TITLE:

A spatial model of upper-trophic level interactions in the eastern Bering Sea

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PERIOD OF RESEARCH: August 1996 - September 1998

GOAL AND OBJECTIVES

This project proposed to investigate the hypothesis that spatial processes which affect the overlap and availability of juvenile pollock to predators, particularly adult pollock, are important determinants of juvenile pollock survival rates. In order to investigate this hypothesis, we first developed a non-spatial model of predation interactions and are developing a spatially resolved model of upper trophic level predators on juvenile walleye pollock, with particular emphasis on cannibalism. The models will serve as a focus for synthesizing information on juvenile and adult pollock and other upper trophic level predators on juvenile pollock.

PROJECT DESCRIPTION:

Adult walleye pollock have been the dominant component of the pelagic fish consumer guild in the eastern Bering Sea over the last 15 years. The primary fish prey of this guild is juvenile walleye pollock and cannibalism appears to be the main source of predation mortality on juvenile walleye pollock, at least during the 1980's. Cannibalism occurs primarily on age-0 and age-1 walleye pollock and some yearclasses appear to suffer higher mortality rates due to cannibalism than others.

It has been hypothesized that predator switching to more abundant yearclasses may be one mechanism explaining the higher mortality rates of certain yearclasses of walleye pollock, such as the 1985 yearclass. However, there is also evidence that spatial separation of juveniles from adults in some years could be important in reducing cannibalism rates. For example, the above-average 1982 yearclass of pollock was quite abundant as 1-year olds in the middle shelf habitat while 1-year olds of the below-average 1987 yearclass were found mainly in the outer shelf area where most adult pollock reside. These two yearclasses were spawned from adult populations of similar size. However, a surface current model suggests that onshelf and northward transport was stronger in 1982 than in 1987 and may have transported larvae to areas of low adult abundance. Other factors, such as the extent of the cold pool of bottom water in the middle shelf and degree of vertical stratification, also have the potential to change the spatial overlap and vulnerability of juvenile pollock to cannibalistic adults.

A series of models to address these questions are being developed. First, a multispecies virtual population analysis model of the predation interactions in the eastern Bering Sea was developed to examine hypotheses about predation interactions and multispecies effects of fishing in a non-spatial context. This model will also be used to assess the multispecies implications of fishing by forecasting the population changes that might occur under different hypothetical fishing scenarios. Finally, a spatial model of upper trophic level predators on juvenile walleye pollock is being constructed which will be initialized with the juvenile pollock abundance estimates from MSVPA. Predators of pollock will be allocated to different geographic regions corresponding to the seven biophysical domains outlined in the SEBSCC concept paper and seasonal movements will be simulated based on available data. Other processes relating to upper trophic level predators that affect their population abundance and predation rates on juvenile pollock include: food consumption, prey selection, growth, natural mortality, and fishing removals**.** Some of these processes, such as food consumption and growth rates are temperature dependent. As physical circulation models, nutrient-phytoplankton-zooplankton (NPZ)models , and individual-based models of pollock larval transport and survival are developed and validated, their outputs can be linked to the spatial predation model.

RESULTS

We have completely parameterized a multispecies virtual population analysis (MSVPA) model which characterizes the predation interactions between major groundfish populations and one marine mammal predator, northern fur seal, in the eastern Bering Sea for the time period 1979-1995. Multispecies virtual population analysis (MSVPA) is a retrospective method of analyzing catch-at-age data in conjunction with information on diet linkages between species to obtain more realistic estimates of numbers-at-age and natural mortality for juvenile fish, particularly walleye pollock.. Juvenile pollock abundance in the spatial model will be derived from MSVPA outputs. We have completed parameterization of the MSVPA for the eastern Bering Sea and are now conducting a sensitivity analysis of the model.

The MSVPA model, as currently parameterized for the eastern Bering Sea, includes the following species as predators: walleye pollock, Pacific cod, Greenland turbot, yellowfin sole, arrowtooth flounder, and northern fur seal. Arrowtooth flounder and northern fur seals are entered as "other predators", which means that VPA's are not performed for these species. Instead, inputs on their consumption rates, diet, and population abundance are input so that their predation on VPA prey species in the model can be calculated . Prey species are walleye pollock, Pacific cod, Greenland turbot, yellowfin sole, rock sole, and Pacific herring (Table 1). The modeled time period is 1979 to 1995 and we have included an extensive amount of diet data from 70 predator/year/quarter combinations derived from close to 40,000 stomach samples collected during that time period. We added arrowtooth flounder and northern fur seals to the model, added substantial amounts of diet data, and updated and re-tuned the VPA inputs to reflect the 1995 stock assessment data. The single-species VPA's have been tuned to fit the outputs of the more complex stock assessment models that are presently being used for most groundfish species in the eastern Bering Sea.

Table 1. Species included in the eastern Bering Sea multispecies virtual population analysis model (MSVPA).

Common name	**Scientific name**	**MSVPA or Other Predator**	**Prey**
Walleye pollock	*Theragra chalcogramma*	MSVPA predator	Yes
Pacific cod	*Gadus macrocephalus*	MSVPA predator	Yes
Greenland turbot	*Reinhardtius hippoglossoides*	MSVPA predator	Yes
Yellowfin sole	*Pleuronectes asper*	MSVPA predator	Yes
Arrowtooth flounder	*Atheresthes stomias*	Other predator	No
Northern fur seal	*Callorhinus ursinus*	Other predator	No
Rock sole	*Lepidopsetta bilineatus*	No	Yes
Pacific herring	*Clupea pallasi*	No	Yes

Sensitivity analysis of the Bering Sea MSVPA revealed which input parameters were most important in determining the values of selected key output variables. For example, model input perturbations of ration and parameters determining population size of arrowtooth flounder, walleye pollock and Pacific cod were the most significant variables explaining changes in model estimates of age-1 walleye pollock population size. Perturbations in input parameters for predators such as Greenland turbot, northern fur seal, and yellowfin sole were not important in explaining changes in age-1 walleye pollock population size. These analyses give us information as to which predators contribute most to the predation mortality of a particular groundfish species. This will help guide future modeling and field sampling plans on these species interactions.

Model results show that most predation mortality for the prey species in the model (walleye pollock, Pacific cod, Greenland turbot, yellowfin sole, rock sole, and Pacific herring) occurs on juveniles that have not yet recruited to the fishery. Model estimates of population abundance for exploited ages of each prey species are similar to those provided by single species models. However, abundance estimates of juveniles, particularly walleye pollock, are substantially larger than estimates from single-species model (Figure 1). Walleye pollock was the main prey species consumed by MSVPA predators, and cannibalism constituted the majority of the predation mortality of age-0 fish. The dominant predators on age-1 pollock included adult pollock, Pacific cod, arrowtooth flounder, and northern fur seals. In some years, Pacific cod consumed the largest biomass of walleye pollock prey relative to other predators (Figure 2). However, most of the biomass of pollock consumed by cod tended to be from older pollock.

Ricker stock recruitment curves were fitted to estimates of walleye pollock spawning stock biomass and age-0 and age-1 recruit numbers from MSVPA and single-species virtual population analysis (SSVPA) (Figure 3). The SSVPA recruitment curves exhibit more of a downward bend at the right hand side of the fitted curves. The coefficients of determination (R^2) from all the model fits were low, ranging from 0.06 to 0.22. The highest R^2 of 0.22 was from the fit of age-0 recruits to spawning biomass estimates from MSVPA.

The MSVPA model estimated rates of total natural mortality for juvenile walleye pollock in the eastern Bering Sea are comparable to rates estimated by other models and methods (Table 1). Livingston (1993) calculated age 0-1 predation mortality for 1985-87 using diet, ration, and groundfish and marine mammal predator population estimates and obtained annual instantaneous rates that were higher than MSVPA estimates for age-0 but very similar to MSVPA model estimates for age-1 pollock mortality. Age-2 predation mortality estimated in that paper is low compared to the other sources because it did not include the residual natural mortality rate of 0.3 used in MSVPA and Livingston and Methot (1996). Total natural mortality rates estimated from an integrated catch-at-age model of walleye pollock with predators produced estimates of age-1 M that were comparable to MSVPA estimates for the recent modeled time period but were lower for the 1963 to 1980 period not included in the MSVPA model of the eastern Bering Sea. Estimates of age-2 mortality from MSVPA seem high relative to other estimates and suggest the possibility that residual natural mortality rate (M1) for age-2 pollock used in the MSVPA model should be lowered.

Table 2. Comparison of instantaneous natural mortality rates at age for juvenile pollock in the eastern Bering Sea derived from several different methods. (Mortality rates of age-0 pollock apply to the second half of the year only.)

Source	Time Period	Age-0	Age-1	Age-2
MSVPA model	1984-1993	1.05	1.55	0.77
Livingston (1993)	1985-1987	2.84	1.90	0.31
Livingston and Methot (1996)	1984-1992	-	1.50	0.35
Livingston and Methot (1996)	1963-1980	-	0.59	0.35
Wespestad and Terry (1984)	1963-1980	-	0.85	0.45

The initial increase and then decline in total biomass consumed of walleye pollock during the 1982 to 1987 period generally reflects the trends in population biomass of two dominant pollock predators: adult pollock and Pacific cod. Estimated total biomass of pollock consumed by predators was higher than fishery removals of pollock during the time period, which ranged from 859,000 t to 1,455,000 t. Given the strength of the predation on pollock by adult pollock and cod, it will be important to investigate how changes in fishing intensity of these two species could affect pollock recruitment. When sensitivity analyses are completed on MSVPA, we will begin forecasting the effects of different fishing strategies using the estimated suitabilities from the model.

Although predation on age-0 pollock was dominated by cannibalism, there were several important predators on age-1 pollock including cod (an exploited species) and arrowtooth flounder and northern fur seal (two non-exploited species). About half the estimated number of age-1 pollock consumed were eaten by these non-exploited species and suggests the possibility that there may be limited ability to influence recruitment of pollock into a fishery using various fishing strategies. An integrated catch at age model of pollock that included pollock, cod, and northern fur seals as predators, using the same basic food habits data sources for this MSVPA model, estimated much lower predation mortality rates on age-1 pollock from these predators. That model had difficulty fitting model parameters relating to cod and fur seals, given the other sources of data and suggests the need to examine more closely the inputs relating to these predators. The importance of arrowtooth flounder as a predator on age-1 pollock is highlighted by the results of this MSVPA. Other models of predation on pollock in the eastern Bering Sea should probably include this important predator, particularly since its biomass has been steadily increasing on the eastern Bering Sea shelf from under 100,000 t in 1982 to over 500,000 t in 1996.

The relationship between spawning stock and recruitment of pollock is different depending on whether estimates from single species virtual population analysis (SSVPA) or MSVPA are used. Although the total amount of variability explained by the MSVPA recruitment curve, particularly for age-0 recruits, is somewhat higher than the amount explained by the SSVPA curve, there is still a great deal of variability around the respective curves. The time series of recruitment used here contains only 13 points and the estimated recruitment curves would probably be improved with a longer time series of data. An important contrast will be to compare recruitment variability estimated from this non-spatial model and the spatially-explicit model to see if we are able to explain more of the recruitment variability in pollock by considering spatial variability in predation.

PRODUCTS

Models

A multispecies virtual population analysis model of groundfish in the eastern Bering Sea.

Publications

Livingston, P.A. and J. Jurado-Molina. In review. A multispecies virtual population analysis model of the eastern Bering Sea. Submitted to ICES mar. Sci. Symp. Series.

Jurado-Molina, J., and P.A. Livingston. In prep. A description and analysis of the eastern Bering Sea multispecies virtual population analysis model. NOAA/NMFS Processed Report.

Presentations

Jurado-Molina, J. 1997. A multispecies approach to stock assessment in the Bering Sea. Presented Nov. 1997 as a Quantitative Seminar of the School of Fisheries , University of Washington, Seattle, WA.

Jurado-Molina, J. 1998. A multispecies approach to stock assessment in the Bering Sea. Presented April, 1998 at the Graduate Symposium in Fish Populations and Management, School of Fisheries, University of Washington, Seattle, WA.

Posters

Livingston, P.A. and J. Jurado-Molina. 1997. A multispecies virtual population analysis model of the eastern Bering Sea. Poster presented at: 1997 ICES Recruitment Symposium, Baltimore, MD.

Outlook:

We have spent the majority of research effort for this project on validating and documenting the MSVPA model, a crucial step that was not included in our original proposal. Validation of the model included a sensitivity analysis of the model to perturbation of key input parameters, analysis of the varying assumptions that can be made about the values of other food available to predators, and statistical analysis of the variability in estimates of prey suitability. The results from these analyses are now being documented in a draft report of the eastern Bering Sea MSVPA model and its results, which will be sent out for review upon completion and published as a NMFS processed report and later as chapters in a doctoral dissertation, and as peer-reviewed publications. Since September 1998, we have updated the model to reflect the 1998 stock assessment information and we have a developed a forecasting model as a companion model to the MSVPA that will be able to consider the possible multispecies implications of fishing. This will be used in 1999 to provide advice to the North Pacific Fishery Management Council groundfish plan teams, who have expressed concern about the ecosystem implications of unbalanced exploitation rates. The MSVPA will continue to be used and updated to incorporate new food habits and stock assessment information. A prototype version is also being developed that will explicitly consider uncertainty in the inputs.

We are presently parameterizing the spatial model of upper trophic level predation in the eastern Bering Sea. We have obtained area specific data for bottom temperature, pollock catch, survey, and other biological information such as growth. We are also compiling information on pollock spatial abundance patterns by size which will be used to do a retrospective analysis of walleye pollock distribution by season in the eastern Bering Sea in cold, warm, and average years in order to determine how differently pollock distribute themselves across the Bering Sea shelf by age and season and how physical factors may influence these distributions. This will be important information needed to refine the spatial model's definition of pollock movement. We hope to have a parameterized spatial model and begun some initial validation work by the end of 1999.

Our initial proposal was to link this spatial model to lower trophic level models. These models are not yet ready for linking but we intend to do the linking when the models are completed and validated. It is evident from this modeling exercise that we lack knowledge of zooplankton abundance and distribution (a necessary input to a spatially explicit model of pollock feeding) and that we have a lot of retrospective analysis to do to refine our characterization of pollock movement patterns and mechanisms influencing movement. We lack seasonal understanding of pollock distribution since independent surveys are typically conducted only during summer. Further research could include: N-P-Z model development, quantitative zooplankton sampling, seasonal survey of pollock distribution and feeding habits, expanded area of summer surveys to determine age-0 and age-1 pollock distribution in that season, and a tagging program to better understand pollock movement patterns from the juvenile to adult stage.

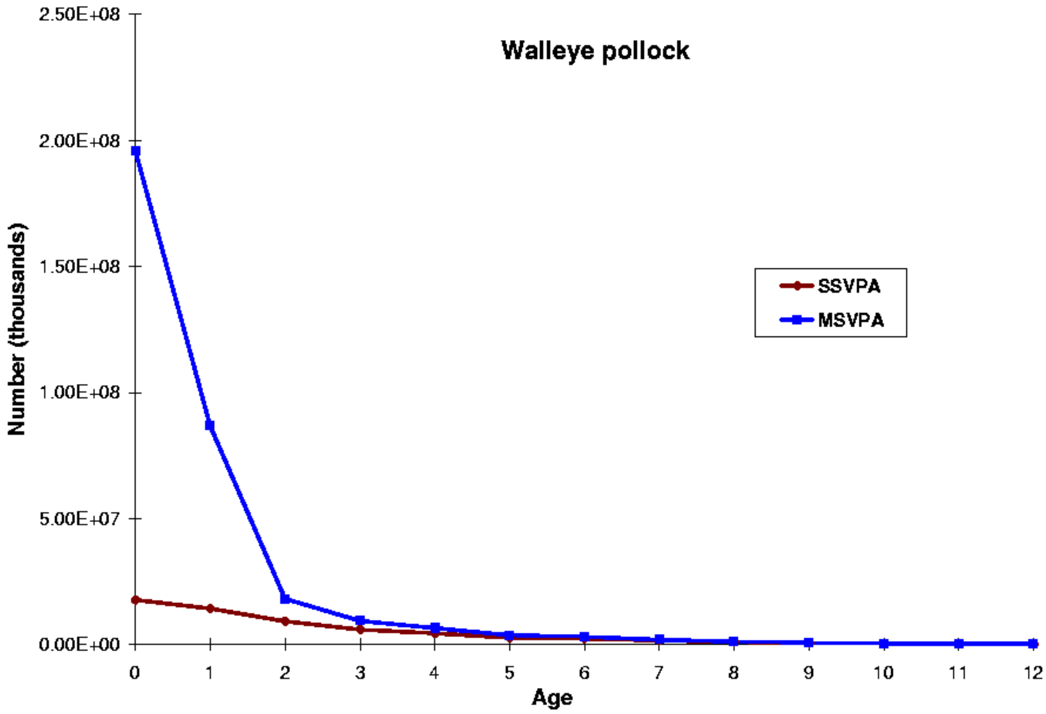

Figure 1.–MSVPA and SSVPA estimates of walleye pollock number at age, averaged over the time period of 1984 to 1993 in the eastern Bering Sea. (Age-0 mortality rate from MSVPA and SSVPA is a half-year rate.) Back to text

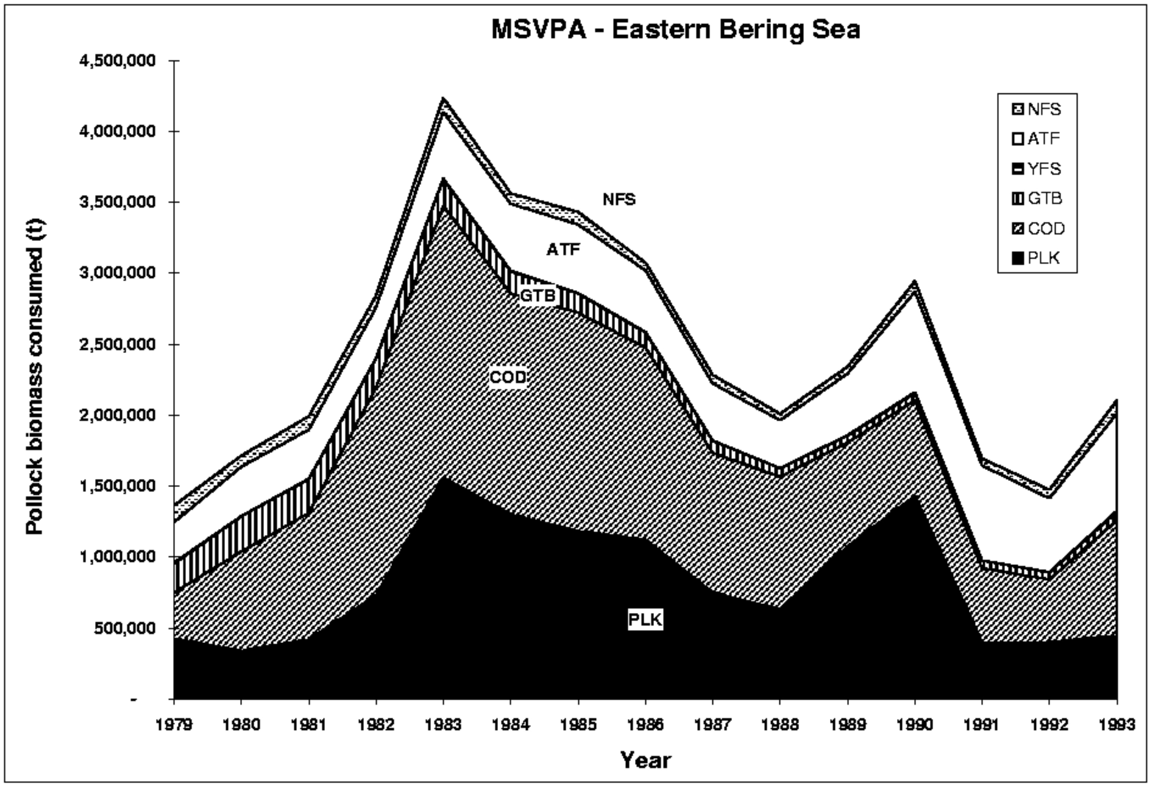

Figure 2.–MSVPA estimates of biomass of walleye pollock consumed by northern fur seals (NFS), arrowtooth flounder (ATF), yellowfin sole (YFS), Greenland turbot (GTB), Pacific cod (COD), and walleye pollock (PLK) from 1979 to 1993 in the eastern Bering Sea.

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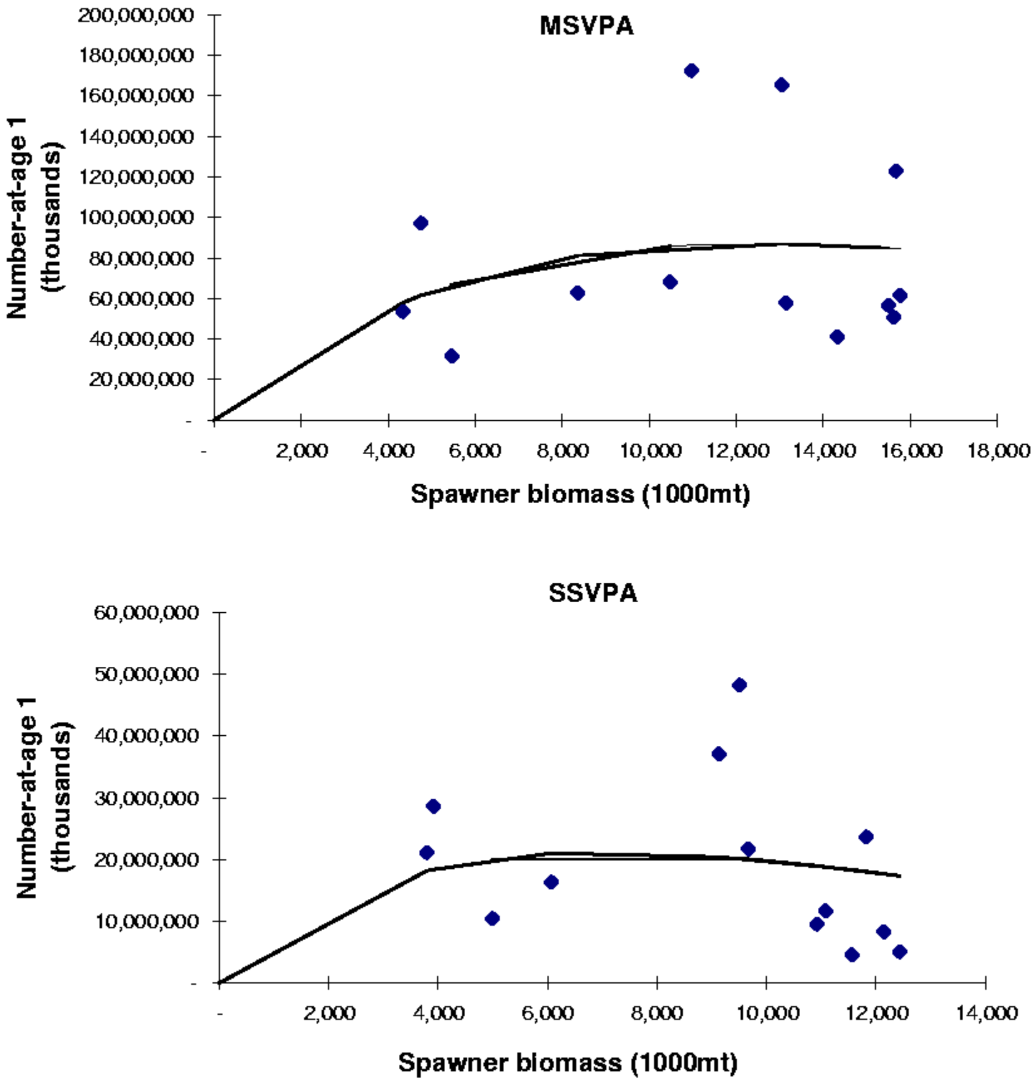

Figure 3.–Spawning stock biomass and age-1 number-at-age relationships for walleye pollock estimated from MSVPA (upper panel) and SSVPA (lower panel).

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