine ecosystems in Europe and North America to create a multi-component index of predation on mid-trophic level species and to quantify how the index and its components have varied through time. First, we developed a multi-component index of predation. Second, we examined this index at the mass-balance model equilibrium biomasses (static analysis), and third, across the time series of biomasses (dynamic analysis). The static and dynamic analyses were useful for understanding predation in different ways. For a list of ecosystems and prey species included and the food web models used, see Table 1. Abundance information is from the database compiled in Fu *et al.* (2012).

*Developing the predation index*

First, we developed a predator index that is unique to each prey species. The simplest estimate of an index of predation might simply sum the abundances of all predators that are known to consume a given prey species. The ideal estimate would explicitly quantify each predator’s contribution to natural mortality every year, accounting for a host of ecological factors we are unlikely to ever fully resolve. Here, we attempt to find a middle ground that captures more complexity than a simple sum, but still makes a number of simplifying assumptions in order to allow us to calculate the index for multiple prey species across many ecosystems.

Our predator index is a weighted sum of predator abundances where the weighting factors are determined by estimates from static food web models of the predator consumption rates and diets. Specifically, the weights are calculated as the product of consumption rate per unit biomass and the fraction of predator diet that consists of the prey. Both of these inputs come from a static model based on a distinct time period relative to our abundance time series. Still, this is a simple, albeit imperfect, way to judge predator fluctuations that improves upon a straight summation by weighting some predators more than others. The weight for predator *i* with respect to the predator index for prey *j*, *Wi,j* is written as:

where *QB* is the annual consumption to biomass ratio and *Di,j* is the fraction of predator species *i*’s diet that species *j* makes up. Some food web models divided species into juvenile and adult stages, but our time series of abundance data did not. We therefore averaged the weights for the juvenile and adult life stages based on their relative biomasses in the static model. When prey species were divided into juvenile and adult stages, we quantified predation on the juvenile stage because predation tends to be more important and detectable when it targets those ages (Oken and Essington, 2015). While juvenile functional groups in food web models tend to be more data-poor, we note that, as prey species, we use diet information of groups *consuming* juveniles, and do not use juvenile diets or consumption rates (unless the juveniles are themselves predators).

We attempted to select the important mid-trophic level species within a system as prey species. Experts from each ecosystem in the analysis had initially classified all species in the system based on taxonomic grouping and size, among other characteristics (Fu *et al.*, 2012). In general, we selected as prey any food web functional group that contained forage fish, clupeids, gadids and pleuronectids that were classified as “small,” and any other species or species groups local experts thought were key for transferring energy from low to high trophic levels.

*Static analysis*

First, we calculated the predation index at the biomasses associated with the static model equilibria. To do this, we multiplied the weights in equation (1) by the baseline biomasses from the static models, an approximation of species’ relative abundances in the ecosystem. Therefore, the contribution of predator functional group *i* to the static predator index for prey group *j*, *Pi,j* is:

where *Bi,0* is the static model biomass of functional group *i.* Furthermore, the total predator index for prey group *j*, *Pj* is the sum of *Pi,j* over all predators *i*.

Using this static predation index, we examined the proportion of baseline predation mortality (from the equilibrium model) that was attributable to the species for which we have biomass time series data. To do so, we checked which functional groups contained at least one species found in the abundance time series, and calculated what fraction of predation mortality those functional groups made up.

We also used these static calculations to assess the hypothesis that predation is distributed diffusely among many different species. One key advantage to using the static calculations for this analysis was that we were able to include all predators, even those not included in the abundance data. We ranked predators in descending order of the *Pi,j* and then compared the proportion of predation mortality attributable to the top ranked and second ranked predator for each prey species.

*Dynamic analysis*

We then examined how the predator index and its component parts varied through time. We again used the weights from equation (1) to calculate the dynamic predator index, but used the time series of predator biomasses instead of the single value in the static food web model. In addition, the time series data had more taxonomic detail than the food web models. When several species were part of the same functional group in the food web model, they were included as separate components in the index, but all received the same weight that was calculated for that functional group. This assumes that all species within a functional group have grossly similar diets and consumption rates. Thus, the contribution of predator species *ik* within functional group *i* to the predator index for prey group *j*,at time *t*, *Pi,k,j­(t)*, is:

Once again, the total dynamic predator index, *Pj(t)* is the sum over all predator species of the *Pi,k,j(t)*. Missing data were imputed using linear interpolation.

We used the variance ratio as a metric of synchrony or asynchrony within a given predator guild. The variance ratio is commonly used to measure compensatory dynamics (Gonzalez and Loreau, 2009), and can be interpreted as a metric of correlation in a multivariate dataset (as opposed to bivariate). We calculated the variance ratio of the predator index for prey group *j, VRj* as:

The variance ratio measures the degree of synchrony (Fig. 1, black line) or asynchrony (Fig. 1, light gray line) within a guild, and is equal to one when the components are, on average, statistically independent (covariances sum to zero, Fig. 1, dark gray line). Therefore, it allows us to test whether predator assemblages display patterns consistent with compensatory dynamics (asynchrony) or independently fluctuating predator populations, both of which would cause predator diversity to stabilize the predator index, or if predator assemblages display synchronous dynamics consistent with similar responses to a shared driver, which would inflate predator variability and make the system more susceptible to community cascades.

We then examined how the variance ratio was related to diversity (species richness) of the predator guild. We used species richness as a metric of diversity because the expected value of the variance ratio is directly proportional to the number of components over which it is calculated, if average pairwise correlation among the species remains constant with the addition of more predator populations. We therefore wished to account for this expected relationship to reveal deviations from it that would signify stronger or weaker correlations among predator species within the assemblages. However, species richness is potentially problematic because it treats all species as identical so that rare or relatively unimportant predators inflate the species richness To solve this problem, we recalculated the variance ratio and species counts for a subset of the original guild of predator species: the minimum number of predators that account for at least 90% of the time average of the total dynamic predator index. In this way, we accounted for the majority of predation, but when many predators made up only a small portion of total predation, they did not inflate the diversity metric.

To measure precision and uncertainty in the inferences drawn from the variance ratios regarding synchrony of the predator assemblages, we bootstrapped the variance ratios under the null assumption that predator populations are independent (i.e., an expected variance ratio of one, consistent with the statistical averaging hypothesis). If the observed variance ratio falls in the tails of the distribution of bootstrapped variance ratios, this is evidence that the predator populations are not statistically independent, and either display synchrony or asynchrony. To account for the serial nature of the time series data, we used phase scrambling, which is effective for statistics like the variance ratio that are independent of statistical location (Davison and Hinkley, 1997; Solow and Duplisea, 2007). When a single species dominates the predator index, but there are still many component species, the null distribution of the variance ratio tended to become extremely tightly centered about one; the variance of the sum and the sum of the variances are both nearly equal to the variance of the dominant species. Therefore, for ease in plotting the distributions, we only bootstrapped the variance ratios of the core predator species. This had no qualitative impact on results, besides the aforementioned cases.

All analysis was done in R version 3.3.0 (R Core Team, 2016). Bootstrapping was done with the boot package (Canty and Ripley, 2016).

**Results**

In the nearly one-third of cases (19/30), we had time series for species that covered functional groups accounting for at least 50% of total predation mortality, as quantified in the mass balance models (Fig. 2). The Gulf of Maine and Georges Bank were exceptions, where gelatinous zooplankton account for greater than 70% of predation mortality across prey functional groups and systems. While forage species are not a significant component of gelatinous zooplankton diets, their consumption rate in the model that was two to three orders of magnitude more than predatory fish caused the effect to dominate. The other exceptional cases were due to marine mammals: Atlantic herring in the Barents Sea where whales and seals account for 89% of predation and Pacific herring in the Eastern Bering Sea where seals account for 81% of predation.

The diversity of predation sources varied widely among species and systems (Fig. 3,4). In approximately one-third (9/30) of the prey species, there was a single predator functional group accounting for over 50% of predation. While this metric is dependent on the degree of taxonomic detail in the food web model, three of those prey functional groups (Gulf of Alaska Pacific herring- 86% and Walleye Pollock- 54%, Eastern Bering Sea Pacific herring- 55%) came from two of the most detailed models, with over 120 functional groups each. Four prey functional groups had a single predator account for at least 90% of the average total predator index (which only includes predators for which there is time series data, Fig. 4). These were Baltic Sea sprat (Atlantic cod are the predator), both sand lance and other small pelagics in the Eastern Scotian Shelf (Grey seals), and Pacific herring in the Gulf of Alaska (Arrowtooth flounder). The North Sea tended to have predation that was most evenly distributed, with no predator group accounting for more than a quarter of the total in any prey group, based on the static analyses.

When testing the relationship between diversity and stability of the assemblages, it is important to understand how the stability metric (variance ratio) might be expected to vary with diversity. If additional species in the predator assemblage maintain the same average variance and pairwise covariance of the assemblage, the variance ratio will change linearly as the number of species increases, with a slope equal to the ratio of the average covariance and variance. Thus if predator assemblages display similar covariance structures across systems, the variance ratios should fall roughly along a straight line that decreases (or increases, in the case of positively covarying species) with species richness. Conversely, one system with many weakly anti-correlated species will experience a dampening of total predation to a similar extent as another system with fewer strongly anti-correlated species, and the two systems will have similar variance ratios.

We did not see a common non-independent covariance structure among different predator assemblages, which would be indicated by a linear trend in the variance ratios with changes in species richness (Fig. 5). A simple linear regression of the variance ratio against species richness that forces a variance ratio of 1 when there is a single species had a slope term that was essentially equal to zero for both the analysis with all species (slope = -0.004, *P* = 0.434), and the analysis with only the core predators (slope = -0.013, *P* = 0.549). In addition, the mean of both sets of variance ratios was approximately one: 1.02 and 0.99 respectively. That is, the variance ratios are approximately evenly distributed around one, and this is constant across predator diversities (Fig. 5). These results collectively provide evidence that across ecosystems, on average, predator populations are statistically independent. This indicates there is likely a stabilizing effect of predator diversity on the total predator index, but the data do not provide cross-system evidence for compensatory dynamics among the predator populations.

Examination of uncertainty in the variance ratios further supported the conclusion of a general pattern of statistically independent populations, though with exceptions mainly occurring by region, not species. When we bootstrapped components of the predator index under the null assumption that populations are independent of one another (i.e., forced the theoretical variance ratios of the bootstrapped assemblages to be one), the observed variance ratios usually fell well within the distribution of bootstrapped variance ratios (Fig. 6), providing no evidence that the assemblages are not statistically independent. Assemblages departing from this general rule were tightly clustered by ecosystem. Nine of the 30 observed variance ratios fell outside of the middle 90% of bootstrapped variance ratios. Of these nine non-independent predator assemblages, four came from the Eastern Bering Sea, where all four variance ratios were significantly less than one (asynchronous), and four came from the North Sea, where all four variance ratios were significantly greater than one (synchronous). The final non-independent assemblage was planktivorous small pelagics in the Northern Gulf of St. Lawrence (synchronous). Thus, while in general predator diversity confers stability in the predator index due to statistical averaging, exceptions to that rule tend to occur by ecosystem rather than by prey functional group. This is likely in part because predator assemblages on different prey functional groups in the same ecosystem are still ultimately composed of the same biomasses. We do note that the weights on those biomasses differed among prey functional groups. In the Eastern Bering Sea, no prey functional group shared the same top predator (as quantified from the static analyses). In the North Sea, adult Whiting was generally the top predator, but the second most important predator was different for each prey functional group.

One key limitation of static models is that systems can undergo major changes. While our method of calculating the predator index was reasonable in most cases, it was less successful when there was a major reorganization of the system in the time series. In the Eastern Scotian Shelf, the time series data indicated that grey seals account for an overwhelming amount of predation throughout the time period (Fig. 4). However, using the equilibrium biomasses in the food web model, seals account for only 15% (Northern sand lance) and 2% (Small pelagics) of the predation. For contrast, in the Gulf of Alaska, which did not undergo a major reorganization, the dominance of a single predator (Arrowtooth flounder) was consistent across the static and dynamic analyses. Thus, the assumptions from equilibrium food web models tended to be most problematic for systems that experienced major system shifts over the time period, such as the collapse of Atlantic cod. In such cases, it is useful to understand how diets and consumption patterns have changed in order to accurately quantify a predator index.

**Discussion**

We conducted a unique and unprecedented analysis of predator dynamics across ecosystems in North America and Europe. In general, we found that when predator assemblages are diverse, the independently fluctuating predator populations stabilize the amount of predation that populations at lower trophic levels experience. However, this was not uniformly the case. We found one system (North Sea) where predator populations were synchronous and thus predator diversity amplified variability in the total predation. We also found one system (Eastern Bering Sea) where predator populations were asynchronous, a pattern consistent with compensatory dynamics. Finally, we found several cases across systems where the predator assemblages were simply not diverse, and a single predator dominated. In such cases there is no diversity to dampen variability in predation. Therefore, while we observed that statistical averaging was generally the dominant mode of predator assemblage variability, there are few universal rules in ecology, and understanding individual communities will always be crucial, particularly for natural resource management. In cases when predation variability is not dampened by predator diversity, whether due to synchrony among predators or lack of diversity, it is particularly important for managers to maintain relatively stable population sizes because predator populations cannot balance each other out, increasing the potential for trophic cascades to effect major changes in the system.

There is a rich literature linking diversity, stability, and ecosystem functioning, particularly in terrestrial ecosystems (e.g., May, 1973; Tilman, 1996; Doak *et al.*, 1998; McCann, 2000; Gonzalez and Loreau, 2009). While research on the topic has also been conducted in marine ecosystems, empirical evidence has been harder to obtain because of the difficulties of experimentation in these large connected systems (Naeem, 2006). However, comparative studies that utilize ecosystems as “experimental units” can begin to answer some of these questions (Jensen *et al.*, 2012; Link *et al.*, 2012). We used a comparative approach to show that in large marine ecosystems any observed dampening of variability in the total amount of predation prey populations experience is usually due to statistical averaging, and only in rare exceptions did we observe further dampening due to asynchronous populations that would be consistent with compensatory dynamics. That is, different predator populations were more or less independent of one another. When predator assemblages are diverse, this confers a stabilizing effect on the total predation, but this stabilization likely does not occur because communities have assembled themselves to maximize utilized niche space.

There is some empirical evidence that stronger top-down control is correlated with less diverse and higher latitude systems, though establishing the actual driver is challenging because many factors, including diversity, covary with latitude (Frank *et al.*, 2006, 2007; Boyce *et al.*, 2015). Establishing evidence for (or ruling out) potential mechanisms by which a particular factor could influence trophic control is an important step in determining what actually drives trophic control. This work shows that more diverse predator assemblages could reduce the strength of top-down control by temporally stabilizing the total amount of predation prey species experience through statistical averaging (but generally not through compensatory dynamics). Essentially, in more diverse systems, predation intensity is relatively constant. While we did not test the latitudinal hypothesis explicitly, we note that our systems did span a range of latitudes, and we did not see less dampening of the predator index at higher latitude systems. In fact, the Eastern Bering Sea, our northernmost system in the Pacific, was the only system that showed consistent patterns of asynchrony among predators. One mechanism for factors to influence trophic control is to affect the variability of the predator assemblage; we did not see evidence for latitude itself (or other correlated factors) to mediate top-down control via that mechanism, though such factors could certainly influence top-down control in other ways (e.g., DeLong *et al.*, 2015; O’Connor *et al.*, 2009; Siuda *et al.*, 2010).

While our predator index is a significant improvement over past efforts that either gave all weight to one predator, or equal weight to all predators, the new index is far still from perfect at characterizing predation risk. One of the chief weaknesses is that the weights, or relative importance of each predator population’s biomass, do not change through time. This is particularly problematic because the weights depend diet information, which is known to change through time and space (Brodeur *et al.*, 2014), particularly when systems undergo major structural shifts. Unfortunately, times series of ecosystem information such as diets are only available for a small number of systems, and so accounting for changes in diets while also maintaining a comparative approach is challenging, underscoring the utility of the snapshot food web models (Pikitch *et al.*, 2014).

Complex food webs are often thought to be less responsive to changing predator abundances (Power, 1992; Strong, 1992). However, evidence has shown that predation can play a crucial role in population dynamics in complex marine systems; in the Southern Gulf of St. Lawrence, predation is thought to be a key factor preventing demersal fish populations from recovering following collapse due to overfishing (Swain and Benoît, 2015). Therefore, understanding and predicting more nuances in the relative importance of predator control is important. We have shown that, in general, more diverse marine predator assemblages are less variable, and this is more likely to be due to independently fluctuating populations rather than compensatory dynamics. Diverse systems should thus be less susceptible to dramatic trophic cascades. However, we also found that marine predator assemblages are not uniformly diverse, and are therefore not automatically buffered from top-down effects. Because of this, understanding whether a given prey species or system is likely to experience predator control requires specific knowledge of the food web, an important step in implementing an ecosystem-based approach to fisheries management. As trophic cascades can be major hurdles towards sustainable resource management, predator populations and assemblages in low diversity systems or systems that display synchrony among predators should be managed with particular precaution to prevent more examples of large system shifts in the future.

**References**

Baum, J. K., and Worm, B. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology, 78: 699–714.

Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B., Cooper, S. D., *et al.* 2005. What Determines the Strength of a Trophic Cascade? Ecology, 86: 528–537.

Boyce, D. G., Frank, K. T., Worm, B., and Leggett, W. C. 2015. Spatial patterns and predictors of trophic control in marine ecosystems. Ecology letters, 18: 1001–1011.

Brodeur, R. D., Buchanan, J. C., and Emmett, R. L. 2014. Pelagic and demersal fish predators on juvenile and adult forage fishes in the Northern California Current: spatial and temporal variations. CalCOFI Report, 55: 96–116.

Canty, A., and Ripley, B. D. 2016. boot: Bootstrap R (S-Plus) Functions. R package version, 1.3-18.

Christensen, V., and Pauly, D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological modelling, 61: 169–185.

Davison, A. C., and Hinkley, D. V. 1997. Bootstrap Methods and Their Applications. Cam. bridge University Press, Cambridge, ISBN 0-521-57391-2.

DeLong, J. P., Gilbert, B., Shurin, J. B., Savage, V. M., Barton, B. T., Clements, C. F., Dell, A. I., *et al.* 2015. The body size dependence of trophic cascades. The American Naturalist, 185: 354–366.

Doak, D. F., Bigger, D., Harding, E. K., Marvier, M. A., O’Malley, R. E., and Thomson, D. 1998. The Statistical Inevitability of Stability‐Diversity Relationships in Community Ecology. The American Naturalist, 151: 264–276.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., *et al.* 2011. Trophic Downgrading of Planet Earth. Science, 333: 301–306.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science, 308: 1621–1623.

Frank, K. T., Petrie, B., and Shackell, N. L. 2007. The ups and downs of trophic control in continental shelf ecosystems. Trends in Ecology and Evolution, 22: 236–242.

Frank, K. T., Petrie, B., Shackell, N. L., and Choi, J. S. 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. Ecology Letters, 9: 1096–1105.

Fu, C., Gaichas, S., Link, J. S., Bundy, A., Boldt, J. L., Cook, A. M., Gamble, R., *et al.* 2012. Relative importance of fisheries, trophodynamic and environmental drivers in a series of marine ecosystems. Marine Ecology Progress Series, 459: 169–184.

Gonzalez, A., and Loreau, M. 2009. The Causes and Consequences of Compensatory Dynamics in Ecological Communities. Annual Review of Ecology, Evolution, and Systematics, 40: 393–414.

Holsman, K. K., Essington, T., Miller, T. J., Koen-Alonso, M., and Stockhausen, W. J. 2012. Comparative analysis of cod and herring production dynamics across 13 northern hemisphere marine ecosystems. Marine Ecology Progress Series, 459: 231–246.

Jensen, O. P., Branch, T. A., and Hilborn, R. 2012. Marine fisheries as ecological experiments. Theoretical Ecology, 5: 3–22.

Lindegren, M., Checkley, D. M., Ohman, M. D., Koslow, J. A., and Goericke, R. 2016. Resilience and stability of a pelagic marine ecosystem. Proc. R. Soc. B, 283: 20151931.

Link, J. S., Gaichas, S., Miller, T. J., Essington, T., Bundy, A., Boldt, J., Drinkwater, K. F., *et al.* 2012. Synthesizing lessons learned from comparing fisheries production in 13 northern hemisphere ecosystems: emergent fundamental features. Marine Ecology Progress Series, 459: 293–302.

Lucey, S. M., Cook, A. M., Boldt, J. L., Link, J. S., Essington, T. E., and Miller, T. J. 2012. Comparative analyses of surplus production dynamics of functional feeding groups across 12 northern hemisphere marine ecosystems. Marine Ecology Progress Series, 459: 219–229.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press.

McCann, K. S. 2000. The diversity–stability debate. Nature, 405: 228–233.

Minto, C., and Worm, B. 2012. Interactions between small pelagic fish and young cod across the North Atlantic. Ecology, 93: 2139–2154.

Naeem, S. 2006. Expanding scales in biodiversity-based research: challenges and solutions for marine systems. Marine Ecology Progress Series, 311: 273–283.

O’Connor, M. I., Piehler, M. F., Leech, D. M., Anton, A., and Bruno, J. F. 2009. Warming and Resource Availability Shift Food Web Structure and Metabolism. PLOS Biol, 7: e1000178.

Oken, K. L., and Essington, T. E. 2015. How detectable is predation in stage-structured populations? Insights from a simulation-testing analysis. Journal of Animal Ecology, 84: 60–70.

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. Trends in ecology & evolution, 14: 483–488.

Pershing, A. J., Mills, K. E., Record, N. R., Stamieszkin, K., Wurtzell, K. V., Byron, C. J., Fitzpatrick, D., *et al.* 2015. Evaluating trophic cascades as drivers of regime shifts in different ocean ecosystems. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 370: 20130265.

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., *et al.* 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries, 15: 43–64.

Polis, G. A. 1999. Why Are Parts of the World Green? Multiple Factors Control Productivity and the Distribution of Biomass. Oikos, 86: 3–15.

Polis, G. A., and Strong, D. R. 1996. Food Web Complexity and Community Dynamics. American Naturalist, 147: 813–846.

Power, M. E. 1992. Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy. Ecology, 73: 733–746.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., *et al.* 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters, 5: 785–791.

Siuda, A. N., Dam, H. G., and others. 2010. Effects of omnivory and predator-prey elemental stoichiometry on planktonic trophic interactions. Limnology and Oceanography, 55: 2107–2116.

Solow, A. R., and Duplisea, D. E. 2007. Testing for Compensation in a Multi-species Community. Ecosystems, 10: 1034–1038.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology, 73: 747–754.

Swain, D. P., and Benoît, H. P. 2015. Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. Marine Ecology Progress Series, 519: 165–182.

Tilman, D. 1996. Biodiversity: Population Versus Ecosystem Stability. Ecology, 77: 350–363.

Worm, B., and Myers, R. A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology, 84: 162–173.