



Geographic variation in Pacific herring growth in response to regime shifts in the North Pacific Ocean



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ABSTRACT

Pacific herring populations at eight North Pacific Rim locations were simulated to compare basin-wide geographic variations in age-specific growth due to environmental influences on marine productivity and population-specific responses to regime shifts. Temperature and zooplankton abundance from a three-dimensional lower-trophic ecosystem model (NEMURO: North Pacific Ecosystem Model for Understanding Regional Oceanography) simulation from 1948 to 2002 were used as inputs to a herring bioenergetics growth model. Herring populations from California, the west coast of Vancouver Island (WCVI), Prince William Sound (PWS), Togiak Alaska, the western Bering Sea (WBS), the Sea of Okhotsk (SO), Sakhalin, and Peter the Great Bay (PGB) were examined. The half-saturation coefficients of herring feeding were calibrated to climatological conditions at each of the eight locations to reproduce averaged size-at-age data. The depth of averaging used for water temperature and zooplankton, and the maximum consumption rate parameter, were made specific to each location. Using the calibrated half-saturation coefficients, the 1948–2002 period was then simulated using daily values of water temperature and zooplankton densities interpolated from monthly model output. To detect regime shifts in simulated temperatures, zooplankton and herring growth rates, we applied sequential *t*-test analyses on the 54 years of hindcast simulation values. The detected shifts of herring age-5 growth showed closest match (69%) to the regime shift years (1957/58, 1970/71, 1976/77, 1988/89, 1998/99). We explored relationships among locations using cluster and principal component analyses. The first principal component of water temperature showed good correspondence to the Pacific Decadal Oscillation and all zooplankton groups showed a pan-Pacific decrease after the 1976/77 regime shift. However, the first principal component of herring growth rate showed decreased growth at the SO, PWS, WCVI and California locations and increased growth at the Sakhalin, WBS and Togiak locations after 1977. The SO location belonged to the same cluster as the location in with the eastern North Pacific. The calibrated half-saturation coefficients affected the degree to which growth was sensitive to interannual variation in water temperature versus zooplankton. For example, the half-saturation values for the SO location resulted in very efficient feeding that shifted the sensitivity of herring growth from food to temperature. The model results demonstrate how geographic specificity of bioenergetics parameters, coupled with location-specific variation in temperature and food, can combine to determine local and regional responses of fish growth to climate forcing.

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1. Introduction

Many studies have demonstrated the strong influence of basin scale climatic variability on marine ecosystems (Kawasaki, 1983;

Chavez et al., 2003; Alheit and Bakun, 2010). In the North Pacific Ocean, physical and ecological variability often have a coherent basin-wide expression owing to the global processes that drive them, such as the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (King, 2005). In some cases, the coherent basin-wide physical and ecological variability show “regime shifts” that signify large time- and space-scale shifts between two alternative steady states (Mantua et al., 1997;

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Francis et al., 1998; Chavez et al., 2003). Ecosystem regime shifts have been identified as changes in plankton production (Chiba et al., 2008), fish distribution (Mueter and Litzow, 2008; Spencer, 2008), fish abundance (Francis et al., 1998), fish recruitment (Hollowed et al., 2001), species composition (Chavez et al., 2003; Conners et al., 2002), biodiversity (Conners et al., 2002; Hoff, 2006), and trophic linkages (Aydin and Mueter, 2007). Despite the recognition that the basin-scale oceanic system is forced by climate, the upper ocean response and consequent changes in the ecosystem structure are localized, being modulated by specific regional conditions that affect how the climate signals are expressed in physical and biological responses. Therefore, regime shifts can have opposite effects on species living in different domains, or can affect similar species living within a single domain in opposite ways (Benson and Trites, 2002). Mechanistic modeling of marine ecosystems provides a method for quantifying ecosystem and upper trophic level responses to climate on regional scales, which when combined with similar analyses in other regions, can lead to increased understanding of broad-scale coherence in biological responses.

Relevant biological and physiological data have been collected for decades on Pacific herring (*Clupea pallasii*) and Pacific saury (*Cololabis saira*), and were used to develop a bioenergetics fish growth model coupled to the commonly used a lower trophic level NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) NPZ model (NEMURO.FISH – Ito et al., 2004 and Megrey et al., 2007a,b). In this paper, we build on the NEMURO.FISH analysis of Rose et al. (2007a), and focus on Pacific herring across multiple regions in the North Pacific. Pacific herring have been observed to display widespread geographic synchrony. For example, the exceptionally strong year-class in 1977 was observed over a broad geographic range. Recruitment was strong in northern British Columbia, Canada, parts of southeastern and central Alaska, and in the Bering Sea (Hollowed and Wooster, 1995; Hollowed et al., 2001; Hay et al., 2001). This 1977 year-class developed in different populations with different spawning times, with a range of about 3 months from the earliest to the latest mean spawning time. Estimated spawning in 1977 was not exceptionally high or low in any of the populations that were examined, including all in British Columbia and many in Alaska (Hay et al., 2001). Consequently, the simplest explanation for the geographically widespread synchrony of the 1977 cohort was a geographically widespread increase in survival from eggs to the juvenile and recruit stages (Hay et al., 2001).

NEMURO.FISH was previously applied to simulate herring weights-at-age and growth from 1948 to 2000 for three locations along the Pacific coast of the North American Continent: west coast of Vancouver Island (WCVI), Prince William Sound (PWS), and Togiak, Alaska (Rose et al., 2007a). Simulated herring at all three locations showed a shift in growth during the mid and late 1970s. Herring growth decreased in WCVI and PWS, and increased in Togiak; these changes were coincident with the simulated warming and decreased density of the predatory zooplankton group. Temperature and zooplankton densities affected the predicted herring growth responses in both Alaskan locations, with zooplankton dominating the model response for PWS and temperature dominating the model response for Togiak.

Although some of the simulated shifts of herring growth responses reported in Rose et al. (2007a) were consistent with the observed responses, the availability of observations is generally limited. Otolith growth analysis is one of the effective methods to investigate fish growth response to climate regime shifts (Matta et al., 2010). However, it is commonly difficult to obtain a systematic data set that includes a comprehensive set of environmental variables, prey conditions, and fish growth, all measured and reported on temporal and spatial scales that allow straightforward

and rigorous statistical analyses. The implementation of a higher trophic model coupled to a general lower trophic model to estimate variability in fish growth and population dynamics is a feasible alternative to field data analyses for studying long-term ecosystem responses to regime shifts at multiple locations (Rose et al., 2007a, 2008). Since the model captures the variability in physical forcing, zooplankton dynamics, and fish responses at suitable temporal and spatial scales. Of course, use of model output has the caveat that analysis of “model data” is completely dependent on the skill of the underlying models.

Species-specific and east–west comparisons of fish responses to climate variability were previously conducted using NEMURO.FISH for Pacific herring and saury (Megrey et al., 2007b). However, this east–west comparison was conducted assuming identical conditions for herring in the same subarctic region where saury migrate in summer, and thus their projections were illustrative but limited in their realism. In addition, Pacific herring show considerable differences in weight- and size-at-age between the eastern and western North Pacific (Hay et al., 2008). The broad geographical differences may relate not only to temperature and food differences, but also to geographical variation in herring-related biological factors (e.g. consumption rates, prey preferences, behavior) due to adaptation to local conditions. Therefore, the regional responses of Pacific herring to climate variability may be a combination of environmental and biological differences.

In this paper, we expand the target area of Rose et al. (2007a) from the west coast of North America to the broader pan-Pacific area in order to investigate latitudinal and longitudinal variation and temporal patterns in Pacific herring growth in response to climatic variability and regime shifts within the entire North Pacific basin. Specifically, we added the herring populations of California, the western Bering Sea (WBS), the Sea of Okhotsk (SO), Sakhalin, and Peter the Great Bay (PGB) to the previously studied WCVI, PWS, and Togiak locations (Fig. 1). Model output was analyzed to identify regime shifts. Regime shifts within and among locations were compared to determine if herring responses were consistent across locations. We also analyzed how the different bioenergetics-related characteristics of the herring within locations influence the geographical responses of Pacific herring growth to climate change.

2. Materials and methods

2.1. Overview

The approach we used was basically the same as that used in Rose et al. (2007a). We used output from a NEMURO simulation of the nutrient–phytoplankton–zooplankton (NPZ) dynamics as input to the herring bioenergetics model. The bioenergetics model simulated the daily growth and weight of an average herring individual based on daily-interpolated monthly water temperatures and zooplankton densities. In the present study, as with the Rose et al. (2007a) analysis, the fish bioenergetics model was uncoupled from the NEMURO NPZ model. As such, the simulated herring had no effect on zooplankton densities and we did not need to simulate herring abundances. Other applications of NEMURO.FISH have included the feedback of herring on their prey and simulated recruitment and abundances by age of the herring to generate population dynamics (e.g., Rose et al., 2008). However, the application of Rose et al. (2008) was limited to a single box model, rather than the summarized output from a 3-dimensional coupled hydrodynamics–NPZ model. The alternative of running the fish bioenergetics for many individuals dynamically coupled to the 3-dimensional model to allow for density-dependent effects was deemed unnecessary to capture the major geographic differences

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