**Background and questions:**

There is significant debate in the scientific community regarding the pervasiveness of top-down effects in coastal marine ecosystems, and on fish in particular. Some ecological theories predict that complex speciose food webs with multiple weak trophic linkages, like the food webs found on continental shelves, are buffered from dramatic trophic cascades driven by changing predator abundances (Strong 1992). This is partly 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). Diversity is often thought to promote stability in a number of other ecological contexts, as well (e.g., Tilman 1996; Hilborn *et al.* 2003); recent studies have sought to evaluate this hypothesis by borrowing the idea of portfolio effects from economics (Figge 2004; Schindler *et al.* 2010; Anderson, Cooper & Dulvy 2013). In the case of marine fisheries, however, heavy fishing pressure has reduced populations of many oceanic predators (Baum & Worm 2009), so that the abundances of different predators within an ecosystem may actually be changing together in response to both fishing and management. In addition, although these ecosystems are diverse, it is possible that one or two species in fact cause the majority of predation mortality.

Any examination of productivity in exploited coastal marine ecosystems must acknowledge the underlying role of the environment in regulating population dynamics (Vert-Pre *et al.* 2013; Szuwalski *et al.* 2014). Small pelagic fish that are subject to particularly high rates of predation (Pikitch *et al.* 2014) are also among the most sensitive to changing environmental conditions; as a result, density dependent equilibrium-based models often fail (MacCall 2009). However predators do exert an important influence on population dynamics, and are one component among the myriad environmental drivers that govern productivity (Baum & Worm 2009). Understanding the contributions of both environmental and trophodynamic forces as drivers of productivity remains an important question both to better understand marine ecosystems and to develop better practices for ecosystem-based management (Link *et al.* 2012).

*The goal of this work is to determine, across ecosystems, 1) is the variation in the total amount of predation on mid-trophic level fish mediated by a portfolio effect, and if not 2) how does it modulate the extent of environmentally-driven changes in productivity.*

**Proposed approach:**

First, we will use a combination of published food web models coupled with surveys and stock assessment abundance information from the CAMEO database to identify important predators and evaluate the “predator field,” which I define as an index of predation mortality from a suite of predator species that changes through time. Second, we will test whether the predator field is more or less variable than might be expected were it composed of a single species. Third, we will develop methods to identify and quantify the relative contribution of changing predator fields on stock productivity, as measured on top of a low frequency environmental signal.

We have developed a metric to weight the relative importance of each predator species on a given prey species, as most marine fish are subject to predation from a variety of species, each with different diet preferences, consumption rates, and abundances. This metric uses balanced Ecopath models (Christensen & Pauly 1992) that were parameterized for the various ecosystems of interest. Ecopath models assume the following equilibrium holds:

(1)

That is, the biomass rate of change for each species, *i*, is zero, and is equal to production minus fishing minus predation. We used the alpha terms from Eq. 1 as the weighting for each predator species, multiplied these weightings by the time series of abundances of the predators (from the data), and summed over all predators in order to obtain an overall measure of predation that a prey species experiences. I refer to this final quantity as the predator field. To calculate the alpha terms, first total prey consumed per predator biomass is calculated as the product of the predator consumption to biomass ratio and the fraction of diet that the prey comprises. This quantity is used to calculated alpha by dividing by the equilibrium prey biomass to obtain the fraction of prey biomass consumed per unit biomass of each predator. Multiplying alpha by the time series of observed predator biomasses then gives the time series of the predator field, *Pi(t)*, which is the prey consumption rate per prey biomass:

. (2)

When Ecopath models divided the prey species into separate compartments for adults and juveniles, we examined predation on juveniles, as previous work (Oken & Essington 2014) indicated that was where we were most likely to detect an effect of predation.

We will measure portfolio effects to assess whether the predator field is less variable than one would expect it to be were it a single predator species exerting the same amount of predation pressure. There are a number of possible methods to calculate portfolio effects (Anderson *et al.* 2013), the crudest of which is to compare the coefficient of variation (CV) of the entire predator field to the average CV of each individual predator signal (Figge 2004). However, more complicated versions exist (e.g., Thibaut & Connolly 2013). We also note here the limitation that biomass time series are not available for every predator species, with the largest gaps for seabirds and marine mammals.

We are exploring potential models to assess how predation mediates environmental influences on annual surplus production of prey. The method currently proposed is a hidden markov model (HMM), which has been used to study recruitment regimes of forage fish (Munch & Kottas 2009). HMMs assume that there is an underlying unobserved state of the system, or a regime, that can change on longer time-scales. In this case the regime governs the overall level of productivity. On top of the unobserved regime is an observed process that can depend on explanatory variables, in addition to the underlying state: population productivity will depend on standing biomass, and we will test whether it also depends on the predator field. This is thought to be a good model because mid-trophic level fish, and particularly forage fish, undergo significant low-frequency shifts in productivity over time, and previous work (Oken & Essington 2014) found that simple surplus production models with time-invariant parameters are often ineffective at detecting effects of predation.

**Current progress:**

We have quantified the predator field for all forage fishspecies, as well as pleuronectids and gadids classified as “small” in the CAMEO database. We have done this in most ecosystems, but still need to collect information from Ecopath models for the Gulf of Maine/Georges Bank (Link *et al.* 2006), Southern Gulf of St. Lawrence (Morisette *et al.* 2003), and Eastern Bering Sea (Aydin *et al.* 2002). For the Southern Gulf of St. Lawrence, we are currently using a model for the Northern Gulf of St. Lawrence. Visual inspection of these predator fields indicates that the predator field is quite variable, and the hypothesis that oceanic ecosystems have weak top-down control due to a buffered predation mortality rate does not seem supported (Figure 1). There was generally not an immediately apparent effect of predation on surplus production on fish stocks. This result caused us to rethink our approach, and we are now hoping to model the effect of predation on top of prey productivity that is environmentally regulated.

Macintosh HD:Users:okenk:Dropbox:BypassProposal:pred-field.pdf

Figure 1 Total predator field split up by predator species, across ecosystems and prey species.

**Works Cited**

Anderson, S.C., Cooper, A.B. & Dulvy, N.K. (2013) Ecological prophets: quantifying metapopulation portfolio effects. *Methods in Ecology and Evolution*, **4**, 971–981.

Aydin, K.Y., Lapko, V.V., Radchenko, V.I. & Livingston, P.A. (2002) *A Comparison of the Eastern Bering and Western Bering Sea Shelf and Slope Ecosystems through the Use of Mass-Balance Food Web Models*. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center.

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

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

Figge, F. (2004) Bio-folio: applying portfolio theory to biodiversity. *Biodiversity & Conservation*, **13**, 827–849.

Hilborn, R., Quinn, T.P., Schindler, D.E. & Rogers, D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, **100**, 6564–6568.

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

Link, J.S., Griswold, C.A., Methratta, E.M. & Gunnard, J. (2006) Documentation for the energy modeling and analysis exercise (EMAX). *Northeast Fisheries Science Center Reference Document*, **6**, 166.

MacCall, A.D. (2009) A short scientific history of the fisheries. *Climate change and small pelagic fish* (eds D.M. Checkley, Jr., J. Alheit, Y. Oozeki & C. Roy), pp. 191–255. Cambridge University Press.

Morisette, L., Despatie, S.-P., Savenkoff, C., Hammill, M.O., Bourdages, H. & Chabot, D. (2003) Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence(mid-1980 s). *Can. Tech. Rep. Fish. Aquat. Sci./Rapp. Tech. Can. Sci. Halieut. Aquat.*, 100.

Munch, S.B. & Kottas, A. (2009) A Bayesian modeling approach for determining productivity regimes and their characteristics. *Ecological Applications*, **19**, 527–537.

Oken, K.L. & Essington, T.E. (2014) How detectable is predation in stage-structured populations? Insights from a simulation-testing analysis. *Journal of Animal Ecology*, n/a–n/a.

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Heppell, S.S., Houde, E.D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R.S., Geers, T.M., Gownaris, N. & Munch, S.B. (2014) The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, **15**, 43–64.

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

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A. & Webster, M.S. (2010) Population diversity and the portfolio effect in an exploited species. *Nature*, **465**, 609–612.

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

Szuwalski, C.S., Vert-Pre, K.A., Punt, A.E., Branch, T.A. & Hilborn, R. (2014) Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries*, n/a–n/a.

Thibaut, L.M. & Connolly, S.R. (2013) Understanding diversity–stability relationships: towards a unified model of portfolio effects. *Ecology Letters*, **16**, 140–150.

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

Vert-Pre, K.A., Amoroso, R.O., Jensen, O.P. & Hilborn, R. (2013) Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 1779–1784.