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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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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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.

2. Methods

2.1. Overview

We used output from a NEMURO simulation of the NPZ dynamics as input to a herring bioenergetics model. The bioenergetics model used here, NEMURO.FISH, simulated the daily weight of an average herring individual based on inputted daily water temperature and zooplankton densities. However, NEMURO was uncoupled with the bioenergetics fish model. Examples of bioenergetics and population dynamics models dynamically coupled to the NEMURO model are given in Megrey et al. (2007) and Rose et al. (in press). Because we used output from a 3D-NEMURO simulation, the simulated herring had no effect on zooplankton densities (*i.e.*, the models were uncoupled). Thus, there was no need to predict the recruitment of young-of-the-year (YOY) herring each year or to follow numbers of herring in each age-class, as was done in previous applications that used NEMURO coupled with the herring bioenergetics model.

The NEMURO application, from which we used temperature and zooplankton as inputs to the bioenergetics model, was a 3D implementation for the Northern Pacific (Aita et al., 2003, 2007). The 3D-NEMURO simulation represented the NPZ dynamics for 1948–2002 using, as much possible, observed data for driving variables. We used the output of the 3D-NEMURO simulation at three locations (WCVI, PWS, and BS) as input to the bioenergetics model and simulated the daily growth of herring for 1948–2000. We then applied the sequential *t*-test analysis to detect regime shifts (STARS) algorithm (Rodionov and Overland, 2005) to the simulated temperatures, zooplankton, and herring growth rate (annual change in weight between ages 3 and 4) to identify statistical shifts in their average values. We compared these shifts within and among locations to determine if herring responses were consistent across populations. Simulations were also preformed that used various combinations of averaged (climatological) and time series temperature and zooplankton densities to determine whether predicted herring responses were due to the interannual variation in temperature or in zooplankton.

2.2. Herring bioenergetics model

The daily weight of an individual herring was followed from entrance into the population at about 3 months of age in June through their maximum age (10 years for WCVI and PWS; 15 years for BS). At the beginning of each model year marked by the approximate spawning time (March 15), we started a new year-class cohort as eggs which then entered the population in June of the same year. Just after spawning (March 20), we promoted individuals to the next age. The actual numbers in the age-classes were irrelevant as the herring consumption did not affect the NEMURO-predicted zooplankton densities. The herring model used units of grams wet weight per cubic meter (g m^{-3}); we converted between the 3D-NEMURO units of micromoles nitrogen per liter (μM N L^{-1}) and the herring model units of g m^{-3} assuming dry weight was 20% of wet weight and nitrogen was 7% of dry weight. Weights-at-age were outputted from

the bioenergetics model just before spawning so that age-1 individuals were just about 12 months of age, age-2 individuals were just about 24 months old, *etc.* For the purposes of these analyses that focused on growth of age-3 and older individuals, we ignored the differences in spawning times among the locations (Hay et al., 2001) and ignored any influence that differences in YOY growth might have on subsequent adult growth.

The growth rate in weight W (g wet weight) of an individual herring was computed as:

$$\frac{dW}{dt} = [C - (R + S + F + E)]\frac{CAL_z}{CAL_f}W \tag{1}$$

where C is realized consumption rate, E the excretion rate, F the egestion rate, R the respiration rate, S the specific dynamic action, CAL_z the energy density of zooplankton and CAL_f is the energy density of herring (J g^{-1}). The units of C, E, F, and S are g prey (g fish)$^{-1}$ day^{-1}. The ratio of zooplankton to herring energy densities converted all of the process rates from g prey (g fish)$^{-1}$ day^{-1} to g fish (g fish)$^{-1}$ day^{-1}. The energy density of herring varied over the year (Megrey et al., 2007). On the day of spawning (March 15), the average weight of an individual in each mature age-class was reduced by subtracting off their weight times their age-specific fraction mature times 0.25 (*i.e.*, 25% loss of weight for individuals in fully mature age-classes). Realized consumption rate (C) depended on a maximum consumption rate and the simulated zooplankton densities.

Maximum consumption rate and respiration rate were computed as functions of weight and temperature, while egestion rate, excretion rate, and specific dynamic action were computed based on realized consumption (Megrey et al., 2007). The herring bioenergetics model was configured using modified versions of the usual formulations in the Wisconsin bioenergetics model (Hanson et al., 1997). Respiration rate was computed as the product of allometric effect (power function of herring weight) and a Q10 temperature relationship, with parameters specific to YOY, age-1, and age-2 and older herring.

Realized consumption was computed using a multispecies functional response (Rose et al., 1999) with the small, large, and predatory zooplankton as prey types:

$$C_{ij} = \frac{C_{MAX}((PD_j v_{ij})/K_{ij})}{1 + \sum_{k=1}^{3}(PD_k v_{ik})/K_{ik}} \tag{2}$$

where C_{ij} is the consumption rate of the jth zooplankton group ($j = 1$ is small zooplankton, $j = 2$ is large zooplankton, and $j = 3$ is predatory zooplankton) by a herring in the ith age-class, PD_j the density of the jth zooplankton group (in g m^{-3}) on each day, C_{MAX} the maximum consumption rate (g prey (g fish)$^{-1}$ day^{-1}), v_{ij} the vulnerability and K_{ij} is the half-saturation coefficient (g m^{-3}) of the jth zooplankton group to the ith age-class herring. Vulnerabilities and half saturation coefficients were specified separately for YOY, age-1, and age-2 and older herring. Vulnerabilities were specified based on general descriptions of ontogenetic shifts in herring diets, with $V_{13} = 0$ (YOY herring do not eat predatory zooplankton) and $V_{31} = 0$ (age-2 and older herring do not eat small zooplankton); all other vulnerabilities

had non-zero values. Consumption by an individual herring in the ith age-class (C in Eq. (1)) is the sum of the consumption rates over the three zooplankton groups.

2.3. 3D-NEMURO output

The 3D-NEMURO model simulation used the NPZ dynamics of the NEMURO model (Kishi et al., 2007) imbedded into each cell of the CCSR Ocean Component Model configured for the Northern Pacific Ocean (Aita et al., 2003, 2007). Each cell was 1° latitude by 1° longitude, with a vertical thickness of 5 m in the upper 100 m, 10 m between 100 and 200 m, and thicker below 200 m; surface to bottom involved 54 cells. NEMURO represented the NPZ dynamics in each cell with 11 state variables: nitrate, ammonium, small phytoplankton, large phytoplankton, small zooplankton, large zooplankton, predatory zooplankton, particulate organic nitrogen, dissolved organic nitrogen, particulate organic silicate, and silicate. All NEMURO state variables were tracked in the units of micro-moles nitrogen per liter (μM N L^{-1}).

The rate of change of each state variable in NEMURO was expressed as the sum of process rates that affected that state variable. Photosynthesis, respiration, excretion, predation by modeled zooplankton, and other mortality affected each phytoplankton state variable; grazing, egestion, excretion, predation by modeled zooplankton, and other mortality affected each zooplankton state variable. Nutrient state variables were reduced by photosynthesis uptake, increased by various combinations of phytoplankton and zooplankton respiration, excretion, mortality, and converted among nutrient forms via first-order, temperature-dependent decomposition reactions. Phytoplankton photosynthesis, respiration, and mortality, and zooplankton grazing and other mortality, were all temperature-dependent. Vertical migration of the large zooplankton to deeper cells was simulated for October through March in cells north of 20° North and for April through September for cells south of 20° South.

We used the output for the 3D-NEMURO simulation of 1948–2002. Daily average values of sea surface temperature, fresh water flux, surface wind stress, and solar radiation data were estimated from National Centers for Environmental Prediction (NCEP) data, and were used as driving variables in the 3D-NEMURO simulation (Aita et al., 2007). We extracted NEMURO-predicted monthly values for water temperature, and small, large, and predatory zooplankton densities in the individual column of spatial cells that corresponded to our three locations (Fig. 1): WCVI (48°N, 125°W), PWS (60°N,147°W), and BS (57°N,160°W). We used the output from a 3D-NEMURO simulation slightly different from the simulation results reported in Aita et al. (2007). The earlier simulation that we used here had a slower sinking velocity of PON in deep waters where export rate was high. Other than the changed sinking velocity, the earlier and Aita et al. (2007) simulations used identical parameters, driving variables, and boundary conditions. While the two simulations differed in their predicted magnitude of some of the state variables, the results of both simulations were qualitatively similar and both generated similar broad temporal and spatial
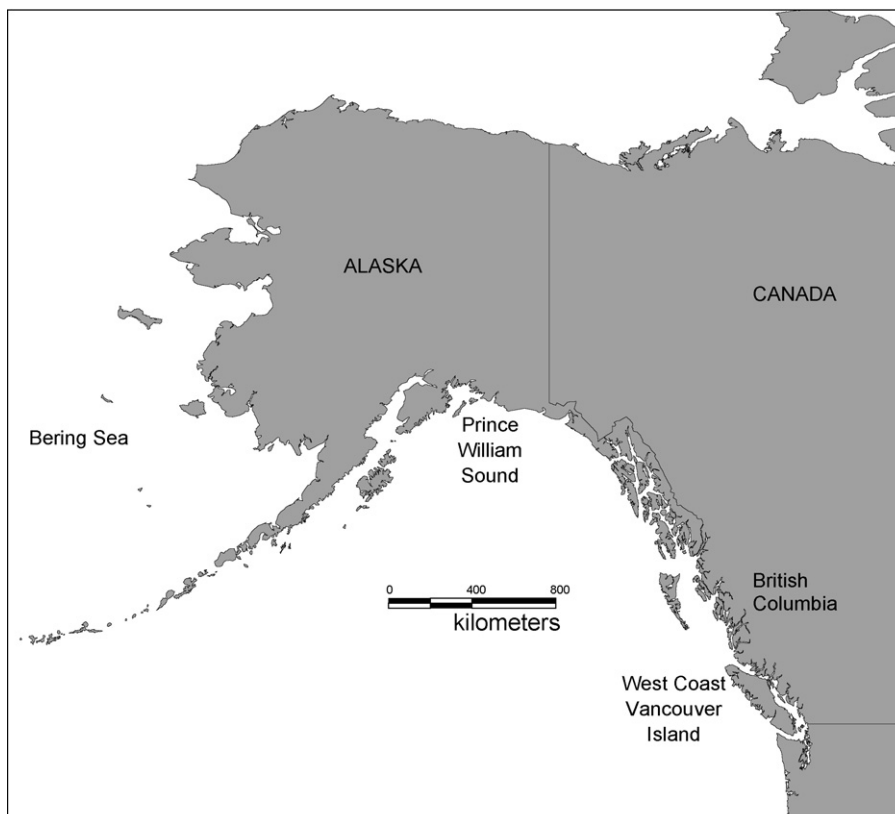

Fig. 1 – Locations of the West Coast Vancouver Island (WCVI), Prince William Sound (PWS), and Bering Sea (BS) populations of herring along the West coast of Canada and Alaska.
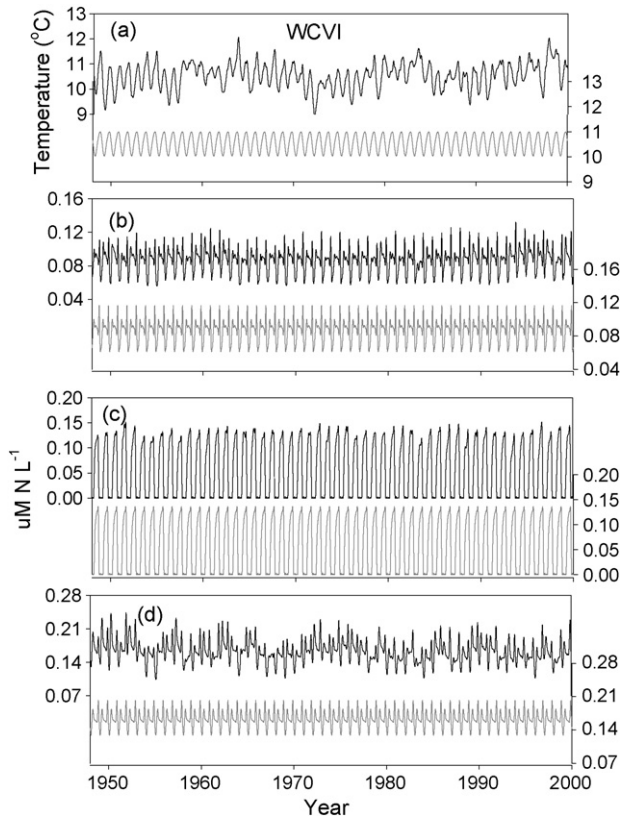
Fig. 2 – Time series and climatological (a) temperature, (b) small, (c) large, and (d) predatory zooplankton densities for WCVI from the 3D-NEMURO simulation. Time series are shown with black lines and climatology is shown with gray lines.
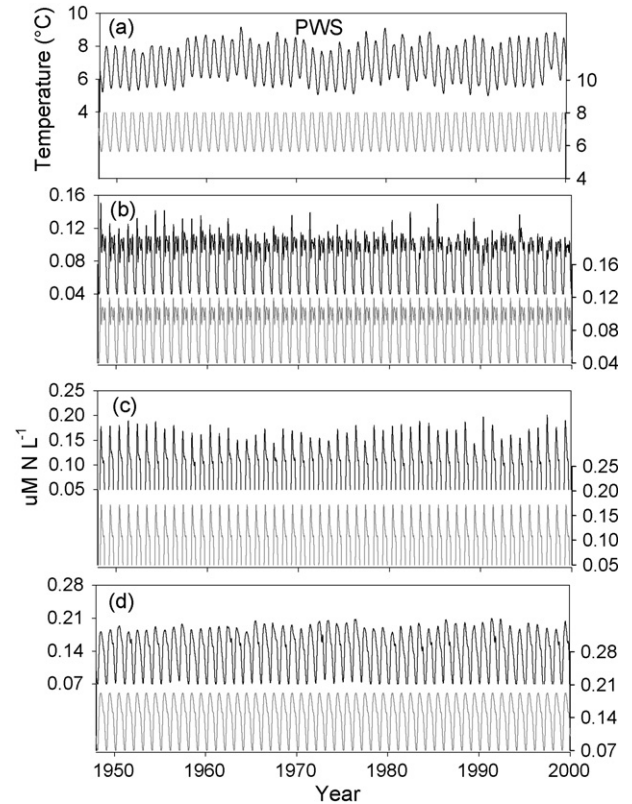

Fig. 3 – Time series and climatological (a) temperature, (b) small, (c) large, and (d) predatory zooplankton densities for PWS from the 3D-NEMURO simulation. Time series are shown with black lines and climatology is shown with gray lines.

patterns of nutrient, phytoplankton, and zooplankton dynamics for the North Pacific.

We then constructed time series by averaging the output over the top 50 m of the water column to obtain single depth-averaged values of temperature, and small, large, and predatory zooplankton densities for each month from 1948 to 2002 at each location. We refer to these monthly values as "time series" (see black lines in Figs. 2–4). For some simulations, we averaged the depth-averaged monthly temperature and zooplankton densities by month over the entire 1948–2002 period to obtain a single set of monthly values, which we refer to "climatological" (gray lines in Figs. 2–4). In model simulations, we repeated this set of monthly climatological values year after year for 54 years. For all bioenergetics model simulations, we linearly interpolated daily values of temperature and zooplankton densities from the monthly values.

2.4. Calibration of herring model

The herring model required calibration because the zooplankton densities generated by the 3D-NEMURO model were generally lower than those used in our previous one-box application of the bioenergetics model to WCVI (Rose et al., 2007). We had calibrated the herring bioenergetics model as coupled to the NEMURO model (Megrey et al., 2007), which itself had been

calibrated using site-specific zooplankton field data (Rose et al., in press). Understandably, the large-scale application of NEMURO to the entire Northern Pacific basin used a generic and spatially constant set of parameter values for phytoplankton and zooplankton growth and mortality rates. Predicted zooplankton densities from the 3D-NEMURO simulation, isolated at specific locations, were lower than the zooplankton densities simulated in the WCVI application. Recalibration of the half-saturation parameters of the herring, the K_{ij}'s in Eq. (2) which determine realized consumption, was necessary to obtain realistic herring growth using the 3D-NEMURO simulated zooplankton densities.

We used parameter estimation (PEST) software (Doherty, 2004) to automatically calibrate the values of the feeding half-saturation (K) parameters. Use of an objective calibration method, rather than adjustments to parameter values based on subjective visual fits, should increase our confidence that simulated differences in herring growth among locations were truly due to temperature and zooplankton differences rather than due to *ad hoc* calibration decisions.

PEST uses a variation of the Gauss–Marquardt–Levenberg algorithm to determine the values of parameters that minimize the weighted sum of squared deviations between predicted and observed values (Doherty, 2004). PEST approximates the relationship between observations and model
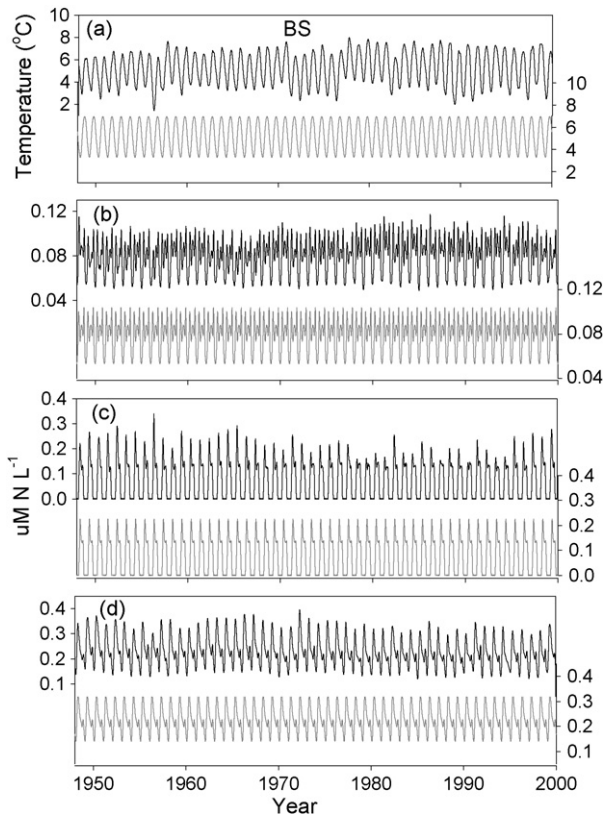
Fig. 4 – Time series and climatological (a) temperature, (b) small, (c) large, and predatory zooplankton densities for BS from the 3D-NEMURO simulation. Time series is shown with black lines and climatological is shown with gray lines.

parameters using a Taylor series expansion, which involves using small changes to parameters to approximate the Jacobian matrix (the matrix of partial derivatives of observations with respect with parameters). New values of parameters are determined based on the gradient of the objective function. PEST stops searching when the objective function does not go lower over several iterations, when the changes in parameters dictated by the update vector are very small, or when the number of iterations or other internal calculations is triggered.

Calibration of the K parameters was based on steady-state predictions of weights-at-age compared to observed mean weights-at-age. Climatological temperature and zooplankton densities were used every year for a 52-year simulation, and predicted weights-at-age in year 50 were compared to observed mean weights-at-age. The calibration simulation was designed so that the model predictions of herring weights-at-age reached steady-state values under repeating environmental conditions. The seven values of K that had non-zero vulnerabilities (Megrey et al., 2007) were allowed to vary in the calibration (Table 1). All K values were started at 0.5 g m^{-3}. PEST determined the values of the seven K parameters that minimized the sum of the squared deviations between predicted and observed weights-at-age. We determined K values separately for each of the three locations. We were interested in how interannual variation in temperature and zooplankton densities affected herring weights-at-age and growth rates. Our approach was to calibrate to average conditions at each location, and then examine how interannual variation around the average conditions affected herring growth. Because we obtained different values for the K parameters for each location, we did not simulate the effects of separately varying individual zooplankton groups.

2.5. Design of simulations

Two sets of simulations were performed using the 3D-NEMURO output and the herring bioenergetics model calibrated for each location: time series response and temperature *versus* zooplankton effects. All simulations were for 1948–2000; we stopped the bioenergetics simulation at 2000 to permit accurate interpolation of daily values. All simulations used an initial 20 years of climatological temperature and zooplankton to minimize the effects of the assumed initial values for weights-at-age.

The first set of simulations involves single simulations at each location that used the time series temperature and time series zooplankton densities for 1948–2000. We computed herring growth as the change in weight (grams wet weight) between ages 3 and 4, and associated this growth rate with the year of the age-3 (*i.e.*, year signifies the year of the summertime growing season). Annual growth rate should reflect the conditions of that particular year, whereas weights-at-age also reflect cumulative conditions over several previous years. Previous analyses have focused on weights and growth

Parameter	Definition	WCVI	PWS	BS
K_{11}	YOY for small zooplankton	0.147	0.104	0.059
K_{12}	YOY for large zooplankton	0.441	1.048	0.352
K_{21}	Age-1 for small zooplankton	0.469	0.546	0.065
K_{22}	Age-1 for large zooplankton	0.425	0.197	0.336
K_{23}	Age-1 for predatory zooplankton	0.435	0.437	0.352
K_{32}	Age-2 and older for large zooplankton	0.757	0.604	0.457
K_{33}	Age-2 and older for predatory zooplankton	0.541	0.490	0.530

Table 1 – Calibrated values of the half-saturation feeding parameters (K values, g m^{-3}) for the three locations

Calibration was performed using the PEST software and year 50 output of weights-at-age from the bioenergetics model simulation with climatological (averaged) temperature and zooplankton densities. WCVI, West Coast Vancouver Island; PWS, Prince William Sound; BS, Bering Sea.

rates of ages 3–5 for comparative analyses (*e.g.*, Schweigert et al., 2002). In order to detect shifts in the monthly temperature and zooplankton densities, we computed annual values of each. We applied the STARS statistical method (Rodionov and Overland, 2005) to the simulated time series of herring growth rate and the annual average values of temperature and zooplankton densities to identify shifts in mean values. The STARS method was applied to all simulated time series using its default settings ($p = 0.1$, cutoff length = 10, and Huber parameter = 1). We present the results for age-3–4 growth rate; similar results were obtained using weight-at-age of age-4 and -10, and growth rate computed between ages 4 and 5.

The second set of simulations, designed to compare temperature *versus* zooplankton effects, consisted of the simulations from the first set plus three additional simulations at each location. The first set of simulations used the time series values of temperature and zooplankton densities. As part of the second set of simulations, we then simulated herring weights-at-age for time series temperature and climatological zooplankton densities (temperature effect), climatological temperature and time series zooplankton densities (zooplankton effect), and with both temperature and zooplankton densities at their climatological values (*i.e.*, same as calibration). Predicted herring growth rates for 1948–2000 were compared at each location to determine the contribution of temperature *versus* zooplankton to the predicted herring response under time series conditions.

3. Results

3.1. Calibration

Calibrated steady-state weights-at-age were very similar to observed values for all three locations (Fig. 5), and the resulting *K* parameter values were reasonable (Table 1). Particularly good fits were obtained for age 3 through about age 8. We used weights-at-age for age-3 and -4 to compute an annual growth rate. Simulated weights at the very young ages and oldest ages tended to deviate slightly from observed values. Predicted weight at age 2 was consistently lower than observed values for all three locations, and was probably due to our use of single *K* values for all age-2 and older ages. We sacrificed a closer fit for age-2 in order to ensure better fits for ages 3 through 8.

3.2. Time series responses

All three locations showed a shift in herring growth during the late 1970s (Figs.6a, 7a, 8a). Herring growth decreased in WCVI and PWS, and increased in BS. Coincident with these shifts in herring growth was warming of temperature (Figs.6b, 7b, 8b) and a decrease in predatory zooplankton density (Figs.6e, 7e, 8e). There was also a relatively small increase in small zooplankton density in BS (Fig. 8c).

All three locations also showed initial signs of possible shifts in herring growth, temperature, and zooplankton densities at the end of the simulation during the late 1990s (Figs. 6–8). However, detection of shifts in growth rate, temperature, and zooplankton densities for years at the end of
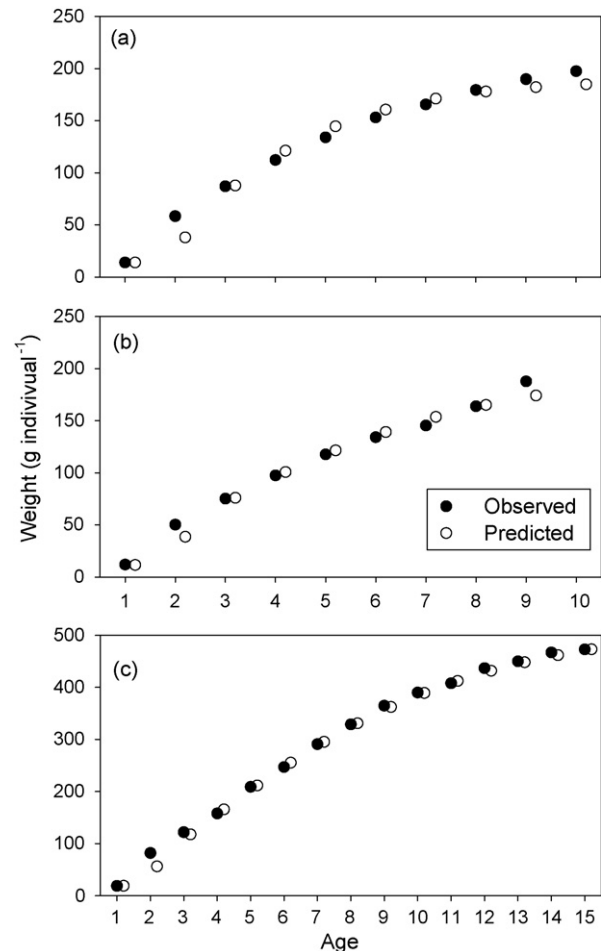

Fig. 5 – Calibrated and observed values of herring weights-at-age for (a) WCVI, (b) PWS, and (c) BS. Seven *K* parameters were calibrated using the PEST software. Predicted weights at age were outputted from the bioenegetics model during year 50 of a 52-year simulation and represent steady-state values. Observed weights-at-age were averaged for 1951–2003 for WCVI (very similar to averages during 1980–2000), for 1980–2000 for PWS, and for 1978–2000 for BS (Togiak stock). Observed weights at age-1 and age-2 for PWS and age-1, -2, and -3 for BS were unavailable and were estimated based on the ratio of observed mean weights for WCVI. For example, age-1 weight for PWS was computed as the [(weight at age-1 for WCVI)/(weight at age-3 for WCVI)] × (weight at age-3 for PWS), and weight at age-1 for BS was computed as [(weight at age-1 for WCVI)/(weight at age-4 for WCVI)] × (weight at age-4 for BS).

the records is not robust, and should be viewed as only suggestive that conditions may be changing (Rodionov and Overland, 2005).

For WCVI, there were also shifts detected in temperature (late 1950s and early 1970s; Fig. 6b) and in small zooplankton (early 1960s; Fig. 6c) that were not detected in the herring growth rate (Fig. 6a). Predatory zooplankton, like herring growth rate, did not show any shifts besides the shift in the late 1970s (Fig. 6e). No shifts were detected for large
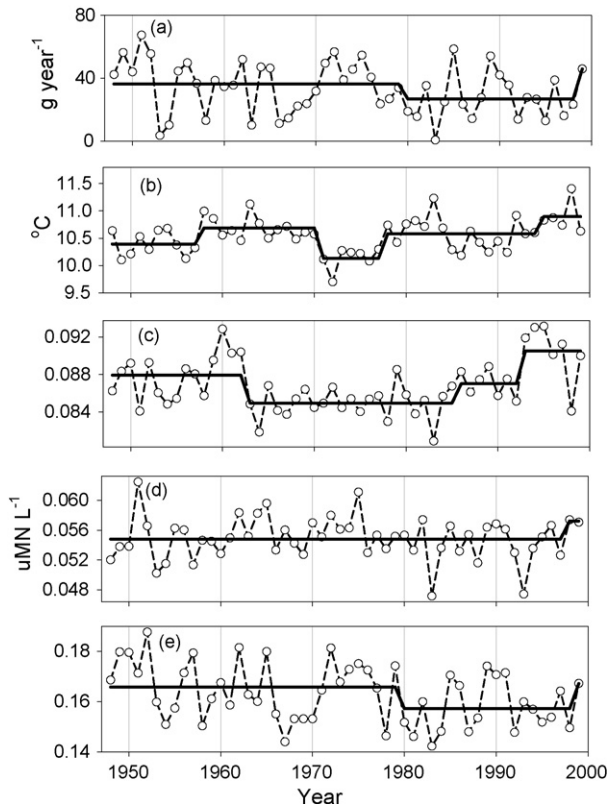
Fig. 6 – Simulated (a) herring growth rate (age 3–4) and annual average, (b) temperature, (c) small zooplankton density, (d) large zooplankton density, and (e) predatory zooplankton densities for WCVI for 1948–2000. Model predicted growth rates are shown with circles; solid lines are average values between statistically identified shifts in mean values.
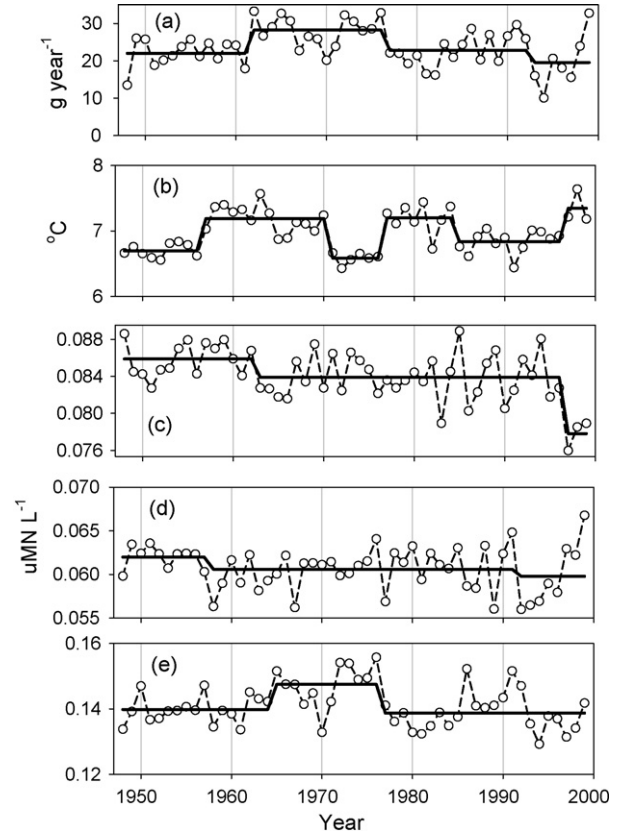

Fig. 7 – Simulated (a) herring growth rate (age 3–4) and annual average, (b) temperature, (c) small zooplankton density, (d) large zooplankton density, and (e) predatory zooplankton densities for PWS for 1948–2000. Model predicted growth rates are shown with circles; solid lines are average values between statistically identified shifts in mean values.

zooplankton, except for highly uncertain shift at the very end of the simulation (Fig. 6d).

The responses of herring in PWS and BS were more complex than those predicted for WCVI. Both Alaskan locations showed faster herring growth beginning around 1960 (Figs.7a and 8a), which was not obviously related to shifts in temperature or zooplankton densities (Figs.7b–e and 8b–e). PWS herring also showed a small decrease in growth rate just after 1990 (Fig. 7a), which was coincident with a small, but significant, decrease in large zooplankton density (Fig. 7d).

Herring growth in BS showed several shifts in addition to the shift that was predicted in the late 1970s for all three of the locations. Herring growth in BS decreased after 1970 (and before the increase in the late 1970s) (Fig. 8a) that could have been associated with a decrease in large zooplankton (Fig. 8d), although small zooplankton (Fig. 8c) increased at about the same time. More likely, the decrease in predicted BS herring growth between 1970 and 1977 was due to cooler temperatures that were not statistically significant according to the STARS analysis, but appeared at least visually to be consistently cooler (Fig. 8b). The short duration of the lowered temperatures (before their subsequent increase in the late 1970s) may have contributed to the lack of statistical detection of a

mean shift. Growth rate of herring in BS also decreased in the late 1980s (Fig. 8a), coincident with a cooling of water temperatures (Fig. 8b).

3.3. Temperature and zooplankton effects

The relative importance of variation in temperature and zooplankton density on herring growth response in the time series simulations differed by location (Fig. 9). Interannual variation in zooplankton densities caused the time series response in herring growth for WCVI. The simulation that only varied zooplankton densities (temperature maintained at averaged monthly values every year) generated almost the identical time series of herring growth rates as the simulation in which temperature and zooplankton densities were both varied (dashed line similar to solid line in Fig. 9a).

Temperature and zooplankton densities both played roles in PWS and BS herring growth responses, with zooplankton dominating the response for PWS and temperature dominating the response for BS. For PWS, the varying zooplankton simulation tended to track the time series response (dashed line tracking the solid line in Fig. 9b), although there were periods of deviation when the varying temperature sim-
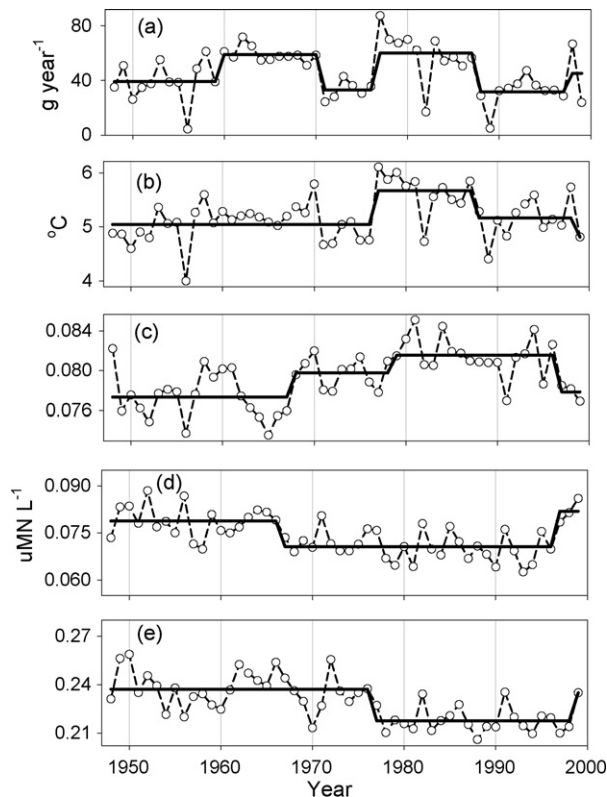
Fig. 8 – Simulated (a) herring growth rate (age 3–4) and annual average, (b) temperature, (c) small zooplankton density, (d) large zooplankton density, and (e) predatory zooplankton densities for BS for 1948–2000. Model predicted growth rates are shown with circles; solid lines are average values between statistically identified shifts in mean values.
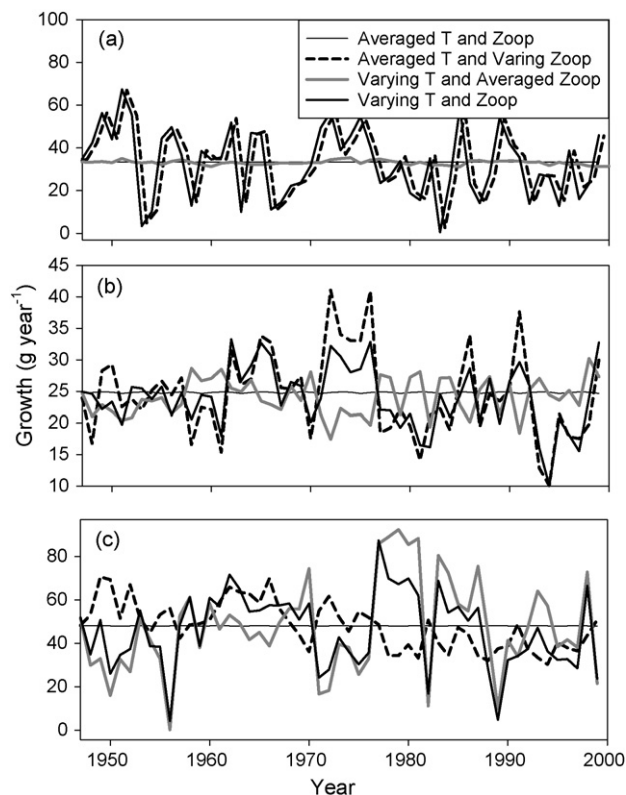

Fig. 9 – Predicted herring growth rate (age 3–4) for 1948–2000 at (a) WCVI, (b) PWS, and (c) BS for climatological temperature and zooplankton densities, climatological temperature with time series zooplankton densities, time series temperature with climatological zooplankton densities, and for time series temperature and zooplankton densities. Climatological conditions repeated a single year of monthly values obtained by averaging values by month over years. The climatological temperature and zooplankton densities correspond to the same simulation used for model calibration. The time series temperature and zooplankton densities simulation is the same as that presented in Figs. 6–8.

ulation also played a role. For example, around 1970, the time series simulation for PWS showed the same two-peak pattern as the varying zooplankton simulation but at a lower magnitude; during this same period the varying temperature simulation (solid gray line) resulted in lowered herring growth rate (Fig. 9b).

Temperature played a major role in response of herring in BS (gray line tracking solid line in Fig. 9c), although like with PWS, there were time periods when the time series response was intermediate between the varying temperature and varying zooplankton densities simulations. For example, during the late 1970s and early 1980s, the time series response was a mix of the varying temperature and varying zooplankton simulations (solid line in between the solid gray and dashed lines in Fig. 9c).

4. Discussion

Our approach of using output from a broad-scale NPZ model as input to a herring bioenergetics model has advantages and drawbacks. The major advantage to the approach is that we were able to use a consistent set of temperature and zooplankton densities over a long (52-year) historical time frame

at multiple, and geographically isolated, locations. It would be difficult to reconstruct field data to generate 50 years of monthly temperature and zooplankton densities at our three locations. The alternative of using three different models configured to each location would also restrict comparison of predictions made by the models. For instance, we would not know whether the differences in simulated herring growth at the three locations were due to true geographic differences in temperature and zooplankton dynamics or due to differences among the NPZ models and how they were applied to each location. Our use of output from a single, broadly applied NPZ model provides a reasonable method for obtaining consistent long-term time series of temperature and zooplankton densities.

The drawbacks of a single NPZ model uncoupled from the fish model include a sacrifice of realism for generality and the inconsistent accounting for zooplankton mortality. The NEMURO model was applied to a broad geographic area, so

location-specific biological details may have been missed and the spatial resolution for site-specific predictions was coarse. For example, all locations in the 3D-NEMURO simulations used the same set of phytoplankton and zooplankton parameter values (Aita et al., 2007), and 1° by 1° cells do not permit detailed simulation of near-shore (*e.g.*, upwelling) areas. Extracting predictions from one, or a few spatial cells, is unfair to the present 3D-NEMURO application, as detailed simulation of a particular location was not the goal of that modeling.

Examples of other potentially important site-specific features relevant to our application that could be missed with our analysis are top-down effects on WCVI herring growth due to variation in hake predation affecting herring recruitment (Ware, 1991), and the recent changes in jellyfish abundance in the Bering Sea (Brodeur et al., 2002). Ware and Thomson (2005) recently documented strong bottom-up linkage between primary production and resulting fish production in coastal areas of the northeast Pacific. Further extensions to our analysis could involve investigation of how averaging over multiple horizontal cells affects the temperature and zooplankton density time series, comparisons of predictions between the broadly applied NPZ model to those from more detailed localized models, and how to include potential top-down effects on herring growth.

In addition to the potential missing of important site-specific features, a second potential drawback to the use of the output from a broadly applied NPZ model is problems with zooplankton mortality rates. Use of uncoupled NPZ and bioenergetics models creates potential accounting problems with the mortality of zooplankton. The NPZ model included its own mortality terms for zooplankton, which were reflected in the outputted densities, and herring consumption effects on zooplankton were not explicitly included. One could question whether the simulated zooplankton densities from the 3D-NEMURO model, with its own predation rate assumed for zooplankton, were realistic prey densities for herring. Also, use of uncoupled models prevents any density-dependence in simulated growth from emerging from model simulations. Density-dependent growth can affect mortality, maturity, and reproduction rates that can influence fish population dynamics (Rose et al., 2001). We could force density-dependence by lowering herring growth rate based on herring biomass, but specification of the function requires an *a priori* decision of the density-dependence effect. Fully coupled models would allow for herring consumption to be removed from the zooplankton densities and thus for density-dependent growth to be an outcome of the simulations (*e.g.*, Rose et al., in press). With proper caution, extracting results from a broadly applied lower trophic level model to use as input to other models provides a powerful method for comparing the long-term dynamics of upper trophic levels across geographic locations (Runge et al., 2004).

Our analysis using output from the 3D-NEMURO model as input to our bioenergetics model showed shifts in simulated herring growth rate around the 1977 regime shift at all three locations (Figs.6a, 7a, 8a). While the 3D-NEMURO output showed warming temperatures at all three locations beginning in the late 1970s (Figs.6b, 7b, 8b), herring growth was predicted to decrease in WCVI and PWS and to increase in BS. One explanation for this is that zooplankton played a major role in determining the herring growth response for WCVI and PWS (Fig. 9a and b), where predatory zooplankton densities declined beginning in the late 1980s. In contrast, herring response for BS was dominated by temperature (Fig. 9c), and the warmer temperatures likely caused faster growth in BS, despite lowered predatory zooplankton densities. Furthermore, there was also a small increase in small zooplankton density in BS beginning in the late 1980s, which may have helped offset the effects of the lowered predatory zooplankton densities. In general, temperature and zooplankton densities generated by 3D-NEMURO were, at most, weakly correlated with each other at each location ($R^2 < 0.2$), so temperature and zooplankton densities could be treated as independent factors in our simulations. All three locations also showed signs of a shift during the last few years of the simulations, which could correspond to the 1998 regime shift. However, detecting shifts near the end of a time series is problematic (Rodionov and Overland, 2005).

Comparisons of model predictions of herring growth to historical data are not straightforward but do provide some suggestion that the simulations are reasonably realistic. We examined observed weights-at-age data for WCVI and PWS as a direct comparison to model-predicted herring growth rates. The model results for BS were not compared to observed data because observed weights-at-age for the Bering Sea begin in 1980. We also tried to compare our predicted herring responses to general responses of fish reported for each of the three regions.

Long-term records of herring weights-at-age exist for PWS and WCVI (Schweigert et al., 2002). Given the time periods of the predicted shifts in growth rates and the availability of weights-at-age data, two direct comparisons were possible. The predicted shift downward in growth rate for before and after about 1980 for WCVI (38.9 g year^{-1} for 1971–1980 *versus* 28.2 g year^{-1} for 1981–1999; Fig. 6a) agreed with the lower average weight at age-4 observed in the field data (150.1 g *versus* 142.9 g). Similarly, the slow growth rate period predicted in PWS for 1992–1997 (17.7 g year^{-1} *versus* 22.0 g year^{-1} for the earlier period of 1981–1989; Fig. 7a) agreed with the lower average weight at age-4 observed in the field data for the same time periods (88.5 g *versus* 96.4 g). Additional direct model to data comparisons are difficult because of the time gaps in the observed weights-at-age data.

Previous studies have also analyzed the long-term observed weights-at-age data for herring. Schweigert et al. (2002) analyzed weights-at-age data for 11 herring populations, including WCVI, PWS, and BS, and suggested that annual growth rates seemed to respond to ENSO events, with warmer waters having a negative effect on growth. He also suggested that herring growth has generally decreased since 1977 in many British Columbia and Alaska stocks, which is consistent with our predictions of lowered growth rates since 1977 for WCVI (Fig. 6a) and PWS (Fig. 7a). However, Schweigert et al. (2002) concluded that the response in herring weights-at-age, growth rate, and condition factor time series were not simple reflections of environmental indices and were not consistent across all populations. Brown (2002) focused on the observed weights-at-age data for PWS and showed that herring weights-at-age were positively correlated to annual zooplankton biomass and that weights were low in the late 1970s

and early 1990s. The periods of low weights-at-age somewhat coincide with our two downward shifts simulated for herring growth rate for PWS (Fig. 7a). Wespestad (1991) found that herring biomass in the eastern Bering Sea showed two peaks in the early 1960s and early 1980s. He conjectured that fast individual growth rate would be associated with good recruitment, which is the opposite pattern we would expect if density-dependent growth was operating. If recruitment and growth are positively related, then this would imply a time series of herring growth rates with two peaks similar to our predicted time series (Fig. 8a). We recognize that our attempt to compare observed and predicted herring growth responses contains many problems and such comparisons involve multiple caveats. So we offer these comparisons in an attempt to be synthetic and exploratory; agreement between observed and predicted patterns of herring growth rates is perhaps fortuitous in some situations.

There is some evidence that our predicted reversal of herring responses between WCVI and BS is plausible. Cooler conditions were associated with higher recruitment for WCVI herring, while in northern British Columbia and Gulf of Alaska warmer conditions were associated with higher recruitment and production (Brown, 2002). Benson and Trites (2002) also reported that after the 1977 shift most fish species increased in the Bering Sea and Gulf of Alaska while most fish did poorly in the California Current. Our simulated reversal may be due to different reasons than occurred in nature, as the only differences in our simulations among locations were temperature and zooplankton densities. Lowered zooplankton densities reduced simulated growth rates of herring in WCVI, while warmer temperatures increased growth rates in BS.

Even in our virtual world of 3D-NEMURO output and simulated herring growth, detecting and explaining regime shift effects on herring growth is complicated. PWS and BS herring both showed increased growth just after 1960, when there were no obvious coincident shifts in temperature and zooplankton densities (Figs. 7 and 8). At first, we were concerned that these early-predicted shifts in herring growth were due to the effects of initial conditions in the bioenergetics model simulations. Simulating 20 years of averaged temperature and zooplankton densities should have taken care of any initial conditions effects. But to be sure we also repeated the time series simulations using other initial conditions and consistently detected a shift in herring growth rate around 1960 in PWS and in BS but not in WCVI. Other shifts were detected in temperature and zooplankton densities that did not manifest themselves in herring growth. We applied the STARS method the same way across all time series. Some shifts deemed statistically significant in temperature and zooplankton densities may be ecologically unimportant to modeled herring growth, while other shifts deemed not statistically significant may result in herring growth responses.

Understanding regime shift effects on fish is critical to their proper management, yet unraveling the influence of climate on fishes is a challenging task. Our analysis was in a virtual world that we control and yet we were unable to easily explain some of our simulated responses. We suspect that if we looked hard enough we could find a climate-related index that shifted during a particular time window of interest (e.g., Fig. 2 in Rodionov and Overland, 2005). The long time history of data needed, combined with the complex life histories of many fishes, make detecting shifts in fish growth or recruitment difficult and establishing cause and effect between responses and climate a challenging goal. Extensive collaboration and coordination among climatologists, oceanographers, and fisheries ecologists (e.g., Kendall et al., 1996) will be required to make progress on understanding climate effects on fish populations. We are optimistic that advances in data collection methods and modeling capabilities, and the formation of the necessary collaborative networks of scientists, are steadily approaching the point when we can soon generate realistic forecasts of climate effects on fish population dynamics.

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