Variability and stability in predation landscapes: a cross ecosystem comparison on the potential for predator control in temperate marine ecosystems

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**Abstract:** The importance of predator consumption in shaping population, community, and ecosystem scale processes is an active area of study. In general, it is thought that when food webs have multiple top predators, fluctuations in any single population have only a small influence on variability of the guild at large, meaning that predator diversity stabilizes the predator landscape that prey experience. The degree to which this phenomenon occurs depends on the how populations within the predator assemblage vary. The greatest dampening of variability occurs when populations vary asynchronously, consistent with compensatory dynamics, while the least dampening occurs when populations vary synchronously, possibly in response to a shared environmental driver or similar exploitation history. We utilized a database of biomasses of (mainly) commercial fish species across ten large marine ecosystems paired with information on diet composition and feeding rates to develop a novel multi-component index of predation that allowed us to ask two main questions. First, how diverse are sources of predation in large marine ecosystems. Second, based on synchrony of the assemblages, how much does diversity stabilize variability in the predation landscape. 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. Abundances of predator populations within these assemblages generally varied independently of one another (neither synchronous nor asynchronous), implying an intermediate stabilizing effect of 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, functional complementarity, synchrony

**Introduction**

Understanding what drives the population- and community-scale consequences of predator-prey interactions is a key question in ecology. 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 been implicated in the slow population growth rate of Atlantic cod (*Gadus morhua*) in two nearby ecosystems. Food webs characterized by strong predator control tend to have dynamics that are non-linear, hard to understand, and unpredictable (Pace *et al.*, 1999). Management of these food webs is difficult due to their susceptibility to dramatic community shifts and unpredictable responses to anthropogenic or other exogenous perturbations, making such ecosystems important to identify (Estes *et al.*, 2011).

One way to examine the strength of predator control in a community is to quantify the extent to which changes in predator abundances induce changes in prey dynamics (MacArthur, 1955; Paine, 1980). Mechanistically, this means that prey vital rates (principally, natural mortality) exhibit changes through time in response to changes in the predator landscape. The strength of predator control then depends both on how much the predator landscape varies through time and how sensitive prey vital rates are to such variations (Essington and Hansson, 2004). In complex speciose systems, ecologists often predict that prey should experience a relatively constant rate of predation because prey are subject to a diverse assemblage of predators whose temporal dynamics are not synchronized, diminishing the influence of fluctuations in a single population (Power, 1992; Polis and Strong, 1996). This stability in the predator landscape reduces the strength of control caused by any single predator (Strong, 1992). However, diverse predator landscapes do not render dramatic community shifts impossible if exploitation or any other driver suddenly depletes the entire guild of predators at once (Baum and Worm, 2009).

The degree to which diversity dampens fluctuations of the entire predator assemblage, potentially decreasing susceptibility of prey to predator control, depends on the extent to which predator population dynamics are synchronized (Fig. 1). When predators are strong competitors, reduction of one predator (i.e. due to an exogenous driver) can lead to increases in others, resulting in *asynchronous* populations (Gonzalez and Loreau, 2009) and strongly stabilizing predator landscapes experienced by prey populations (sometimes referred to as compensatory dynamics or functional complementarity). When predator populations fluctuate independently of each other, statistical averaging implies that as species are added to the system, their fluctuations become more likely to balance each other out (Doak *et al.*, 1998), resulting in an intermediate level of stabilization. Finally, if predator populations exhibit similar responses to a shared exogenous driver or experience a similar history of exploitation, predator populations will be *synchronous* (Baum and Worm, 2009), which will weaken the effect of predator species richness on stabilization of predator landscapes.

There is some evidence supporting the hypothesis that less diverse predator assemblages are associated with stronger predator control of prey populations. The dominance of predator control in marine systems, as measured by a negative correlation between adjacent trophic levels, has been found to be associated with lower predator diversity (Frank *et al.*, 2006; Boyce *et al.*, 2015). However, 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). Lindegren *et al.* (2016) found evidence supporting the hypothesis of functional complementarity in predators in the Southern California Current, and concluded that this stabilized predation intensity and contributed to the observed strong linear effect of environmental drivers on ecosystem dynamics. There remains a need to take a comparative cross-system examination (Link *et al.*, 2012) that explicitly explores the mechanism by which predator diversity could stabilize variability of predator assemblages, thereby decreasing the strength of predator control.

To understand linkages among predator diversity, stability, and predator control, we first must develop time series composed of meaningful metrics of predation intensity that account for the different roles each predator species plays. To date, metrics of predation have generally taken one of two approaches. Both approaches are easy to compute and understand, yet 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 each prey species is eaten by a diverse assemblage of consumers, and the ability to partition predation by predator species allows the testing of hypotheses regarding 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 higher consumption rates, feeding preferences, or higher levels of habitat overlap (CITE). 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 outsized 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 it only considers one predator population. New metrics are needed to bridge the divide between these two endpoints.

In this study, we take a unique comparative database of multispecies abundances and predator feeding habits and consumption rates across ten large marine ecosystems in North America and Europe (Table 1). We use the database to quantify species richness in marine predator assemblages associated with individual prey groups, and the frequency and extent to which predator diversity may stabilize the predator landscape experienced by prey. We create a novel multi-component index that assesses predator assemblages from the perspective of different prey populations and then: 1) quantify whether and in what cases predation tends to come from a small or large number of consumers, and 2) quantify whether populations within predator assemblages are synchronous (consistent with a similar fishing history or other shared driver), asynchronous (consistent with compensatory dynamics), or independent (consistent with statistical averaging).

**Methods**

We combined published static food web models (Christensen and Pauly, 1992) with abundance information from surveys and stock assessments across ten large marine ecosystems in North America and Europe 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). Ecosystems from across the Atlantic and Eastern Pacific all varied in their length and intensities of exploitation, latitude, and perceived major drivers of community structure and dynamics. 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), and is based on fishery-independent surveys or stock assessment model output, with consistent sources within each system.

*Developing the predation index*

First, we developed a predator index that is unique to each prey functional group. Prey functional groups are defined as a combination of one or more populations assumed to have similar life history characteristics and roles in the ecosystem (e.g., rates of productivity, habitats, consumption rates, key predators). The simplest estimate of an index of predation might merely sum the abundances of all predators that are known to consume a given prey. 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 weighting factors are calculated as the product of consumption rate per unit biomass and the fraction of predator diet that consists of the prey. Both inputs come from a static food web model based on a distinct time period relative to our abundance time series. In the predator index for prey *j*, the weighting factor of predator *i* *Wi,j* is written as:

(1)

where *QBi* is the annual consumption to biomass ratio (a single quantity) of predator *i*, and *Di,j* is the fraction of predator species *i*’s diet that prey 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 selected mid-trophic level species within a system as prey species. Experts from each ecosystem used 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 functional group that contained forage fish, clupeids, and gadids and pleuronectids that were classified by experts as “small,” as well as any other species or species groups that were thought to be 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 mass balance. To do this, we multiplied the weights in equation (1) by the baseline predator 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 the static predation index that included all or most species in the ecosystem, we examined how comprehensively the subset of species for which we had time series data quantified predation mortality. 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 predator species. One key advantage to using the static calculations for this analysis was that we were able to include all predators included in the models, even those for which we did not have time series of 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 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. 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 biomasses. If no earlier (or later) years had estimates for a single species, the value from the first (or last) year with information was inserted.

We measured the degree of synchrony or asynchrony (Fig. 1) of a predator guild (i.e., subdivided predator index for a given prey group) using the variance ratio. The variance ratio is commonly used to test for compensatory dynamics (Gonzalez and Loreau, 2009), and can be interpreted as a metric of correlation in a multivariate dataset (as opposed to bivariate). The variance ratio of the predator index for prey group *j, VRj* was:

(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 (i.e., pairwise covariances of all predator populations sum to zero), less than one when components are, on average, asynchronous (i.e., negative sum of covariances, consistent with compensatory dynamics), and greater than one when components are, on average, synchronous (i.e, positive sum of covariances, consistent with a shared driver).

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. We also 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 average, over time, 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 there were many rare or unimportant predators, 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 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, which is 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**

We first sought to determine whether the predator species for which we had time series of abundance accounted for a sizable fraction of the baseline mortality. For over one-half of prey (15/26), we had time series data for at least one predator species within functional groups accounting for 50% or more of the of total predation mortality (Fig. 2). Key predators that usually lacked time series data were marine mammals and gelatinous zooplankton. Whales and seals accounted for 89% of predation on Barents sea Atlantic herring, and seals accounted for 81% of predation on Eastern Bering Sea Pacific herring. In every prey group in both the Gulf of Maine and Georges Bank, gelatinous zooplankton (Cnidaria, Ctenophores, colonial Siphonophores, colonial Salpidae) accounted for greater than 70% of predation mortality. This was because the consumption to biomass ratio 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 though forage fish represented only a small diet fraction, and furthermore meant that gelatinous zooplankton were the chief consumers of forage fish.

*Diversity of predator assemblages*

The number of predation sources varied widely among species and systems; the components of the predator indices were not always distributed among many species (Fig. 3,4). Based on the static analyses, over 50% of predation came from a single predator functional group for approximately one-third (9/26) of the prey groups (Fig. 3). Five of those nine functional groups were composed of a single species, underscoring that predation mortality can come from a small number of species. 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 dynamic analyses, 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).

*Synchrony of predator assemblages*

Across ecosystems, there was no overall tendency for predator populations to be either synchronous or asynchronous (Fig. 5). A consistent pattern of synchrony or asynchrony across assemblages is indicated by a positively or negatively sloping relationship between the variance ratio and species richness. However, we saw no significant slope in the relationship between the variance ratio and species richness (all species slope = -0.006, *P* = 0.298; core species slope = -0.020, *P* = 0.404). Furthermore, the mean of both sets of variance ratios was approximately one (1.03 and 0.99 for all predators and core predators, respectively), indicating an even balance between synchronous and asynchronous assemblages.

Bootstrapping confirmed that there was generally insufficient evidence to reject the null hypothesis that predator populations vary independently. 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 18 out of 26 assemblages, the observed variance ratio was within the middle 90% of the bootstrapped distribution. When predator species are independent of one another, there is an intermediate stabilizing effect of predator diversity on the total predator index; the data do not provide consistent cross-system support for further stabilization through asynchrony and compensatory dynamics.

Predator assemblages that did show evidence for either synchrony or asynchrony were clustered within a few ecosystems (Fig. 6). Of the eight non-independent predator assemblages, four came from the Eastern Bering Sea, where all four variance ratios were less than one (asynchronous), and four came from the North Sea, where all four variance ratios were 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.

**Discussion**

We developed a novel index of predation to study the potential for predator control across marine ecosystems. We find evidence of many cases across systems of low predator richness, implying that although the food webs may be complex, predator guilds on individual prey are not always so. This could potentially lead to higher variability of the predator landscape. On the other hand, for prey where predation is distributed across several predators, we find that predator populations tend to vary independently of one another, implying that the diversity of predator assemblages leads to an intermediate level of stabilization on the total amount of predation that populations at lower trophic levels experience. However, this is not uniformly the case. We observe one system (North Sea) where predator populations are synchronous and thus predator diversity will only minimally dampen 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 find one system (Eastern Bering Sea) where predator populations are asynchronous, a pattern consistent with the hypothesis of compensatory dynamics. Therefore, while the idea of statistical averaging 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). 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 predator control on prey populations 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 govern predator control: more diverse predator assemblages could reduce the strength of predator control by temporally stabilizing the total amount of predation that 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, as all curves are approximately linear over short ranges. However, major ecosystem 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 when 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 Eastern Scotian Shelf is an example of a system where the use of a static food web model led to inconsistent results. 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, even 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 findings of this study contribute to our understanding of the linkage between food web composition and the potential for predator control. Predation can play a crucial role in population dynamics in complex marine systems. For example, 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, variability of predation mortality should be somewhat stabilized in diverse predator assemblages, potentially decreasing the strength of predator control in such systems. However, when examining predator assemblages from the perspective of specific prey, we found that marine predator assemblages are not uniformly diverse, and systems are therefore not automatically buffered from predator control. 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 resulting from strong predator control 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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