Thermal habitat dynamics in the Northwest Atlantic and the role of the winter habitat squeeze in density dependent regulation of forage species populations.

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1. Introduction

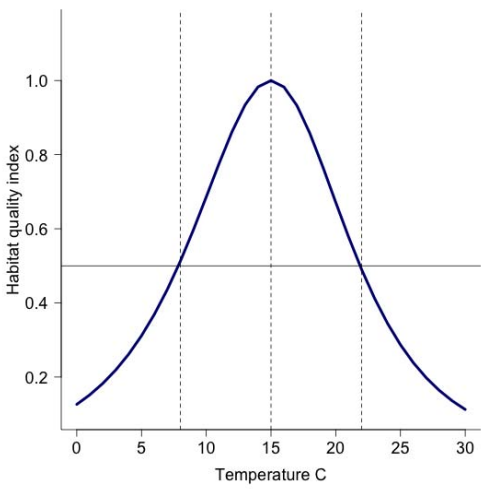

Figure 1. Prototype mechanistic thermal habitat model for longfin inshore squid based on parameterization of a Boltzmann-Arrhenius function using inshore NEAMAP and offshore NEFSC bottom trawl surveys.

Production and age-structured assessment models assume factors regulating population productivity are stable in space and time. Violations of this assumption are common and affect the ability of assessment's to predict future population size (UN FAO 2000). We assert that many factors affecting critical processes regulating populations including habitat volume are unstable because the underlying physical environment of the ocean is unstable. To capture impacts of an unstable environment on fish populations, we propose to develop an index of the effects of winter thermal habitat volume on density dependent mechanisms of population regulation that has strong theoretical foundations in the metabolic theory of ecology and population ecology and is supported by empirical analysis. Since we develop our index for important forage species, it should provide a valuable indicator for ecosystem-based fisheries management as well as single species stock assessment.

Volumes of the habitats organisms use are implicit and assumed to be fixed in traditional population and fish stock assessment models in which density-dependent birth and death rates regulate population growth. Because habitat volume is believed to be stable over short, ecological time scales, changes in population density affecting rates of predation, competition, and/or reproductive success are assumed to vary directly with population size within fixed geographic ranges or management regions. However, the assumption that habitat is stable in the ocean is untenable. Many spatially dynamic properties and processes of the ocean's fluid are fundamental habitat defining characteristics in the sea where fluid transport partly regulates productivity and most organisms are ectothermic, osmoconforming, and nearly neutrally buoyant during at least part of their life histories (Steele, 1991). At given population sizes, densities of organisms occupying habitats defined by dynamic fluid properties should change as habitat volumes change. Changes in population density with changes in habitat volume could affect mortality, growth and other important density dependent vital rates.

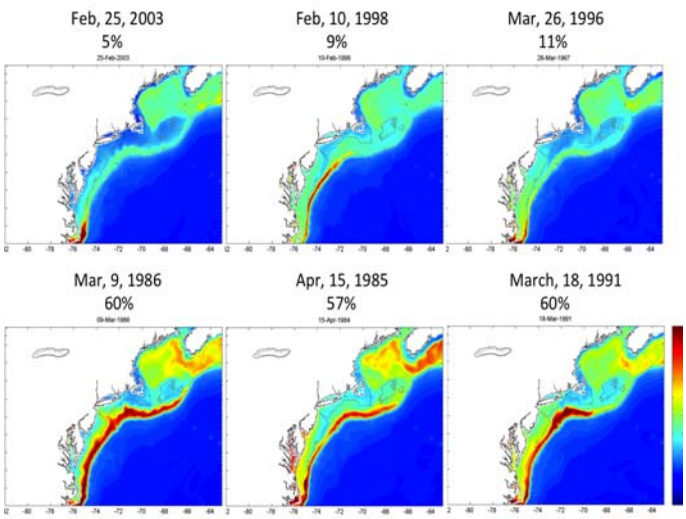

Figure 2. Annual minimum habitat volumes projected by coupling the prototype thermal habitat model (Fig. 1) to ROMS bottom water temperature hindcasts. Dates indicate when volume minima are estimated to occur. Top panels: Dates of the 3 smallest annual minima. Bottom panels: dates for three largest annual minima estimated from between 1958 to 2007 (see figure 3). Percentages are minimum areas expressed as percent of maximum habitat volume recorded.

Causes and consequences of changes in fish population density with habitat volume have been discussed by several authors. Prince et al (2010) used satellite telemetry to describe habitat compression for sailfish and blue marlin associated with increases in the size of the oxygen minimum zone in the extra-tropical Atlantic. They argued that increases in billfish and tuna densities with habitat compression potentially increase the vulnerability of animals to longline fisheries and creates biases in indices of population size used in stock assessments. Brodziak & Mountain (2002) analyzed autumn surveys of 12 fish stocks on the North East US Continental Shelf (NEUS) and showed that longfin inshore squid, bluefish, scup, monkfish, and silver hake densities decreased with increases in the volume of continental shelf water.

Temperature is the primary factor defining fundamental niches and habitats particularly for ectotherms in the sea (Sunday et al. 2010; Hochachka & Somero, 2003; Anderson-Teixeira et al. 2009). Thermal habitat is particularly important and dynamic in the NEUS, which experiences some of the largest seasonal fluctuations in water temperature on the planet (Shearman & Lentz, 2010). Many fish native to the NEUS, including most analyzed by Brodziak & Mointain (2002), are migratory and use shallow nearshore habitats as summer feeding and nursery grounds and deep offshore habitats along the shelf break to overwinter when shallow shelf waters are cold (Low et al. 1982). Among stocks exhibiting this type of onshore-offshore migratory thermoregulation are longfin inshore squid (*Doryteuthis pealeii*) and Atlantic butterfish (*Peprilus triacanthus*); short lived, pelagic species central to the NEUS food web and economically important to the regional fisheries (Link et al. 2008).

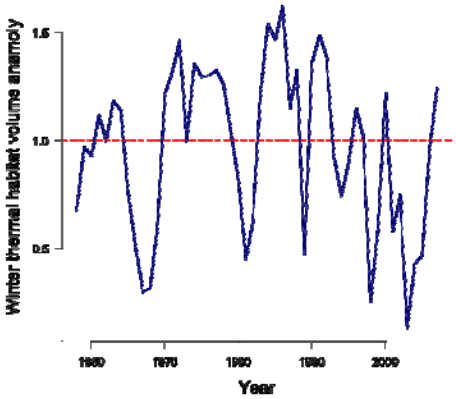

Figure 3. Winter habitat volume anomaly (hVt in Fig.5) derived from projections of the prototype mechanistic habitat model coupled to ROMS model hindcasts of bottom temperature depicted in Fig 1 & 2

2. Background

We have developed a series of statistical and mechanistic thermal habitat models for NEUS species including longfin inshore squid and Atlantic butterfish to quantify habitat dependent biases in stock assessment survey indices and to develop a better understanding of the relationship between habitat dynamics and population dynamics (Fig. 1). The foundation for these model are empirical habitat models that used ocean observations originally developed with FATE funding (Manderson et al.

2011; Palamara et al. 2012) and subsequently refined and evaluated in cooperation with the fishery industry. We are developing a 3rd generation mechanistic habitat models based upon metabolic theory for longfin squid and butterfish that we can couple to Regional Ocean Modeling System (ROMS) hindcast of daily bottom water temperatures from 1958 to 2008 (Fig. 2). This allows us to analyze pronounced seasonal and interannual changes in the location and volume of thermal habitats these animals may occupy. Based on preliminary output, annual habitat volume minima occur in February or March when thermal habitat is confined to the shelf break. There is strong interannual variation in minimum habitat volumes which range from 4% to 60% of the maxima. During warm ocean winters, thermal habitat extends along the shelf break from Cape Hatteras, the southern extent of our projections, ~750 km to the northeast and the canyons located due south of Georges Bank. During cold winters, thermal habitat extend only 350 km or less to the north to canyons south of the Hudson Canyon. These variations in minimum winter habitat volume are linked to winter cooling of North West Atlantic shelf waters as well as shelf slope front, shelf slope sea and gulfstream dynamics. These dynamics are regulated by large scale climate and remote buoyancy forcing in the North West Atlantic (Greene et al. in press; Bisagni et al. 2009; Linder et al. 2004)

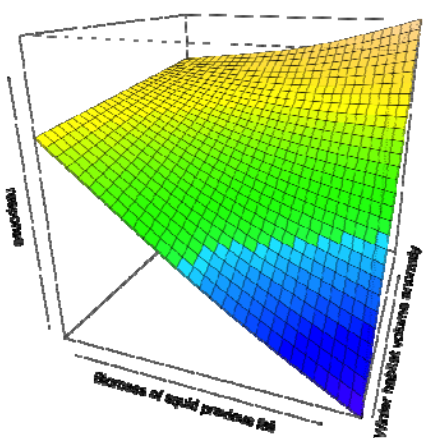

Figure 4. Longfin inshore squid population size in the spring appears to vary with our winter habitat volume anomaly (fig. 3) when the population is large the previous fall based on analysis of biomass estimates from the 2010 stock assessment (52nd SAW; table B24). This suggests that important density dependence processes affecting the animals in the winter are modulated by thermal habitat volume.

We have used data from the most recent stock assessment (52nd SAW 2010) to perform a preliminary empirical analysis of the relationship between spring estimates of longfin inshore squid population size, our winter habitat volume anomaly and population size the previous fall (Fig. 4). This analysis indicates that spring population size varies with minimum winter habitat volume when the squid population is large the previous fall. This suggests that mechanisms of density dependent population regulation are modulated by winter habitat volumes when the population is large. Moustahfid et al. (2009) showed longfin inshore squid are important prey for many species on the outer continental shelf during the winter when natural mortality for squid appears highest.

Based on the information and preliminary analysis above we hypothesize that:

Dynamic changes in thermal habitat volume modulate density dependent predation mortality for critical forage species overwintering on the outer NEUS continental shelf. Furthermore since dynamic changes in thermal habitat volume in the Northwest Atlantic are controlled by large scale climate and oceanographic forcing, modulations of density dependence by habitat volume provides a mechanistic link between remote climate forcing and population dynamics of forage species overwintering on the outer shelf.

3. Approach

The objective of our proposed study is then to perform empirical and theoretical analyses required to fully develop and support this hypothesis and to develop a useful set of indicators for ecosystem and stock assessment that rest on the ecological mechanisms. We will develop

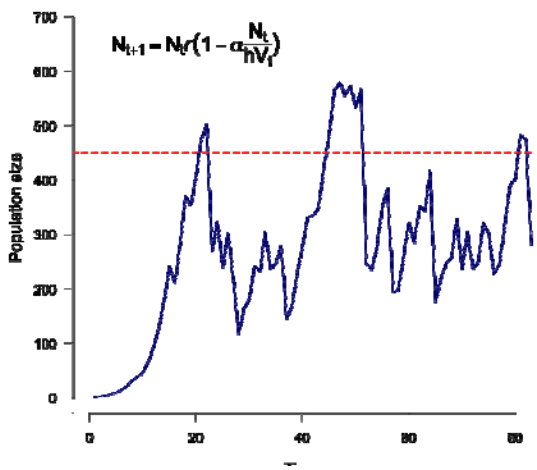

Figure 5. Single simulation of a discrete time logistic population model in which the minimum winter habitat volume anomaly (hVt; Fig 3.) was sampled and integrated into density dependence. Alpha = per-capita density dependent effect, r is population growth rate, N is population size. The red line indicates population size at 1/alpha which is equal to the carrying capacity (K) that does not vary when habitat volume is considered to be implicit and

indicators for ecosystem and stock assessment based on mechanistic links between density dependence, thermal habitat dynamics and climate forcing by performing the following tasks:

Task 1: Evaluate the temperature estimates from the 50 year ROMS hindcast.

The ROMS hindcast will be provided to this project at no cost to the proposed project. Under this task we will use available bottom temperature data to evaluate and quantify uncertainties in ROMs hindcasts of bottom water temperature used to project thermal habitat. In-situ temperatures provided by the NEFSC fisheries independent survey, NEFSC survey fleet data and IOOS ocean observatories will be used to quantify the uncertainty in temperature hindcasts.

Task 2: Develop thermal habitat model and estimates of thermal habitat volume.

To quantify thermal responses of species using the outer NEUS continental shelf as overwintering habitat we will use the habitat modeling approaches and several models we are already developing on a closely linked project (*"Accounting for habitat-dependent observation error in bottom trawl survey indices for pelagic stocks using butterfish (Peprilus triacanthus) as a model"*, Manderson lead PI)) funded by the NOAA office of Science and Technology HAIP (e.g. Fig 1 & 2). One of our goals will be to determine whether species specific responses are similar enough that a general thermal response for the winter shelfbreak community could be used to develop a general winter thermal habitat volume anomaly. We will evaluate and quantify uncertainties of thermal habitat models using cross validation and independent datasets including industry based temperature and catch data available from the NEFSC COOP program.

Finally we will couple habitat models to ROMS validated in task 1 to estimate thermal habitat volumes in the Northwest Atlantic with emphasis on winter habitat along outer shelf.

Task 3: Identify NEUS fish and invertebrate stocks for which winter habitat volume appears to modulate density dependent mortality. Identify potentially important remote oceanographic and climate drivers of dynamic changes in winter habitat volume.

Focusing on species overwintering on the outer continental shelf, we will quantify variation in estimates of spring population size in relation to winter habitat volume and population size the previous fall (as in Fig. 4). We may be able to use this approach identify species potentially benefiting from winter thermal habitat squeezes (e.g., some predators including fishers), as well as those negatively impacted (some prey). We will use analysis of NEFSC food habits database and models of prey consumption (e.g. Moustahfid et al. 2009) to determine species populations affected by modulations of density dependent predation mortality by winter habitat volume. Finally we will conduct a thorough literature review of physical oceanographic and climate mechanisms potentially regulating thermal habitat dynamics in the NEUS. Based on this review

we will use statistical modeling to identify regional remote climate and oceanographic factors driving changes in thermal habitat dynamics and habitat modulated density dependence.

Task 4: Apply modeling framework to determine ecosystem and stock indicators.
We will develop and use the habitat volume index in a quantitative theoretical framework integrating habitat and population dynamics for species identified in task 3 (Fig 5). Surplus production models use a simple parameterization similar to Fig. 5. We will therefore use a modified surplus production model that captures variability in carrying capacity associated with changes in habitat volume. We will fit modified surplus production models for species identified in task 3 to demonstrate the feasibility of incorporating dynamic habitat into stock assessment.

4. Benefits

Analyses, modeling activities and products we develop will be integrated with materials reviewed and delivered by our working group already formed using NOAA S & T HAIP funding (*"Accounting for habitat-dependent observation error in bottom trawl survey indices for pelagic stocks using butterfish (Peprilus triacanthus) as a model"*, Manderson (PI)) and organized to inform the SSC charged with butterfish assessment for the Mid-Atlantic Fisheries Management Council (MAFMC). This working group includes stock assessment scientists (Tim Miller, NEFSC; Olaf Jensen, Rutgers) including the SSC chair for butterfish assessment (Rob Latour, VIMS), a MAFMC staff member (Rick Seagraves), as well as representatives from the fine mesh trawl fishing industry. As a result, the proposed work significantly leverages modeling, outreach activities and a processes already developed on NOAA S & T HAIP funding, as well as other cooperative activities undertaken with partners active in the Mid Atlantic Regional Coastal Ocean Observation System (MARACOOS). Analyses and products will also be shared with the NEFSC Ecosystem Assessment Program (EcoAP) charged with developing ecosystem assessment and management in the North West Atlantic (Both Manderson and Townsend are associated and interact frequently with the EcoAP group).

5. Deliverables

1. Analyses and products will be developed and delivered to the MAFMC in collaboration and consultation with federal, academic, industry and MAFMC partners involved in the working group for integrating habitat into butterfish stock assessment formed with NOAA HAIP funding.
2. Two reports to the FATE program describing data and analytical, and modeling results
3.Peer-reviewed publications describing: Empirical and theoretical analysis of the mechanistic link between climate, habitat dynamics, and habitat modulated density dependence. These will include recommendations on application of empirical and theoretical analysis to stock and ecosystem assessments as well as for process studies validating hypothesis and analysis

5. Schedule of Work

	Year 1	Year 2
Task 1	XXXXXXXXXXXXXXXXXXXXXXXXXXXX	
Task 2	XXXXXXXXXXXXXXXXXXXXXXXXXXXX	
Task 3	XXXXXXXXXXXXXXX	
Task 4	XXXXXXXXXXXXXXXXXXXXXXX	
Final Report (All Partners)		XXX

6. References

Anderson-Teixeira KJ, Savage VM, Allen AP, Gillooly JF (2009) Allometry and Metabolic Scaling in Ecology. In: eLS. John Wiley & Sons, Ltd

Bisagni JJ, Kim H-S, Chaudhuri A (2009) Interannual variability of the shelf-slope front position between 75° and 50° W. Journal of Marine Systems 78:337–350

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

Dell AI, Pawar S, Savage VM (2011) Systematic variation in the temperature dependence of physiological and ecological traits. Proceedings of the National Academy of Sciences 108:10591-10596

Greene CH, Pershing AJ, Monger BC, Schnepf NR, Louise P. McGarry1 IMB, Paula S. Fratantoni, David G. Mountain, Robert S., Pickart\ AP, Rubao Ji, James J. Bisagni, Changsheng Chen, Sirpa, M.A. Hakkinen DBH, Jia Wang, Charles Hannah, Erica Head, Peter, Smith PCR, Alessandra Conversi (in press) Remote Climate Forcing of Regime Shifts in Northwest Atlantic Shelf Ecosystems.

Hochachka PW, Somero GN (2002) Biochemical Adaptation: Mechanism and Process in Physiological Evolution, Vol. Oxford University Press, Oxford

Linder CA, Gawarkiewicz GG, Pickart RS (2004) Seasonal characteristics of bottom boundary layer detachment at the shelfbreak front in the Middle Atlantic Bight. JOURNAL OF GEOPHYSICAL RESEARCH 109

Link J, Overholtz W, O'Reilly J, Green J, Dow D, Palka D, Legault C, Vitaliano J, Guida V, Fogarty M, Brodziak J, Methratta L, Stockhausen W, Col L, Griswold C (2008) The Northeast U.S. continental shelf Energy Modeling and Analysis exercise (EMAX): Ecological network model development and basic ecosystem metrics. Journal of Marine Systems 74:453-474

Low RA, Ulrich GF, Blum F (1982) Development potential of underutilized trawl fish in the South Atlantic Bight. Marine Resources Research Institute. In, Book Tech Memo 82. South Carolina Wildlife & Marine Resources Department

Manderson J, Palamara L, Kohut J, Oliver MJ (2011) Ocean observatory data is useful for regional habitat modeling of species with different vertical habitat preferences. Marine Ecology Progress Series 438:1-17

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, GOODYEAR CP, 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

Shearman RK, Lentz SJ (2010) Long-Term Sea Surface Temperature Variability along the U.S. East Coast. Journal of Physical Oceanography 40:1004-1017

Steele JH (1991) Can ecological theory cross the land-sea boundary? Journal of Theoretical Biology 153:425-436

Sunday JM, Bates AE, Dulvy NK (2010) Global analysis of thermal tolerance and latitude in ectotherms. Proc Royal Soc B: Doi: 10.1098/rspb.2010.1295

United Nations Food and Agriculture Organization [UN FAO]. 2000.Research implications of adopting the precautionary approach to management of tuna fisheries. FAO Fisheries Circular. No. 963. Rome, FAO. 2001. 74p.

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