Patterns of variability in predation on marine fish

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**Abstract**

**Keywords:**

**Introduction**

Ecological theories often predict that complex speciose food webs with many weak trophic linkages, such as those found on continental shelves, are buffered from dramatic trophic cascades driven by changing predator abundances (Strong, 1992). This is because species are subject to a diverse assemblage of predators whose dynamics are not synchronized in time, and prey therefore experience a relatively constant rate of predation (Power, 1992). That is, major changes in a single predator population are unlikely to cascade through the food web. Ecosystem and predator-prey models driven from the bottom up tend to have dynamics that are more linear, easy to understand, and 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).

Functional or niche complementarity (closely related to compensatory dynamics) occurs in diverse assemblages of similar species that have complementary responses to the environment, resulting in asynchronous populations (Gonzalez and Loreau, 2009). Essentially, total predation (or any other metric) remains less variable than the individual populations because one populationcompensates for changes in another, either due to competitive interactions (anticorrelated, Tilman, 1996) or simply because populations are independent (uncorrelated, Doak *et al.*, 1998). This is often the mechanism that is hypothesized to lead to the increasing dominance of resource control, and thus increased stability, in more diverse ecosystems. It also means that if historically we have observed a system to be driven from the bottom up, but exploitation depletes the entire guild of predators at once, the system can still respond with dramatic cascades (cite).

Empirical evidence in large marine ecosystems for both trophic control and functional complementarity is mixed. While trophic control certainly varies in space, possibly along latitudinal gradients (Boyce *et al.*, 2015; Frank *et al.*, 2007), conclusions can also depend on which data are analyzed and how they are interpreted (Beaugrand *et al.*, 2003; Frank *et al.*, 2011; Koeller *et al.*, 2009; Worm and Myers, 2003). There is evidence that bottom-up control in marine systems is correlated with higher predator diversity (Boyce *et al.*, 2015), though simple correlations between predators and prey can be poor indicators of trophic control (Pershing *et al.*, 2015), and other work has found no relationship between diversity and the strength of trophic cascades (Borer *et al.*, 2005). The hypothesized mechanism for a relationship between diversity and trophic control, functional complementarity, has generally been difficult to assess in large marine ecosystems because of data requirements. Lindegren *et al.* (2016) found evidence for functional complementarity in several guilds, including predators, in the Southern California Current, but there is still a need to take a comparative cross-system examination of these topics (Link *et al.*, 2012).

If more variable predator assemblages are associated with top down control, then the abundance of predators must be quantified, but how to do so is not always clear. As a result, several approaches have been developed, and the appropriate tool depends on the question. One common approach is to sum the abundances of all piscivorous species (e.g., Frank *et al.*, 2005; Lucey *et al.*, 2012; Lindegren *et al.*, 2016); however, this ignores the fact that, for a given prey species, some of those predators are more important relative to their biomass than others. This can be due to higher consumption rates (e.g., hemeotherms versus ectotherms) or different diet preferences among the predators. A second approach to obtaining a predator time series is to select a single predator species (e.g., Worm and Myers, 2003; Holsman *et al.*, 2012; Minto and Worm, 2012). In addition to prey almost always experiencing predation from multiple predator species, this also prevents any examination of functional complementarity or diversity-stability relationships because there is only one predator population. Finally, a third approach is to use dynamic ecosystem models, such as Ecopath with Ecosim (Christensen and Walters, 2004). These require either extensive data on diets and size structure that rarely exist, or many simplifying assumptions, some of which may not always be readily apparent to either the modeler or the reader. In addition, only studying systems for which such a model has been parameterized limits the range of systems available for comparative analysis.

In this study, we take a unique comparative database of multispecies abundances across large marine ecosystems in North America and Europe to examine patterns of variation in predator assemblages and explore the mechanism by which diversity is thought to promote both resource control and community stability. We combine these abundance data with coarse 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 sources 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 (functional complementarity, Fig. 1a), independently (Fig. 1b), or synchronously (response to shared environmental driver, Fig. 1c). 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 mass-balance equilibrium 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 key mid-trophic level species and to quantify how the index and its components have varied through time. We examined this index at the mass-balance model equilibrium biomasses (static analysis), and across the time series of abundances (dynamic analysis), as the two sets of 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 for the CAMEO working group (see Fu *et al.*, 2012 for details).

First, we developed a predator index that could be applied to different prey species. The most naïve 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 naïve 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. The weighting factors are determined by estimates from mass-balance food web models of the predator’s consumption rate and the fraction of the predator’s diet that the prey of interest makes up. In this way, it roughly quantifies, from the perspective of a given prey, how predation pressure may be shifting through time, where biomass of more important predators is more heavily weighted. Therefore, the predation index for prey species *i,* *Pi* is written:

where *QB* is the annual consumption to biomass ratio, *Dj,i* is the fraction of species *j*’s diet that species *i* makes up, *Bj* is the biomass of predator ­*j*, and *Bi* is the mass-balance equilibrium biomass of prey *i*. Because some food web models divide species into juvenile and adult stages, but our abundance data did not, we weighted the consumption and diet parameters for the juvenile and adult life stages based on their relative biomasses in the equilibrium 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 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 also 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 gadids and pleuronectids that were classified as “small,” forage fish, clupeids, 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 examined what proportion of predation mortality from the equilibrium model we were able to capture with our biomass time series that mainly tracked commercial fish species. To do this, in equation (1) we used the associated mass-balance equilibrium biomasses for the predators, an approximation of species’ relative abundances in the ecosystem. We then checked which functional groups contained at least one species found in the abundance time series.

We also used the static calculations to assess whether a single functional group in the mass-balance model tends to dominate the predation or if predation is, as is often hypothesized, 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 quantified what proportion of predation mortality the top predator makes up, as well as the proportion from the second most important predator.

*Dynamic analysis*

We then examined how the predator index and its component parts varied through time. We again used equation (1) to calculate the predator index, but the biomass of the predator, *Bj* became a vector over time of species abundances. 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, which assumes that all species within a functional group have grossly similar diets and consumption rates. Missing data were replaced were linearly interpolated.

We used the variance ratio as a metric of functional complementarity within a given predator guild. The variance ratio is a commonly used metric to assess evidence for functional complementarity and compensatory dynamics (Gonzalez and Loreau, 2009). We calculated the variance ratio of predation on prey species *i, VRi*,  as:

where *Pi,j* is the contribution of predator *j* to the predator index of prey i *(*i.e., unsummed version of equation 1).The variance factor measures the degree of either synchrony (Fig. 1c) or functional complementarity (Fig. 1a) within a guild, and is equal to one when the components are, on average, statistically independent (covariances sum to zero, Fig. 1b).

We then examined how the variance factor was related to diversity of the predator index, measured in number of species. We used species counts as a metric of diversity because the number of components in the variance ratio is directly related to its theoretical value (keeping average correlation among components constant), and we wished to be able to account for this trend. However, species counts are not the best metric of diversity because many rare species (or in this case, species that account for a small fraction of predation) will inflate the count. To solve this problem, we recalculated the variance factor and species counts for a subset of the original guild of predator species: the minimum number of predators such that we accounted for at least 90% of the average of the total predator index (i.e., 90% of the predation for which we had time series data). 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 artificially inflate the diversity metric. We refer to this as the reduced variance factor.

To assess uncertainty, we bootstrapped the variance ratios under the assumption that predator populations are independent. 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. 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). With a large number of components, the null distribution of the variance factor tended to become extremely tightly centered about one. Therefore, for ease in plotting the distributions, and because we felt the reduced variance factor better quantified the diversity-stability relationships, we only bootstrapped the reduced variance factors (maximum of 26 predator species vs. 9).

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. 2a). 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. 2b,c, 3). 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 species (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. The North Sea tended to have predation that was very evenly distributed, with no predator group accounting for more than a quarter of the total.

Sometimes the biomass estimates from the food web models were different than the time series data. 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. 3). 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. However, in other cases, such as Gulf of Alaska herring, both the food web model and the time series data indicated a single dominant predator (Arrowtooth flounder). The assumptions from equilibrium food web models tend to be most problematic for systems that experienced major system shifts over the time period: the collapse of cod and growth of seal populations on the Scotian Shelf and in the Gulf of St. Lawrence.

If all systems shared a similar correlation, or level of synchrony, among predator species, we would expect to see the variance factor consistently increase (synchronous) or decrease (asynchronous) linearly as the number of species increased. However, instead we see patterns that generally vary by region, and variance factors that are approximately even distributed around one, where populations are statistically independent (Fig. 4, 5). Most predator assemblages show a variance factor within the range we would expect to see if the magnitude of average correlation among species is less than 0.05 (Fig. 4); this was particularly the case for the full variance factor (Fig. 4a). That is, there is sometimes dampening of variability of the predator index with an increased number of predator populations, but this is more often due to more statistically independent populations, and not necessarily greater use of the niche space. For the reduced variance factor, although more species fall outside the region contained by the 0.05 lines, the lines themselves lie very close to the horizontal line at one. This means that for systems with a smaller numbers of species, it is more difficult to differentiate among competing hypotheses for the variance factor.

Four prey functional groups had a single predator account for at least 90% of the average total predator index (Fig. 5). These were 1) Baltic Sea sprat, where the key predator is cod, and cannibalism by sprat is the only other predator that is a fish, 2) both sand lance and other small pelagics in the Eastern Scotian Shelf, where the key predator is grey seal, and Pacific herring in the Gulf of Alaska, where the key predator is arrowtooth flounder.

Two regions stood out as consistently having populations within predator assemblages that were not independent (Fig. 5). The North Sea displayed patterns of synchrony among predators. This could be either due to the species responding similarly to a shared environmental driver, or all predators sharing a similar history of exploitation. The Eastern Bering Sea displayed patterns of functional complementarity among predators. We also note the importance of examining different predator assemblages for different prey species, even within the same region. In the Southern Gulf of St. Lawrence, one prey species showed a synchronous predator assemblage, while the other prey species tended to have asynchronous assemblages (though all three/four were in the middle 95% of the null distribution).

**Discussion**

Contrary to some ecological theory, food web linkages in large marine ecosystems are not uniformly diffuse. We conducted a unique and unprecedented analysis of sources of predation across ecosystems in North America and Europe. While sometimes predation comes from a range of sources, in other cases a single predator dominates the signal. In addition, evidence for functional complementarity among predator assemblages, a process thought to dampen top-down control and stabilize ecosystems, is also mixed. We mainly found evidence that different predator populations vary in a statistically independent manner, with a similar number of exceptions of predator assemblages that displayed synchrony and asynchrony (i.e., functional complementarity). This may help explain unexpected marine ecosystem shifts in response to predator collapses, and should serve as a warning in defense of precautionary management of higher trophic level populations.

There is a rich literature on diversity, stability, and ecosystem functioning, particularly in terrestrial ecosystems (e.g., May, 1973; Tilman, 1996; McCann, 2000). 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 any observed dampening of variability in the total amount of predation prey populations experience is usually a statistical artifact, and not evidence of true functional complementarity and niche partitioning that asynchrony would signal. That is, different predator populations were more or less independent of one another. While this means that the variance of the total predator assemblage is simply the sum of the individual population variances, the standard deviation of the sum is less than the sum of individual predator standard deviations, and so variability is still somewhat dampened under metrics such as the standard deviation or coefficient of variation.

There is some empirical evidence that higher latitude systems have stronger trophic cascades because they are less diverse and therefore have simpler food webs with stronger linkages (Frank *et al.*, 2007; Boyce *et al.*, 2015), but the mechanism for this has not yet been explored. While we did not test the latitudinal hypothesis explicitly, we did not see mechanistic evidence for it. In the Gulf of Alaska, Arrowtooth flounder is a single dominant predator, whereas in the Eastern Bering Sea, north of the Gulf of Alaska, we saw the most notable evidence for asynchrony and functional complementarity. The North Sea showed more synchrony across predators than the more northerly Barents Sea, also indicating that the southern food web is possibly more susceptible to dramatic shifts. And in the West Atlantic, none of the ecosystems showed strong evidence for synchrony or asynchrony, and the variance factor was in fact just as variable among different prey functional groups within a single ecosystem (the Southern Gulf of St. Lawrence) than among the five areas.

Our predator index is far from perfect at characterizing predation risk. While it represents an improvement over summing all possible predators, or over choosing a single dominant predator, it still has important weaknesses. Chief amongst them 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 include diet information, which is known to change through time (cite), particularly when systems undergo major structural shifts. Unfortunately, diet time series are only available for a small number of systems, and so accounting for changes in diets while also maintaining a comparative approach is challenging.

Theory predicts that complex food webs should 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, and can in fact prevent populations from recovering from overfishing, even in the absence of further exploitation (Swain and Benoît, 2015). Whether we observe a system to be driven from the bottom up or the top down depends in part on where we have historically observed the most variability in the food chain (Has someone said this? it seems obvious to me). Marine predator assemblages can in fact show high levels of variability, either because a single population is extremely dominant, or because of synchrony within the assemblage. Either case provides a mechanism for top-down control in large marine ecosystems. Therefore, an observed history of an environmentally driven system does not preclude it from a future trophic cascade if the predator assemblage undergoes large changes. Predator populations and assemblages should be managed with precaution to prevent more examples of large system shifts in the future.

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