# Questions

Initially, we wanted to know in what sort of cases do we see an influence of predation on population productivity, when looking across species and ocean basins. It turns out we often see no signal, which begs the question why.

First, one common theory is that marine food webs are complex, and predation comes from many different species. This complexity stabilizes the total amount of predation any species experiences. That is, the total portfolio of predation is less variable than each individual predator species. According to this logic, in simpler systems with single predators, such as the Baltic Sea, we should see a predation signal in prey productivity.

Second, we generally only had abundance data for commercially exploited species, particularly groundfish that are easy for surveys to capture. Therefore, perhaps we are not capturing the true time series of predation that fish are experiencing because we are missing key predator species such as birds and mammals. According to this logic, in systems where we have data that capture a larger proportion of predators, we should see a predation signal in prey productivity.

# Data

Data mainly consist of time series of trawl surveys from across the North Atlantic and North Pacific (Table 1). These time series exist for a wide range of species. Surveys have already been corrected for catchability and are scaled up to total population biomasses. In some ecosystems (mainly the Pacific), we have stock assessment model output instead.

In concert with the abundance data, we also have Ecopath models that have been parameterized and balanced for many of the above ecosystems. In two cases we used Ecopath models for neighboring ecosystems: the North Gulf of St. Lawrence Ecopath model was used for South Gulf of St. Lawrence data, and the Eastern Scotian Shelf model was used for Western Scotian Shelf data.

Finally, for forage fish species for which we had productivity data (i.e., catch and abundance) and appropriate Ecopath models, we looked to see if recruitment estimates were also available in the RAM Legacy database.

Table 1 Prey stocks and ecosystems we have examined, and whether recruitment estimates are available in the RAM legacy database.

|  |  |  |  |
| --- | --- | --- | --- |
| **Species** | **Ecosystem** | **Ecosystem code** | **Recruitment?** |
| Atlantic herring | Baltic Sea | BALT | Yes |
| Sprat | Baltic Sea | BALT | Yes |
| Atlantic herring | Barents Sea | BS | No |
| Capelin | Barents Sea | BS | Yes |
| Pacific herring | Gulf of Alaska | GoA | No |
| Pacific herring | Hecate Strait | HS | Yes |
| Atlantic herring | North Sea | NORT | Yes |
| Lesser sandeel | North Sea | NORT | No |
| Atlantic herring | South Gulf of St. Lawrence | sGoSL | Yes |
| Capelin | South Gulf of St. Lawrence | sGoSL | No |
| Atlantic herring | Western Scotian Shelf | WSS | Yes |

# Questions and input we are interested in from you (to think about as you read):

1. Right now, we only consider forage fish. Would we gain a lot more insight from expanding this to medium-small hakes, and other bathypelagics, for example?
2. We’re having a really hard time detecting a signal from predation, even in cases where it is considered more expected. Is there something we missed? A better explanation as to why we’re not seeing it?
3. Is there a way to study predation using a model “in between” a totally age-structured one and a totally aggregated surplus production one? Delay-difference?
4. Is variation in production due to recruitment swamping anything we see from predation? Can we test that? Can we extract a signal from predation anyway *after* accounting for recruitment? (Perhaps using biomass per recruit as a metric instead of biomass?) Or is that the point— variation in recruitment swamps everything?
5. Anything else?

# Analyses

We tested, across ecosystems, which forage fish species have surplus production time series that are significantly affected by predation. We tested two main hypotheses as to when we might see a predation signal. First, fish in simple food webs with a small diversity of predators are more likely to be regulated by predation than fish in complex food webs with many different predators. Second, we are more likely to detect a predator effect when the measured predator signal (which mainly consists of commercially exploited groundfish) accounts for a larger proportion of the total predation mortality. We measured annual surplus production of prey as the change in biomass after accounting for fishery catch, where prey biomasses were first smoothed with a Kalman filter to avoid unrealistic spikes in productivity.

To evaluate both hypotheses, we first needed to quantify the total predation, and then examine the relationship between prey productivity and total predation across species and ecosystems. Quantifying predation is challenging as most marine fish are subject to predation from a variety of species, each with different diet preferences, consumption rates, and abundances. As a result, we required a metric to weight the relative importance of each predator species on a given prey species. To do so, we used Ecopath models that were parameterized for the various ecosystems of interest. Ecopath models assume the following equilibrium holds:

(1)

That is, the rate of change of biomass of each species, *i*, is zero, and is equal to production minus fishing minus predation, which is accounted for by the final summation. We used the alpha terms from that summation as the weighting for each predator species, and multiplied these weightings by the time series of abundances of the predators (from the data) in order to obtain an overall measure of predation that a prey species experiences. We refer to this quantification of predation mortality from a suite of predator species as a prey’s “predator field.” Alpha terms are equal to the predator consumption:biomass ratio multiplied by the fraction of the predator diet that the prey of interest makes up, divided by the equilibrium prey biomass. When Ecopath models divided the prey species into separate compartments for adults and juveniles, we examined predation on juveniles, as work from chapter 1 indicated that was where we were most likely to detect an effect of predation.

We have examined the relationship between prey surplus production and the predator field in two ways. First, we measured the correlation between the predator field and prey surplus production. Second, we fit a Schaefer model assuming process errors with an additional linear term for predation, as was done for the simulations from my first chapter. In this latter case, the predator field was de-meaned, and we examined the p-value of the predation term’s t-value for indication of top-down effects. That is, we fit the following linear model, where SP is annual surplus production, B is prey biomass, P is predator field, and estimated parameters are population growth rate r, carrying capacity K, (linear) predator effect beta, and the residual standard deviation:

To test the first hypothesis, that a more diverse predator field is more stable, and therefore cannot account for changes in prey surplus production, we have visually inspected how the total predator field changes through time, broken up by the Ecopath model functional groups.

To test the second hypothesis, that a fuller quantification of predation makes it more likely to detect a significant top-down effect, we measured what proportion of predation mortality we were able to account for with the time series of biomass trawl surveys available. As we needed a single snapshot in time for this calculation, we assumed the equilibrium predator abundances from the Ecopath models.

Finally, we examined the relationship between recruitment and the predator field. This is not an avenue we have pursued very seriously, but it is included for completeness.

# Preliminary results

Examining the relationship between prey surplus production and the predator field showed only weak correlations. A preliminary statistical test for a non-zero correlation revealed a significant (P < 0.05) correlation in only two cases: Baltic sprat and North Sea sandeels. In addition, Gulf of Alaska herring were nearly significant (P = 0.057). However, this rather crude preliminary test does not account for temporal autocorrelation, which undoubtedly exists.



Fig. 1 Prey surplus production versus predator field. The number in the upper-right corner is the correlation between the two. A star indicates statistical significance (P < 0.05), but the preliminary test did not account for temporal autocorrelation, so is quite liberal. Ecosystem codes are listed in Table 1.

Next, we looked at the relationship between predation and prey surplus production after accounting for a Schaefer biomass-surplus production relationship. Examining the predation term from this slightly more complex model reveals that our conclusions regarding predation from the full surplus production model are different than those from the simpler correlation test (Table 2). In particular, we now only conclude that there is a significant effect of predation on North Sea sandeels. Gulf of Alaska herring are again nearly significant, as are North Sea herring. However, Baltic sprat, a stock that is commonly accepted to be regulated by predation, no longer shows a significant relationship. Possibly, surplus production partially drives changes in sprat biomass, and the model incorrectly determines that the causal relationship is reversed. Therefore it does not attribute enough of the variation in surplus production to predation.

Table 2 Significance of predation term in surplus production models. The farthest right column is the P-value from the predation term (i.e., < 0.05 implies predators are important). Ecosystem codes are listed in Table 1.

region prey.spp demean.pred

1 BALT Atlantic herring 0.6194877283

2 BALT Sprat 0.2481059681

3 BS Atlantic herring 0.8681035387

4 BS Capelin 0.1236510733

5 GoA Pacific herring 0.0675461340

6 HS Pacific herring 0.9839787731

7 NORT Atlantic herring 0.0906217671

8 NORT Lesser sandeel 0.0003708616

9 sGoSL Atlantic herring 0.8016093161

10 sGoSL Capelin 0.8363723208

11 WSS Atlantic herring 0.7127709297

We also note that for most stocks, there is minimal evidence of a biomass-surplus production relationship (Fig. 2). In most cases, the linear and quadratic biomass terms were statistically different from zero, but not necessarily ecologically so. Any attempt to estimate a reference point, for example, would yield highly unreliable results.



Fig. 2 Prey surplus production versus smoothed prey biomass. In most cases, the plots show minimal evidence of the expected parabola-type relationship. Horizontal line is where surplus production equals zero (i.e., equilibrium). Ecosystem codes are listed in Table 1.

Results do not support the first hypothesis, that predation is more likely to be detected in simple food webs because the predator field, being composed of fewer species is more likely to be highly variable. In all ecosystems, the predator field appears quite variable (Fig. 3). It does not seem more variable in ecosystems with fewer components (colors). We do note that predation in both the Baltic and Gulf of Alaska, two ecosystems where predation was detected, appears to be dominated by a single species. This at least supports the idea that predation is likely to be detected in simpler ecosystems; it does not support the idea that this is due to a type of portfolio effect. However, this support breaks down in the case of the North Sea sandeel, which has a high diversity of predators. There is also a notable difference in patterns we see between trawl surveys and stock assessment model output (Baltic- BALT, Gulf of Alaska- GoA, Hecate Strait- HS).



Fig. 3 Time series of the predator field (total height) broken down by Ecopath compartments (each color is the contribution to mortality from a different compartment). Ecosystem codes are listed in Table 1.

To test the second hypothesis, we examined which species were contributing to predation and quantified the proportion of predation we were able to account for with time series data. Ecosystems in the Northwest Atlantic, the Baltic, and the Gulf of Alaska have very high coverage (Fig. 4). Other cases like Hecate Strait and Barents Sea herring have very low coverage (Fig. 4). Coverage percent seems unrelated to whether we detect a predation signal, as we only have time series data for 37% of North Sea sandeels, which had the strongest predator effect across species and ecosystems. Often, a single missing species would help capture the majority of predation (Barents Sea minke whales, Hecate Strait squid). In some cases, such as the Baltic Sea and Gulf of Alaska, one or two species are responsible for the bulk of the predation. As noted above, both of these species showed some sort of relationship between production and predator abundance. In other systems like the Scotian Shelf and North Sea, many different species contribute. North Sea species also showed a relationship between predation and prey productivity above. Here



Fig. 4 Total predation mortality at Ecopath model equilibrium abundances, separated by Ecopath compartment. Predator species with data are outlined in gray. Missing species are outlined in black. Ecosystem codes are listed in Table 1. Y-axis is mortality rate. Only the top ten predator species are included (selected separately for each prey species).

Finally, we looked at the relationship between recruitment and the predator field. This does not account for the stock-recruit relationship though, as this analysis has not been an avenue we have really pursued.

Fig. 5 Recruitment versus predator field. Number in the upper right-hand corner is the correlation between the two. Ecosystem codes are listed in Table 1.

# A few conclusions

There seems to be some evidence that prey species that experience predation from one or two sources (Baltic sprat, Gulf of Alaska herring) show larger responses to predation in their productivity, lending evidence to the hypothesis that simpler systems are driven from the top down, and complex systems from the bottom up. However, this does not seem to be due to a portfolio effect whereby experiencing predation from a variety of sources dampens the variability on predation through time. The importance of predation is likely not related to the proportion of mortality we are able to account for, as predation seems very important for North Sea sandeels, and we do not account for a high proportion of their predation. Recruitment currently doesn’t seem like a very useful path to go down, particularly as it further reduces the available stocks.