ICES CM 2014/P:07. Thermal habitat compression and density-dependent overwintering mortality in longfin inshore squid: Theory, empirical support, and a possible application enhancing the flexibility of fisheries management

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Summary:

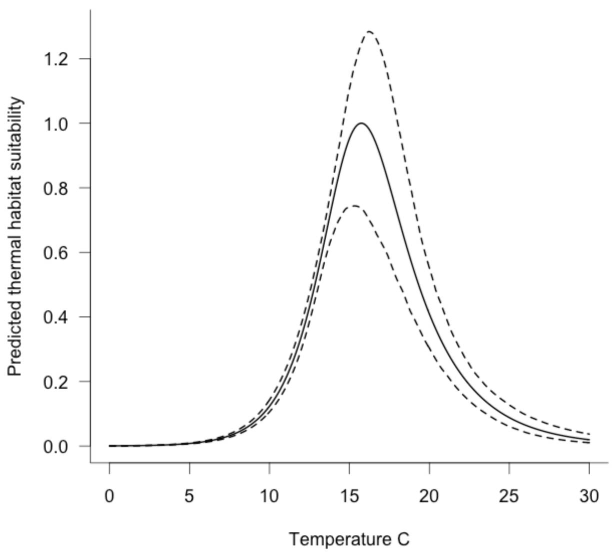

Figure 1. Thermal niche model for longfin inshore squid used to calculate thermal habitat quality. The model which represented a population level response to temperature was made using maximum likelihood to estimate the parameters of the Johnson and Lewin equation, a unimodal extension of the Boltzmann-Arrhenius function, from catch and temperature data. The function was rescaled to produce habitat quality values ranging from 0-1. Solid line represents the median response while dashed lines represent 2.5% and 97.5% confidence intervals. The niche model was coupled to the ROMS hindcast temperatures to simulate daily thermal habitat quality over the study domain from 1959-2007.

Most models of marine fish population dynamics, including those used for managing fisheries, are spatially implicit and assume that populations occupy habitats that remain effectively stationary over ecologically relevant time scales. When this assumption holds true density dependent mechanisms of population regulation (e.g. competition, cannibalism, disease transmission, predation mortality, fishing mortality, reproductive success) vary directly with changes in absolute population size. When the assumption that habitat is stationary is not true, however, density dependent processes can vary in strength with changes in the volume of suitable habitat as well as the absolute size of the population occupying that habitat. Under these circumstances density dependent feedbacks resulting from changes in absolute population size are modulated by changes in habitat volume.

In marine ecosystems, water column properties including seawater temperature and oxygen are habitat defining features for most organisms and are particularly important for mobile ectotherms, like squids, that behaviorally regulate physiology by habitat selection and movement. In temperate regions where seawater temperature is highly variable, like the northwest Atlantic, we hypothesize that dynamic changes in thermal habitat volume can interact with absolute population size to modulate density-dependent processes such as predation mortality. We present an analyses indicating that for longfin inshore squid (*Doryteuthis pealeii*) which support an important commercial fishery and are central to the food web on the North East United States Continental Shelf, the volume of thermal habitat during the winter is approximately 2-4 times smaller than during the fall when the habitat volume is highest. In addition yearly variation in the volume of thermal habitat are also highest during the winter. Thus winter habitat could be an important bottleneck driving interannual variation in important population regulating processes.

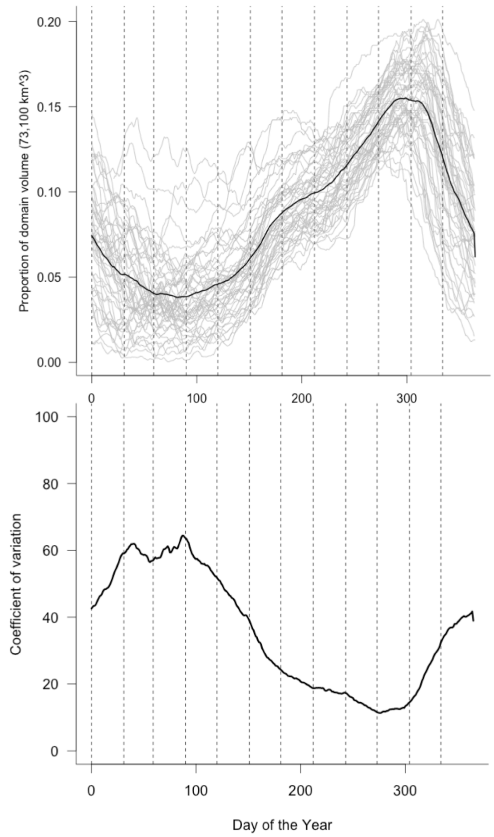

Figure 2. Top panel. Simulated thermal habitat quality weighted volume for each day in the northwest Atlantic for longfin inshore squid from 1959 to 2007 expressed as a proportion of the theoretical maximum computed by assuming all voxels in the 73,100 km^3 model domain had the highest suitability (=1). Bottom panel shows the coefficient of variation of thabitat quality weighted volume for each day of the year based on the 1959 to 2007 simulation. Dashed vertical lines indicated the first day of each month.

We show that, when the size of the squid population entering the overwintering grounds is large, the size of the squid population during the spring varied directly with winter habitat availability. When the size of the population entering the overwintering ground is small habitat availability did not affect population size.

We believe our results indicate that during some winters the availability of thermal habitat can be an important bottleneck affecting population processes. We interpret our result in the light of previous studies indicating that predation and fishing mortality are elevated during the winter and that oceanographic processes affect recruitment in long fin squid. We believe that with further study, relationships between spring population size, fall population size, winter habitat volume and predation mortality could be used to make short term forecasts of seasonal recruitment. These forecasts could be used to design fisheries management measures that are more flexible and responsive to the physical dynamics of the ecosystem than is currently the case.

Introduction

For many pelagic organisms in the sea, habitats are primary defined by water column processes and properties affecting the vital rates of individuals that underly population growth. Changes in habitat volumes due to changes in water column features such as temperature, oxygen and even prey concentrations {Richardson, 2014 #3438; Prince, 2010 #3151}, can cause changes in the concentrations of animals as they seek to optimize performance in highly dynamic seascapes. When changes in environmental features cause changes in organism concentrations over sufficiently large volumes and long time periods, the cumulative effects of variations in the strength of interspecific interactions with wild and human predators and intraspecific interactions such as competition and cannibalism should affect population.

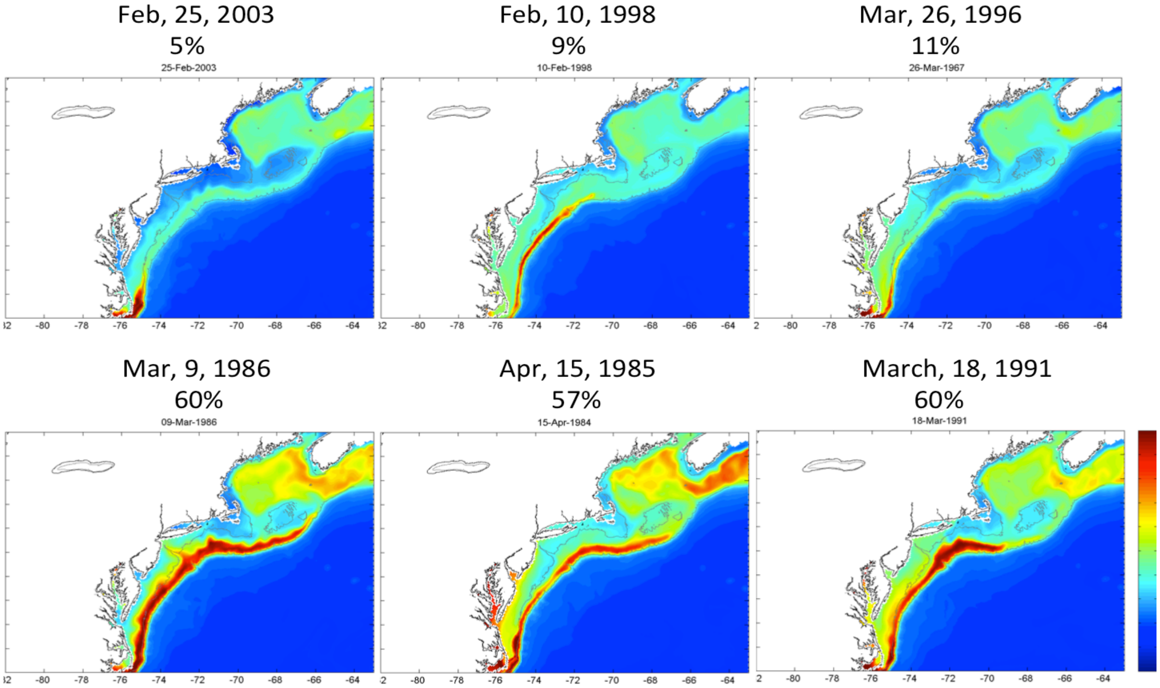

Figure 3. Maps showing thermal habitat quality (red high, blue low) for long fin inshore squid on days of the year when habitat quality was at a minima. Only quality in the bottom layer is shown. Top panels: Dates of the 3 smallest annual minima and dates of three largest annual minima. Percentages are quality weighted volumes expressed as a percent of the maximum. During the late winter and spring thermal habitat for squid was confined to the outer edge of the continental shelf

Seasonal variability in ocean temperatures on the North East US continental shelf is among the greatest in the world. Most important species in the ecosystem are ectotherms that occupy warm productive waters in the near shore during the summer months, but retreat offshore to the outer edge of the continental shelf where an envelope of relatively warm water persists during the winter months. This warm offshore water is crucial overwintering habitat for number of species including longfin inshore squid,. Recruitment in longfin inshore squid appears to be sensitive to variations in oceanographic conditions and the animals appear to suffer highest mortality from natural and human predators offshore during the wintertime {MOUSTAHFID, 2009 #2821; Brodziak, 2002 #2808 }.

We investigated a potential link between winter habitat availability and overwintering mortality in Longfin Squid. We simulated longfin Squid thermal habitat dynamics at the extent of the Northwest Atlantic by coupled a thermal niche model to a 50 year hindcast of water temperatures from a Regional Ocean Modeling System (ROMS) numerical circulation model. We describe seasonal habitat dynamics and use the coupled model to develop an index of winter habitat availability. We use this index to develop a simple statistical model testing the degree to which spring population size varies in squid with overwintering habitat availability and/or the size of the population entering overwintering grounds the previous fall. We discuss our results in the light of earlier studies investigating predation and oceanographic effects on recruitment in longfin squid.

Materials and Methods

We used maximum likelihood estimation, catch and temperature data to develop a parametric thermal niche model for Longfin Squid. We then coupled the niche model to seawater water temperatures hindcast daily from 1959 to 2007 by a 3-D Regional Ocean Modeling System

(ROMS; {Shchepetkin, 2003 #3008;Shchepetkin, 2005 #3007; Kang, 2013 #3301}) numerical ocean circulation model. The ROMs model had a horizontal resolution of 7 km and a vertical resolution of 40 terrain-following levels (e.g., 1 m resolution in a 40 m water column). The model domain used in our analysis extended from 45°N to 32°N, 77°W to 64°W. We used the thermal niche model to assign a thermal habitat quality index ranging from 0 (unsuitable) to 1 (highly suitable) based on temperature to each 3 dimensional voxel in the model domain over the hindcast time period. We used these daily projections of habitat quality in 3 dimensions to visualize and develop indices describing thermal habitat dynamics for longfin squid.

To compute an index of the availability of thermal habitat at the extent of the regional sea we calculated the cumulative quality weighted volume of thermal habitat for the model domain for each day of the hindcast by multiplying the volume of each model voxel by its thermal habitat quality. We summed the quality weighted voxels in the 73,100 km^3 model domain. The index allowed us to evaluate changes in thermal habitat quality for squid at the scale of the domain over time scales ranging from days to decades over the temporal extent of the hindcast. To describe spatial habitat dynamics we examined time series of vertical cross sections and 2 dimensional maps of thermal habitat quality.

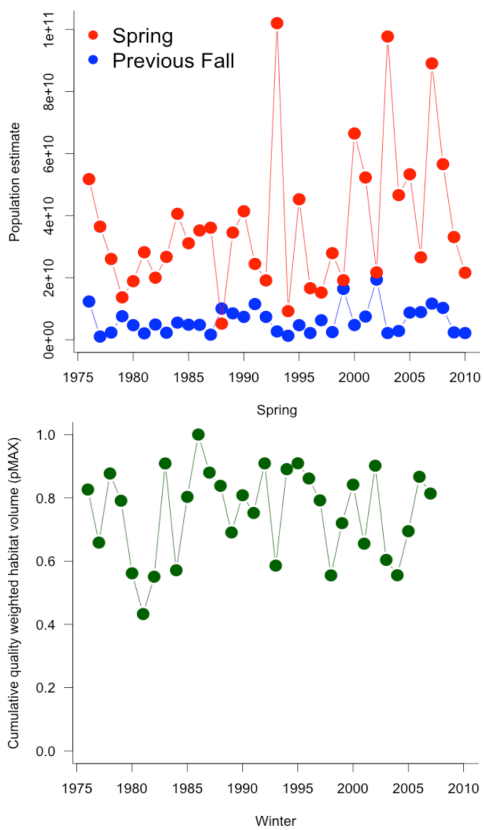

Figure 4. top panel. Estimates of longfin inshore squid population size during spring (blue) and the previous fall (red) from the 2010 NEFSC stock assessment. Bottom panel. Cumulative habitat quality weighted volume over the winter period extending between the end of the fall and beginning of the spring surveys used to develop population estimates

We chose to examine the effects of thermal habitat availability on longfin squid population dynamics during the winter because the results of our analysis indicated that habitat availability was lowest and most variable during the wintertime (see below). We used swept area biomass estimates for the Longfin inshore squid population developed for the most recent (2010) NEFSC stock assessment (http://www.nefsc.noaa.gov/publications/crd/crd1101/crd1101.pdf). Swept area biomass estimates were developed primarily with data collected in the National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) annual fall (September–November) and spring (March–May) bottom trawl survey. A four month period elapses between the median date of the end of the fall survey (day of the year DOY = 306) and the start date of the spring survey (DOY = 64). As a result, we developed an index of winter thermal habitat availability for each year by summing the quality weighted thermal habitat volume for the northwest Atlantic for each day over this 4 month period.

We used generalized additive modeling to examine the degree to which variation in spring swept area biomass estimates was related to swept area biomass of the population entering overwintering grounds the previous fall and the index of the availability of thermal habitat during the winter. In our interpretation of the results, we assumed the primary process affecting population dynamics during the winter period was predation mortality from wild and human predators. We assumed that there is not significant reproduction during the winter months and that although immigration of small juveniles from the South Atlantic bight may occur but rates are relatively low {Hanlon, 2012 #3071}. Further we assumed that emigration rates to the South Atlantic bight was also low.

Results and Discussion

The thermal niche model parameterized using concentrations of squid in bottom trawls and bottom temperatures measured from 2009 through 2013 throughout the Northwest Atlantic rose gradually from cold temperatures through a half maximum of ~ 13°C to an optimal temperature (T_{opt}) of ~ 16 °C (Figure 1). The function then declined rapidly through an upper half maxima at ~ 21°C to low values at temperatures above ~ 25 °C. Evaluation of the niche model with catch and temperature data not used in model training indicated that probabilities of habitat occupancy were well explained.

The availability of suitable thermal habitat for longfin squid in the Northwest Atlantic was about 3 times smaller on average during the spring than during the fall based on the habitat simulation made by coupling the niche model to daily hindcasts of ocean temperature from the ROMS model (Figure 2 top). During November and December the availability of suitable thermal habitat was highest and represented 20% (5^{th} and 95^{th} confidence limits, 17% and 23%) of a theoretical maximum computed by assuming that all voxels in the 73,100 km^3 model domain had the highest suitability (=1). Interannual variation in availability of suitable thermal habitat was also smallest during the fall (CV=8.2%, Early October; Figure 2 bottom).

The availability of suitable thermal habitat was at a minimum during Febuary, March or April. During the late winter early spring period suitable habitat represented approximately 7% of theoretical maximum computed by assuming all voxels in the model domain had the highest suitability (Figure 2 top). Interannual variation in availability of suitable thermal habitat was largest in during the late winter early spring period (CV=60%, Early February; (Figure 2 bottom).

During "cold" ocean winters, the simulation indicated that suitable thermal habitat extends north along outer edge of the continental shelf break from Cape Hatteras as far north and east the Hudson Canyon (Figure 3). During "warm" winters thermal habitat extended northeast from Cape Hattaras to Lydonia and Corsair canyons just south of Georges Bank. Results of the similation indicated suggested that the volume of suitable habitat during the winter months could be an important bottleneck during some years.

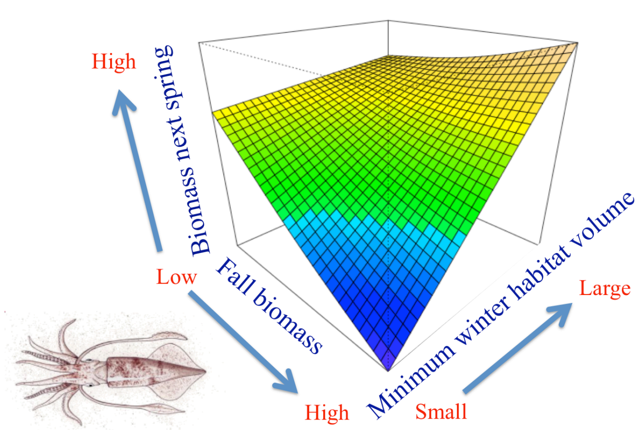

Figure 5. Results of GAM showing that population size in the spring is partially related to interaction between winter habitat availability and the size of the population entering overwintering grounds the previous fall

Generalized additive modeling indicated that squid population size in the spring was related to the interaction between the size of the population entering the overwintering ground the previous fall and the availability of thermal habitat during the winter and early spring even though a large portion of the variability was left unexplained. When the size of the population entering the overwintering grounds was large, the size of the squid population during the spring varied directly with winter habitat availability (Figure 4). When the size of the population entering the overwintering ground was small habitat availability did not affect population size. Earlier surplus production modeling indicates that substantial squid mortality occurs due to predation by wild and human predators during the winter months {MOUSTAHFID, 2009 #2821}. Further recruitment in longfin inshore squid appears to be related to shelf water volume {Brodziak, 2002 #2808} Our results that suggest that the strength of interactions with predators including with conspecifics and humans is modulated by the availability of thermal habitat during the winter may provide a mechanistic link between these studies. Interaction with predators may be particularly strong during years when a large population entering overwintering grounds in the fall is concentrated within a small volume of thermal habitat. During winters when winter habitat volume is very large, interaction strengths with predators may be relatively weak even when the population entering the overwintering habitat is large. We believe that our results indicate that effects of large scale dynamic changes in habitat volume on organism concentrations can partially decouple a density dependent regulatory process from changes in absolute populations size.

We believe that with further investigation and support relationships between population size and winter habitat quality could be used to make short term, seasonal forecasts of population size during the spring and summer periods. These forecasts could be used to develop fisheries management measures that are more flexible and responsive to the physical dynamics of the ecosystem than is currently the case.

References

Brodziak JKT, Mountain DG (2002) Some biological responses to increased shelf water volume in the mid-Atlantic Bight of the Northeast USA Continental Shelf Ecosystem. In: ICES CM, Book 2002/Q:04. ICES

Hanlon R, Buresch K, Moustahfid H, Staudinger M (2012) Doryteuthis pealeii (Lesueur, 1821), longfin inshore squid. In: Rosa R, Pierce G, O'Dor R (eds) Advances in Squid Biology, Ecology and Fisheries. Nova Science Publishers

Kang D, Curchitser EN (2013) Gulf Stream eddy characteristics in a high-resolution ocean model. Journal of Geophysical Research: Oceans 118:4474-4487

MOUSTAHFID H, TYRRELL MC, LINK JS (2009) Accounting Explicitly for Predation Mortality in Surplus Production Models: an Application to Longfin Inshore Squid. North American Journal of Fisheries Management 29:1555–1566

Prince ED, Luo J, Phillip Goodyear C, Hoolihan JP, Snodgrass D, Orbesen ES, Serafy JE, Ortiz M, Schirripa MJ (2010) Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. Fisheries Oceanography 19:448-462

Richardson DE, Palmer MC, Smith BE (2014) The influence of forage fish abundance on the aggregation of Gulf of Maine Atlantic cod (Gadus morhua) and their catchability in the fishery. Canadian Journal of Fisheries and Aquatic Sciences:1-14

Shchepetkin AF, McWilliams JC (2003) A method for computing horizontal pressure-gradient force in an oceanic model with a nonaligned vertical coordinate. J Geophys Res 108:3090

Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Modelling 9:347-404