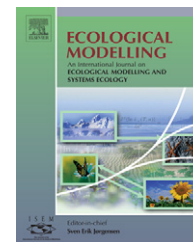




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North Pacific basin-scale differences in lower and higher trophic level marine ecosystem responses to climate impacts using a nutrient-phytoplankton–zooplankton model coupled to a fish bioenergetics model

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ABSTRACT

We present a modeling approach where we use one common model formulation of a 11 state variable lower trophic level model that includes two groups of phytoplankton, three groups of zooplankton, and representations of nitrogen and silicate embedded in a three-dimensional ocean general circulation model (OGCM) and forced with a common climate forcing. Results are applied to a fish bioenergetics model for two geographically distinct ocean regions off Japan including the Oyashio, mixed, and Kuroshio subregions and off California including the subarctic, transition and subtropical subregions. The model is applied to two fish species (Pacific saury: *Cololabis saira* and Pacific herring: *Clupea harengus pallasii*) with different life histories in each region and the influence of three different “regime shift” periods was explored. With this approach, we narrow the observed biological response and model dynamics to reflect local conditions and eliminate differences related to the model formulations in each region. In general, the trend in temperature was negatively correlated with trends in the zooplankton community. Out-of-phase herring growth trends were observed between the Japan and California regions ($r = -0.259$, $p = 0.02$). In-phase growth trends between herring and saury were observed at the California region ($r = 0.61$, $p < 0.01$). We did note some evidence of a basin-scale PDO mode response. During 1980–1985, simulated saury and herring in both regions showed a consistent increase in weight-at-age. In the Oyashio subregion, temperature decreased and all three zooplankton groups increased beginning around 1980. The same pattern of a decrease in temperature and an increase in zooplankton densities was observed between 1980 and 1985 in the subarctic subregion of California. Results are discussed in the context of ecosystem-based fisheries management.

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1. Introduction

The response of marine ecosystems to climate change is one of the most significant sampling and modeling challenges presently faced by the ocean research community (deYoung et al., 2004). Although many important marine ecosystems worldwide are being intensely studied, the mechanisms by which climate change leads to ecosystem responses are not fully understood. Providing mechanistic understanding is especially critical when trying to assess the impacts of climate change on target populations at the basin-scale.

In the North Pacific Ocean, physical and ecological variability often have a coherent basin-wide expression owing to the global processes that drive them, e.g., ENSO, PDO, etc. (King, 2005). Despite the recognition that the basin-scale oceanic system is forced by climate, the upper ocean response and consequent changes in ecosystem structure are localized depending on modulation by specific local expressions of physical and biological attributes.

Significant and coherent changes in the state of the ocean, across large geographic areas such as the whole North Pacific basin, should be manifested in regional marine ecosystems if long-term changes in climate variability influence ecosystem productivity. Indeed, broad scale physical and biological changes have been noted throughout the North Pacific basin. Around 1977, population abundance, productivity and distribution, across all trophic levels in ecosystems throughout the North Pacific underwent rapid changes (Hare and Mantua, 2000). In the eastern Pacific, coherent changes were observed in fish stocks and recruitment patterns (Hollowed and Wooster, 1992, 1995; Beamish and Bouillon, 1993; Hare et al., 1999; McFarlane et al., 2000; King, 2005) and zooplankton biomass, timing and community composition in the northeastern Pacific gyre (Brodeur and Ware, 1992; Mackas et al., 1998, 2001). In the western Pacific, similar observations of coherent decadal scale variability patterns in the winter Kuroshio/Oyashio current ecosystems have been made in plankton biomass (Sugimoto and Tadokoro, 1998), winter abundance of large copepods (Nakata and Hidaka, 2003), and fish abundance and fisheries CPUE for sardine, mackerel, and Pacific saury (Yatsu and Ueno, 2004).

A widely used index for decadal changes in the state of the North Pacific Ocean is the Pacific Decadal Oscillation index (PDO). The PDO tracks the dominant spatial pattern of sea surface temperature variation across the North Pacific and the major low frequency changes in North Pacific climate. Shifts in the PDO are often used to delineate different regime periods (Mantua et al., 1997). It has been well established that in the North Pacific climate regime shifts took place in 1977, 1989, and 1998 (King, 2005). The climate shift that occurred in the late 1970s was associated with an abrupt transition from a negative to a positive phase of the PDO. This pattern resulted in anomalously warm waters along the west coast of North America, and cooler waters in the western North Pacific (Mantua et al., 1997; Yasunaka and Hanawa, 2002). Prior to 1989, the main mode of variation was in an east–west pattern and it is referred to as the classic PDO mode. Since 1989, a different north–south pattern has emerged, often referred to as the Victoria mode (Bond et al., 2003). Further information

on the characteristics of the classic PDO and Victoria modes can be found in Mantua et al. (1997), Minobe (1997), Hare and Mantua (2000) and Bond et al. (2003). As discussed by King (2005), the most noteworthy feature of this collection of observations is that observed changes in the marine ecosystems are evident on the scale of the whole North Pacific, and that the changes persist on time-scales of a decade or longer.

Despite a substantive observational database, we still lack quantitative knowledge of how major oceanic ecosystems respond to North Pacific climate variability. Understanding the processes that regulate marine ecosystems is essential to assessing and predicting impacts of climate variability on marine biota and on the human communities that depend on them. Unfortunately, the observational records are short relative to the time scale of regime shifts, as well as spatially incomplete, and hence it is not certain if modes observed during this century are regular in structure, intensity, and timing. Moreover, these patterns cannot be observed in isolation. Andrew C. Revkin, science and environmental writer for the New York Times, proposed the analogy of pointillist paintings with being able to see patterns in nature “the picture is revealed only when a large number of points are regarded as a whole” (Revkin, 2006).

Simulation modeling serves as a tool for quantitatively synthesizing our current knowledge and is well suited to exploring long-term ecosystem response to climate change over broad regions. However, models only represent a caricature of the complexity of the real world (Libralato et al., 2006). Nonetheless, simulation experiments allow exploration of questions and hypotheses that are difficult to address with limited field data. Use of a single model, or multiple models developed to be comparable, enables a more straightforward comparison of predicted responses among different species and among regions. Often, such comparisons of predictions are confounded by differences in responses being inseparable from true biological differences or because different models were applied by different investigators to the species and regions of interest.

Using modeling approaches and data sets described in this issue (Kishi et al., 2007; Ito et al., 2007; Megrey et al., 2007; Rose et al., 2007b), our study focuses on two highly productive, economically important and dynamically distinct ecosystems of the North Pacific at similar latitudes: the California Current System (CCS) and the Kuroshio/Oyashio extension current System (KOS). The CCS extends along the west coast of North America from British Columbia, Canada to northern Baja California, Mexico. The KOS is a swift ocean current extending from the coast of Japan to the central North Pacific, forming the West Wind Drift Current, which bifurcates as it reaches the west coast of the North American continent. The southern arm of the bifurcation forms the CCS. We have focused on the CCS and KOS regions as key response locations to Pacific decadal climate variability, for the reasons discussed above.

Our objective is to present the results of a simulation model of the growth response of Pacific herring (*Clupea harengus pallasi*) and Pacific saury (*Cololabis saira*) to long-term climate changes in the KOS (we term Japan) in the western Pacific and the CCS (we term California) in the eastern Pacific (Fig. 1). We use a nutrient-phytoplankton–zooplankton lower trophic level (LTL) model, NEMURO (Kishi et al., 2007) embedded in a

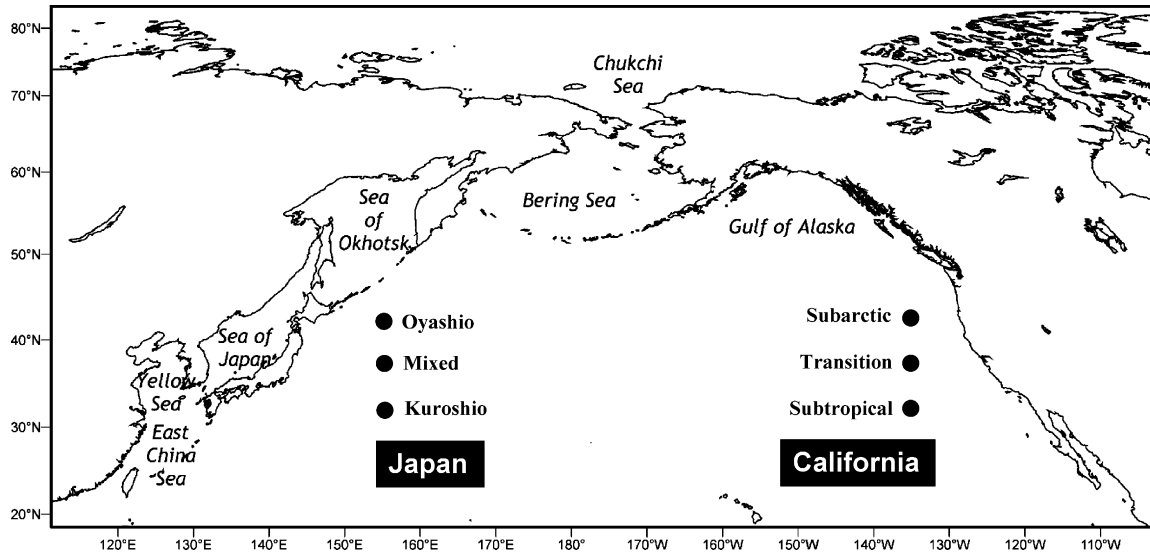


Fig. 1 – Regions in the eastern (California) and western (Japan) North Pacific where growth dynamics of saury and herring were simulated with the NEMURO.FISH model.

3D circulation model of the North Pacific, 3D-NEMURO (Aita et al., 2007) to force a higher trophic level (HTL) fisheries-bioenergetics growth model of Pacific herring and Pacific saury. Two questions related to the biological response of marine ecosystems to climate forcing are addressed: (i) given the long-term changes in temperature and zooplankton predicted by the 3D-NEMURO simulation model, how do these changes propagate up the food web and become expressed in fish growth?; (ii) what role do life-history characteristics play in mediating climate forcing and its impact on the biological response of higher trophic level organisms? Our overarching null hypothesis is that two fish species with different life histories, in two different regions, will show similar biological responses when modeled with a common lower trophic level and fish bioenergetics model, location-specific HTL bioenergetic growth models, and a common basin-scale climate forcing.

2. Materials and methods

2.1. The models

Three different models were used in this analysis and they are related as follows. The first model is a process-oriented nutrient-phytoplankton–zooplankton model (NPZ) called NEMURO and it is described by Kishi et al. (2007). Within NEMURO, 11 state variables are represented including two biological groups of phytoplankton and three groups of zooplankton. NEMURO equations describe the biogeochemical fluxes of nitrogen and silicon. NEMURO is often referred to as a point model because it only simulates a single spatial box that represents the water column from the surface down to the bottom of the mixed layer at a specific latitudinal and longitudinal location. The second model used was an extension to the NEMURO model to include a higher trophic level component by coupling it to a fish bioenergetics model

(NEMURO.FISH) and including process equations to describe growth and life-history characteristics of Pacific herring (*Clupea harengus pallasii*) (Megrey et al., 2007; Rose et al., 2007b) and Pacific saury (*Cololabis saira*) (Ito et al., 2004, 2007). Both herring and saury are distributed generally around the perimeter of the North Pacific, and are planktivores throughout their entire life cycle, eating mainly copepods and euphausiids. In the third model (3D-NEMURO), the NEMURO NPZ model was embedded in a global three-dimensional ocean general circulation model (OGCM) of the North Pacific (Aita et al., 2003; Aita et al., 2007). The NEMURO equations are calculated at every 3D-NEMURO latitude/longitude grid point.

There are two possible types of linkages possible between NEMURO, 3D-NEMURO and NEMURO.FISH: coupled and uncoupled. In the coupled configuration, daily water temperature and the densities of three size-classes of zooplankton (small, large, and predatory) from NEMURO or 3D-NEMURO are used to determine daily consumption rate and respiration rate of the fish, resulting in predictions of daily growth in body weight. A population dynamics component keeps track of the numbers of individuals in each age class over time. Population-level fish consumption is treated as an additional zooplankton mortality term in the NPZ model (NEMURO or 3D-NEMURO), and population-level fish excretion and egestion contribute to the nutrient cycling dynamics in the NPZ. Examples of this approach can be found in Megrey et al. (2007) and Rose et al. (in press). In the uncoupled configuration, NEMURO or 3D-NEMURO output is used to force NEMURO.FISH, and growth (not population dynamics) is predicted at a specific latitude/longitude location. If 3D-NEMURO is used to force NEMURO.FISH, then output is available at multiple locations, and basin-scale fish growth comparisons can be made.

In this study, we used NEMURO.FISH in an uncoupled configuration with output variables from a 3D-NEMURO simulation used as input to both the herring and saury version of the NEMURO.FISH model. Because 3D-NEMURO and NEMURO.FISH were uncoupled (i.e., run sequentially),

we predicted only growth rates of an individual fish from NEMURO.FISH. Thus, no fish population dynamics or density-dependent fish predation effects on the NPZ dynamics were estimated. Results of coupled configurations have been reported in Megrey et al. (2007) and Rose et al. (in press).

3D-NEMURO simulated the NPZ lower trophic level dynamics for the northern Pacific for 1948–2002. The time period for the 3D-NEMURO simulation was selected independently of this study (see Aita et al., 2007), but the simulation period was selected to span several known regime shift periods (1976–1977, 1988–1989, 1998–1999). We extracted monthly temperature and zooplankton densities for the KOS and CCS regions and subregions from the 3D-NEMURO simulation and used these as inputs to the fish bioenergetics model to simulate weight-at-age of saury and herring for 1948–2002. The 3D-NEMURO domain had 1° latitude by 1° longitude cells, with a vertical thickness of 5 m in the upper 100 m, 10 m between 100 m and 200 m, and thicker below 200 m. The 3D-NEMURO simulation was forced by daily means of the NCEP/NCAR (National Centers for Environmental Prediction, NOAA National Weather Service/National Center for Atmospheric Research) reanalysis six-hourly dataset taken from 1948 to 2002 (Aita et al., 2007). Monthly values of water temperature and small, large, and predatory zooplankton densities were stored for the KOS (Japan) and the CCS (California) regions. Each region was subdivided into three subregions representing a northern latitude cold water subregion, a mid latitude mixed temperature subregion, and a southern latitude warm water subregion (Fig. 1). In the western North Pacific these subregions were called Oyashio (155°E, 42°30'N), mixed water (155°E, 37°30'N), and Kuroshio (155°E, 32°30'N). In the eastern North Pacific, subregions were called subarctic (135°W, 42°30'N), transition (135°W, 37°30'N), and subtropical (135°W, 32°30'N). The three Japan subregions are where saury are located off Japan (Ito et al., 2004); for the California region, we selected the same three latitudes but at longitudes equidistant from the California coast as the saury subregions were from the coast of Japan.

We analyzed the model-generated monthly time series of temperature, zooplankton densities, and the annual weights-at-age and annual growth increments of herring and saury for the study period. The time series version of the extracted data consisted of values of temperature and zooplankton densities averaged over top 50 m at each of the 3D-NEMURO subregions; thus, we obtained single values of temperature and small (ZS), large (ZL), and predatory zooplankton (ZP) densities for each month for each of the six subregions. Climatological versions of the temperature and zooplankton densities were determined by averaging all January values, all February values, etc., to obtain a climatological year, and then repeating the climatological year. The climatological year was used for two purposes. In the first, we used climatological year to force the model during calibration of feeding-related parameters of saury and herring. Once the model was calibrated, we used the climatological year for a 20-year spin-up period prior to using the time series values. The spin-up allowed fish weights-at-age and annual growth rates to reach their steady-state calibrated values. Thus, effects of initial conditions were removed, allowing us to interpret simulated growth beginning in 1948.

2.2. Model simulations

Calibration and time series simulations were performed for herring and saury in the Japan and California regions. Even though this approach is not biologically realistic (e.g., herring are not found in the western Pacific off Japan and saury and herring are not found in the offshore subregions of the California coast), forcing herring and saury to experience the same environmental and prey conditions enables direct comparison of their responses. We compared simulated weight-at-age (g wet weight) and annual growth rate ($\Delta\text{weight} - \text{g wet weight year}^{-1}$) for 1948–2002 for herring and saury in both regions.

2.3. Saury version of NEMURO.FISH

The saury version of NEMURO.FISH used in this study was as described by Ito et al. (2004, 2007). Briefly, the saury version simulates the daily growth of a saury through nine life stages as they migrate among the three oceanographic subregions: the Kuroshio subregion (warm water), the mixed area subregion, and the Oyashio subregion (cold water). These subregions are represented off California (eastern Pacific) by the subtropical, transition, and subarctic subregions. Individual growth was predicted from its larval stage to its maximum age of 2 years. Saury undertake large annual migrations through the three subregions that depend on their size (age) and the water temperature. Adult saury undergo most of their growth in body weight in the Oyashio subregion. As an individual fish moves from one subregion to another, it experiences the temperature and zooplankton densities specific to the subregion. Parameter values for the saury version of NEMURO.FISH were as reported in Ito et al. (2004) and Mukai et al. (2007).

The same migration rules for saury at the three California subregions were the ones used for Japan. As a response variable, we used the predicted saury body weight on September 1 (Julian day = 245) of their second year of life and computed growth rate ($\Delta\text{weight} - \text{g wet weight year}^{-1}$) as the change in body weight over the 8-month period between September 1 and the preceding February (their birthday upon entering their second year of life).

2.4. Herring version of NEMURO.FISH

The herring version of the NEMURO.FISH model used in this study was identical to that described by Megrey et al. (2007) and Rose et al. (2007b). The herring version simulates the daily growth of an individual herring in a single spatial area that corresponds to their summer feeding grounds. Because herring are intertidal spawners, they depend on suitable inshore habitat for at least a part of their life cycle. Pacific herring are spring spawners throughout their range, laying adhesive eggs on available substrata and hatching free-floating larvae within 2–3 weeks. Juveniles spend their first summer in inshore waters feeding on copepods, and then migrate offshore to join immature and adult stocks in the summer feeding grounds during the fall of their first year or during the late spring of their second summer. Parameter values for the herring version of NEMURO.FISH are as in Megrey et al. (2007).

For the present study, herring were forced to inhabit the northernmost subregion off California (the subarctic subregion) and Japan (the Oyashio subregion). As a response variable we used predicted body weight just before spawning on March 15 (Julian day = 74) in the fourth year of the herring's life, i.e., an individual nearly 48 months of age. Growth rate ($\Delta\text{weight} - \text{g wet weight year}^{-1}$) was computed as the change in weight between ages 4 and 5.

2.5. Calibration of feeding-related parameters to climatological conditions, subregions and species

Both the saury and herring versions of NEMURO.FISH required calibration for 3D-NEMURO to produce realistic region and subregion-specific weights-at-age. We used the PEST automatic calibration method (Doherty, 2004) to determine the values for feeding-related parameters (the half-saturation constants, the K 's, of the multispecies functional-response consumption term in the bioenergetics model (see Megrey et al., 2007), and the scaling parameter of the weight-effect on maximum consumption, a_c , for saury only). Calibrated values predicted steady-state weights-at-age that were similar to observed values. See Rose et al. (2007a) for additional details related to its application in NEMURO and NEMURO.FISH. 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. PEST approximates the relationship between observations and model 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 to parameters). New parameter values were determined based on the gradient of the objective function. PEST stops searching when the objective function ceases to be minimized 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 calculation thresholds is triggered.

We used the climatological monthly temperatures and zooplankton densities for the Japan and California subregions, which resulted in steady-state predictions of weights-at-age specific to species and subregion. We used herring weight-at-age in year 52- of a 54-year climatological simulation, and we used saury weights-at-age in year 6 of a 10-year climatological simulation. The parameters that were calibrated were the half-saturation constants (the K 's) of the multispecies functional-response consumption term in the bioenergetics model (see Megrey et al., 2007), and scaling parameter of the weight-effect on maximum consumption (a_c) for saury only. We used observed weights-at-age of saury from Japan (Ito et al., 2004) to calibrate the saury model to the Japan region and used the same calibration values for the California region.

Observed saury weight-at-age data originate from observations of saury otoliths. However, saury has a hyaline zone in the otolith that is formed during egg production and the season prior to spawning. It is very difficult to estimate the age of saury adults because the hyaline zone obscures the growth increment and precludes accurate aging. Kurita et al. (2004) developed a method to estimate the hatch date from the age at which the otolith increment width reached a maxi-

mum for the second time. With this technique, it has become possible to estimate the age of saury even if there is a hyaline zone. Observed weight-at-age data, derived from the work of Suyama et al. (2006) and Kurita et al. (2004) was originally reported by Okuda (2002).

For herring, we used the San Francisco herring weights-at-age presented in Lassuy (1989, Table 2). These estimates are based on data presented in Spratt (1981) who reported seasonally combined age and length composition data from two seasons (1973–1974 and 1974–1975, $n=743$ fish) as an age-length key based on sampling catches in San Francisco Bay (data given in Table 9 of Spratt (1981)). Mean length-at-age was estimated by fitting a regression to the length-age data using a least squares regression $y=A+B(\ln x)$ where \ln is the natural logarithm, y =length (mm body length), A = y intercept, B =slope (rate of growth), and $\ln x$ =logarithm of age (months) (data given in Table 10, $A=-0.792$, $B=49.3$ and Fig. 5 of Spratt (1981)). Length-at-age were converted to weight-at-age using a length-weight data set of 1070 herring collected from 1973 through 1977 from San Francisco Bay. The length-weight relationship was determined from the regression $W=AL^B$ where W =fish weight (g), L =fish length (mm), A = y intercept and B =slope (data from Table 12, $A=0.49665E-5$, $B=3.20555$ and Fig. 6 of Spratt (1981)). The coefficients of the length-weight relationship reported above are averages of parameters fit separately to male ($n=529$, $A=0.5815E-5$, $B=3.1673$) and female ($n=541$, $A=0.4118E-5$, $B=3.2438$) data since Spratt (1981) determined that males and females did not have statistically different length-weight relationships in San Francisco Bay.

The saury and herring weight-at-age data were used as observations to calibrate both regions. All K values for saury and herring were initialized at 0.01. The weight-effect parameters of maximum consumption were initialized at 0.8. The “log” option of PEST was used. All weights-at-age were weighed equally during calibration except for age-1 herring which were given a weighting factor of 2.0. We weighted the age-1 observation more heavily than the other herring age groups because initial herring calibration runs showed that the calibration tended to overestimate the weight of age-1 herring.

2.6. Detection of regime shifts

The STARS algorithm (sequential t-test analysis to detect regime shifts) of Rodionov and Overland (2005) was used to determine regime shifts based upon modeled temperature, zooplankton densities, and weight-at-age of herring and saury for the Japan and California regions. Temperature, small, large, and predatory zooplankton densities were averaged over months for each year to obtain single annual values. We used standard recommended STARS operating parameters (i.e., probability=0.1, cutoff length=10, Huber parameter=1) to identify statistical shifts in the averaged annual values. We then compared these shifts at the Japan and California regions.

We also examined the temperature time series from all the subregions for evidence of coherent changes consistent with the previously identified 1976–1977, 1988–1989, and 1998–1999 regime shifts. We calculated a mean average temperature (SST) pre- and post-regime shift for the 1976–1977, 1988–1989

and 1998–1999 regime shift period using a 10-year window. For each period we calculated the difference of the mean SST_{1977–1986} minus mean SST_{1967–1976}, mean SST_{1989–1998} minus mean SST_{1979–1988}. Because the time series did not allow a 10-year mean to be calculated for the last regime we used a 4-year window; thus for the last regime we have mean SST_{1999–2002} minus mean SST_{1995–1998}.

2.7. Time series simulations

Once the parameters were calibrated for each species in each subregion using the climatological temperature and zooplankton densities, we then simulated the period 1948–2002 using the time series values of temperature and zooplankton densities. Predicted annual weight-at-age (age-4 for herring; September of second year for saury) and growth rate (ages 4–5 for herring; February–September for saury) were compared for 1948–2002 for Japan and California. Pearson correlation coefficients were calculated to assess the degree of correspondence between pair wise combinations of predicted weight-at-age time series. STARS was applied to annual average temperature, zooplankton densities, and saury and herring weights-at-age for both regions.

3. Results

3.1. Calibration

Both the saury and herring versions of NEMURO.FISH predicted weights-at-age for Japan and California similar to observed weights-at-age (Fig. 2). The calibrated half-saturation constants (the *K*'s) of the multispecies functional-response consumption term in the bioenergetics model and scaling parameter of the weight-effect on maximum consumption (*a_c*) (see Megrey et al., 2007) for both species in both regions are given in Table 1.

3.2. Analysis of regime shifts and long-term trends in temperature and zooplankton

In general, for all three subregions off Japan, temperature and zooplankton densities showed inverse long-term trends. In the Oyashio subregion (Fig. 3), temperature (Fig. 3a) showed a consistent decline from 1948–2002 (Fig. 3a), while both small (Fig. 3b) and large zooplankton (Fig. 3c), and predatory zooplankton (Fig. 3d) showed gradual increases. In the mixed subregion (Fig. 4) and the Kuroshio subregion (Fig. 5), the pattern was reversed; temperature gradually increased (Figs. 4a and 5a), but the zooplankton response varied by subregion and zooplankton group (Figs. 4b–d and 5b–d).

STARS identified a consistent regime shift off Japan between 1978 and 1980. Temperature and all three zooplankton groups showed significant shifts around 1980 in the Oyashio subregion (Fig. 3). Temperature showed a shift just prior to 1980 in the mixed subregion (Fig. 4a), and temperature and both small and large zooplankton showed shifts around 1980 in the Kuroshio subregion (Fig. 5a–c).

The general inverse relation between temperature and zooplankton density predicted off Japan was less apparent off California. At the end of the simulated period, however, temperature decreased while zooplankton densities increased in all three subregions (Figs. 6–8).

STARS identified a fairly consistent regime shift just before 1990 with increased temperature and decreased zooplankton density in the subarctic subregion off California (Fig. 6), and decreased predatory zooplankton in the transition subregion of the California region (Fig. 7d). As with Japan, much of the temperature and zooplankton density time series showed shifts near the end of the simulated period.

The data from the analysis of a 10-year mean pre- and post-regime shift for the three regime shift periods by subregion is presented in Table 2. Even though STARS did not identify 1976–1977, 1988–1989 and 1998–1999 as a shift, results generally show evidence of consistent east-west asynchrony,

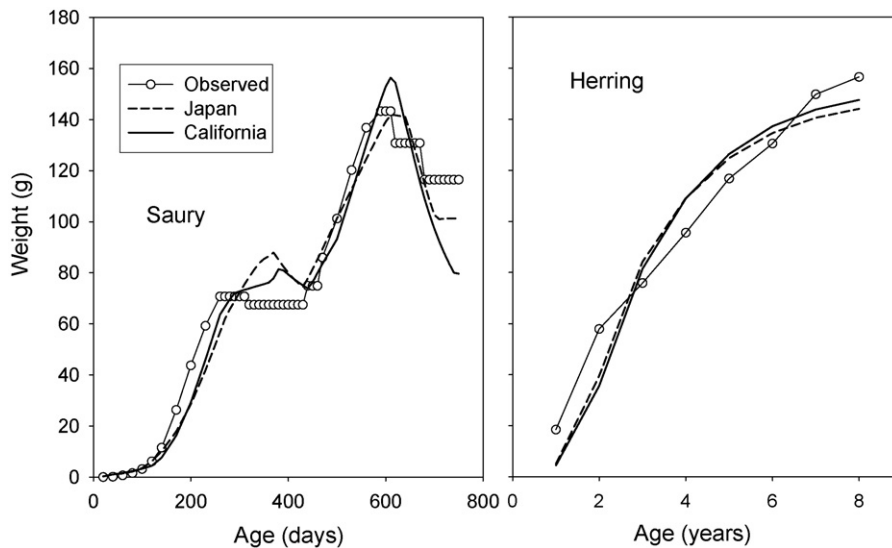


Fig. 2 – Saury and herring growth (g wet weight) from calibrated model simulations compared to observed values for two regions in the North Pacific. White circles show observed values; black lines show model fits using California herring size-at-age data; dashed lines show model fits using Japan saury size-at-age data.

Table 1 – Calibrated feeding parameters for saury and herring in the Japan and California NEMURO.FISH models

Parameter	Saury		Herring	
	Japan	California	Japan	California
K_{11}	0.00217	0.00971	0.00147	0.000611
K_{12}	Not used ^a	Not used ^a	0.0582	0.00367
K_{13}	Not used ^a	Not used ^a	Not used ^a	Not used ^a
K_{21}	0.0261	0.0335	0.00595	0.00736
K_{22}	0.0429	0.0206	0.0126	0.00843
K_{23}	Not used ^a	Not used ^a	0.00555	0.0112
K_{31}	Not used ^a	Not used ^a	Not used ^a	Not used ^a
K_{32}	0.0285	0.176	0.0235	0.00539
K_{33}	0.00253	0.00617	0.0365	0.00196
a_c	0.443	0.670	Fixed at 0.2 ^b	Fixed at 0.2 ^b

Calibrated parameters include the scaling parameter for the weight-effect on maximum consumption rate (a_c) and the half-saturation constants (K_{ij}) for the multispecies functional response consumption term in the bioenergetics model. i denotes fish stage (saury—1 for life stage 1, 2 for life stage 2 and 3 for life stages 3–9; herring—1: age 1; 2: age 2; 3: ages 3–10) and j denotes the prey type [1: small zooplankton (ZS), 2: large zooplankton (ZL) and 3: predatory zooplankton (ZP)]. Initial values were 0.8 for a_c and 0.01 for all K_{ij} values.

^a This parameter corresponds to a life stage that does not consume this zooplankton prey type so the K value is not used in the model.

^b Values constrained during calibration.

especially in the northern latitude subregions, except for the 1988–1989 regime shift. For the 1976–1977 and 1998–1999 regime shift, eastern and western regions at northern latitudes showed opposite trends in changes in temperature. For the 1998–1999 regime shift, considered one of the weaker ones, the asynchrony in temperature was evident at all latitudes between the east and west regions, with positive temperature occurring in the western Pacific pre 1998 and cooler temperature occurring in the eastern Pacific post 1999.

3.3. Growth of two different species in the same subregion

Weights-at-age of herring and saury off Japan were out of phase from 1948 to 1980 and then synchronized after 1980, while herring and saury weights-at-age off California were in-phase over the entire simulation period (Fig. 9). The initially out-of-phase and then in-phase herring and saury weights-at-age for Japan resulted in a slightly negative but non-significant correlation ($r = -0.097$, $p = 0.42$). The higher degree of synchrony between herring and saury weights-at-age off California resulted in a significant, positive correlation ($r = 0.608$, $p < 0.01$).

For both species in both regions (Fig. 9), annual growth rates showed very similar temporal patterns. Correlation between herring and saury growth rates were also positive but non-significant off Japan ($r = 0.199$, $p = 0.10$), and significantly positive off California ($r = 0.654$, $p < 0.01$). Because of the similarity between the temporal patterns in weight-at-age and annual growth rates, we focus on weight-at-age in the subsequent presentation of results.

3.4. Growth of the same species between two different subregions

The same time series simulation shown in Fig. 9, reorganized to highlight differences between regions (Fig. 10), showed that saury weights-at-age were generally synchronous between

Japan and California, while herring weights-at-age were out of phase between Japan and California. Predicted saury weight-at-age was highly correlated between Japan and California ($r = 0.36$, $p = 0.002$). In contrast, predicted weight-at-age for herring between Japan and California was significantly negatively correlated ($r = -0.26$, $p = 0.03$).

Application of the STARS algorithm to saury and herring weights-at-age time series (Fig. 10) showed that herring became heavier at age off Japan beginning around 1980 (Fig. 10a) and both species shifted towards smaller weights-at-age beginning around 1988 off California (Fig. 10b). Herring also increased in weight-at-age beginning around 1980 for the California region but this was not identified by STARS as a statistically significant shift. A few other shifts in weight-at-age were also identified by STARS, including an increase around 1970 for herring off California and a decrease for saury off Japan just before 1960. Both herring and saury showed shifts in the mid to late 1990s in both regions (Fig. 10b and d), but these are highly uncertain because they are so close to the end of the simulated time period.

3.5. Fish growth responses to environmental regime shifts

Both saury and herring responded similarly to the two major shifts (beginning in 1978–1980 and the early 1990s) apparent in the 3D-NEMURO simulated temperature and zooplankton densities time series. However, these shifts in saury and herring weights-at-age were mixed in with other detected shifts in their weights-at-age, and the 1980 and 1990 shifts were not consistent across all temperature and zooplankton types.

Between 1980 and 1985, simulated saury and herring weights-at-age in both regions showed consistent increases (Fig. 10). Based on STARS, only the upward shift in weight-at-age for herring in the Japan region was statistically significant. In the Oyashio subregion, where most fish growth occurs, temperature decreased and all three zooplankton groups increased beginning around 1980 (Fig. 3). The same decrease in

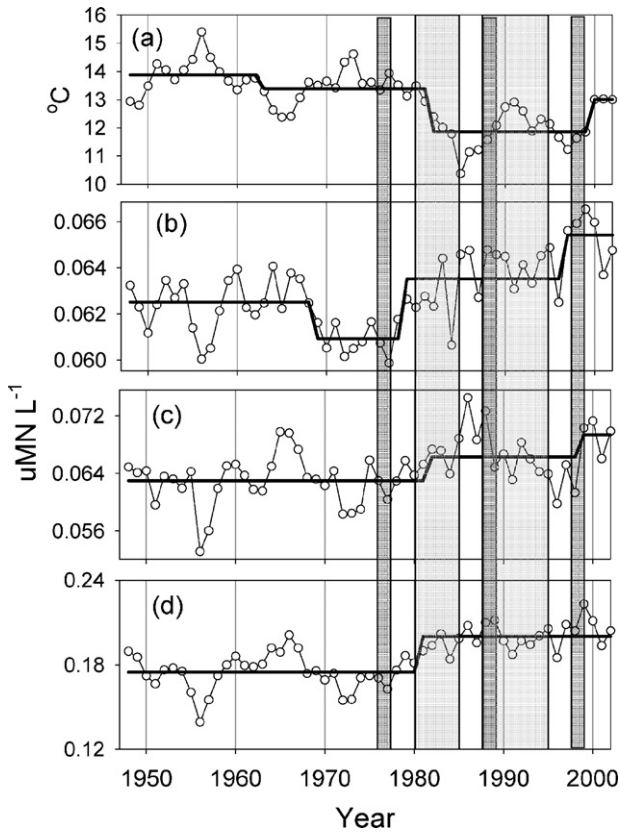


Fig. 3 – (a) Simulated annual average water temperature (°C), (b) small zooplankton density, (c) large zooplankton density, and (d) predatory zooplankton densities for the Oyashio subregion at the Japan region for 1948–2002. Zooplankton density is in units of $\mu\text{MN l}^{-1}$. Simulated model observations are shown with circles; the heavy solid lines are average values between statistically identified shifts in mean values using STARS. Dark grey vertical bars highlight the 1976–1977, 1988–1989 and 1998–1999 regime shifts. Light grey vertical bars identify periods of major ecological shifts (1980–1985 and 1988–1995) that do not correspond to the 1976–1977, 1988–1989, 1998–1999 regime shift periods mentioned earlier.

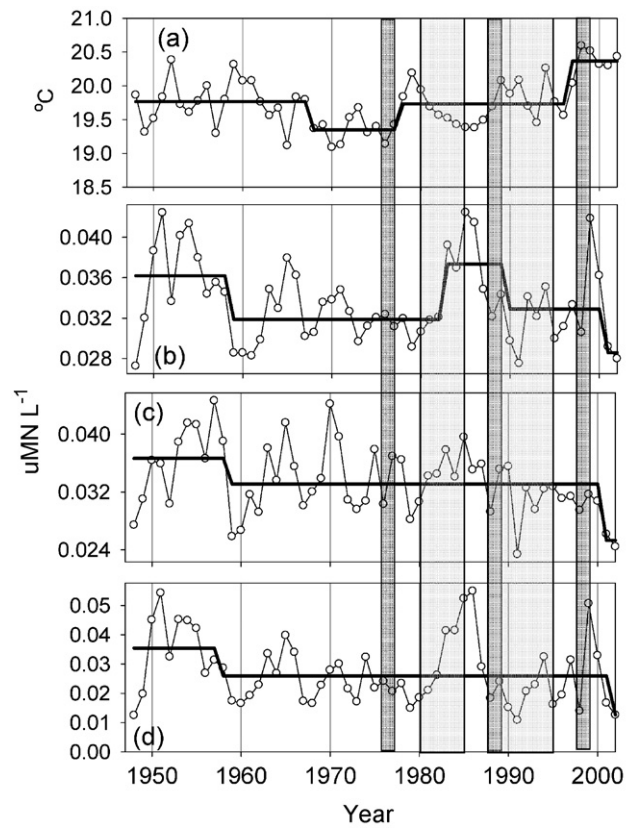


Fig. 4 – (a) Simulated annual average water temperature (°C), (b) small zooplankton density, (c) large zooplankton density, and (d) predatory zooplankton densities for the Mixed subregion at the Japan region for 1948–2002. Zooplankton density is in units of $\mu\text{MN l}^{-1}$. Simulated model observations are shown with circles; the heavy solid lines are average values between statistically identified shifts in mean values using STARS. Dark grey vertical bars highlight the 1976–1977, 1988–1989 and 1998–1999 regime shifts. Light grey vertical bars identify periods of major ecological shifts (1980–1985 and 1988–1995) that do not correspond to the 1976–1977, 1988–1989, 1998–1999 regime shift periods mentioned earlier.

temperature and increase in zooplankton densities between 1980 and 1985 in the subarctic subregion off California is apparent in Fig. 6, but none of these were identified by STARS as statistically significant shifts.

Beginning around 1988 and through the early 1990s, both saury and herring weights-at-age decreased off Japan and California (Fig. 10) and were identified as significant off California by STARS. For Japan, these increases in weight-at-age were suggestive but not definitive. These shifts in Japan corresponded to a period of increasing temperature and decreasing zooplankton densities in both Oyashio and mixed subregions (Figs. 3 and 4); however, only the decrease in small zooplankton in the mixed area subregion was statistically significant. The same pattern of increase in temperature and decrease in zooplankton densities in the subarctic subregion of California for 1988 to about 1995 were all identified as statistically significant by STARS (Fig. 6).

4. Discussion

We used the output of a lower trophic level model coupled to a global three-dimensional OGCM (3D-NEMURO) as input to a fish bioenergetics model, and compared saury and herring growth responses to the conditions simulated for 1948–2002 at two regions of the North Pacific. Our approach was to look first at upper trophic level response (i.e. we started by looking for shifts in the fish growth response, then looked to see if these fish growth shifts were coincident with observed shifts in temperature and zooplankton density).

The models described in this paper are similar to efforts undertaken in other geographic regions. Similar to the work herein, many examples (Hinckley et al., 1996; Werner et al., 1996) have successfully combined lower trophic level and higher trophic level models, including the use of a NPZ models to provide food for fish larvae (Hermann et al., 2001). Most

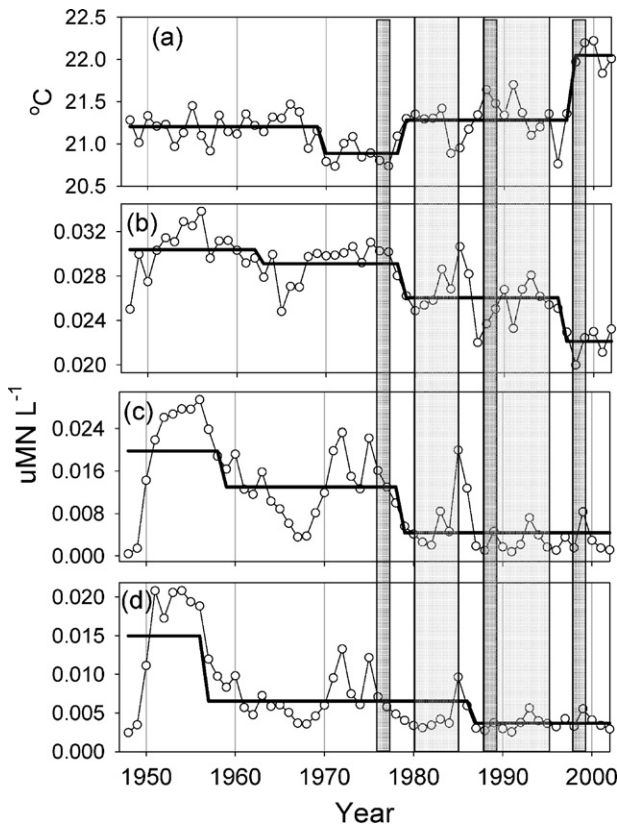


Fig. 5 – (a) Simulated annual average water temperature ($^{\circ}\text{C}$), (b) small zooplankton density, (c) large zooplankton density, and (d) predatory zooplankton densities for the Kuroshio subregion at the Japan region for 1948–2002. Zooplankton density is in units of $\mu\text{MN L}^{-1}$. Simulated model observations are shown with circles; the heavy solid lines are average values between statistically identified shifts in mean values using STARS. Dark grey vertical bars highlight the 1976–1977, 1988–1989 and 1998–1999 regime shifts. Light grey vertical bars identify periods of major ecological shifts (1980–1985 and 1988–1995) that do not correspond to the 1976–1977, 1988–1989, 1998–1999 regime shift periods mentioned earlier.

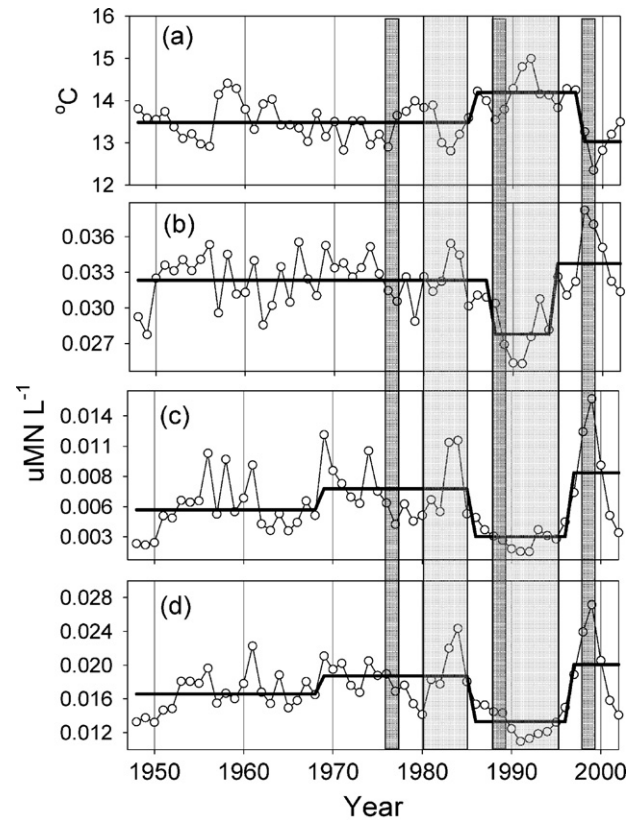


Fig. 6 – (a) Simulated annual average water temperature ($^{\circ}\text{C}$), (b) small zooplankton density, (c) large zooplankton density, and (d) predatory zooplankton densities for the subarctic subregion at the California region for 1948–2002. Zooplankton density is in units of $\mu\text{MN L}^{-1}$. Simulated model observations are shown with circles; the heavy solid lines are average values between statistically identified shifts in mean values using STARS. Dark grey vertical bars highlight the 1976–1977, 1988–1989 and 1998–1999 regime shifts. Light grey vertical bars identify periods of major ecological shifts (1980–1985 and 1988–1995) that do not correspond to the 1976–1977, 1988–1989, 1998–1999 regime shift periods mentioned earlier.

of these applications have used an uncoupled configuration. Wisconsin-based bioenergetics models (Hansen et al., 1993; Ney, 1993; Hanson et al., 1997) are quite common and have been widely applied in fisheries science (e.g., Hartman and Brandt, 1995; Essington, 2003; Tang et al., 2003). Other more complicated initiatives exist as well. As part of the West Coast US GLOBEC program, a suite of nested physical and biological models have been developed for the Gulf of Alaska (e.g., Hermann et al., 2002) that include: (1) multiply nested circulation models spanning basin to regional to local scales; (2) a lower trophic level (NPZ) model including salmon prey items, driven by circulation fields; and (3) an individual-based salmon model which receives circulation and NPZ model output. The GLOBEC effort is continuing, with the goal to create a tool to investigate interannual and decadal changes in the physical environment of the central Gulf of Alaska and its effects on biological production. Runge et al. (2004) provide

a recent review of coupled lower and upper trophic level modeling efforts, and deYoung et al. (2004) provides the context for basin-scale comparisons.

For the 1976–1977 and 1988–1989 regime shifts identified in the 3D-NEMURO model output, our models showed consistent growth responses in both fish species. The period from 1980 to about 1985 had decreased temperature and increased zooplankton and led to faster growth and larger weights-at-age of saury and herring in both Japan and California, while the period of the early 1990s had increased temperature and decreased zooplankton densities and led to slower growth and small weights-at-age of both species in Japan and California. Thus, with strong and consistent signals from the lower trophic levels, herring and saury growth responded in very similar ways. However, the STARS regime shift detector did not identify all changes in temperature, zooplankton densities, and herring and saury weights-at-age as statistically

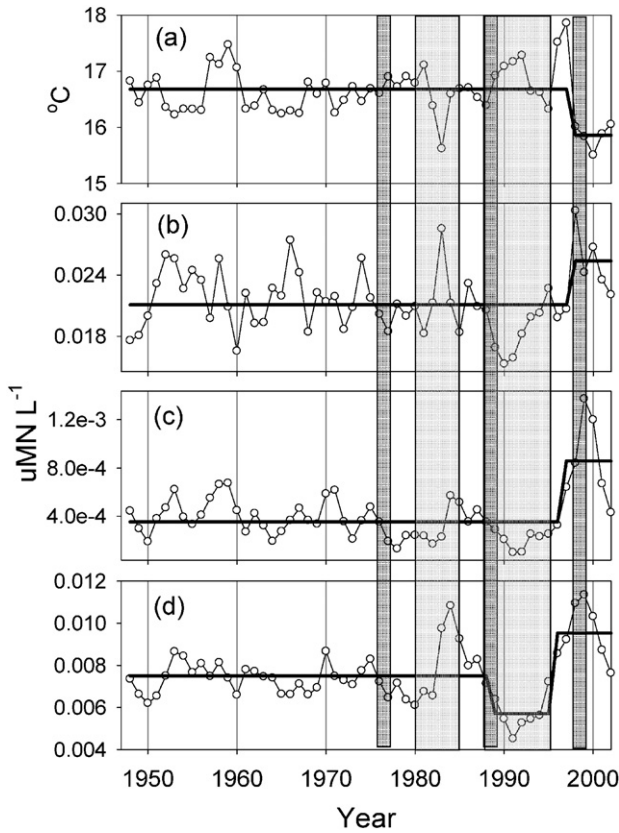


Fig. 7 – (a) Simulated annual average water temperature (°C), (b) small zooplankton density, (c) large zooplankton density, and (d) predatory zooplankton densities for the transition subregion at the California region for 1948–2002. Zooplankton density is in units of $\mu\text{MN L}^{-1}$. Simulated model observations are shown with circles; the heavy solid lines are average values between statistically identified shifts in mean values using STARS. Dark grey vertical bars highlight the 1976–1977, 1988–1989 and 1998–1999 regime shifts. Light grey vertical bars identify periods of major ecological shifts (1980–1985 and 1988–1995) that do not correspond to the 1976–1977, 1988–1989, 1998–1999 regime shift periods mentioned earlier.

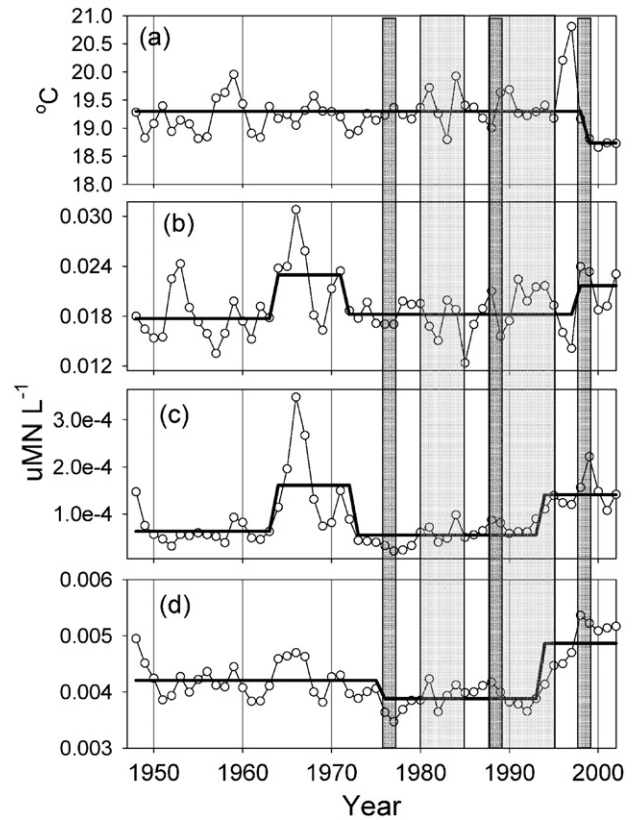


Fig. 8 – (a) Simulated annual average water temperature (°C), (b) small zooplankton density, (c) large zooplankton density, and (d) predatory zooplankton densities for the subregion at the California region for 1948–2002. Zooplankton density is in units of $\mu\text{MN L}^{-1}$. Simulated model observations are shown with circles; the heavy solid lines are average values between statistically identified shifts in mean values using STARS. Dark grey vertical bars highlight the 1976–1977, 1988–1989 and 1998–1999 regime shifts. Light grey vertical bars identify periods of major ecological shifts (1980–1985 and 1988–1995) that do not correspond to the 1976–1977, 1988–1989, 1998–1999 regime shift periods mentioned earlier.

significant shifts, while other changes during other time periods were identified as significant shifts. Some of the shifts were identified only visually and observations made in the earlier studies cited above helped guide their recognition. Even with the roughly 50 years of model-generated inputs and simulated growth, it was still difficult to interpret the relationship between temperature, zooplankton densities, and fish growth.

Current thinking (King, 2005) assumes that the ecosystem response to regime shifts will be most evident within the lower trophic levels or for pelagic planktivorous fishes whose interannual variations are closely coupled to lower trophic levels. Changes in the productivity characteristic of primary and secondary producers should quickly reveal changes in population abundance very shortly after a regime shift has occurred. However, several years are required in order to distinguish long-period regime changes from short-period interannual

variation. Our analyses showed that the statistical approach of the STARS regime shift detector objectively identified regime shifts, however we believe that some shifts not identified as statistically significant may still be biologically important to upper trophic levels, and some shifts identified as statistically significant may not be biologically important to upper trophic levels.

While we identified shifts in the 1980s and 1990s in the modeled temperature and zooplankton density time series, we did not see obvious evidence of the well-documented 1976–1977, 1988–1989, and 1998–1999 regime shifts. Temperature and zooplankton densities off both Japan and California showed evidence of these well known regime shifts, but the shifts were not consistent for all variables or they were identified several years before or after the expected year of the shift. The most coherent 1977 regime response was seen in

Table 2 – Shifts in the 10-year mean value of the temperature time series from 3D-NEMURO during the 1976–1977, 1988–1989, and 1998–1999 regime periods

Latitude-geographic location	Region	Subregion	Regime period		
			1976–1977	1988–1989	1998–1999 ^a
North–West	Japan	Oyashio	–	+	+
North–East	California	Subarctic	+	+	–
Middle–West	Japan	Mixed	+	+	+
Middle–East	California	Transition	+	+	–
South–West	Japan	Kuroshio	+	+	+
South–East	California	Subtropical	+	+	–

Signs indicate change in state (increasing mean temperature between the two 10-year periods indicated by a plus; decreasing mean temperature between the two 10-year periods indicated by a minus). Comparisons are made for two major geographic regions (west-Japan and east-California) and among the three subregions within each region separated by latitude (North, Middle, South).

^a Because of the length of the time series, only a 4-year mean was used for this regime. Ten-year means were used for the other two regime periods.

the Kuroshio subregion, showing an increase in temperature (Fig. 3a) and declines in both small and large zooplankton (Fig. 3b and c). The only clear evidence of a response to the 1976–1977 regime shift off California was seen with predatory zooplankton in the subtropical subregion (Fig. 8d), although declines in both small (Fig. 8b) and large zooplankton (Fig. 8c) occurred shortly prior to 1977. Evidence of the 1988–1989 regime shift off Japan was limited to reduced small zooplankton density in the mixed subregion (Fig. 4b) and reduced predatory zooplankton density immediately prior to 1989 in the Kuroshio subregion (Fig. 5d). For California, the response to the 1988–1989 regime shift was most evident in the subarctic subregion, which showed a reduction of small zooplankton

(Fig. 6b), but shifts in temperature (Fig. 6a), large zooplankton (Fig. 6c), and predatory zooplankton (Fig. 6d) preceded 1989. The 1998–1999 regime shift was evident in both regions but additional years beyond 2002 must be simulated for the 1998 shift to be identified with confidence.

In fish populations, the response to regime shifts may not be immediately apparent because factors that affect population abundance will not be observed until the year class is old enough to be observed in surveys or fisheries. This lag time can range from 2 to 3 years for fish such as Pacific herring, to 2 years for Pacific saury. Different life history strategies, and their expression in biological traits such as longevity, are good predictors of fish population and growth

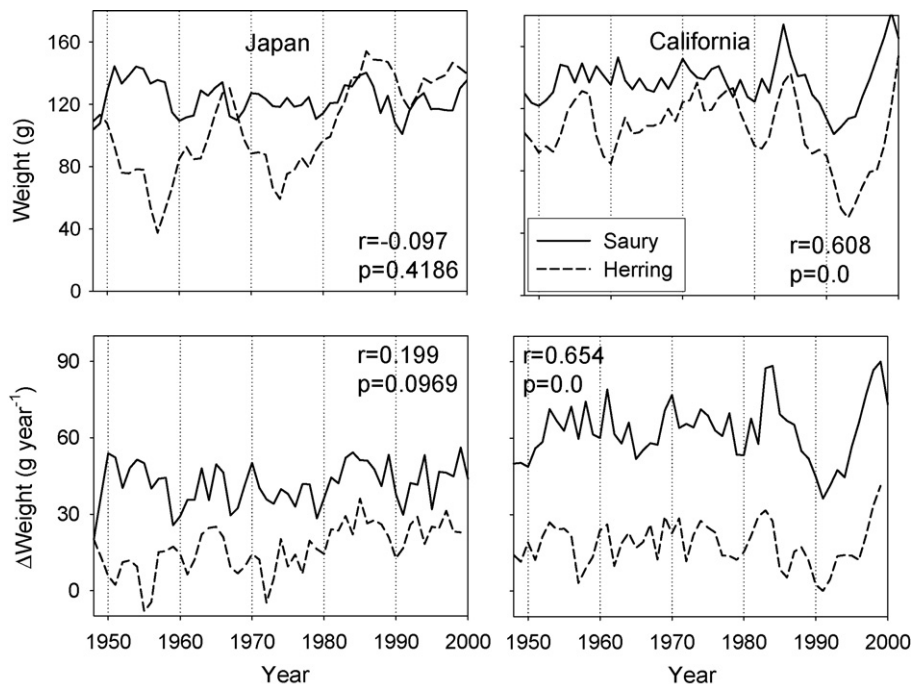


Fig. 9 – A comparison of simulated saury and herring growth off Japan and California. Shown are growth (g wet weight; top row panels) and growth rate (Δ weight – g wet weight year⁻¹; bottom row panels) within the Japan (left column panels) and California (right column panels) regions. Pearson correlation coefficients for the two trends within each panel are given along with the probability of rejecting the null hypothesis $H_0: r = 0.0$. See text for calculation of Δ weight.

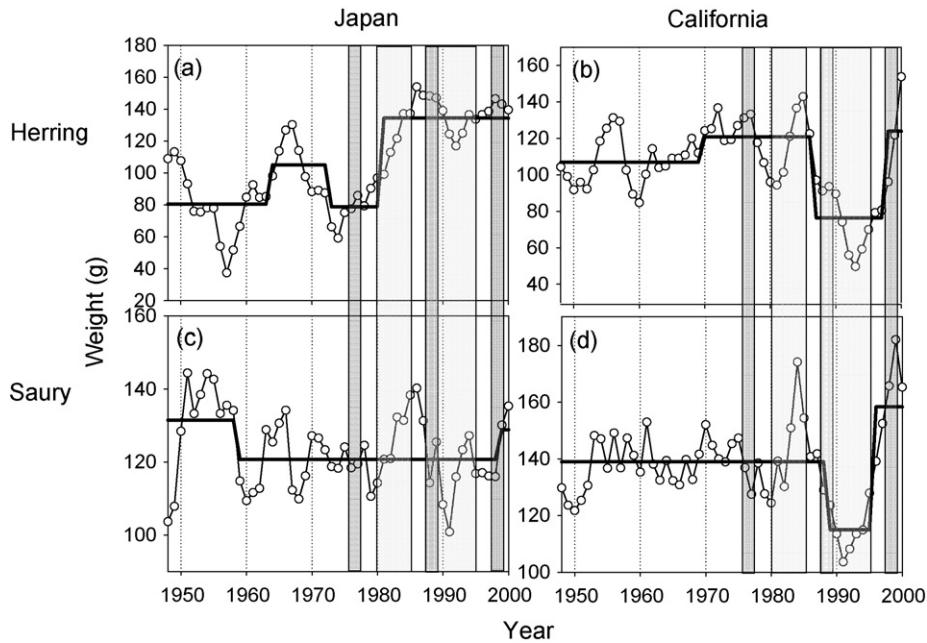


Fig. 10 – Simulated growth (g wetwt) of herring in the Oyashio subregion of the Japan region (a), herring in the subarctic subregion of the California region (b), saury in the Oyashio subregion of the Japan region (c), and saury at the subarctic subregion of the California region (d) for 1948–2002. Predicted growth from the model is shown with circles; the heavy solid lines are average values between statistically identified shifts in mean values using STARS. Grey vertical bars highlight the 1976–1977, 1988–1989 and 1998–1999 regime shifts. Light grey vertical bars identify periods of major ecological shifts (1980–1985 and 1988–1995) not corresponding to the three regime shift periods mentioned earlier.

responses to long-term climate and ocean changes (King and McFarlane, 2003). We have seen evidence of this in our comparison of saury and herring growth responses to differences in biological factors, environmental factors, and their inter-relationships. In our analysis, saury, because of their short life span, responded more quickly than herring to changes in the environment and their growth response showed greater interannual variability (Fig. 9). The longer-lived herring more effectively integrated changes in environmental conditions and exhibited a smoother growth response that was characterized by longer cycles (greater autocorrelation).

One of the more intriguing results of this study was the complicated pattern of predicted weights-at-age being out of phase in some cases and synchronous in others. Weights-at-age of herring and saury off Japan were initially out of phase and then synchronized after 1980, and were synchronous off California (Fig. 9). Saury weights-at-age were generally synchronous between Japan and California, while herring weights-at-age were out of phase between Japan and California (Fig. 10). Two possible factors that could account for these differences are subtle patterns in the temperature and zooplankton time series that differ between regions and subregions, and the longer life-span of the herring creating autocorrelation in weight-at-age.

We tested the impact of bottom-up effects via controlled simulations using different combinations of time series and climatological forcing similar to the analysis performed by Rose et al., 2007b. We repeated simulations under two contrasting situations. One was driven by climatological temperature and time series zooplankton. The other was driven

by time series temperature and climatological zooplankton. These results (not reported here) were suggestive of bottom-up control, as they indicated that the importance of temperature versus zooplankton in driving the responses in weight-at-age differed between species and regions. But additional simulations are required before definitive conclusions can be drawn.

We also considered that the potential for stronger autocorrelation in weight-at-age for the longer-lived herring might contribute to the predicted patterns of out-of-phase and synchronous responses. We explored this possibility by running a simulation where the herring weight-at-age at the beginning of each year was set to the same mean starting value, thereby removing any autocorrelation in growth (results not reported). Predicted herring growth rates with autocorrelation in weight removed were very similar to the predicted growth rates with autocorrelation. At this time, we do not have an explanation of these patterns of out-of-phase and synchronous responses, although differences between species and regions are promising as they suggest the importance of temperature and zooplankton.

Hsieh et al. (2005) cautioned that biological time series in the North Pacific show nonlinear dynamics and alternate stable states and they warn that the ocean-atmosphere-biological system is not amenable to simple interpretation. The nonlinearities and localized effects of regimes can cause situations where the same regime shift has opposite effects on the same fish species in different geographic areas, and opposite effects on different fish species within the same geographic area (Benson and Trites, 2002). An implicit assumption

of our analysis is that there are two mutually exclusive regimes and consequent states of the ecosystem. King (2005) clearly point out that decadal climate variability in the North Pacific is not a two-state system represented by a single mode (e.g., alternating cool/warm states), but is a result of more than one climate mode.

We did note some evidence of a basin-scale PDO mode response. King (2005) concludes that each region of the ocean does not respond in the same manner to a regime shift and states that the 1998–1999 regime shift had the greatest impact in the most southerly regions of the North Pacific basin (i.e., the central North Pacific and the California Current System). We saw this pattern in our temperature and zooplankton density time series but the signal is not as clear at the higher trophic level. Also of interest was the ecosystem response at the different regions to the regime shift periods. The 1976–1977 regime shift was governed by the Pacific/North American pattern, while the 1988–1989 regime shift was closely related to the Arctic Oscillation (Yasunaka and Hanawa, 2002). Moreover, the Victoria mode shows a rapid shift in 1998–1999. Examination of the east–west response in Table 2 shows a consistent and opposite sign response between in the 1998–1999 regime shift period. The Oyashio subregion also showed this pattern in the 1976–1977 regime period and the results are consistent with Mantua et al. (1997) who reported warmer water in the eastern Pacific (California) and cooler water in the western Pacific (Japan). The Victoria mode, which appeared in 1998–1999 showed a north–south response. We can see that water temperatures were similar south of the Oyashio and Subarctic subregions (42°N) in both the western (Japan) and eastern (California) sides of the Pacific. Therefore, responses to regimes were strongly dependent on region.

To summarize our findings, we saw opposite changes in water temperature and zooplankton production in both the Japan and California regions. We believe that temperature alone was not directly affecting zooplankton biomass but rather temperature was a proxy for available nutrient supply originating from vertical mixing exchange similar to results observed in Aita et al. (2007). For the 1976–1977 and 1988–1989 regime shifts, we saw consistent growth responses in both fish species. The period from 1980 to about 1985 had decreased temperature and increased zooplankton and led to faster growth and larger weights-at-age of saury and herring in both Japan and California. In contrast, the period of the early 1990s had increased temperature and decreased zooplankton densities and led to slower growth and small weights-at-age of both species in Japan and California. Thus, with strong and consistent signals from the lower trophic levels, herring and saury growth responded in very similar ways. Weights-at-age of herring and saury in the Japan region were initially out of phase and then synchronized after 1980, and were synchronous for the California region. Saury weights-at-age were generally synchronous between Japan and California, while herring weights-at-age were out of phase between Japan and California. Our analyses showed that the statistical approach of the STARS regime shift detector objectively identified regime shifts, however we believe that some shifts not identified as statistically significant may still be biologically important to upper trophic levels, and some shifts identified as statisti-

cally significant by STARS may not be biologically important to upper trophic levels.

Important elements missing from our modeling exercise include no intra-specific or inter-specific interactions among the higher trophic level species (i.e., ours was a density-independent, single-species approach). There was no density-dependent growth response because the LTL and the HTL were uncoupled. Inter-specific interactions are undoubtedly important in real marine ecosystems. Ito et al. (2007) discuss species interactions between sardine and saury that affected saury dynamics. For simplicity, we have chosen not to address intra- and inter-specific interactions among the upper trophic level taxa in this application; thus, our results are suggestive rather than conclusive.

Considering these outcomes relative to our initial hypotheses we can conclude that changes arising from regime shifts can propagate up the food web and get expressed in fish growth, and that life-history characteristics play an important role in mediating climate forcing and its impact on the biological response of higher trophic level organisms. Our null hypothesis that two fish species with different life histories in two different regions will show similar biological responses to the same regime shifts was rejected.

Despite the interesting results, one may question the practical utility of these types of modeling exercises. We maintain that there is direct relevance of the modeling tools described herein towards efforts to implement ecosystem-based fisheries management. Managing resources from an ecosystem perspective is a daunting challenge that requires simultaneous consideration of several essential elements. These include: (1) effective monitoring of the physics and marine ecosystem characteristics of the lower and higher trophic levels (i.e., composition, abundance and distribution of biological components); (2) descriptions of physical/chemical/biological interactions and trophic and multi-species linkages; and (3) understanding the mechanisms that influence the response of individual organisms to changing environmental conditions such as climate change, climate variability and global warming. Ultimately all of these factors would be assembled and synthesized into a model, or suite of models, whose goal would be to characterize the changing states of ecosystems and to forecast the impact of climate change or man-induced influences such as fishing. The ability to assess and predict impacts on the marine ecosystem or fishery productivity forecasts, to the effects of climate change or global warming, naturally follow. From these, decision support tools for adaptive, ecosystem-based management of fisheries, coastal development, and marine resources should evolve. We feel that the models described in this study exhibit many of these necessary characteristics and offer a path towards better management under uncertain future environmental conditions. When fishery managers understand the complex ecological and socioeconomic environments in which fish and fisheries exist, they may be able to anticipate the effects that fishery management will have on the ecosystem and the effects that ecosystem change will have on fisheries. Certainly coupled climate-LTL-HTL type models have a role to play.

Although scientists have been studying ecosystem processes for decades, long term scientific research is still needed. We advocate continued environmental and biological moni-

toring. Observations made today become the baseline of the future. Retrospective analyses, modeling studies, and field research must also continue in the hope that, eventually after adding more observations, ‘dots’ in Revkin’s pointalist painting analogy, “the large array of observations, regarded as a whole” will reveal their secrets and we will have the information needed to identify the mechanisms by which climate change leads to ecosystem response. Only when we have an understanding of these relationships can we begin to effectively incorporate knowledge of the state of the ecosystem into ecosystem-based fisheries management (FAO, 2003; Browman and Stergiou, 2004).

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