Revisiting functional responses: Insight from a multi-guild, Bayesian approach for the northwest Atlantic

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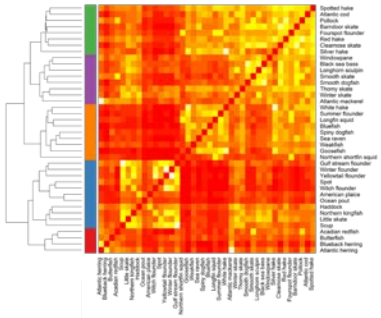


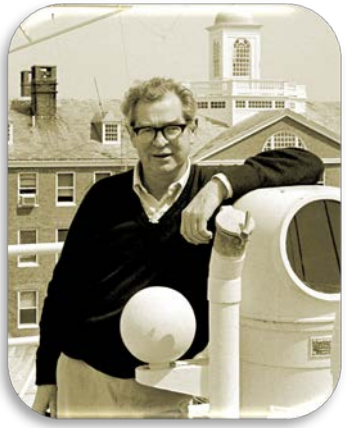
Trophic Grouping

Major Objectives

- Examine functional responses of 19 predators spanning three feeding guilds for the northeast US continental shelf.

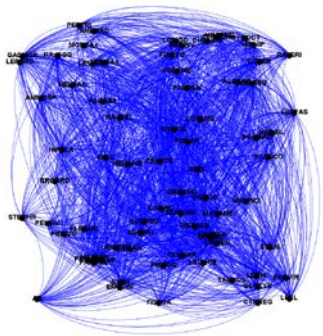
1. Expand knowledge of predator-prey interactions and predator abundance to prey density relationships with empirical data.
2. Piscivores, benthivores, and planktivores (19 predators, 14 prey).
3. Apply robust methods for handling uncertainty.

Rationale



J. Steele, Woods Hole

- Predator-prey interactions shape community structure, regulate prey populations, and present energy requirements for community sustainability.
- Key to modeling trophic interactions and predator abundance in end-to-end models with strong influence on model behavior.
- Much work on functional responses; estimating responses across multiple feeding guilds with a robust modeling approach is less studied.
- Need for empirically-driven functional responses of various trophic groups (Steele et al. 2013) plus additional interests.

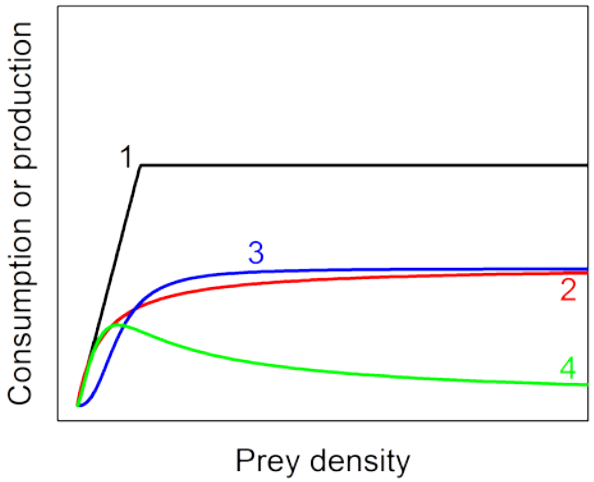


Food Web

Background

- Holling's disk equation (Holling 1959) relating consumption or abundance (*Y*) to prey density (*x*):
- *a* = attack rate, *h* = handling time, n = functional response form.
- Functional response Types 1, 2, 3, and 4.
- Type 4 (modified Holling's to allow for n1 and n2), if n1 = 1 and n2 ≥ 2.
- High uncertainty in trophic relationships for most marine ecosystems; thus, a need for exploration.

$$Y = \frac{a \cdot x^n}{1 + a \cdot h \cdot x^n}$$



Trawl survey

Data for NE US Shelf

- Fish feeding ecology & right whale calf abundance: seasonal time series of per capita consumption from NMFS bottom trawl survey, 1973-2016. Annual time series of calf abundance from NMFS right whale surveys, 1990-2011.

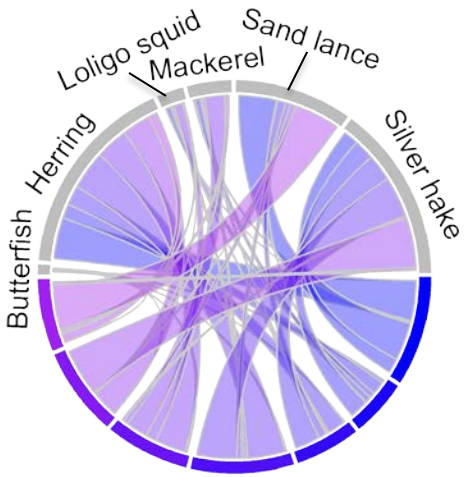
- Fish abundance: seasonal time series, stratified mean numbers per nautical mile^2 from NMFS bottom trawl survey, 1973-2016.

- Benthic invertebrate abundance: mean number per grab volume by season-shelf region from NMFS macrobenthic surveys, 1956-1965.

- Plankton abundance: seasonal time series as mean number per volume of water sampled from NMFS ECOMON and bottom trawl surveys, 1977-2015.

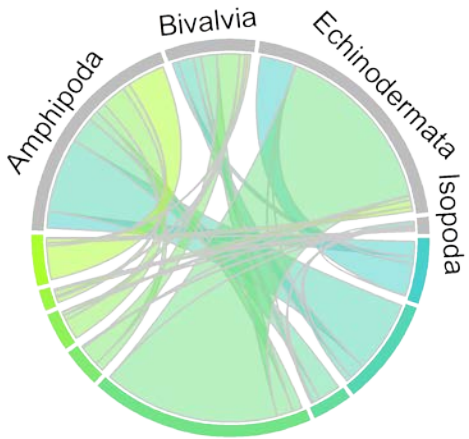
To Eat and Be Eaten

Piscivores



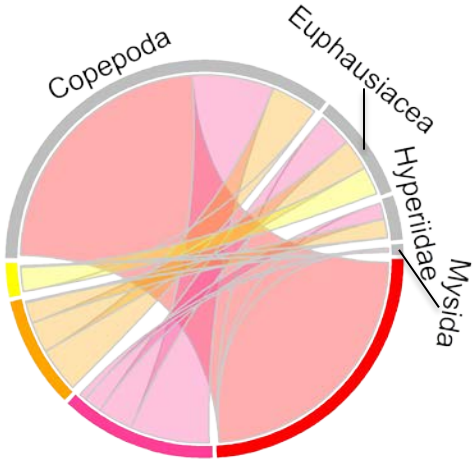
- Winter skate
- White hake
- Spiny dogfish
- Silver hake
- Pollock
- Goosefish
- Cod

Benthivores



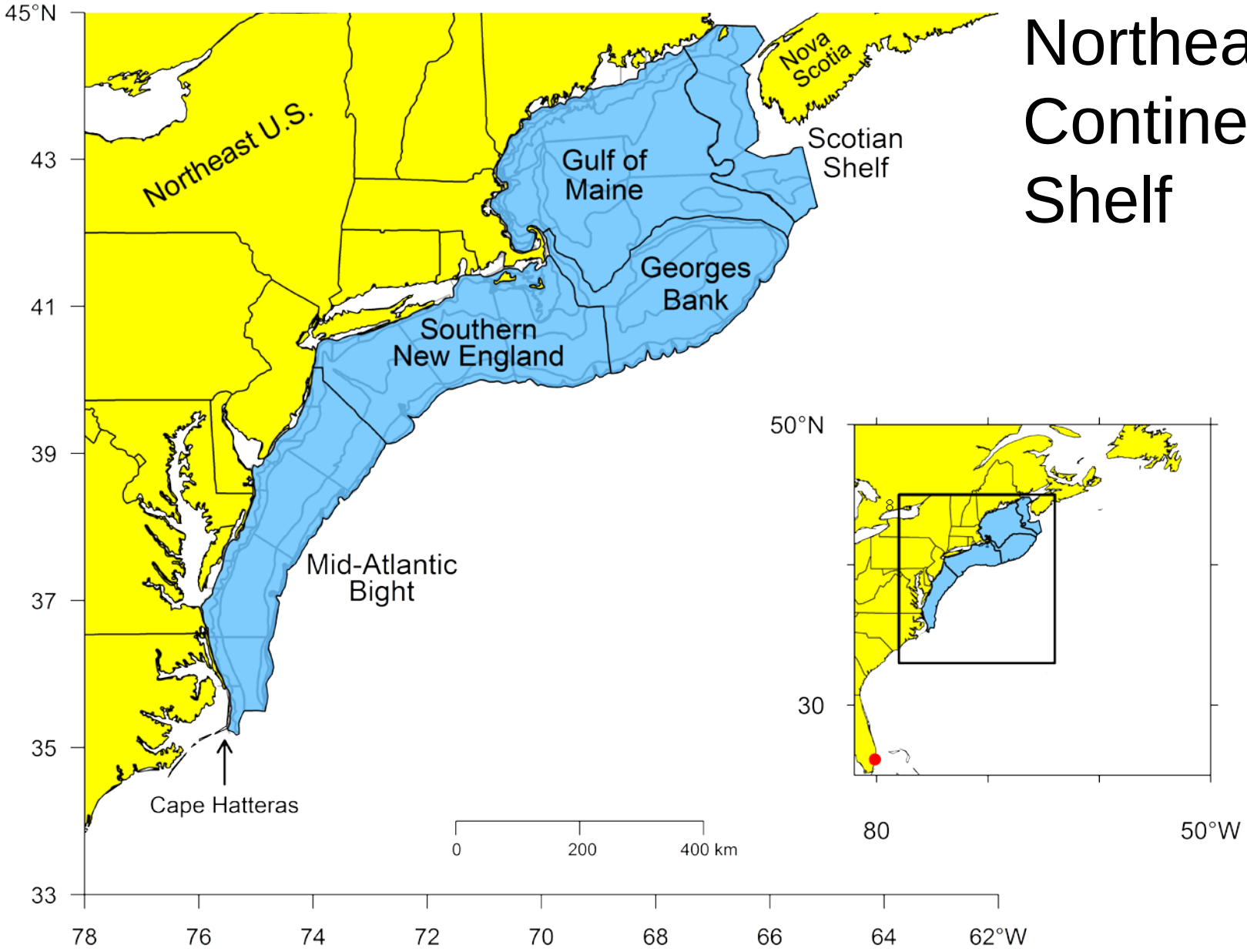
- Yellowtail flounder
- Witch flounder
- Winter flounder
- Red hake
- Ocean pout
- Longhorn sculpin
- Little skate
- Haddock

Planktivores



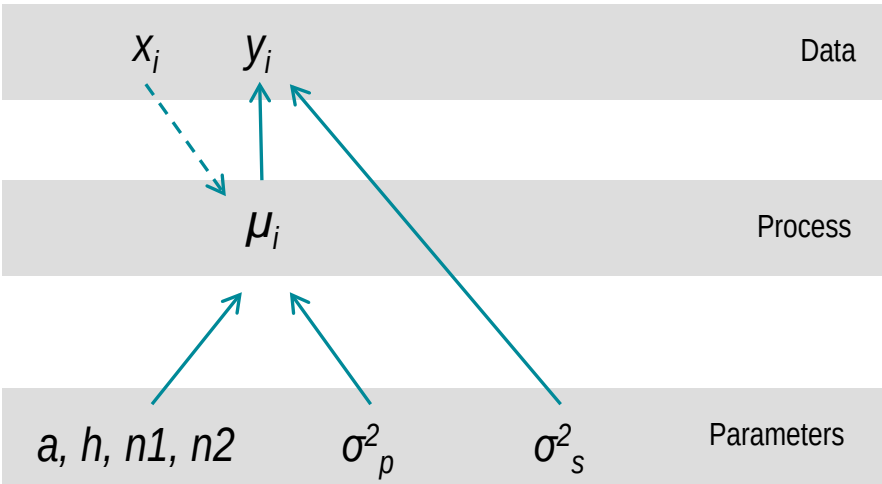
- Silver hake
- Atlantic mackerel
- Atlantic herring
- Right whale

Northeast U.S. Continental Shelf



Bayesian Modeling

Network



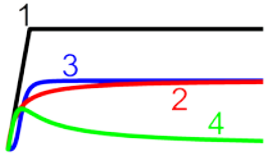
Deterministic model

$$g(a, h, n1, n2, x_i) = \mu_i = \frac{a \cdot x_i^{n1}}{1 + a \cdot h \cdot x_i^{n2}}$$

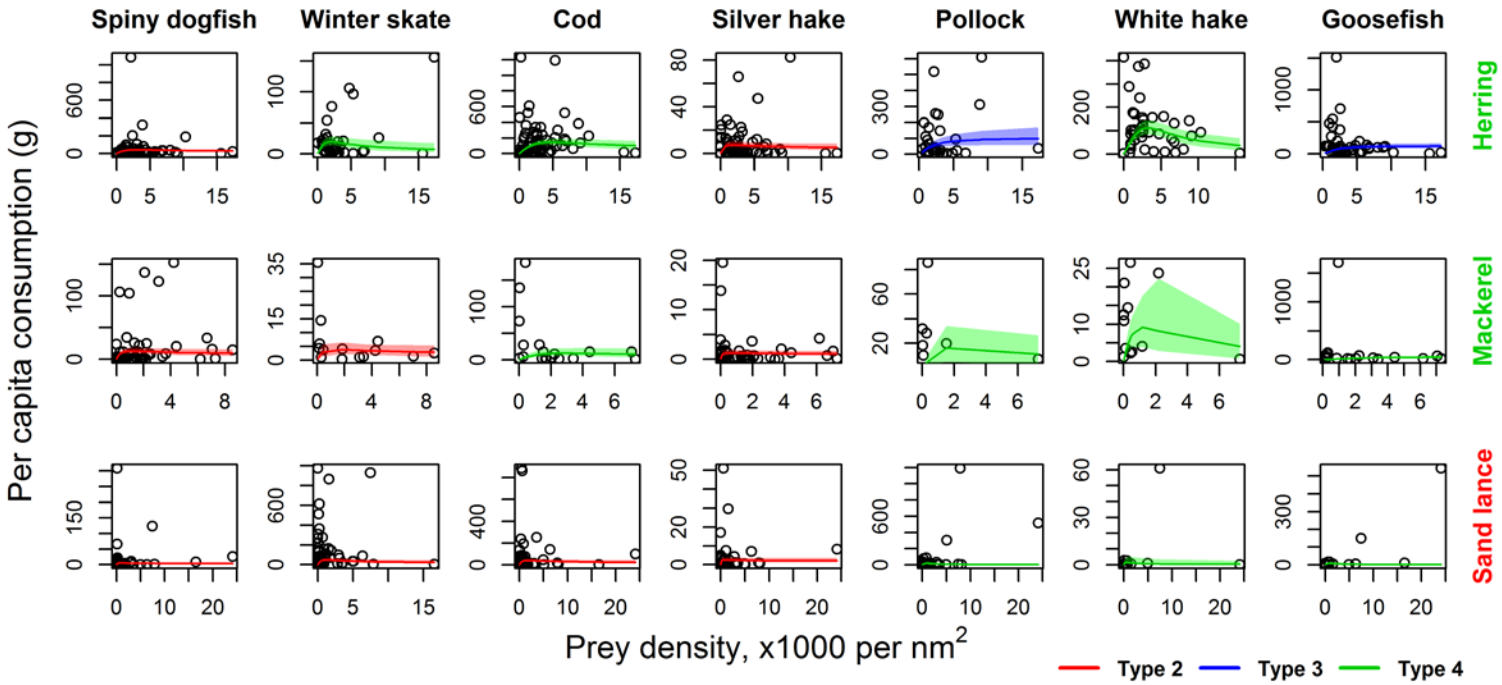
x_i = Prey density
y_i = Per captia consumption or right whale calf abundance
a = attack rate
h = handling time
$n1$ = exponential term allowing for various responses
$n2$ = exponential term allowing for various responses
σ^2_p = process error
σ^2_s = observation error

Full conditional equation

$$\begin{aligned}
&[\mu, a, h, n1, n2, \sigma_s^2, \sigma_p^2 \mid \boldsymbol{Y}] \\
&\quad \propto \prod_{i=1}^{N} Gamma\left(y_i \middle| \frac{\mu_i^2}{\sigma_s^2}, \frac{\mu_i}{\sigma_s^2}\right) \\
&\quad \times gamma\left(\mu_i \middle| \frac{g(a, h, n1, n2, x_i)^2}{\sigma_p^2}, \frac{g(a, h, n1, n2, x_i)}{\sigma_p^2}\right) \\
&\quad \times gamma\,(a|0.25, 0.25)\; gamma\,(h|0.25, 0.25) \\
&\quad \times gamma\,(n1|0.25, 0.25)\; gamma\,(n2|0.25, 0.25) \\
&\quad \times inverse\ gamma\,(\sigma_s^2|0.25, 0.25) \\
&\quad \times inverse\ gamma\,(\sigma_p^2|0.25, 0.25)
\end{aligned}$$



Piscivore Responses



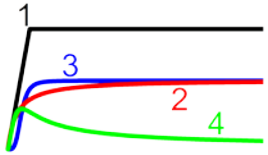
Average Prey Length (mm) ± 2xSE

204 ± 3.0

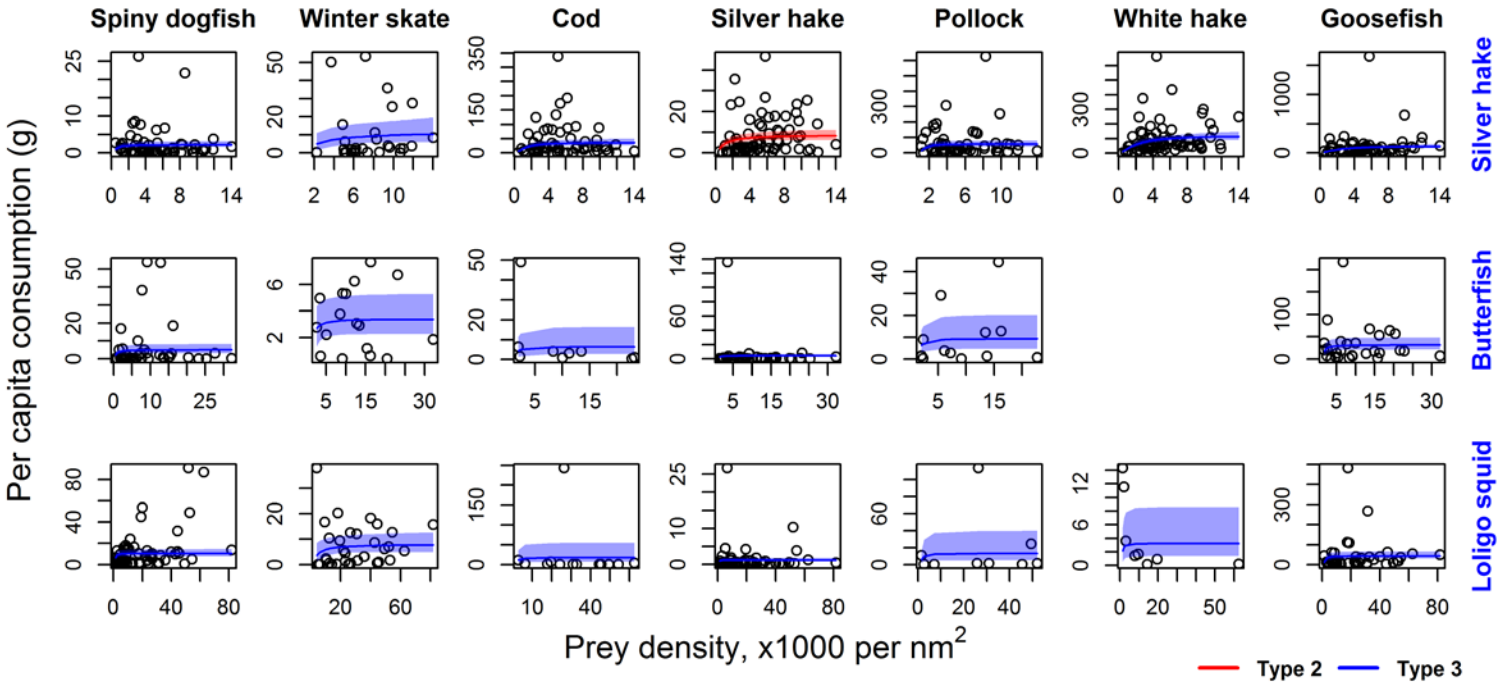
196 ± 6.4

126 ± 1.6

- Primarily Type 2 and 4 responses (red and green) for larger pelagic and small bentho-demersal prey fishes.
- Predator- and prey-dependent functional responses.
- Decreased feeding for some species with increased prey density (Type 4).

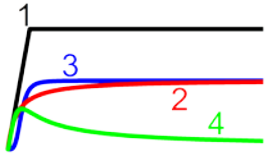


Piscivore Responses

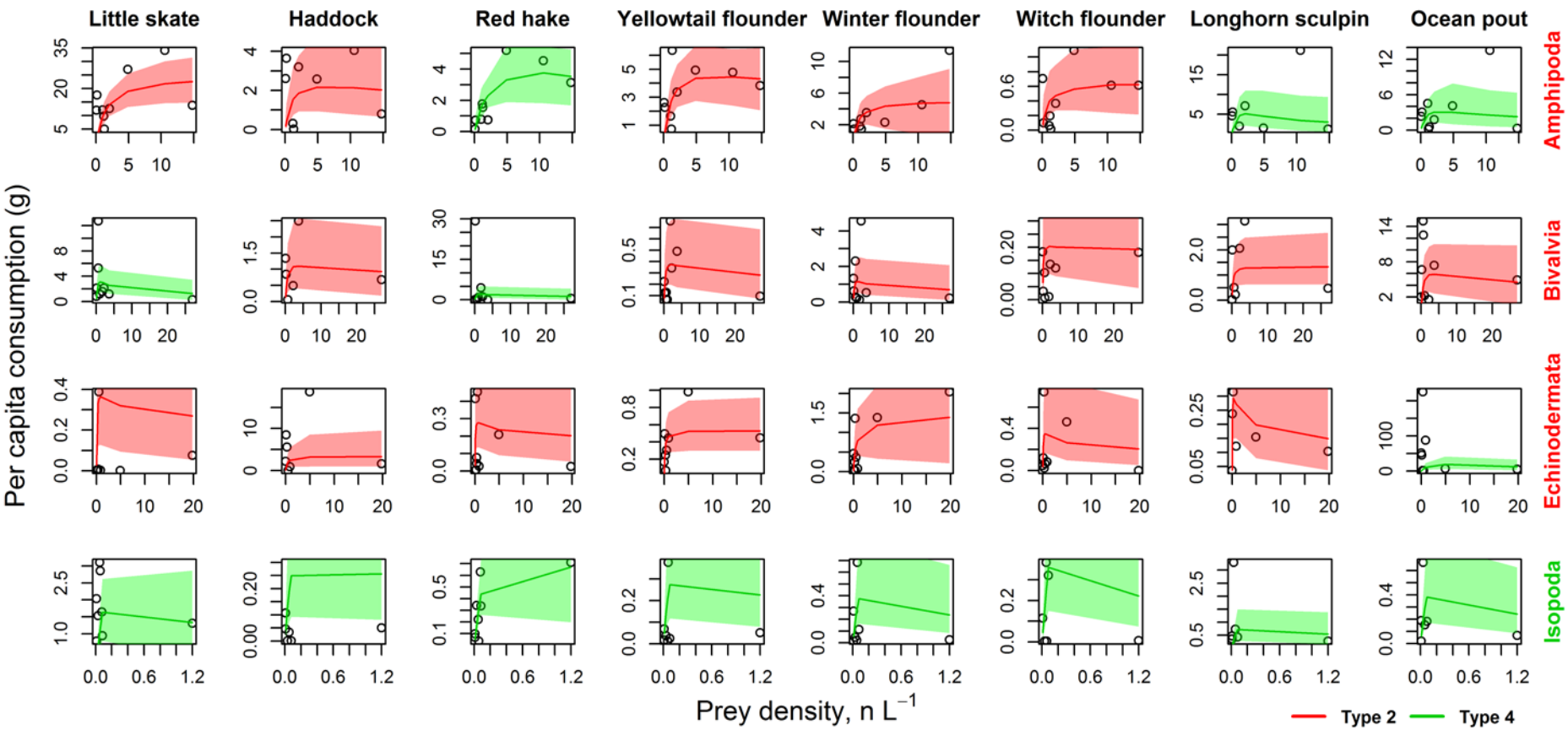


	Average Prey Length (mm) ± 2xSE
Silver hake	149 ± 2.7
Butterfish	98 ± 3.2
Loligo squid	75 ± 2.5

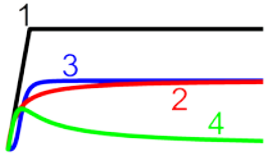
- Primarily Type 3 responses (blue) for smaller pelagic (denser aggregations) and abundant demersal prey fishes and squid.
- Silver hake cannibalism (Type 2, red).
- Implied learning or waiting period with small pelagic prey.



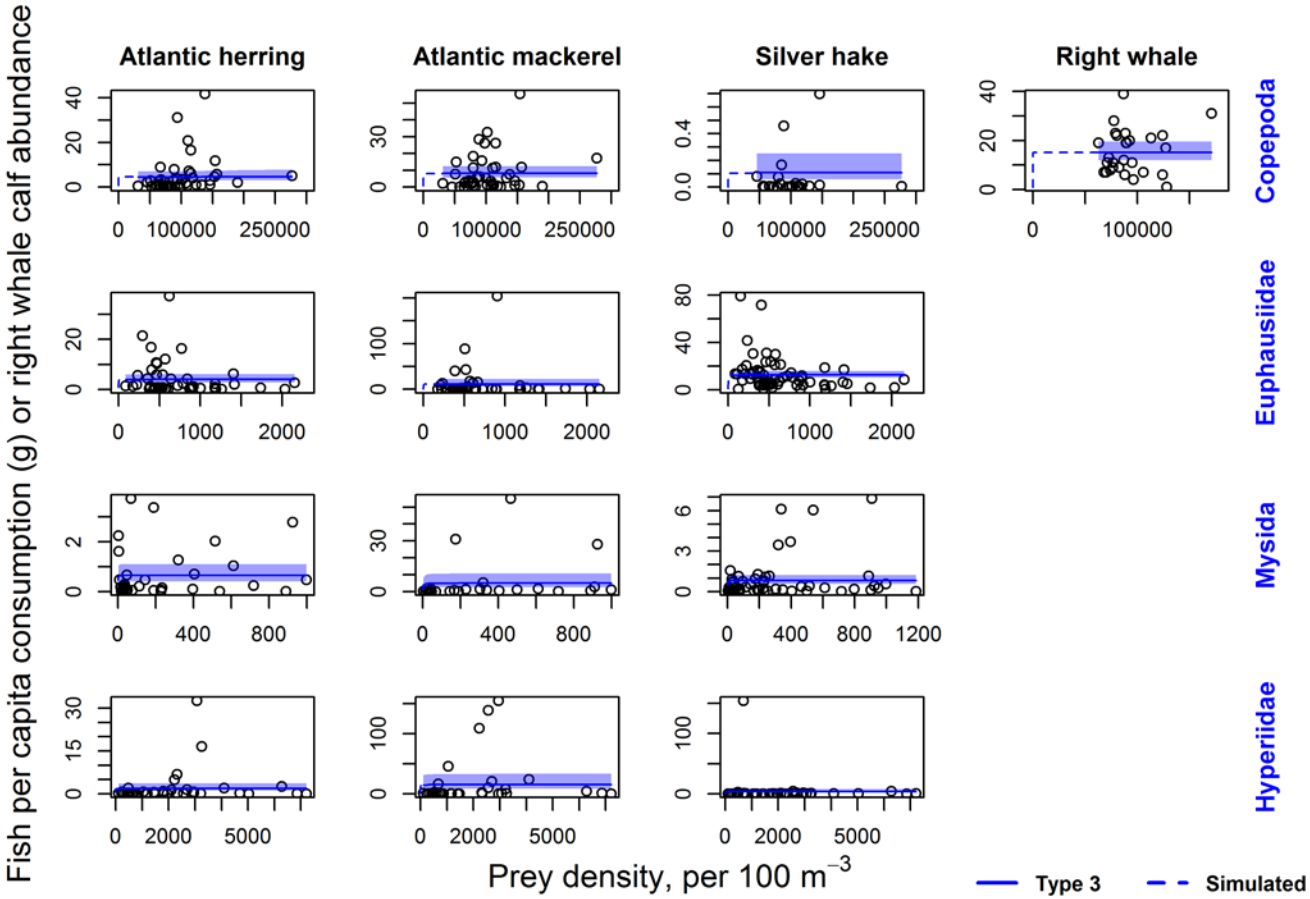
Benthivore Responses



- Primarily Type 2 responses (red); Isopoda exception (Type 4, green).
- Implied feeding until satiation, but handling time is apparent.



Planktivore Responses



- Type 3 responses, suggesting prey switching, learning, or waiting.
- Again, Type 3 responses present with dense prey aggregations.

FSV Bigelow

Summary

- Response Types 2, 3, and 4 present, and show primarily prey-dependent, but also predator-dependent results.
- Type 2 or 4: larger pelagic and one bentho-demersal fish prey.
- Type 3: smaller, densely aggregated pelagic fish prey, highly abundant demersal fish prey, and “planktonic” prey.
- Type 2 or 4: benthic invertebrate prey.

A. O'brien

Discussion

- Previously, predator-based or trophic-group approach.
- We suggest a prey-based approach which may limit use of broad trophic groups (e.g. piscivores).
- Potential overestimation of predation with higher densities of prey (ignoring Type 4 response).
- With these refined ecological inputs, we can improve multi-species and ecosystem models and continue to advance fisheries management.

Questions?