Patterns of variability in predation on marine fish

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**Abstract:** The relative importance of predator consumption in shaping population, community, and ecosystem scale processes is 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. When there are many predator populations, increases in one can be compensated for with declines in another. In such cases, the predator diversity causes the overall predation mortality to remain a relatively stable. The two hypothesized mechanisms for this phenomenon 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 paired 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 had a single predator group that accounted for over half of all predation. Populations within predator assemblages generally varied independently of one another; this supported the theory that statistical averaging leads to a stabilizing effect of high predator diversity on predation mortality. However, we also observed ecosystems with both synchronous and asynchronous predator assemblages. Assemblages that are either synchronous or that have low diversity have a greater potential to vary dramatically and induce large-scale changes throughout the system. Quantifying and understanding this potential can help identify systems where precautionary management of predators may be particularly valuable.

**Keywords:** predator control, top-down control, diversity-stability theory, predation, compensatory dynamics

**Introduction**

Trophic processes have the potential to drive large changes in the abundances of populations both in marine systems and elsewhere. Food webs characterized by top-down regulation tend to have dynamics that are more non-linear, harder to understand, and less predictable (Pace *et al.*, 1999). Management of these food webs is difficult due to their susceptibility to community shifts and unpredictable responses to anthropogenic or environmental perturbations (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). For example, both predation (Swain and Benoît, 2015) and climate (Rose, 2004) have explained the non-recovery of the same focal species (Atlantic cod) in two different nearby ecosystems. Therefore, understanding what drives the population- and community-scale consequences of consumption is a key question in ecology.

The influence of predation on prey likely depends, in part, on community structure and dynamics (MacArthur, 1955; Paine, 1980). Ecologists often predict that species in complex, diverse food webs with many weak trophic linkages are buffered from top-down control because of compensatory responses of predators (Strong, 1992). In these systems, 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 change in abundance (Power, 1992; Polis and Strong, 1996). Under this view, keystone species (Paine, 1966) are uncommon, and the sheer diversity of predator populations generally prevents “community-level” trophic cascades – those that impact the entire system rather than specific species – 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 utilized niche space, so that one species compensates for changes in another (Tilman, 1996). Second, the statistical averaging hypothesis suggests that stabilization occurs because populations vary independently of one another, so that as species are added to the system, their fluctuations become more likely to balance each other out (Doak *et al.*, 1998). In more diverse ecosystems, either mechanism can dampen fluctuations in predation, reducing the chances that predation drives large changes in prey biomass; this in turn increases prey stability.

Empirical evidence in large marine ecosystems for compensatory dynamics and the corresponding 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). Cross-ecosystem assessments of relationships between diversity and trophic control, either functional complementarity or statistical averaging, have generally been difficult for large marine ecosystems because of extensive data requirements and slow rates of population turnover (Naeem, 2006). However, studies examining diversity-stability and compensation have occurred in individual ecosystems. For example, Lindegren *et al.* (2016) found evidence supporting the hypothesis of functional complementarity in predators in the Southern California Current. There remains 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 approaches that both benefit from being easy to compute and understand, but also have key weaknesses. The first approach 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 eaten by a diverse assemblage of consumers and allows testing of 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 consume significant prey biomass. Most importantly it prevents any examination of functional complementarity or diversity-stability relationships because there is only one predator population. New metrics are needed to bridge the divide between these two endpoints.

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 how often increased predator diversity can 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) test whether populations within predator assemblages are synchronous (consistent with a similar fishing history or shared environmental driver), asynchronous (consistent with compensatory dynamics), or independent (consistent with statistical averaging). Predator assemblages that are more synchronous display more temporal variability, which is amplified by increased predator diversity; systems with such predator assemblages should be more susceptible to predator control. In contrast, diversity dampens temporal variability of asynchronous predator assemblages; these systems should be less susceptible to predator control (Fig. 1). We explore whether one of these three modes of variation is dominant both across and within large marine ecosystems.

**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, which requires spatially explicit time series of abundance, feeding rate, and diet composition, which 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 that 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 values 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. The weight for predator *i* with respect to the predator index for prey *j*, *Wi,j* is written as:

(1)

where *QB* is the annual consumption to biomass ratio (a single quantity) 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 younger ages (Oken and Essington, 2015). Although juvenile functional groups in food web models tend to be more data-poor, we note that we use diet information of groups *consuming* juveniles, not the actual 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 by experts as “small,” and any other species or species groups that 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:

(2)

where *Bi,\** 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 predator species for which we have biomass time series data. To do so, we checked which predator functional groups contained at least one predator 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 time series. 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 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 predator 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 predator 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:

(3)

Once again, the total dynamic predator index, *Pj(t)* is the sum over all predator species of the *Pi\_k,j(t)*. Missing biomass estimates were imputed by linearly interpolating between the two most adjacent years with estimates. If no earlier (or later) years had estimates for a single species, the value from the first (or last) year with estimates was inserted.

We used the variance ratio as a metric of synchrony or asynchrony within a given predator guild (Fig. 1). 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:

(4)

where the variances of each predator species or assemblage are calculated over time. The variance ratio is equal to one when the components are, on average, statistically independent (covariances sum to zero), less than one when components are, on average, asynchronous (consistent with compensatory dynamics), and greater than one when components are, on average, synchronous (consistent with a shared driver). The first two cases cause predator diversity to stabilize the predator index, whereas in synchronous predator assemblages, species diversity inflates predator variability and makes the system more susceptible to predator control.

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. Deviations from this expected relationship 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 (which we refer to as the “core” predator species). 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.

Because population dynamics are inherently noisy, it was important to determine the probability of the observed variance ratios occurring by chance alone. To do so, we bootstrapped years from each weighted biomass time series for each predator species under the null assumption that predator populations are independent (i.e., an expected variance ratio of one, consistent with the statistical averaging hypothesis), and then, for each bootstrap iteration, recalculated the variance ratio of the assemblage. 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, a parametric bootstrap method that resamples the phases of the empirical Fourier transform while keeping fixed the moduli, thereby maintaining the mean and spectral characteristics of the time series. This is an effective method for statistics such as 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 that accounted for the top 90% of predation. This had no qualitative impact on results beyond 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 two-thirds of prey functional groups (19/30), we had time series for species that covered predator 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 accounted for greater than 70% of predation mortality across prey functional groups and systems. Notably, forage species are not a significant component of gelatinous zooplankton diets. However, the consumption rate of gelatinous zooplankton in the model was two to three orders of magnitude greater than that of predatory fish. This caused gelatinous zooplankton to consume a large biomass of forage fish, even with a small diet fraction, and furthermore meant that gelatinous zooplankton were the chief consumers of forage fish. The other exceptional cases were due to marine mammals: Atlantic herring in the Barents Sea where whales and seals accounted for 89% of predation and Pacific herring in the Eastern Bering Sea where seals accounted for 81% of predation.

The number of predation sources varied widely among species and systems (Fig. 3,4). In approximately one-third (9/30) of the prey species, a single predator functional group accounted for over 50% of predation. Five of those nine functional groups were composed of a single species, underscoring that predation mortality can come from a small number of species. 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.

Across ecosystems, on average, predator populations were statistically independent from one another (Fig. 5). Correlation among predators causes the variance ratio to deviate from one, but this deviation is amplified as the number of species increases. Thus, the same average correlation strength among species will result in a variance ratio farther from one in systems with more species. A consistent pattern of synchrony or asynchrony across assemblages is best indicated by a positively or negatively sloping relationship between the variance factor and species richness. However, we saw no significant slope in the relationship between the variance factor and species richness, indicating no consistent pattern of synchrony or asynchrony (all species slope = -0.004, *P* = 0.434; core species slope = -0.013, *P* = 0.549). Furthermore, the mean of both sets of variance ratios was approximately one (1.02 and 0.99 for all predators and core predators, respectively), indicating an even balance between synchronous and asynchronous assemblages.

Testing the null hypothesis that predator populations vary independently of one another further supported the conclusion that, in most assemblages, they do. When we bootstrapped components of the predator index under the null assumption that populations are independent (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). In 21 out of 30 assemblages, the observed variance ratio was within the middle 90% of the bootstrapped distribution. When predator species are independent of one another, there is a stabilizing effect of predator diversity on the total predator index; however, the data do not provide consistent cross-system support for further stabilization through compensatory dynamics.

Predator assemblages that were not statistically independent were mainly, though not entirely, clustered by ecosystem (Fig. 6). Of the 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). Thus, exceptions to the pattern of independence among predators tended 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 were composed of the same set of biomass time series, only weighted differently. The final non-independent assemblage was planktivorous small pelagics in the Northern Gulf of St. Lawrence (synchronous). Notably, the other assemblages in the Northern Gulf of St. Lawrence were weakly asynchronous. Therefore, exceptions to independent predator assemblages can also occur for individual prey functional groups.

One key limitation of static models is that systems can undergo major changes that are not reflected in the model and that therefore lead to inconsistencies in the results. The Scotian Shelf and Gulf of St. Lawrence are both systems that experienced major shifts during the collapse of Atlantic cod. In the Eastern Scotian Shelf, the time series of biomasses used in the dynamic analysis 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, as we did in the static analysis, seals account for only 15% (Northern sand lance) and 2% (Small pelagics) of the predation. Thus, the model biomass for the reference years (1995-2000) does not match our available seal biomass for that same time period, perhaps due to new assessments of seal biomass that have become available since construction of the model. It is also likely that such a substantial change in biomass has been associated with changes in consumption patterns. The Southern Gulf of St. Lawrence actually had food web models built both before and after the collapse. While results for three of the prey functional groups were robust to choice of time period, the predator assemblage for flounders was not (supplementary materials). The number of core predators of flounders (from the dynamic analysis) was six for the model before the collapse and only four for the model after, largely because of the increased role of seals. The variance ratio based on the model before the collapse was less than one (asynchronous, variability is dampened), whereas based on the model after the collapse it was greater than one (synchronous, variability is magnified), though neither variance ratio was significantly outside of the bootstrapped distributions.

**Discussion**

We found evidence supporting the hypothesis that when predator assemblages are diverse, the independently fluctuating predator populations generally stabilize the amount of predation that populations at lower trophic levels experience; however, this was not uniformly the case. However, we observed one system (North Sea) where predator populations were synchronous and thus predator diversity amplified variability in the total predation. This synchronicity could be due to a similar fishing history or a shared response to an environmental driver. We also found one system (Eastern Bering Sea) where predator populations were asynchronous, a pattern consistent with the hypothesis of compensatory dynamics. Finally, there were several cases across systems where a single species dominated the predator assemblage so that the variability of the assemblage was similar to the variability of the dominant predator. Therefore, while the idea of statistical averaging (i.e., summing independent time series) can largely explain characteristics of predator assemblage variability, there are few universal rules in ecology, and understanding individual communities will always be crucial. In cases when predation variability is not dampened by predator diversity, whether due to synchrony among predators or low diversity, prey populations should be more susceptible to predator control.

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), but less in marine ecosystems where empirical evidence is harder to obtain because of the difficulties of experimentation in such large connected systems (Naeem, 2006). However, a small number of studies have looked for evidence of compensatory dynamics in individual marine ecosystems (Duplisea and Blanchard, 2005; Shackell and Frank, 2007; Gifford *et al.*, 2009; Lindegren *et al.*, 2016). They have generally found mixed results, and their varying methodologies likely make the studies only grossly comparable (e.g., accounting for serial autocorrelation, see Solow and Duplisea, 2007). Our comparative study has allowed us to systematically test for evidence of asynchrony in predator assemblages across North America and Europe, and we found little evidence supporting compensatory dynamics. One large terrestrial study found that compensatory dynamics are rare across natural systems (Houlahan *et al.*, 2007); however, a similar examination over marine ecosystems has yet to be undertaken. Here, we also found that compensatory dynamics are likely to be the exceptional case, and extend the results of Houlahan (2007) to both marine ecosystems, and ecosystems with long and varying histories of exploitation, which have long since left their “natural” state.

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 which variable actually drives trophic control. This work offers a mechanism for predator diversity to drive trophic control: 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. Therefore, if we assume that diversity and latitude are correlated (Hillebrand, 2004), predator diversity could cause observed spatial variation in trophic control.

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 has limitations. In particular, the weights, based on static food web models, are constant and do not accurately quantify the predator assemblages when predators display non-linear functional responses. This becomes most apparent for systems that have undergone major reorganizations, such as those that experienced the collapse of Atlantic cod. When there is a narrow range of predator and prey biomasses, most functional responses can be approximated as linear over the observed values. However, major changes generally induce a wider range of observed biomasses, causing the linear approximation to break down. For a prey density initially in the middle section of a type III functional response (typical of generalists like most marine predators), our linear assumption will overweight the predator if prey abundance increases dramatically and underweight the predator if prey abundance decreases. This means that if non-linear functional responses are accounted for, the predator index will be less variable. If the incorrect weightings are proportional across predators, the relative importance of a predator species would be unaffected, but the variances may still be incorrect. Unfortunately, time series of ecosystem information necessary to parameterize a functional response curve are only available in a small number of cases (Szoboszlai *et al.*, 2015). This makes accounting for such complexities while also maintaining a comparative approach challenging, underscoring the utility of the snapshot food web models (Pikitch *et al.*, 2014).

The findings of this study contribute to our understanding of the linkage between food web composition and the potential for predator control. Previous 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). This underscores the importance of understanding and predicting more nuances in the relative strength of predator control. We found that, in general, systems with diverse predator assemblages should be less susceptible to dramatic trophic cascades, which can be major challenges to sustainable and stable resource management. 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 should be managed with particular precaution, avoiding both sudden decreases (e.g., overfishing) or increases (e.g., rapid mammal reintroductions) in predator populations, as high variability in individual populations may have far-reaching consequences for the community.

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