ECOLOGICAL MODELLING 202 (2007) 184–195

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/ecolmodel

Simulated herring growth responses in the Northeastern Pacific to historic temperature and zooplankton conditions generated by the 3-dimensional NEMURO nutrient–phytoplankton–zooplankton model

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ARTICLE INFO

Article history:
Published on line 13 November 2006

Keywords:
3D-NEMURO
Bioenergetics
Climate
Fish
Growth
Pacific herring
NPZ model
NEMURO
NEMURO.FISH
North Pacific
Regime shift

ABSTRACT

The infrequent occurrence of climate regime shifts and the long-lived life history of many harvested fish species imply that quantitative understanding of the effects of climate shifts on fish will require long-term data spanning decades. We use the output of the 3-dimensional (3D) NEMURO nutrient–phytoplankton–zooplankton model applied to the Northern Pacific as input to a Pacific herring (*Clupea pallasi*) bioenergetics model, and predict herring weights-at-age and growth from 1948 to 2000 for the West Coast Vancouver Island (WCVI), Prince William Sound (PWS), and Bering Sea (BS) locations. The feeding parameters of the bioenergetics model were calibrated from steady-state predictions of herring weights-at-age at each location compared to observed mean weights-at-age. Herring weights-at-age were then simulated from 1948 to 2000 using the 3D-NEMURO generated time series of monthly temperature and zooplankton densities. Herring growth rates, annual temperature, and zooplankton density time series were analyzed statistically for coincident shifts in their mean values. We also simulated herring growth rates using the 1948–2000 time series and averaged (climatological) temperature and zooplankton densities to determine the relative importance of temperature and zooplankton to predicted herring growth responses. All three locations showed a shift in herring growth during the mid and late 1970s. Herring growth decreased in WCVI and PWS, and increased in BS; these changes were coincident with a warming of temperature and a decrease in predatory zooplankton density. Herring growth responses in PWS and BS were more complex than those predicted for WCVI, with additional shifts predicted besides the late 1970s shift. Interannual variation in zooplankton densities caused the herring growth response for WCVI. Temperature and zooplankton

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doi:10.1016/j.ecolmodel.2006.06.020

densities affected the herring growth responses in both Alaskan locations, with zooplankton dominating the response for PWS and temperature dominating the response for BS. We compare our simulated herring growth responses to observed responses, and discuss the advantages and drawbacks of using the output of broadly applied lower trophic model as input to fish models in order to examine long-term responses to regime shifts at multiple locations.

1. Introduction

The effects of climate on marine fish recruitment and populations have been the focus of study for decades (*e.g.*, Cushing, 1982; Laevestu, 1993; McGinn, 2002). Numerous correlative analyses have invoked environmental factors as important in affecting fish population dynamics (*e.g.*, Rose and Summers, 1992), and the large interannual fluctuations in recruitment are often attributed to environmental variation (Fogarty, 1993; Hofmann and Powell, 1998; Chen, 2001; Werner and Quinlan, 2002). Environmental conditions can change gradually due to persistent trends in climate (*e.g.*, gradual warming) or stepwise due to climate regime shifts. A climate regime can be defined as a persistent state in climate, ocean, and biological systems, with a regime shift being an abrupt, non-random change from one state to another (Beamish et al., 2004). Interannual variation can occur within a regime, but the climate conditions within regimes are relatively consistent and persistent compared to the magnitude of change that occurs between regimes (King, 2005). Understanding how gradual and regime shift changes in climate affect the growth, mortality, and reproduction of fish is essential to their proper management. Quantifying how climate changes affect fish populations would allow us to attribute variation in population dynamics to nature *versus* fishing, and would also allow us to adjust harvest levels dependent on favorable and unfavorable climatic conditions (Beamish and Bouillon, 1993; Beamish et al., 2000, 2004).

The infrequency of climate regime shifts and the long-lived life history of many commercially exploited fish species imply that long-term data sets spanning decades are needed. Site-specific analyses looking for climate regime shift responses in biota have been performed for the few well-studied locations with long-term data (*e.g.*, Rebstock, 2002; Mackas et al., 2004). Comparisons of responses among populations can be useful to understanding the cause and effect of multiple environmental factors that covary in the historical record, but such comparisons require long-term data sets at multiple locations. While analysis of responses within specific trophic levels across locations are possible with long-term data (*e.g.*, Hollowed et al., 2001), analyses across trophic levels in multiple locations are much more difficult. Data collection, instrumentation, and methods can vary over time, as well as within and across geographic locations. Use of the output of site-specific models, as an alternative to field data, can also be problematic. Site-specific models often are developed for different purposes, thereby confounding structural and application differences in models with true geographic differences among locations. One approach is to perform more qualitatively oriented *a posteriori* analyses and synthesize the various studies that are available (*e.g.*, Beamish et al., 2004; King, 2005).

We use an alternative approach to the *a posteriori* qualitative analysis by extracting location-specific information from a broadly applied single lower trophic model and using that as input to an upper trophic level model that is applied to multiple locations. In our application, we use the output of the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) nutrient–phytoplankton–zooplankton (NPZ) model applied to the Northern Pacific as input to a Pacific herring (*Clupea pallasi*) bioenergetics model, and predict herring weights-at-age and growth for 1948–2000 at three locations. A major advantage of this approach is that it is quantitative, and it uses a complete and consistently generated set of long-term environmental conditions (albeit model-generated) with a single upper trophic level model. Disadvantages of this approach include that the lower and upper trophic level models are used uncoupled, so the analysis is completely bottom-up (the herring dynamics do not affect the NPZ model), and the broad spatial application of the NPZ model excludes potentially important site-specific details.

In this paper, we present the results of herring growth simulated for 1948–2000 at three locations in the Northeastern Pacific. Predictions of water temperature and zooplankton densities from a 3D application of the NEMURO NPZ model were used as inputs to a herring bioenergetics model. The three simulated locations were: West Coast Vancouver Island (WCVI), Prince William Sound (PWS), and the Bering Sea (BS). All three locations currently or historically supported herring fisheries that are managed as separate stocks (Hay et al., 2001). The three locations offer an opportunity for comparative analysis of the geographic aspects of herring growth responses. Williams and Quinn (2000) analyzed historical weights-at-age data for 14 Bering Sea and Northeastern Pacific herring stocks and assigned our three locations to different clustering groups, implying they differed in temporal patterns of weights-at-age. We simulated herring weights-at-age with North Pacific Ecosystem Model for Understanding Regional Oceanography for Including Herring and Saury (NEMURO.FISH) and statistically analyze the resulting growth rate, and the annual average temperature and zooplankton densities, for shifts in their mean values. We also perform simulations to determine the relative influence of temperature and zooplankton on herring growth responses. Finally, we discuss the advantages and drawbacks of our uncoupled models approach, and compare our simulated herring growth responses to observed responses.