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SPATIO-TEMPORAL DISTRIBUTIONS, ABUNDANCE, AND OVERLAP BETWEEN SABLEFISH (*ANOPLPOMA FIMBRIA*) AND COMMANDER SQUID (*BERRYTEUTHIS MAGISTER*) IN THE EASTERN BERING SEA SLOPE

Martin A. Gonzalez^{1,2}, Caitlin I. Allen Akselrud³, and Cecilia A. O'Leary⁴

¹ University of California, Santa Cruz

² NOAA Educational Partnership Program with Minority Serving Institutions (EPP/MSI)

³ NOAA Southwest Fisheries Science Center, La Jolla, California

⁴ NOAA Alaska Fisheries Science Center, Seattle, Washington

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Spatio-Temporal Distributions, Abundance, and Overlap Between sablefish (*Anoplopoma fimbria*) and commander squid (*Berryteuthis magister*) in the Eastern Bering Sea Slope

Martin A. Gonzalez*¹, Caitlin I. Allen Akselrud², Cecilia A. O’Leary³

*corresponding author: mgonz266@ucsc.edu

¹University of California, Santa Cruz and the NOAA Educational Partnership Program with Minority Serving Institutions (EPP/MSI Program)

²NOAA Southwest Fisheries Science Center, La Jolla, California

³NOAA Alaska Fisheries Science Center, Seattle, Washington

Abstract

The study of species interactions, especially when concerning commercially important species, is important if we wish to better understand how different living marine resources affect each other. The decline of one species could have widespread economic and cascading ecological effects. This is relevant for the interactions between the predator sablefish (*Anoplopoma fimbria*), and one of its major prey species, commander squid (*Berryteuthis magister*). In order to better understand the effect commander squid abundance has on sablefish over space and time, we created a spatio-temporal model to illustrate distribution patterns for the Eastern Bering Sea sablefish stock from 2002 to 2016 using survey data from the Alaska Fisheries Science Center Groundfish Assessment Program’s Eastern Bering Sea Slope survey, with commander squid density as a covariate predictor of biomass. When comparing models with and without the squid covariate, it is clear through model selection that including the squid prey covariate leads to a much better model fit to the data. This analysis shows that adding ecosystem information into species abundance and distribution modeling has the potential to substantially increase model performance and our understanding of changes in densities of individual species through space and time.

Key words: sablefish, commander squid, Bering Sea, ecosystem interactions

Background and Introduction

Sablefish (*Anoplopoma fimbria*) are a commercially important, bathydemersal fish species distributed on the continental slopes, spanning from Mexico to the northern islands of Japan in an arc around the center of the Pacific Ocean (Eschmeyer and Herald, 1983; Yang, 1993; Mateo et al., 2018). Sablefish habitat usage is ontogenetic, whereby younger and generally smaller fish are more abundant in shallower waters while older and generally larger fish are more abundant in deeper waters on the continental slope (Eschmeyer and Herald, 1983; Head et al., 2014; Nims and Butler, 2019; Haltuch et al., 2019). Due to this ontogenetic habitat shift, it is very common to directly correlate sablefish life stages and fork lengths (FL) with habitat regimes, where smaller juveniles 20 - 40 cm in length inhabit the inshore demersal zone, while larger juveniles (40 - 54 cm FL) and adults (FL greater than 54 cm) occupy the offshore demersal zone (Head et al., 2014; Nims and Butler, 2019). Sablefish take five to seven years to reach reproductive maturity and can live up to 102 years old (Haltuch et al., 2019). However, most of the stock is younger than 20 years old (Haltuch et al., 2019).

The commander squid (*Beryteuthis magister*) is an abundant species of squid common in the North Pacific Ocean (Nesis 1997). Commander squid occupy mesopelagic waters during their larvae, paralarvae, and juvenile stages and benthic and near bottom habitats in their adult stages (Nesis, 1997; Katugin et al., 2013). They are presumed to be an aggregative, semelparous spawning species with three spawning seasons (summer, fall, and winter with the summer being the main spawning period) in the Bering Sea, though there have been no direct spawning observations and they have a projected life cycle of two years (Arkhipkin et al., 1996; Nesis, 1997; Arkhipkin et al., 1998; Moltschaniwskyj and Pecl, 2007; Katugin et al., 2013). Adults are known to congregate on the continental slopes of the North Pacific Ocean, Bering, Okhotsk, and Japan seas with seasonal dynamics of squid concentrations reflecting spawning dynamics (Arkhipkin et

al., 1996; Nesis, 1997; Arkhipkin et al., 1998; Katugin et al., 2013). Quantitative studies of commander squid abundance and distribution in the Russian Exclusive Economic Zone (EEZ) demonstrated that the Western Bering Sea (WBS) commander squid is common on and around the continental slope and the Shirshov Ridge, but are rarer in the open seas and away from the slope (Radchenko, 1992).

Known interactions between sablefish and commander squid

Commander squid are an important mid-trophic level species, acting as both a predator and prey species in North Pacific food webs by linking their prey species, such as crustaceans and northern smoothtongue (*Leuroglossus schmidti*), to species which prey on them, including sablefish and local marine mammals (Yang, 1993; Nesis, 1997; Hunsicker et al., 2010; Katugin et al., 2013). Comparatively, the diet of sablefish is divided by size, such that small sablefish diets include small fish and echinuroids (a polychaete worm), while larger sablefish diets include larger fish, cephalopods and shrimp (Sasaki, 1985; Yang, 1993). There is also high geographic variability in the sablefish diet that suggests opportunistic foraging (Brodeur and Livingston, 1988).

In terms of percentage of total weight in the diet, Oegopsida (mostly pelagic squids) and general Cephalopoda (squid, octopus, cuttlefish, or nautilus) formed the third highest component of a sablefish's diet in the Eastern Bering Sea (EBS) during the summer and fall of 1985 to 1986, behind Walleye pollock (*Gadus chalcogrammus*) and general teleost fish (Osteichthyes Teleostei), which were not identified to species level (Brodeur and Livingston, 1988). There was a similar trend in the Gulf of Alaska (GOA) during the summer of 1990 where, in terms of the percentage of total weight in the diet, commander squid were again the third-highest component of the sablefish diet behind Walleye pollock and fishery discards from the local fishing industry (Yang, 1993). In the GOA, the 60 to 69 cm (FL) size class of adult sablefish consumed commander squid,

making up 14% of the diet at that size (Yang, 1993; Head et al., 2014). Total prey weight percentages in diets are expected to be different between the EBS and GOA regions due to differences in fishing vessels and prey fish stock levels, but the trends between size and percent weight of species in the diet are assumed to remain the same (Mito, 1974; Brodeur and Livingston, 1988; Yang, 1993). These patterns between regions indicate that cephalopods generally play an important role in the sablefish diet.

The sablefish population as a whole dramatically declined between 1976 and the early 2010s, after which it experienced large recruitment events in 2013 and 2016 (Johnson, 2015; Tolimieri, 2018; Kapur, 2021). Changes in sablefish abundance are crucial to understand as declines in the stock could lead to drastic economic impacts. Ultimately, it is important to understand the ecosystem dynamics that are driving recent variability in the Alaskan sablefish population biomass because it can have wide ranging effects on the local ecosystem as well as economic impacts due to its status as a commercially important fishery (Goethel et al., 2021). By focusing our analysis on the Bering Sea, we are able to investigate differences in sablefish recruitment and population biomass due to the effects of squid density separately from the Gulf of Alaska region. As such, this predator-prey interaction serves as an important reminder of looking beyond individual-species assessments with ecosystem-based assessments, and the importance of data from the slope survey in the Bering Sea to better understand the relationships between this commercially important benthic scavenger and one of its important prey species.

Objectives

We propose that there are higher rates of commander squid consumption by adult sablefish (greater than 54 cm fork length) during the summer season in the EBS Slope because of an ontogenetic overlap between adult sablefish and overall commander squid aggregations. We also suggest that these squid aggregations stem from either one or both of the following scenarios: 1) pre-spawning squid congregate in the squid spawning grounds, making them more common in adult sablefish diets or 2) spent (post-spawning) squid and squid carcasses are aggregated on the seafloor, making them an easy-to-scavenge prey item for sablefish. The Yang (1993) and Brodeur and Livingston (1988) diet analyses showed a high total weight percentage of squid in sablefish stomachs, which suggests that the first scenario may be more likely than the second, unless foraging sablefish are able to compensate for post-spawning, decreased squid body masses with the sheer number of individuals consumed, as commander squid lose half of their body mass after mating (Nesis, 1997). Our goal is to investigate whether sablefish may be drawn to squid spawning aggregations by modeling the spatio-temporal overlap between sablefish abundance and commander squid density with the data available from the Bering Sea Slope (BSS) Survey between 2002-2016.

Methods

The Alaska Fisheries Science Center (AFSC) Groundfish Assessment Program (GAP) bottom trawl surveys were the source for the spatial and temporal sablefish and commander squid data. The domestic longline survey, while also a good index for sablefish, was excluded due to the complexity of combining multiple surveys, which were beyond the scope of this project. EBS Slope surveys were performed from May to August in the following years: 2002, 2004, 2008, 2010, 2012, and 2016 (NOAA NMFS AFSC GAP Survey; Fisheries One Stop Shop, 2023). Size data is not available in Fisheries One Stop Shop (FOSS), and so the models do not account for the

size of individuals. The EBS Slope survey has a known depth range of 204 m to 1177 m below the surface (NOAA NMFS AFSC GAP Survey; FOSS, 2023). The depth range of survey samples remains consistent throughout the time series for both sablefish and commander squid (Tables 1 and 2). This ensures that the same depths are surveyed each year and that coverage does not change between years. Surveys rarely went past the continental slope into deeper waters below 1177 m, focusing their efforts on the portion of the slope above 1177 m (NOAA NMFS AFSC GAP Survey; FOSS, 2023). Due to known sablefish ontogenetic migration patterns where adults are more abundant at greater depths while younger sablefish are more abundant at shallower depths, it is very likely that the BSS Survey sampled older and longer sablefish on the shelf break and slope region (Maloney and Sigler, 2008; Head et al., 2014). The data include only non-zero observations from the surveys, where standard tow procedures were followed and locations were sampled at predetermined survey stations (NOAA NMFS AFSC GAP Survey; FOSS, 2023).

We investigated the spatial distribution for sablefish and commander squid (Fig. 1) from 2002 to 2016 in the Eastern Bering Sea Slope region using R and the R packages ‘marmap’, ‘ggmap’ and ‘ggplot2’ (Pante et al., 2023; Kahle et al., 2023; Wickham, 2016).

Year	Minimum Depth (m)	Maximum Depth (m)
2002	207	1072
2004	256	1177
2008	299	1154
2010	406	1066
2012	411	1079
2016	210	1116

Table 1: Depth range of captured sablefish from the EBS slope surveys, 2002-2016.

Year	Minimum Depth (m)	Maximum Depth (m)
2002	204	1061
2004	206	1145
2008	205	1171
2010	205	1157
2012	206	1079
2016	210	1022

Table 2: Depth range of captured commander squid from the EBS slope surveys, 2002-2016.

For the spatio-temporal model, we used the Vector Autoregressive Spatio-Temporal (VAST) R package (Thorson, 2019). This allowed us to create a spatio-temporal delta generalized linear mixed model (GLMM) (See Appendix A, B, C). We followed the decision tree laid out in Thorson (2019) in choosing the spatio-temporal model type and settings. We used a Gamma model for the distribution of positive catch rates and a conventional delta-model using a complementary log-log link function for encounter probability and a log-link function for positive catch rates (Thorson, 2015; See Appendix A for model settings and package details). Spatial random effects and spatio-temporal random effects were set to be independent for encounter probability and positive catch rates (Thorson, 2019). Temporal autocorrelation for the encounter probability and catch rate intercepts were turned off (Thorson, 2015). Following the methods of Thorson, 2015, temporal encounter probability autocorrelation was set to follow an auto-regressive-1 (AR-1) process, while positive catch rate autocorrelation was set to follow a random walk (Thorson, 2015).

Two models were produced: a sablefish-only model and a sablefish-squid model. The first model uses only sablefish distribution (km^2) and biomass (kg) data to produce an index of sablefish density through space and time. The second model uses sablefish distribution (km^2) and biomass (kg) data with a commander squid density (kg/km^2) covariate applied to see the effects of

commander squid density on sablefish. The covariate was set up such that there was a spatially varying, zero-centered linear effect due to density (kg/km^2) of commander squid on the encounter probability and positive catch rates of sablefish (Thorson, 2015). Generating the sablefish-squid model was the primary goal of this research project, and used the Bering Sea Shelf survey data from 2002-2016. Unfortunately, we were not able to achieve model convergence with the same subset of data for sablefish only (i.e., without the squid covariate included). An earlier sablefish-only model run included a broader dataset from the Bering Sea Slope and Shelf surveys from 1982-2022. We provide a comparison of the model fits to data using Akaike Information Criterion (AIC; Akaike, 1976), while acknowledging the substantial differences in space and time between these two models.

B. magister vs. *A. fimbria*, Bathymetry and Abundance Map, From 2002 to 2016

BSS Survey Data Only

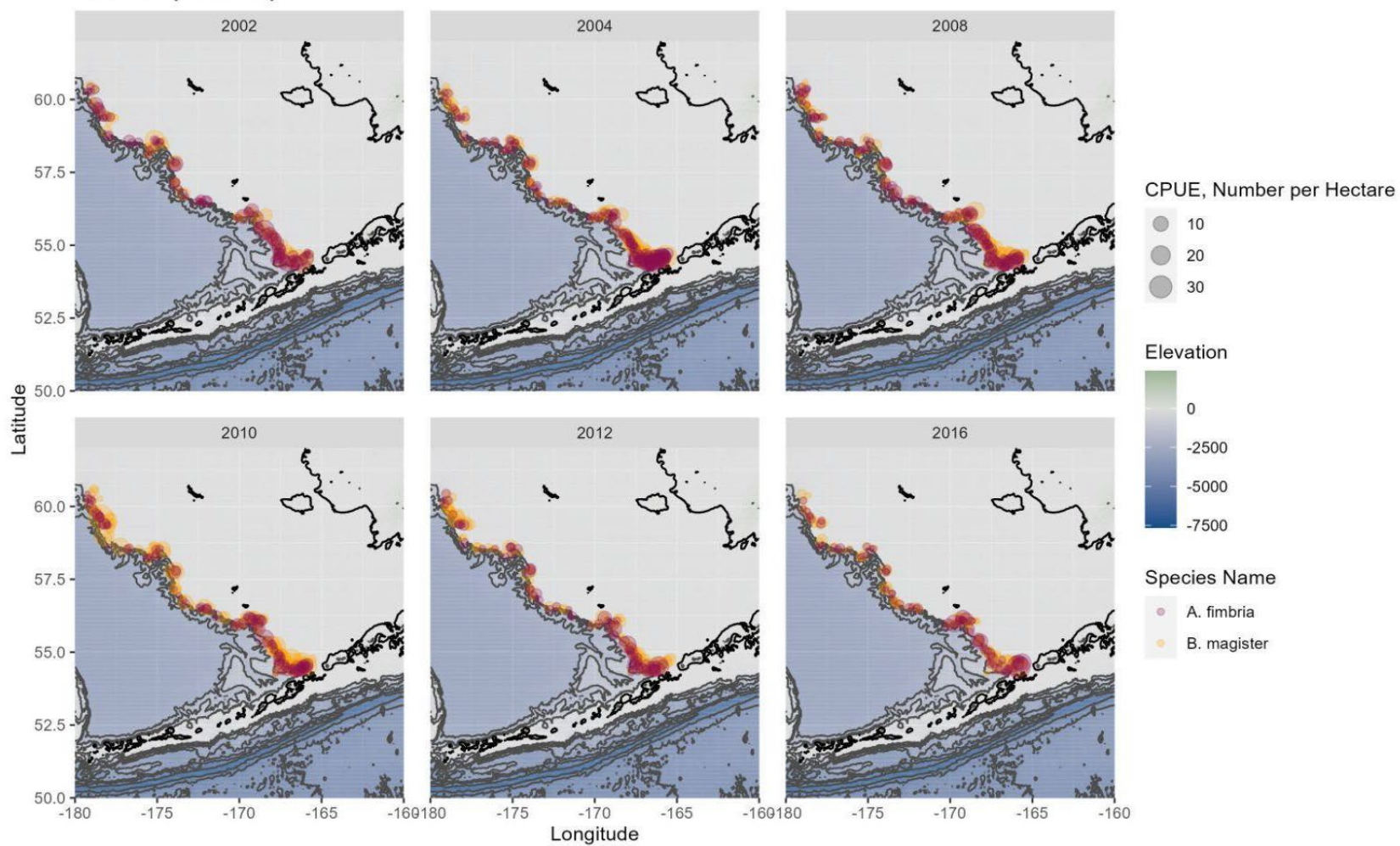


Figure 1: Spatial distribution and abundance for sablefish and commander squid in 2002, 2004, 2008, 2010, 2012, and 2016. Red circles are stations with sablefish present. Orange circles are stations with squid present. The size of the circle is catch per unit effort (CPUE).

Results

The sablefish-squid models converged, producing estimates of sablefish and squid density in space and time. The sablefish-only model using the same spatial and temporal subset of data as the model with the squid covariate did not converge. For comparison, we present an earlier model run that did converge using only sablefish data, but which includes the Bering Sea Shelf in addition to the Slope, as well as a longer time series (see methods for details). The sablefish-squid model is a better fit to the data than the sablefish exclusive model when using Akaike Information Criterion ($\Delta AIC = 5341.92$), though there are substantial differences in the spatial and temporal data used for each. The following results are reported from the sablefish-squid model.

There are high abundances of both sablefish and commander squid in the area centered on 55°N, 167°W throughout the time series, with a decreasing number of overlap occurrences northward and westward (Fig. 1) and diminishing abundances of both species towards shallower waters (Fig. 2). Overall, the shelf break and slope area have higher biomass levels ranging from 14.88 - 1480.30 kg/km² while the inner shelf has much lower biomass levels ranging from 0.002 - 14.88 kg/km² in the most northern and eastern areas of the survey region (Fig. 2). Both the peak sablefish abundance location and biomass trends for the shelf and the shelf break hold for the entire time series with minor variations over time (Fig. 2).

Predicted sablefish biomass generally decreases over time, from 7,316 tons, with a standard error of $\pm 1,127$ tons in 2002 to 1,977 tons ± 336 tons in 2016 (Fig. 3). The effective area of sablefish given a squid covariate varies year-to-year but is generally close to 15,000 km² (Fig. 4). The resulting quantile-quantile plot creates a 1 to 1 linear relationship between the observed and the expected (See Appendix C).

The modeled intercept for sablefish encounter probability remained consistent throughout time (mean = -9.835972, SD = 0.3017226) while the modeled intercept for positive catch rates remains consistent (mean = 5.658457, SD = 0.3252238) from 2002 to 2012 but then decreases in 2016 to 5.0433953 (Appendix Table B.2). The estimates for both parameters demonstrate that the locations where sablefish are caught are not changing over time, but the number of individuals encountered during the surveys has changed over the time series.

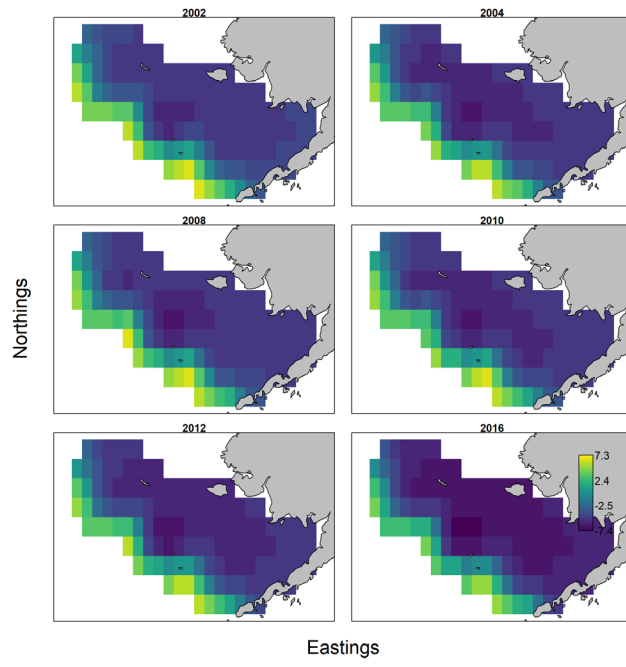


Figure 2: Predicted density of sablefish given the density covariate of commander squid, 2002 to 2016. Scale bar represents the log space transformation of kg/km^2 values.

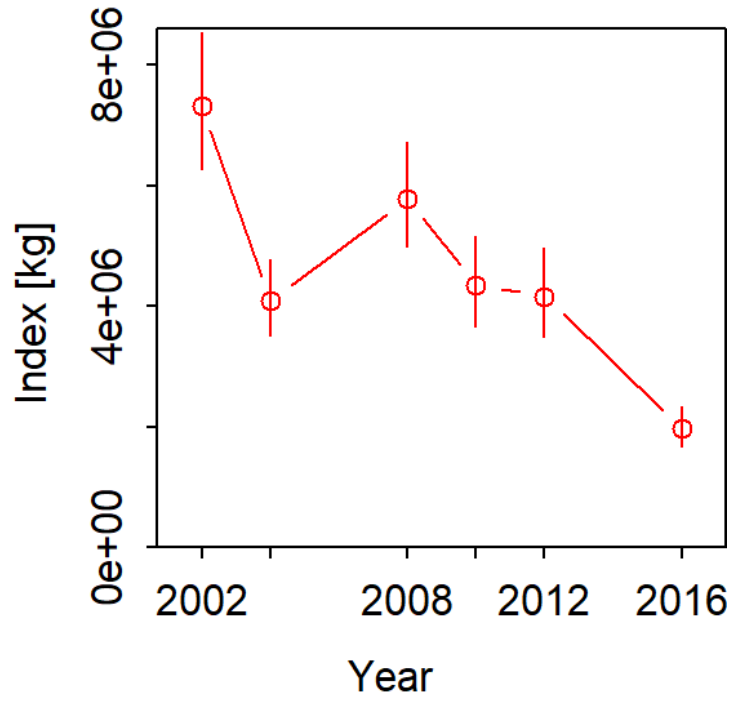


Figure 3: The predicted biomass index estimate, in kilograms, of sablefish given a density covariate of commander squid from 2002 to 2016.

Vertical lines are \pm one standard deviation.

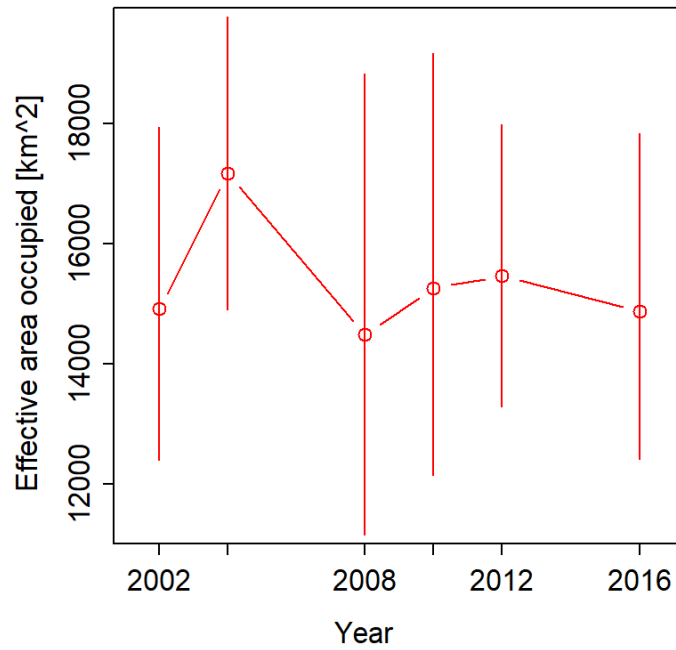


Figure 4: Effective area occupied, in square kilometers, of sablefish given the density effects of commander squid from 2002 to 2016.

Discussion

The importance of the BSS survey must not be understated, as it is through this extension of the GAP EBS survey that the majority of adult sablefish and adult commander squid habitat is surveyed (Eschmeyer and Herald, 1983; Nims and Butler, 2019; Haltuch et al., 2019). Our analysis demonstrates that model predictions of sablefish density are vastly improved when commander squid is used as a covariate. This reinforces the predator-prey link between sablefish and commander squid, and that sablefish may be drawn to commander squid spawning aggregations. By taking an ecosystem approach wherein we account for only one important prey species, we are better able to explain the density distributions of sablefish on the EBS Slope.

Between 2002 - 2016, locations of high sablefish density remained at the same spatial coordinates, but the relative density of these regions decreased over the time series (Fig. 2). We suspect that the reason for the high abundances of sablefish in the area centered on 55°N, 167°W is due to the overlap of sablefish and commander squid spawning grounds (Katugin et al., 2013; Fig. 2). Since the surveys occurred during the summer, which is the prime spawning time for Bering Sea commander squid, there is preliminary evidence to suggest that there is a high spatio-temporal overlap of sablefish and summer spawning commander squid (Fig. 2). Because this high abundance area is present throughout the time series despite a variety of environmental changes, it suggests that the density of commander squid has a strong effect on sablefish abundance and warrants further investigation. The findings here align with our species interaction hypothesis, whereby adult sablefish in the deeper benthic habitats have more spatial overlap during the summer with the commander squid spawning grounds and may be consuming more squid (Yang, 1993; Head et al., 2014). This phenomenon is juxtaposed with juvenile sablefish having less spatial overlap during the summer with the commander squid spawning grounds as they inhabit shallow continental shelf habitats with low commander squid densities (Yang, 1993; Head et al., 2014). To

ensure that either a) this high sablefish abundance given a squid covariate is year-round or b) there are other high sablefish abundance locations given a squid covariate, more modeling must be done and more survey data collected. Because squid serve as a major source of food for sablefish, this behavior could also be seen as a phenological scavenging shift where sablefish seasonally move to this area to scavenge for squid carcasses (Brodeur and Livingston, 1988; Yang, 1993).

The relationship between the effective area occupied by sablefish and predicted biomass estimate is important because some factors, such as changes in oceanic conditions or prey migrations, leads to an overall decrease in the density of sablefish throughout the region (Figs. 2, 3, 4). However, the relative differences in densities remain the same on the shelf break and the inner shelf, indicating that in both high and low sablefish abundance years, there are still areas with lower-than-average density and ones with higher-than-average density (Figs. 2, 3, 4). This indicates that something not explicitly captured by these spatiotemporal models drives a habitat preference for these particular areas. These differences in sablefish abundance, both over time and between different marine habitats in the eastern Bering Sea, should be further explored through targeted diet studies and/or surveys to determine which factors are most critical in determining essential sablefish habitat. Moreover, the sudden decrease in predicted sablefish density in 2016, despite a consistent effective area occupied, should be further investigated. Should a similar situation occur again in the future, it would be helpful to know whether biological or oceanic factors drive the shift in density, which may have impacts on sablefish stock assessments, especially time-varying catchability, and on the fishery as a whole. (Fig. 2, 3, 4; Arreguín-Sánchez, 1996).

Further investigation and additional data are required to better understand the dynamics between this commercially important predator species and one of the most populous squid species

in the region. This is particularly crucial as summer spawning squid aggregations may potentially drive sablefish to forage at those locations. The continuation of the Bering Sea Slope survey time series would greatly benefit this project and other ecosystem dynamic studies on the Bering slope, providing the scientific community access to species that rarely show up in the EBS Shelf survey due to incomplete coverage of their habitats. It is important to understand the inter-species and community dynamics between trophic levels to fully capture the variability in habitat use and biomass, especially when it concerns commercially important species in an area with substantial fishing industries. By further investigating this understudied predatory interaction between the sablefish and commander squid, we can better understand how energy has the potential to flow within the Bering Sea benthos. This knowledge will aid in more effective stock management within an ecosystem framework.

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Appendix A) VAST Settings

Table A.1. VAST settings for the sablefish-only model configuration.

Settings for the sablefish-only model		
Version	-	VAST_v14_0_1
Knots	-	250
Region	-	EBS
Strata	-	one area
FieldConfig	Omega 1	IID
-	Epsilon 1	IID
-	Omega 2	IID
-	Epsilon 2	IID
RhoConfig	Beta 1	0
-	Beta 2	0
-	Epsilon 1	4
-	Epsilon 2	4
VamConfig	Method	0
-	Rank	0
-	Timing	0
OverdispersionConfig	Eta 1	0
-	Eta 2	0
Obs Model	-	(2, 4)
grid_size km	-	25
max_cells	-	5000
knot_method	-	Grid
Method	-	Mesh
use_anisotropy	-	FALSE
fine_scale	-	TRUE
bias.correct	-	TRUE

Table A.2. VAST settings for the sablefish-squid model configuration.

Settings for the sablefish-squid model		
Version	-	VAST_v14_01_1
Knots	-	250
Region	-	EBS
Strata	-	one area
FieldConfig	Omega 1	IID
-	Epsilon 1	IID
-	Omega 2	IID
-	Epsilon 2	IID
RhoConfig	Beta 1	0
-	Beta 2	0
-	Epsilon 1	4
-	Epsilon 2	2
VamConfig	Method	0
-	Rank	0
-	Timing	0
OverdispersionConfig	Eta 1	0
-	Eta 2	0
Obs Model	-	(2, 4)
grid_size_km	-	25
max_cells	-	5000
knot_method	-	Grid
Method	-	Mesh
use_anisotropy	-	FALSE
fine_scale	-	TRUE
bias.correct	-	-

Appendix B) VAST Parameter Estimates

Table B.1. VAST parameter estimates for the converged sablefish-only model.

Parameter estimates for the sablefish-only model			
beta1 ft	-10.32	beta2 ft	4.28
beta1 ft	-9.86	beta2 ft	4.92
beta1 ft	-9.25	beta2 ft	4.55
beta1 ft	-10.44	beta2 ft	5.41
beta1 ft	-9.05	beta2 ft	4.40
beta1 ft	-10.32	beta2 ft	4.07
beta1 ft	-12.23	beta2 ft	3.82
beta1 ft	-10.98	beta2 ft	3.40
beta1 ft	-12.41	beta2 ft	4.75
beta1 ft	-11.51	beta2 ft	4.39
beta1 ft	-11.40	beta2 ft	3.47
beta1 ft	-11.60	beta2 ft	2.90
beta1 ft	-9.37	beta2 ft	5.28
beta1 ft	-9.66	beta2 ft	3.23
beta1 ft	-8.36	beta2 ft	4.44
beta1 ft	-6.76	beta2 ft	4.84
beta1 ft	-8.75	beta2 ft	4.11
beta1 ft	-7.07	beta2 ft	4.50
beta1 ft	-9.18	beta2 ft	5.99
beta1 ft	-9.23	beta2 ft	3.51
beta1 ft	-9.10	beta2 ft	2.68
beta1 ft	-7.24	beta2 ft	4.73
beta1 ft	-7.69	beta2 ft	4.76
beta1 ft	-7.97	beta2 ft	4.83
beta1 ft	-8.23	beta2 ft	2.71
beta1 ft	-7.67	beta2 ft	4.01
beta1 ft	-7.88	beta2 ft	3.58
beta1 ft	-7.93	beta2 ft	3.67
beta1 ft	-7.48	beta2 ft	3.65
beta1 ft	-8.43	beta2 ft	3.38
beta1 ft	-8.00	beta2 ft	3.54
L_omega1 z	4.38	L_omega2 z	2.07
L_epsilon1 z	0.75	L_epsilon2 z	0.02
logkappa1	-4.91	logkappa2	-5.01
Epsilon_rho1 f	1.01	Epsilon_rho2 f	1.06

Table B.2. VAST parameter estimates for the converged sablefish-squid model.

Parameter estimates for the sablefish-squid model	
beta1_ft	-9.98
beta1_ft	-10.19
beta1_ft	-10.18
beta1_ft	-10.46
beta1_ft	-10.66
beta1_ft	-10.54
L_omega1_z	6.74
L_epsilon1_z	0.15
logkappa1	-4.57
Epsilon_rho1_f	0.55
log_sigmaXi1_cp	-4.19
beta2_ft	5.85
beta2_ft	5.57
beta2_ft	5.72
beta2_ft	5.86
beta2_ft	5.91
beta2_ft	5.04
L_omega2_z	1.28
L_epsilon2_z	-0.31
logkappa2	-2.38
log_sigmaXi2_cp	-4.64
logSigmaM	-0.17

Appendix C

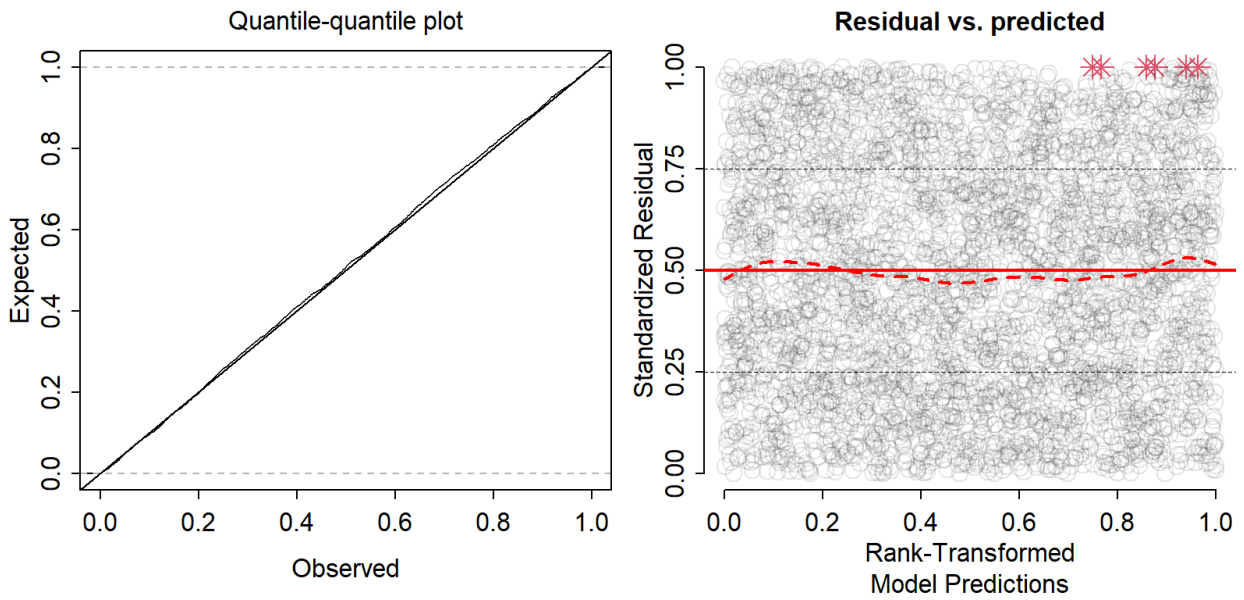


Figure 5: VAST Quantile-Quantile and Residual vs Predicted Plot, sablefish-squid Model