Spatiotemporal analysis of diet and distribution of Atlantic cod and flounder in relation to density

Max Lindmarka,1, Michele Casinib

a Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Marine Research, Turistgatan 5, 453 30 Lysekil, Sweden

b University of Bologna, Department of Biological, Geological and Environmental Sciences, Via Selmi 3, 40126 Bologna, Italy

1 Author to whom correspondence should be addressed. Current address:

Max Lindmark, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Marine Research, Turistgatan 5, 453 30 Lysekil, Sweden, Tel.: +46(0)104784137, email: max.lindmark@slu.se

**Keywords**: Diet, Competition, Spatial analysis, Stomach content data, Spatio-temporal models, Density dependence

Abstract

Introduction

* Find the structure of the intro – key papers etc. Thinking interactions, cooccurrence, diet? Where to start. Check notes for key papers and keep them in a list, maybe in here

Several studies have brought forward the hypothesis that changes in the abundance and distribution flounder have led to increased competition for benthic prey, and a subsequent decline in the proportion of *Saduria entomon* (henceforth Saduria) in cod stomachs. By contrast, a recent study found no effect of local flounder density on the body condition of cod, and that the decline of Saduria in cod stomachs could be due to the cod population changing its distribution away from core Saduria habitats. The first mechanism implies scramble competition, whereas the latter either implies no competition at all, or territorial competition causing cod to occupy new habitats. However, while there is an overlap in their diets (albeit small) and their spatial distribution overlaps to a larger degree in recent years, several aspects, and clues into the interactions between cod and flounder remain largely unexplored.

In this study, we fit spatiotemporal models to diet and density data to quantify how fine-scale density of cod and flounder affect each other’s densities, diet, and condition (as a measure of foraging performance). We find no sign of fine scale negative co-occurrence between the species, and that they both increase in the same spatial area in the southern Baltic but flounder to a larger degree. Moreover, while we find a negative relationship between cod and flounder density and the biomass of Saduria in the stomach of the two species, the total prey biomass is unaffected by density, suggestion these species find prey in proportion to their density and that the density dependence of growth is small. Corroborating this is a long-term analysis cod feeding ratios, revealing that cod stomachs did not contain more prey biomass in time-periods with higher body condition of cod, suggesting that it is not the amount of food that limits the performance of cod.

Results

Results

Discussion

Discussion

Materials and Methods

*Data*

New diet data, standardized CPUE data. Haul-level, important.

Then, old data, with rectangle as the only spatial indicator. Here we have rectangle random effects instead.

* Explain the response variable

*Spatiotemporal models*

To quantify the changes in spatiotemporal distribution, we fit we fit spatial and spatiotemporal predictive-process Generalized Linear Mixed Effects Models (GLMMs). These models include a spatially explicit temporal trend (i.e., local trend), alongside spatial (temporally constant) and spatiotemporal (time-varying) random field. We fit two sets of models, with or without flounder and cod density as covariates for the cod and flounder models, respectively. This is to first evaluate the fine-scale cooccurrence patterns, and the models without covariates are used to calculate other metrics and we want to maintain more independence when quantifying the range shits (English et al., n.d.)). Specifically, we modelled we modelled biomass density with a Tweedie distribution and a log link because densities contain both zeros and positive continuous:

eq

The models were fit using ´sdmTMB´ (Anderson et al., 2019, 2021), which utilizes Template Model Builder (TMB) (Kristensen et al., 2016), R-INLA (Rue et al., 2009) for approximation of Gaussian Markov random fields.

*Long term diet models*

To evaluate differences in feeding ratio between across time periods of different stomach sampling programs (names and years), including older data without haul locations, we used a gamma hurdle model for the feeding ratio. These are two-step models consisting of a binomial model for the probability of presence of prey in the stomach and a gamma model for the conditional part:

eq

We treat ices rectangle as a random factor.

Code and Data Availability

All data (apart from recent stomach data) and R code (lists of studies in literature search, data preparation, analyses and figures) can be downloaded from a GitHub repository (<https://github.com/maxlindmark/cod_interactions>) and will be archived on Zenodo upon publication.

References

Anderson, S. C., Keppel, E. A., & Edwards, A. M. (2019). *A reproducible data synopsis for over 100 species of British Columbia groundfish* (Doc. 2019/041). DFO Can. Sci. Advis. Sec. Res. <www.dfo-mpo.gc.ca/csas-sccs/Publications/ResDocs-DocRech/2019/2019\_041-eng.html>

Anderson, S. C., Ward, E. J., Barnett, L. A. K., & English, P. A. (2021). *SdmTMB: spatiotemporal species distribution GLMMs with ‘TMB’* (R package version 0.0.17.9000) [Computer software]. https://pbs-assess.github.io/sdmTMB/index.html

Barnett, L. A. K., Ward, E. J., & Anderson, S. C. (2021). Improving estimates of species distribution change by incorporating local trends. *Ecography*, *44*(3), 427–439. https://doi.org/10.1111/ecog.05176

English, P. A., Ward, E. J., Rooper, C. N., Forrest, R. E., Rogers, L. A., Hunter, K. L., Edwards, A. M., Connors, B. M., & Anderson, S. C. (n.d.). Contrasting climate velocity impacts in warm and cool locations show that effects of marine warming are worse in already warmer temperate waters. *Fish and Fisheries*, *n/a*(n/a). https://doi.org/10.1111/faf.12613

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., & Bell, B. M. (2016). TMB: Automatic Differentiation and Laplace Approximation. *Journal of Statistical Software*, *70*(1), 1–21. https://doi.org/10.18637/jss.v070.i05

Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *71*(2), 319–392. https://doi.org/10.1111/j.1467-9868.2008.00700.x

Acknowledgements

Acknowledgements

Author Contributions

Author Contributions

Additional Information

Additional Information

Figures