Asia-Pacific Network for Global Change Research

Climate Interactions and Marine Ecosystems: Effects of Climate on the Structure and Function of Marine Food-Webs and Implications for Marine Fish Production in the North Pacific Ocean Marginal Seas

Final report for APN project 2004-10-NSY-Werner

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Final Report submitted to APN

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Overview of project work and outcomes

Non-technical summary

Predicting and understanding effects of global climate change on ecosystems and fish production in oceanic systems is essential if we are to develop quantitative approaches to managing sustainable marine resources. We addressed hypotheses dealing with the environmentally induced variations in fish growth, regime shifts, and changes in energy cycling and structure of marine food-webs. We used a combination of existing data sets, trophodynamic models and a multi-decadal model hindcast scenario to assess the changes in ecosystem structure and function of certain regions in the North Pacific. Geographic areas included the Sea of Okhotsk, coastal areas of Japan off Hokkaido Island, the Bering Sea shelf, Prince William Sounds and the coast near British Columbia. Focusing on herring as the target fish species, existing modeling approaches were used to quantify how climate (e.g., through temperature, stratification, circulation) altered marine ecosystem structure and function. We found that the model results were able to capture the timing in observed shifts in herring population characteristics, with geographic variations latitudinally and zonally across the Pacific basin. We used estimated changes in fish size as a metric for fish production and fish population health. Our modeling approaches have been applied by other research groups to other species.

Objectives

The main objectives of the project were:

1. to use a common marine food-web and fisheries bioenergetics modeling approach, along with long-term area-specific oceanographic and fisheries data sets, to understand the propagation of climate change effects up the marine food-web,
2. to quantify its effects on energy cycling and fish growth and production in distinct geographic regions in the North Pacific and its marginal seas – areas that support important exploited marine fish populations
3. to initiate a discussion of how these results can be integrated into the decision and policy making process by fisheries/resource managers

Amount received for each year supported and number of years supported

The amount received was US$45,000 which supported activities over a 2-year period.

Participating Countries

Participants included representatives China, Japan, Republic of Korea, Russia and the USA. Participants from Canada were funded by the North Pacific Marine Science Organization PICES, http://www.pices.int.

Work undertaken

With Pacific herring as the target fish species, we conducted a successful workshop entitled "Climate Interactions and Marine Ecosystems" held in Honolulu, Hawaii from 10-13 Oct 2004 [see PICES Newsletter, 13(1), 2005; and a recent submission to the PICES Newsletter; both attached in the Appendix of this report]. The workshop and subsequent activities and meetings that culminated in an *Ecological Modelling* special issue focused on addressing three sub-hypotheses:

- *Subhypothesis 1:* geographic variations in fish growth can be explained by differences in environmental conditions and resulting differences in lower trophic conditions. We:

- identified locations with available data sets for lower trophic levels (LTLs) calibration;
- cross-referenced the LTL target list with locations that may have data on Pacific herring, sardines, anchovy, mackerel and other potential target species;
- developed a strategy for analysis of these data via a coupled LTL and fish model to address the hypothesis on geographic variability; and,
- agreed to compile the available datasets with final site and target species selection to be determined depending on the quality of the available information.

- *Subhypothesis 2:* synchronous (or asynchronous) changes in herring growth rates across locations may be accounted for by basin-wide decadal-scale changes in environmental conditions. With full-basin scale solutions as targets for the study of regime shifts in the longer term, we implemented and studied the response of point LTL and coupled LTL-fish models at selected sites in the North Pacific for various regime periods.

- *Subhypothesis 3:* future climate and global change scenarios may affect fish production through changes in structure of the lower trophic levels. We considered conducting exploratory tests of the effects of future conditions by changing bulk model parameters, with the magnitude of the imposed changes guided by the basin and global scale model form other sources, e.g., IPCC reports (Hashioka and Yamanaka, 2006b). While progress was made in the development of oceanic models that capture possible future changes, these models are still unable to resolve ecologically relevant spatial and temporal scales. In anticipation of advances in climate models that will include ecologically relevant scales, we have links with groups in Japan (Frontier Research Institute) and the USA (NCAR) to consider embedding of our modeling approaches that will allow us to explicitly consider responses of fish populations to climate change scenarios.

Results

The results of our APN project providing important, pioneering contributions in the field of quantitative modeling of marine ecosystems to climate change. The main models used are the NEMURO model for lower trophic levels of marine ecosystems (see Kishi et al. 2006) and NEMURO.FISH, its extension that explicitly include a fish component in the model formulation. A significant step forward in our project is the development of ecological models than enable consideration of the oceanic food web from nutrients and micro-organisms through fish, including population level questions. Many of the developments are reported in a special issue of *Ecological Modelling* (co-edited by Kishi, Megrey, Ito and Werner) presently in press (to appear in early 2007), as well as other primary journals. Advances (reviewed in Werner et al. 2006) which we were able to contribute include:

Lower trophic responses: the response of key phytoplankton and zooplankton groups was examined in several papers and their dependence on biogeochemical and physical forcing described (e.g., Aita et al. 2006; Kishi et al. 2006; Yoshie et al. 2006). Their seasonal variability, the shifts in species' composition, as well as their decadal variability was quantified and the details of the lower trophic components of the ecosystem served as input to the models attempting to describe the dynamics of target fish populations Hashioka and Yamanaka (2006a). A forward projection, looking 100 years into the future by Hashioka and Yamanaka (2006b) provided a scenario of possible changes in the ecosystem's structure and dynamics.

Higher trophic levels: the successful modeling of the physics, biogeochemical and lower trophic levels, enabled the construction and implementation of models that consider the dynamics of fish growth and of fish populations. The extension of the basic NEMURO model to include an estimate of fish growth in a fully coupled mode, i.e., where density-dependence is allowed to represent grazing on zooplankton by the fish, is one of the few such efforts presently available (Megrey et al. 2006a; Rose et al. 2006a,b and c). Its uncoupled mode, i.e., where density-dependent effects are not considered, provided testing of scenarios explaining the variation in size distribution of catches of saury and its interannual variability (Ito et al. 2006; Mukai et al. 2006), as well as the long term, interdecadal variability of fish growth including punctuated changes associated with regime shifts (Megrey et al. 2006b; Rose et al. 2006c).

Computational approaches: The general approaches and formulations used in our models (NEMURO and NEMURO.FISH) are relatively well established and broadly used within the modeling community. However some methods introduced in our studies, which we used to calibrate the models and to quantify their sensitivity to the parameters' uncertainty, offered new strategies. Several papers (e.g., Rose et al. 2006a; Wainright et al. 2006; Yoshie et al. 2006; Zuenko 2006) discussed the sensitivity of the model solutions to imposed parameters. The contributions of Rose et al. (2006a) where an objective calibration method that quantitatively minimizes the deviations between predicted and observed values is described, and Yoshie et al. (2006) where a systematic variation of parameters enables a ranking of the model's sensitivity on the various parameters were adopted by several contributions (e.g., Megrey et al. 2006a) and should be considered in future studies that build on similar type models.

Relevance to APN scientific research framework and objectives

The proposed project directly addresses APN's research framework topics "Changes in Coastal Zones and Inland Waters" and "Climate Change and Variability". We considered physical (and chemical) changes in the coastal ocean hindcast for the period 1948-2002. These computed changes allowed us to estimate the impact on the marine ecosystem of the North Pacific, including herring as the target fish species. Being able to hindcast past states opens the possibility to consider future scenarios in the coming years. The magnitude (and direction) of the predicted changes – and the associated uncertainties – will provide valuable information to policy makers and resource managers.

Self evaluation

The project has quite successful in several respects as described above and as reported in the published articles in the primary scientific literature (see below). We advanced the modeling capability of marine ecosystems to explicitly include fish and we also introduced computational approaches that will help in determining sensitivity to parameters and uncertainty in the model solutions. There are two areas that require additional work: *(i)* linking explicitly to climate change scenarios, e.g., from the IPCC contributions, and *(ii)* translating our findings into information that can be used by resource managers, e.g., in the context of Ecosystem Approaches to Fisheries. This area continues to present formidable challenges to the community of researchers and managers, but we believe that our results are necessary steps toward achieving both goals.

Potential for further work

Several key areas are apparent: the inclusion of ecologically relevant scales in climate change scenarios, either directly in the models or using nested approaches; the increase in resolution will bring new mechanisms that will need to be assessed and their importance determined; the development of measures of uncertainty in ecology and population dynamics; the consideration of multiple fish species (note that in a related project funded by APN-CAPaBLE to M. Kishi, work has begun to consider the joint variation and interactions between sardines and anchovies); and the translation of model findings to management-relevant information.

References [(*) denotes Publications resulting in part from APN support]

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Acknowledgments

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NEMURO and NEMURO.FISH models and their applications. We would also like to thank the home institutions (government laboratories and academic institutions) for providing release-time to the many scientists who contributed to this project.

Technical

Note: the technical report that follows is based on the paper published in *Ecological Modelling* by Werner F.E., S. Ito, B.A. Megrey and M.J. Kishi (2006) Synthesis and Future Directions of Marine Ecosystem Models, doi:10.1016/j.ecolmodel.2006.08.019.

Preface

NEMURO, the North Pacific Ecosystem Model for Understanding Regional Oceanography, simulates the temporal evolution and dynamics of the North Pacific's nutrient-phytoplankton-zooplankton food web. NEMURO was extended to NEMURO.FISH using the lower trophic level output of NEMURO as input to a bioenergetic-based model of fish growth and population dynamics. This project explored a rich set of North Pacific case-studies addressing: oceanic biogeochemistry, regional and seasonal variability of phytoplankton and zooplankton, reconstruction of 40-50 years of plankton dynamics, effects of climate on fish growth and population dynamics, automatic calibration methods and model sensitivity, and projections of future ecosystem states under global warming.

1.0 Introduction

The project's overall hypothesis is that global climate change can alter both the structure and function of the marine ecosystem, causing changes in energy cycling, plankton composition and dynamics, and ultimately fish production. The objectives of the project include: *(i)* to use a common marine food-web and fisheries bioenergetics modeling approach, along with long-term area-specific oceanographic and fisheries data sets, to understand the propagation of climate change effects up the marine food-web, *(ii)* to quantify its effects on energy cycling and fish growth and production in distinct geographic regions in the North Pacific; and *(iii)* to initiate a discussion of how these results can be integrated into the decision and policy making process by fisheries and resource managers.

Modeling marine ecosystems requires the integration of a number of physical, geochemical and biological variables and drivers. The task is formidable given the disparate spatial and temporal scales involved in each of the biological and physical subcomponents (Batchelder and Kashiwai, 2006), and the integration required to achieve quantitative statements about individual growth rates or the state of a population. Explaining variability in populations requires consideration of scales that range from mm's and seconds at the level of individual organisms to basin-scales that operate on scales of 1000's km and decades.

No single modeling approach can realistically include all relevant aspects of ecosystem dynamics in a unified formulation, and therefore the development of marine ecosystem models involves compromises and simplifications. Atmospheric forcing is usually decoupled from the ocean and is used as an externally imposed forcing on the ocean through specification of heat and momentum fluxes across the ocean's surface. Turbulence is not modeled explicitly, but rather expressed in terms of diffusivities or viscosities. Circulation, coastlines, bottom topography, boundary layers, mixed-layer depth and other physical features are only approximately resolved. Detailed structures of biological populations are idealized, with considerations of only key species or by grouping species when their functional and behavioral traits appear similar. Fundamental biological processes and vital rates, such as the temperature dependence of feeding, ingestion and assimilation, remain uncertain except for a few well-studied species. The challenge to the modeler is to take those aspects that are (approximately) known, and to build a formulation that still enables the extraction of new results and understanding. That was the charge taken on by the PICES Model Task Team (TT) within the PICES Climate Change and Carrying Capacity Program (Batchelder and Kashiwai, 2006; Kishi et al., 2006b) and a core component of this APN-funded project.

As a result, an immediate goal of the PICES Model TT was to develop a conceptual model representing the minimum trophic structure and bio-physical relationships between and among all the marine ecosystem components thought to be essential in describing ecosystem dynamics in the North Pacific. While several modeling approaches exist for the study of the dynamics of marine ecosystems (Runge et al., 2004), few marine models have explicitly considered the trophic links from nutrients and primary producers, up the foodweb, and through fish. Models that simulate from nutrients through fish are rare because of the large number of species involved, their vastly different reproduction rates, and differences in their complex life histories, abundances, behaviors, and spatial distributions. Commonly used biological and ecosystem modeling approaches include mass-balance or budget models, size-structured or age-structured models, and individual based models (IBMs). Of these approaches, the latter two (size and age-structured models and IBMs) offer advantages in their inherent flexibility to include ontogenetic details about the target organism and mechanistic descriptions of their feeding and swimming behaviors (see Carlotti et al., 2000; Werner et al., 2001). However, these formulations are perhaps best suited for species-specific studies, where the target species' biological traits are relatively well known. Further, if population- or ecosystem-level statements are sought using IBMs, long term simulations that are full life cycle and self-regenerating (model generated individuals reproduce and generate new young) can easily stretch available biological knowledge and can present computational challenges.

Mass-balance model formulations consider the dynamics of material or energy flow among trophic levels. To render the problem tractable, species are usually combined into functional groups with a resulting loss of detail, including the loss of species richness and biological traits such as age- or size-structure and behavior. Lower trophic level mass-balance models that focus on the nutrient-phytoplankton-zooplankton-detritus components are referred to as NPZD models (e.g., Fasham, 1993, 2003; Le Quéré et al., 2005). More comprehensive ecosystem-wide implementation of the mass-balance approach that includes fish, mammals and birds are also actively used, with perhaps the most common approach being the ECOPATH family of models (e.g., Polovina, 1984; Pauly et al., 2000). NPZD models of the open ocean have focused on the pelagic component. When NPZD models are applied to coastal regions and shelf seas, one must consider the coupling between the lower trophic pelagic and benthic components and the explicit inclusion of nutrient fluxes from rivers and other terrigenous sources (Baretta et al., 1995; Moll and Radach, 2003). NPZD models have been coupled to physical circulation models of oceanic and coastal domains, and have been successfully used in studies of nutrient cycles, characteristics of phytoplankton blooms, ocean biogeochemistry, and derivation of carbon budgets (e.g., Allen et al., 2001; Doney et al., 2004). Because lower trophic levels are mostly planktonic, the circulation models' hydrography and hydrodynamics (i.e., physical advection and diffusion) play a large role in determining the spatial distribution of organisms. The spatial representation of higher trophic levels is more difficult as active behavior (e.g., directed swimming, large scale migrations, schooling) becomes important and thus the populations' distributions depend to a lesser degree on hydrodynamics alone.

Hybrid modeling methods are also possible where, for example, higher trophic level IBMs representing fish are coupled to NPZD models that provide the prey fields. However, hybrid approaches in the marine environment to date have focused on larval fish (e.g., Hermann et al., 2001). To our knowledge, hybrid models that include the full life-cycle of higher trophic levels have not yet been implemented in realistic, spatially explicit settings for marine environments. Full life cycle models have been developed for freshwater systems (e.g., Clark and Rose, 1997), but usually with a simplified spatial representation.

Given these considerations, and with the overall goal of describing key elements of the North Pacific ecosystem, the PICES Model TT developed a biomass-based NPZD model as an important initial step in identifying and quantifying the relationship between climate change and ecosystem dynamics (see Batchelder and Kashiwai, 2006). The approach taken was to build a multi-compartment model that described the mass flux and recycling from inorganic nutrients through higher trophic levels. Building on previous NPZD formulations (Fasham, 1993), a model was constructed for nitrogen-limited ocean marine ecosystems (e.g., the North Pacific), with state variables representing functional groups characterizing North Pacific phytoplankton and zooplankton species. Model development tried to balance the need for complexity in order to ensure generality versus the desire to keep the model as simple as possible. The resulting lower trophic level marine ecosystem model was named "NEMURO" (North Pacific Ecosystem Model Understanding Regional Oceanography) and is described in Kishi et al. (2006a; 2006b). NEMURO was extended to include fish as a higher trophic level state variable, leading to the development of NEMURO.FISH (NEMURO For Including Saury and Herring, see Megrey et al. 2006b). Pacific herring (Clupea harengus pallasi) and saury (Cololabis saira) were the two target fish species considered.

2.0 Methodology

NEMURO is a biomass-based model that simulates the temporal evolution and dynamics of the North Pacific's nutrient-phytoplankton-zooplankton food web (see Figure 1).

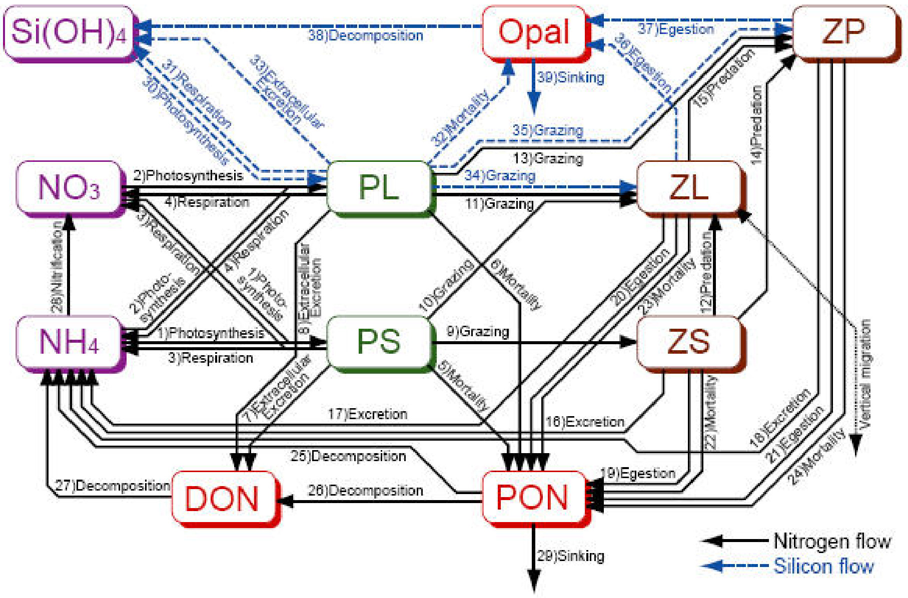

Fig.1: Schematic view of the NEMURO lower trophic level ecosystem model.

Different spatial implementations exist, including a single well-mixed domain that represents the surface layer of the water column (Kishi et al., 2006a), a 1-D vertically structured formulation (Fujii et al., 2006), a 2-D cross-shelf formulation (Wainwright et al., 2006), and a fully 3-D spatially-explicit basin-scale implementation (Aita et al., 2006). In its simplest form, NEMURO is cast as a system of 11 coupled ordinary differential equations, with an equation for the time rate of change of each state variable (see Kishi et al., 2006a), with extensions and additional state variables added in certain applications. The food web is represented with the following state variables: nitrate (NO_3), ammonium (NH_4), small phytoplankton (PS), large phytoplankton (PL), small zooplankton (ZS), large zooplankton (ZL), predatory zooplankton (ZP), particulate and dissolved organic matter (PON and DON) respectively, using nitrogen as the model's mass currency), particulate organic silicate (Opal), and silicic acid ($Si(OH)_4$).

Concentrations of phytoplankton are affected by photosynthesis, respiration, excretion, and predation by zooplankton. Zooplankton concentrations are affected by grazing, egestion, excretion, predation by other zooplankton, and one of the zooplankton groups (large zooplankton, ZL) migrates vertically to overwinter in the deeper layers of the ocean (see Aita et al., 2003). Nutrients are taken-up during photosynthesis, returned to the nutrient pool via phytoplankton and zooplankton respiration, excretion, mortality, and are converted between chemical forms via temperature-dependent decomposition reactions. Most processes use empirical relationships to adjust rates as functions of water temperature (e.g., Q_{10} functions). Photosynthesis also depends on the average light in the water column, and nitrate and ammonium concentrations. Large phytoplankton, representing diatoms, depend additionally on concentrations of silicate. Grazing rates by zooplankton depend on prey concentrations and ambient temperature.

NEMURO depends on over 70 parameters (see Table 1 in Kishi et al., 2006a). Parameters are derived from field or laboratory observations or are extrapolated or borrowed from related species and from other oceanic regions. Some rate parameters are best guesses or specified to ensure realistic model behavior (e.g., externally imposed zooplankton mortality rates). Developing values for these parameters and estimating the models' sensitivity to their values is an important task. The studies by Wainright et al. (2006), Yoshie et al. (2006) and Megrey et al. (2006b) found their model results to be most sensitive to parameter formulations involving maximum photosynthesis and maximum grazing rates, suggesting that narrowing the uncertainty in the estimates of those parameters would be valuable.

Yoshie et al. (2006) undertook a formal sensitivity analysis of NEMURO based on Monte Carlo methods. They found that annual small phytoplankton biomass was most sensitive to the maximum grazing rate of small zooplankton, while large phytoplankton biomass was most sensitive to its own maximum photosynthetic rate parameter. Their analyses also found regional differences in the importance of the parameters. At a location in the northwest Pacific the large phytoplankton biomass was found to be sensitive to zooplankton parameters, while at a northeast Pacific location the same phytoplankton group was more sensitive to phytoplankton parameters. While the analysis of Yoshie et al. (2006) found complex relationships between state variables and parameters, their analyses also showed that the NEMURO model was generally robust to parameter variation and to the method used for the sensitivity analysis.

Some of the observed spatial variations in the state variables cannot be captured with a single set of parameter values. Reasons for this spatial variability may be the scarcity of data that can be assembled for locations of interest, differences in seasons and years in which they were collected (and thus perhaps differences in species dominance), and differences in collection methods. Regardless, it is important not to confound predicted geographic differences with the choice of model parameter values and it is important to ensure that that the model is applied consistently across spatial locations. Rose et al. (2006a) presented an approach to objectively calibrate NEMURO, and contrasted the objective method with the usual ad-hoc method (e.g., investigator adjustment to parameter values until a good fit is obtained). The objective calibration that quantitatively minimized the deviations between predicted and observed values generally fit the field data better than the ad-hoc calibration. Rose et al. (2006a) concluded that, when adequate site-specific field data exist, automated procedures offer a viable approach for the objective calibration of NEMURO. The same automatic calibration approach was then used by Ito et al. (2006b) and Rose et al. (2006b) in their analyses that used NEMURO.FISH.

An alternative approach to estimating NEMURO's parameters was considered by Zuenko (2006). In a model with eight state variables applied at a station in the coastal zone of Peter the Great Bay (Sea of Japan), observations were reproduced using temporally-variable parameter values of phytoplankton and zooplankton growth, grazing and mortality. This approach contrasts with most other contributions in this PICES/APN effort that used temporally and spatially constant parameter values. The parameter's variability was intended to reflect seasonal fluctuations of the species composition and ontogenic changes within the phytoplankton and zooplankton. To account for spatial heterogeneity, Zuenko (2006) included additional terms in the governing equations to account for the unknown advective fluxes of the state variables. Generally, whether parameters should be constant or be allowed to vary is debatable. Uncertainty in the values of the coefficients may be an argument for selecting temporally and spatially constant values. However, changes in species composition over time may justify the use of different parameter values as an alternative to including new state variables and additional parameters.

3.0 Results & Discussion

3.1 Ocean biogeochemistry of the North Pacific

Fujii et al. (2006) extended NEMURO to fifteen-compartments by including calcium carbonate, total alkalinity, total carbon dioxide and partial pressure of CO_2. Within a basin-scale domain, they considered three locations: two in the subarctic northwestern Pacific and one in the northeastern Pacific. Their model results showed significant east-west differences in the seasonal characteristics of both the physical environment and biogeochemistry. Examples of these differences were larger seasonal amplitudes in sea surface temperature, mixed layer depth, surface nutrients, chlorophyll, and CO_2 partial pressure, and higher primary productivity, at the two northwestern Pacific stations. Differences in the magnitude of iron limitation on phytoplankton growth among the locations were also discussed by Fujii et al. (2006). While the importance of iron in establishing the levels and limits of phytoplankton production (Martin et al., 1994; Cullen, 1995; Gao et al., 2003) has been found in several regions of the Pacific, iron limitation in the NEMURO formulation is presently expressed only through the selection of parameter values (e.g., see Denman and Peña, 1999) rather than through explicit process equations that describe iron limitation. In particular, Fujii et al. (2006) found that incorporating iron limitation on diatom growth improved model performance in simulating ecosystem dynamics in the eastern North Pacific by reducing the model's overestimate of the dominance of diatoms. They also found that the computed air-sea CO_2 fluxes increased when they used daily instead of climatological wind data. The increase was attributed to strong winds in late winter, and suggests that the air-sea CO_2 fluxes could be underestimated in the absence of high-frequency wind variability. Phytoplankton growth was found to be light-limited at each of the locations, with diatom growth regulated by silicate rather than nitrate and ammonium, particularly in summer and autumn at the two northwestern Pacific locations. Fujii et al. (2006) concluded that east-west differences in biogeochemistry are caused by differences in the physical environment and by regional differences in iron bioavailability.

3.2 Lower-trophic level studies

Several contributions focused on NEMURO's ability to reproduce and explain observed variations in phytoplankton and zooplankton in space and time. One of these, by Wainright et al. (2006), considered one- and two-dimensional cases at a coastal site off the US west coast. Three other studies (Aita et al., 2006; Hashioka and Yamanaka, 2006a, 2006b) embedded NEMURO in a three-dimensional physical model. They refer to their implementation as 3D-NEMURO, and discuss the relative role of top-down versus bottom-up controls of primary production, hindcasts from 1948 to 2002, and forward projections to the end of the 21st century building on existing climate change scenarios. Aita et al. (2006) consider the entire North Pacific basin, while Hashioka and Yamanaka (2006a, 2006b) focus on the northwestern North Pacific. Lastly, the study by Komatsu et al. (2006), considered a different 3D implementation of NEMURO focusing on a high spatial resolution six-month simulation in the Kuroshio and Kuroshio Extension region.

Wainright et al. (2006) applied a simplified version of NEMURO to the nearshore pelagic zone of the California Current System. Model simplifications included: removal of the temperature dependence from the biological process and adjustment of the temperature-dependent parameters to an average temperature of 10 ºC; the use of a light photosynthetic function without photoinhibition; the grouping of certain parameters related to density-dependent mortality rates, grazing rates, and Ivlev constants; and the elimination of seasonal vertical migration by large zooplankton. Model parameter values were adjusted based upon minimization of the residual mean squared error of the model output compared to observations for a particular year. The solutions were explored in two different physical idealizations: a point-model with no explicit spatial structure and a two-dimensional cross-shelf model of the mixed-layer used to examine the biological response to upwelling. The model predicted low but constant phytoplankton biomass during the upwelling season, which closely fit the low early-summer and fall observations, but were too low compared to the higher mid-summer values. Copepod abundance was underestimated throughout the upwelling season. The authors concluded that, while model results compared reasonably well with observations, further model improvements in the ability to predict copepod production and abundance are needed in order to use the results in a salmon management context.

Hashioka and Yamanaka (2006a) used 3D-NEMURO focused on the western North Pacific to study the seasonal and horizontal variations of phytoplankton groups and their relation to top-down and bottom-up control. Consistent with observations, their results showed that the annually averaged biomass of diatoms, represented as a percentage of total phytoplankton, was 50 to 60% in the subarctic region and less than 30% in the subtropical region. Further, they investigated the seasonal variation of the percentage of diatoms and its relation to bottom-up and top-down control at three sites: the Kuroshio extension, a subarctic site, and a subtropical site. Diatoms at the Kuroshio extension and subarctic sites showed high growth rates from winter to the beginning of the spring bloom – a period without zooplankton grazing pressure – with the percentage of diatoms exceeding 70%. From the end of the spring bloom to the summer period, the percentage of diatoms dropped below 30% due to increased grazing pressure from copepods returning to the surface layers from their overwintering stage and from limitation on photosynthesis resulting from reduced silicate concentrations. At the oligotrophic subtropical site, Hashioka and Yamanaka (2006a) found that the percentage of diatoms was determined mainly by nutrient concentrations throughout the year.

Focusing also on the western Pacific region, Komatsu et al. (2006) constructed a three-dimensional lower trophic model focusing on the role of advection on the size dependent variations of plankton biomass in the frontal region of the Kuroshio and its extension. The model was highly resolved in space using a curvilinear horizontal coordinate system to cover the entire Pacific with mesh size increasing from 1/16° (order 6 km) in the Kuroshio region to 1/4° (order 25 km) farther away. Komatsu et al. (2006) imbedded a 10-compartment version of NEMURO into an eddy-resolving physical primitive equation model that assimilated satellite altimetric data and simulated a six-month period from January to June 30, 1997. One of their findings was that high concentrations of phytoplankton and zooplankton were distributed downstream of the Kuroshio, along the northern edge of the front. At these locations, variation of the biomass was controlled in large part by advective processes. Additional spatial structures (i.e., local maxima), were found in convergence zones associated with meander ridges. In neighboring areas away from the frontal zone and meanders, variation was affected mainly by *in situ* biological growth. Komatsu et al. (2006) concluded that in the frontal region advective processes associated with flow convergences and divergences and ring-stream interaction can cause large spatial differences in plankton biomass. Further, their study suggests that downstream advection of high plankton biomass can provide food at all times for winter-spawned larvae of Pacific saury distributed along the Kuroshio region.

Aita et al. (2006) used 3D-NEMURO to perform a retrospective simulation from 1948 to 2002 to investigate the effects of "regime shifts", such as the well documented mid- to late-1970s shift, on the lower trophic components (phytoplankton and zooplankton) of the North Pacific ecosystem. Their 3D-NEMURO simulation showed a spatially and temporally rich response. Aita et al. (2006) found that the 1970's inter-decadal change of phytoplankton biomass, zooplankton biomass and primary production correlated with the Pacific Decadal Oscillation (PDO; Hare and Mantua, 2000) in the central North Pacific. Variations in sea surface temperature, deepening of the mixed layer depth, and an increase in the nutrient supply, were implicated as the cause of the increased primary production since the regime shift. Phytoplankton and zooplankton concentrations and primary production showed positive correlations with the PDO. In contrast, increased advection of warm water in the northwest and northeastern Pacific regions in the post-shift period caused a decrease in the mixed layer depth with a resulting negative correlation between phytoplankton, zooplankton and primary production and the PDO. In the Gulf of Alaska, decreases in the mixed layer depth after the shift led to more favorable light conditions and an increase in primary production. In the Kuroshio-Oyashio transition region, strengthened advection of low salinity, low temperature water also caused a decrease of the mixed layer depth after the 1970's shift, but cooler water temperatures reduced photosynthesis in this region. In the Bering Sea, the mixed layer depth deepened and, in contrast to observations, the modeled primary production increased. Aita et al. (2006) hypothesized that additional top-down phytoplankton predation, presently missing from the model, may explain the discrepancy between model results and observations at the Bering Sea site. Evidence supporting such a possibility is presented by Brodeur et al. (1999), who show evidence of increases in gelatinous zooplankton in the Bering Sea after the shift.

Hashioka and Yamanaka (2006b) also used 3D-NEMURO and they examined potential global warming impacts on the ecosystems in the western North Pacific. They compared projections of ecosystem state from a particular global warning scenario to present-day conditions. The model simulation showed that global warming increased vertical stratification associated with rising temperatures, and resulted in decreases in surface water nutrient and chlorophyll concentrations at the end of the 21st century. Under warming conditions, the dominant phytoplankton group was shifted from diatoms to smaller phytoplankton. Increased stratification caused the spring diatom bloom to occur a half-month earlier than under present-day conditions. However, decreases in nutrient concentration were predicted to significantly decrease the maximum biomass in the spring bloom compared to present values. In contrast, at the conclusion of the spring diatom bloom, the biomass maximum of the other small phytoplankton groups remained close to present values. The reason offered by the authors was that the small phytoplankton had relatively low half-saturation constants for nutrient uptake and thus lacked sufficient ability to adapt to lower nutrient conditions. Projected changes in other seasons (e.g., from summer to winter) were estimated to be smaller. Hashioka and Yamanaka's (2006b) results agreed with those of Sarmiento et al. (2004); both predicted reduced chlorophyll and longer growing season in the North Pacific.

3.3 Higher-trophic level studies (linking to fish)

The extension of NEMURO to include the effect of higher trophic levels, namely fish, and referred to as NEMURO.FISH, is described in Megrey et al. (2006b). This extension of NEMURO is used in four other: Ito et al. (2006b), Megrey et al. (2006a), Mukai et al. (2006) and Rose et al. (2006c). Previous publications that used NEMURO.FISH include Ito et al. (2004) and Rose et al. (2006b). NEMURO.FISH provides estimates of fish growth and weight-at-age of either Pacific herring or saury in the cases considered here, and can be run in two modes. In the *uncoupled* mode, growth and weight of an individual fish is computed, but the total numbers of fish are not followed and thus there is no effect of the fish on zooplankton concentrations (i.e., the uncoupled mode is a density-independent formulation). In the *coupled* mode, the fish component includes a calculation of the bioenergetics and, additionally, the total numbers of fish are followed, enabling fish consumption to impose a mortality term on the zooplankton – effectively allowing for density-dependent growth of the fish. However, following numbers of fish adds an additional complication, in that the fish's life cycle must be closed and each year a new year-class needs to be added. NEMURO.FISH in the coupled mode allows for long-term simulations by providing the ability to generate new fish recruits within the simulation model. A spawner-recruit relationship, dependent on the prevailing environmental and climatic conditions, is used to estimate the number of new age-1 individuals to be added to the population every year from the spawning biomass a year earlier. Finally, excretion by the fish contributes to the nutrient dynamics by adding to the ammonium compartment of the NEMURO component and fish egestion adds to NEMURO's particulate organic nitrogen compartment

In a site-specific application, Megrey et al. (2006b) used NEMURO.FISH in the coupled mode to simulate the daily average weight and numbers of Pacific herring in each of 10 age classes for multiple years at a site off the west coast of Vancouver Island, Canada.

Good agreement was found between simulated and observed herring growth rates and weights-at-age. Uncertainty and sensitivity analyses, using the same method as used by Yoshie et al. (2006) for NEMURO, identified the importance to herring growth of herring consumption and respiration parameters.

Rose et al. (2006c) used output from Aita et al.'s (2006) basin-scale 3D-NEMURO simulation as input to NEMURO.FISH that was then run in the uncoupled mode. Rose et al. (2006c) simulated the daily growth of herring from 1948 to 2000 at three northeastern Pacific locations. They used the water temperature and zooplankton concentrations from the basin-scale solution of 3D-NEMURO, averaged over the upper water column from the spatial cells in 3D-NEMURO corresponding to the three locations, as input to predict the growth of herring and weight-at-age. Once the simulated daily growth of herring for 1948 to 2000 was obtained, a statistical analysis to detect regime shifts was applied to the simulated temperatures, zooplankton, and herring growth rates. All three locations showed a shift in herring growth during the mid and late 1970's. Associated with the 1970's regime shift, Rose et al. (2006c) found that herring growth decreased at the west coast of Vancouver Island and Prince William Sound locations, but growth increased at the Bering Sea location. At each location, changes were coincident with a warming of temperature and a decrease in predatory zooplankton density. The authors concluded that variation in zooplankton densities caused the herring growth response for the southernmost west coast of Vancouver Island location, and that temperature and zooplankton densities both affected the herring growth responses at the two Alaskan locations. They suggested that variability in zooplankton was more important for the response at the Prince William Sound location, and that temperature dominated the response at the Bering Sea location. Other regime shifts, in addition to that in the 1970's, were found in the Rose et al.'s (2006c) modeled results and their relation to observations are discussed.

Pacific saury was the target fish species in the studies of Ito et al. (2006b) and Mukai et al. (2006). Pacific saury early-fall catch data show multiple peaks in size distribution. Mukai et al. (2006) used NEMURO.FISH in the uncoupled mode to consider whether the dependence of saury growth on spawning season could be a factor in the observed size-distribution of the catch. They showed that in general, winter-spawned saury grew fastest during its first year, and spring-spawned saury showed the slowest growth. However, during the second year, the reverse occurred (i.e., spring-spawned saury show the fastest growth). Mukai et al. (2006) suggested that dependence of growth on spawning season helps explains the size distribution of saury observed in the catch.

Ito et al. (2006b) used NEMURO.FISH in the uncoupled mode and forced by observed sea surface temperature and other climatological data sets from 1950 to 2002 to consider interannual and interdecadal variability of Pacific saury weight in three oceanographic regions of the western Pacific. Autumn, winter and spring saury cohorts were considered, and the differences in observed growth variability were suggested to be related to differences in the life histories among the cohorts. The spring-spawned cohort spawns only once in their life-cycle, while the other two cohorts spawn twice. During autumn, the spring-spawned cohort will not have spawned, while the other cohorts will have already spawned once. As a result, modeled spring-spawned cohorts showed more clearly the effects of environmental variability that affect the early life stages, while the autumn-spawned and winter-spawned cohorts, which have already spawned, have lost the environmental signal. On longer time-scales, Ito et al. (2006b) found that modeled wet weight of Pacific saury showed decadal variability consistent with observations in the Kuroshio and mixed water regions. However, simulated saury weight was not consistent with the observations in the Oyashio region; the amplitude of the variability in predicted weight was smaller than that observed. One possible cause of the model's underestimate of the fluctuation in saury weight is the absence in the model of a competition by Japanese sardine for zooplankton prey. Large biomass of Japanese sardine in the real ocean (but presently not included in the model) may strongly impact zooplankton density in the saury migration region, thus contributing to the increase in variability of observed saury weights.

Megrey et al. (2006b) used NEMURO.FISH to compare growth of Pacific saury and herring at locations off Japan and California. Their approach, as in Rose et al. (2006c), was to use 3D-NEMURO output to force the (uncoupled) NEMURO.FISH model. Megrey et al.'s (2006b) study considered the different life histories of the target fish species at each location and how these differences might influence growth responses to different climate regime periods. They found that sea surface temperature tended to be negatively correlated with the trends in the zooplankton biomass; herring growth trends were out-of-phase between the Japan and California locations; and growth trends were in-phase between herring and saury at the California location. Regarding regime shift signals, Megrey et al. (2006b) found that the 1980 to 1985 period had cooler water temperatures, increased zooplankton biomass, and faster growth and larger weights-at-age of saury and herring in both Japan and California, while the period of the early 1990s had the opposite. They also found shifts in model predicted growth rates for both fish species in both areas but the periods of increased or decreased growth did not coincide with the expected regime shift periods in 1976-77, 1988-89, and 1998-99. Possible factors that helped explain the complex responses (sometimes synchronous and sometimes out-of-phase) observed in the model simulations were that statistically insignificant signals in the temperature and zooplankton time series sometimes had large effects on fish growth rates and greater autocorrelation in herring weights-at-age due to its longer life span.

4.0 Conclusions

The results described summarized above represent important individual contributions to our knowledge about climate effects on North Pacific ecosystems. These contributions, when taken together, also constitute a successful collaborative effort of the PICES Model TT. NEMURO model development started during the 2000 meeting of the TT (see PICES Scientific Report no. 15 and the Preface to the *Ecological Modelling* special issue on NEMURO), marks a major milestone in the development and systematic analysis of the NEMURO family of models.

The approach chosen by the Model TT to use a single, common model as an initial approximation of the North Pacific ecosystem has strengths and weaknesses. An immediate benefit of a single model formulation is that results across the various studies can be interpreted with less concern about the possible effects introduced by individual investigators' at different locations each using their own model formulations. Such differences in formulations are often confounded with specific geographic locations, or with the study of particular climate or environmental events, without consideration of how the specific formulations might themselves be causing differences in predictions. Site-specific models are correctly developed for specific purposes and their validity over larger domains or longer time scales are often unknown. The use of a common NEMURO formulation allowed for cross-comparisons of regional analyses such as Hashioka and Yamanaka (2006a) and Aita et al (2006). Similarly, building on a common foundation enabled the links connecting lower trophic levels to higher trophic (fish) components in NEMURO.FISH to proceed systematically. The development of the saury and herring components of NEMURO.FISH was also done with a common framework so that inter-specific comparisons were possible, removing confounding effects arising from likely different formulations being used for different fish species. An example of the benefits of a common formulation was the study of Megrey et al. (2006a), where the single formulation approach allowed for comparisons across two fish species and two oceanic regions in an attempt to determine if the response to a common climate forcing would manifest itself equivalently in two different fish species. Use of a common formulation to establish baseline studies, like was done with NEMURO and NEMURO.FISH, is necessary to be able to attribute simulated differences in responses to spatial or temporal variation.

Limitations to the applicability of a single formulation approach are readily apparent in cases where the questions posed fall outside the model's capability. Examples are the studies of Hashioka and Yamanaka (2006b) and Fujii et al. (2006), who had to extend the basic NEMURO formulation to include pCO_2 and total alkalinity, in order to address aspects of the carbon cycle for which the initial NEMURO formulation was not equipped. In the case of NEMURO.FISH, some of the idealizations made in constructing a saury model so that it resembled the structure of a herring model may not be fully valid. Although some distinction between the species was introduced by specifying differences in their migratory behaviors, possible differences in their physiology and bioenergetics were ignored mainly for lack of field or laboratory data that could have supported alternative structural formulations (e.g., Ito et al., 2004). Finally, there are known limitations in the representation of the physical environment by using physical fields from a circulation model originally designed for the study of long-term basin-scale processes, and applying these to the study of coastal species like herring. Localized coastal features like upwelling and associated fronts are not resolved, necessitating the effects of such smaller scale processes to be included in the choice of parameters, or to be ignored altogether.

Given the caveats associated with modeling in general and specifically with the use of a single common model formulation, these results include several noteworthy advances:

- *Biogeochemistry:* a "simple" multi-compartment model that captures the essential biogeochemical properties of the North Pacific, including the dynamics of key phytoplankton and zooplankton groups was developed, calibrated and applied to selected locations throughout the North Pacific basin (e.g., Fujii et al. 2006) and was used in synoptic basin-wide studies that considered interannual and decadal variability in the latter half of the 20th century (e.g., Aita et al. 2006).

- *Physics:* the development of the physical model occurred in a parallel effort (e.g., Hasumi, 2000, 2002) and was subsequently made available for coupling with NEMURO. The combined physical and NEMURO model captured the essential details of the large-scale physics, and associated trophodynamics, of the North Pacific. NEMURO focused on the study of lower and higher trophic levels that depended on the spatial and temporal variation of temperature in the upper 100 meters and the cross-basin and latitudinal regional variability in the depth of the mixed layer. The structure provided in the physics enabled detailed studies of the variability of the lower and higher trophic levels, and their comparison with available data. Increased spatial and temporal resolution, together with data-assimilative approaches, enabled the inclusion of additional shear and eddy-induced flow structures and processes affecting lower level trophodynamics in the vicinity of the Kuroshio, as described by Komatsu et al. (2006).

- *Lower trophic responses:* Seasonal and decadal variability and shifts in species composition were quantified by Hashioka and Yamanaka (2006a), Fujii et al. (2006) and Aita et al. (2006). The details of the lower trophic components of the ecosystem served as input to the models describing the dynamics of two target fish species (herring and saury). A forward projection, looking 100 years into the future, by Hashioka and Yamanaka (2006b) provided a scenario of possible changes in the ecosystem's structure and dynamics in response to global warming.

- *Higher trophic levels:* the successful modeling of the physics and lower trophic levels enabled the construction and implementation of models that then considered the dynamics of fish growth and population dynamics. The extension of NEMURO to the coupled version of NEMURO.FISH is an important contribution (Megrey et al. 2006a; Rose et al. 2006b), and represents an example of vertically integrated (physics-to-fish) analysis [also see Bryant et al. (1995)]. The uncoupled mode of NEMURO.FISH provided tests of hypotheses about the variation in the size distribution of saury catch (Ito et al. 2006b; Mukai et al. 2006) and investigation of the bottom-up effects of climate regimes on fish growth over multiple decades (Megrey et al. 2006b; Rose et al. 2006c).

- *Calibration and sensitivity methods:* The general modeling formulations used in NEMURO and NEMURO.FISH (e.g., the class of equations, the closure terms, the solution methods) are well established and broadly used within the modeling community (e.g., see Fasham, 1993; 2003). Methods presented in the special *Ecological Modelling* issue used to calibrate the models and to quantify their sensitivity to parameter uncertainty extended previous efforts (Kuroda and Kishi, 2003). Papers by Rose et al. (2006a), Wainright et al. (2006), Yoshie et al. (2006) and Zuenko (2006) discuss the sensitivity of the model solutions to imposed parameters. The automatic calibration method described in Rose et al. (2006a) and the Monte Carlo sensitivity analysis method described in Yoshie et al. (2006) should be considered in future modeling studies.

5.0 Future Directions

Depending on the application, different levels of physical and biological complexity have been used in the *Ecological Modelling* papers to represent the processes affecting the North Pacific ecosystem. Compromises were required to balance the needs to make NEMURO and NEMURO.FISH as realistic as possible, with the realization that realism requires increased data, more detailed process description, and (often) increased model complexity. Below we discuss some of the enhancements that should be considered for the next generation of the NEMURO family of models.

5.1 Resolution and model structure

5.1.1 Physics

Physical processes determining biogeochemical and biological responses require resolution on the order of kilometers in the open ocean (see McGillicuddy et al., 2003). Fundamentally different dynamics can emerge, depending on the spatial resolution of the model (Komatsu et al., 2006). Coastal areas, where many of the commercially important fish species are found, require even higher resolution in order to capture fronts and other topographically controlled flows. Such details are presently absent from most basin-scale ocean models. Note that as resolution increases, the explicit inclusion of previously unresolved processes is possible, thereby reducing the dependence on externally imposed parameter values (e.g., horizontal diffusion terms). Next steps in either open-ocean or coastal applications of NEMURO or NEMURO.FISH should increase the spatial resolution represented in order to simulate more features from first principles.

5.1.2 Biogeochemistry and lower trophic levels

The need to include additional constituents, such as iron, is well known. While the effect of iron limitation has been parameterized (e.g., Denman and Peña, 1999; Yoshie et al., 2005), the explicit effects of iron in its various forms will likely be required in future efforts (Christian et al., 2002). Similarly, recent understanding of the ocean's acidification and the consequent effect of changes in *pH* on ecosystem dynamics (e.g., Orr et al., 2005) suggest explicit consideration of *pH* would improve the predictive capabilities of NEMURO in some locations. In general, in order to better represent the biological pump of the carbon cycle, additional phytoplankton, zooplankton and bacteria groups are needed (e.g., see Le Quéré et al. 2005). Regarding microbial processes, it has been estimated that 10 to 50% of the primary production passes through the bacterioplankton (McManus and Peterson, 1988), and that very little of the resulting bacterial production is available to mesozooplankton. For example, in the northeast subarctic Pacific Ocean, Rivkin et al. (1999) estimated that only about 3% to 12% of bacterial carbon production was transferred to copepods. Consequently, a large proportion of primary production is respired by the microbial food web in the surface layer, rather than exported to higher trophic level predators or to the deep-sea. Over the last decade, the microbial food-web in aquatic ecosystems has been found to have a potentially significant impact on the amount of primary production that is actually available to mesozooplankton, and hence to higher trophic levels (Moloney and Field, 1991). The functional importance of bacteria is implicitly captured in NEMURO in the decomposition process, which is assumed to occur "instantaneously". While this was an appropriate starting point, the next generation of NEMURO models should explicitly represent additional lower trophic state variables (see Smith et al., 2005). Additional developments of an "**e**xtended" **e**NEMURO model are presently underway (Yamanaka et al., 2004; Yoshie and Yamanaka, 2004).

5.1.3 Zooplankton and fish

Increased biological resolution can imply the separation of the aggregated functional groups, greater detail in the age- and stage-structure of particular species, and the inclusion of additional species. An example of the importance of separating functional groups into their sub-components is offered by Beaugrand et al. (2003) and Reid et al. (2003), where seasonal differences and shifts in dominance of two largely similar North Atlantic zooplanktonic species (*Calanus helgolandicus* and *C. finmarchicus*) are suggested to affect recruitment of Atlantic cod in the North Sea. Explicit consideration of zooplankton ontogeny will be required to properly represent the preferred prey of the early life stages of fish, particularly since first feeding larvae are restricted to eating only the small-sized life stages and most fish exhibit a shift towards larger prey as they get older.

Complex trophic interactions, such as predator-prey and competitive interactions, were minimized or ignored in NEMURO.FISH. Even though additional trophic complexity is difficult to implement, there are instances when it cannot be ignored. Ito et al. (2006b) showed that ignoring the competitive effects of sardine resulted in the overestimation of saury growth. The subsequent inclusion of the effects of sardine predatory effects on zooplankton resulted in more realistic saury growth. Including the effects of competitors and predators of the target species via imposition of assumed changes in the food availability or parameter values of the target species (e.g., higher mortality rate) only allows for some questions to be addressed. Whether the competitors and predators should be explicitly simulated (i.e., approaching the representation of a food web) depends on the questions to be addressed and the availability of sufficient information. NEMURO.**SAN**, which is an extension to NEMURO to consider fluctuations of **S**ardines and **AN**chovy populations in the North Pacific and other regions, will attempt to explicitly include inter-specific competition and predation among multiple fish species (Ito et al., 2006a).

The papers in the *Ecological Modelling* special issue all relied on generating spatial variability in prey fields that were not ideally matched to the spatial scale of fish foraging. Fine scale variation in prey, such as patch frequency and distribution, is undoubtedly important to individual organisms, but such details were beyond the capabilities of the current NEMURO family of models. Despite advances in sampling technology and the ability to describe fine-scale prey fields, modeling efforts rarely include variability in prey fields at the scales relevant to the individual predator (Letcher et al., 1996). In a related aspect, there were no feedbacks between fish behavior and the simulated environment. Behavioral responses to environmental changes are expected, especially in schooling fishes such as herring and saury (Pitchford and Brindley, 2005). A combination of individual-based and population-based models is likely to be required to be able to consider more mechanistic descriptions and to allow fish in the model to dynamically adjust their behavior (e.g., feeding, movement). While advection is critical to understanding the spatial distributions of early life stages of fish, juvenile and adult fish can control their movement on fine to moderate spatial scales.

5.1.4 Bioenergetic formulation

The sensitivity analysis of Megrey et al. (2006b) showed the importance of the parameters describing the consumption and respiration processes in NEMURO. Yet the processes describing the rates of energy gained from foraging and lost via metabolism for all modeled biological taxa in NEMURO are represented using fixed formulations that depend on temperature and body size (Kishi et al., 2006b). Assimilation and growth efficiencies in NEMURO are simply specified as constants. Even with trying to develop bioenergetics models for two fish species, we had to borrow parameter values from other species. Such borrowing of parameter values tends to force convergence of predictions, as species share common parameter values for no other reason than limited information. More detailed descriptions of the mechanistic limits to feeding and respiration processes and the effects of fish size, temperature and prey concentrations are necessary, particularly as we attempt predictions of future scenarios.

5.2 Integration across scales and the use of nested approaches

We recognize that the list of improvements described above would result in an overly complicated model that would likely not be useful for addressing most specific questions. Nested approaches offer an alternative whereby resolution is increased as needed for a particular process, oceanic region, or species, and is then coupled or embedded in a larger, inclusive formulation. For example, coastal regions solved with required high resolution are now commonly nested within larger, but coarser resolution, oceanic domains (e.g., Hermann et al., 2002). Similar strategies regarding biological nesting are summarized by deYoung et al.'s (2004) "rhomboidal" approach to modeling marine ecosystems, which suggests that a key step in representing extended food webs in complex marine systems is to concentrate the biological resolution in the main target species of interest, and to make increasing simplifications up and down the trophic scale from the target species. Competitors, prey and predators would be represented in less detail leading to a rhomboid shaped representation of the ecosystem. Select improvements would be added to NEMURO and NEMURO.FISH as the questions to be addressed dictated that such detail was necessary.

5.3 Uncertainty

Several contributions identified the sensitivity of model results to known ranges in the parameter values used. Generally, model results were not reported with measures of uncertainty. As we look forward and anticipate the need to forecast, or to provide future projections of the state of the ecosystem, the practice of quantifying model results with levels of uncertainty needs to become the rule, rather than the exception. Ensemble, Monte Carlo and other methods exist that can be readily used for this purpose. Climate predictions are issued with associated uncertainty levels (Wigley and Raper, 2001), and some methods developed in that modeling community should be immediately relevant to NEMURO-type modeling. While quantifying the uncertainty in ecological system forecasts will likely bring its own set of challenges, uncertainty estimates should nevertheless be made part of future ecosystem modeling (Clark et al., 2001).

5.4 Data and Forcing

Availability of data and measurements continues to be one of the most important needs in modeling marine ecosystems. In addition to the need to understand the natural systems in question, data collection is needed to validate models, for better forcing of models, or for explicit use in data assimilative schemes. While new programs such as the Global Ocean Observing System (GOOS; IOC, 1998) will result in increased data streams, it will initially be mainly physical data largely for technological reasons simply because biological sensors are more difficult to construct and maintain. Nevertheless, high resolution physical data will be immediately useful to ecological models as more detailed solutions are attempted in space and time, or as Fujii et al. (2006) point out, to more quantitatively capture the air-sea fluxes. As a complement to field observations, there continues to be an equally strong need for laboratory data to better define the vital rate processes of key species that are represented in these models.

One strategy to define the next steps in collecting necessary data is through 'Model Based Observations'. Specific to the North Pacific, several monitoring stations already exist (e.g., Station Papa, ALOHA, KNOT, CalCOFI, Newport line, A-line). If model-based observations are conducted at these stations, increased accuracy of ecosystem models at local, regional and basin scales will be possible. New technologies, like ARGO floats, gliders and profiling mooring systems, enable measurement of primary and secondary production that go beyond point measurements. Future observing systems designed with sensors enabling model based observations will significantly contribute to more rigorous validation and improvement of ecosystem models like NEMURO.

5.5 Public availability and additional development by the community

NEMURO has the potential of becoming a standard "base model" for future developments in several areas – carbon cycling (eNEMURO), multi-species modeling (NEMURO.SAN), and climate change. An important next step to ensure a systematic and integrated effort should be the public release of NEMURO, with complete and clear documentation, to enable broader participation by the research community. There are several very successful examples of community models in the physical oceanographic arena, including the Princeton Ocean Model (POM), the Regional Ocean Modeling System (ROMS), the Hybrid Coordinate Ocean Model (HYCOM), and the Modular Ocean Model (MOM). In the biological arena, Ecopath/Ecosim (Christensen et al., 2000) and ERSEM (Baretta-Bekker and Baretta, 1997) are examples of documented, publicly available modeling frameworks. Providing a modularized code, facilitating the creation of extensions, would allow the creation of a dedicated user and developer groups. Such efforts would accelerate the improvements of NEMURO and provide additional and needed testing of NEMURO's applicability to a wide set of conditions and locations. Modularization of NEMURO would also enable its interface with the emerging Earth System Modeling Framework (ESMF), which is designed to facilitate linkage of systems models and components by providing a common modeling infrastructure (Hill et al., 2004).

5.6 Final remarks

NEMURO was developed as a common ecosystem model for the North Pacific. However, ecosystem models are different from general ocean circulation models. Circulation models are derived from first principles, together with constraints imposed by temperature, salinity and mass conservation equations. Ecosystem models rely much more on empirical relations and the judgment of the developers as to what to include and what to ignore. Hence, developing a generalized ecosystem model is difficult.

To build a true common ecosystem model, the community of researchers needs to come to agreement on unique expressions of key biological traits. A grand challenge is to define unique empirical equations for marine ecosystems. For example, scientists working in one region of the ocean will describe the temperature dependence of target organisms using the data from that region, while scientists at other sites will likely derive a different formulation. The Model TT's effort in implementing NEMURO required the compilation of data from several locations in the North Pacific in order to set the model parameters. To make the data uniform and to be able to compare across sites, conversions needed to be applied. However, the factors themselves varied across sites and varied seasonally. The goal of constructing a "simple" ecosystem model for the North Pacific clearly showed that one of the most basic and important elements that can result from sustained international collaborations is the unification of observational methods, measurements and their interpretation. Such uniformity in approach would greatly help the definition of unique empirical equations for ecosystem modeling in general, and for their inclusion in a common NEMURO-like model.

NEMURO is only one milestone in a long process toward achieving a common ecosystem formulation for use in the North Pacific. The structure of NEMURO was decided through discussions within a broad group of researchers from different fields including physics, biology and fisheries. Formulations and parameterizations were a result of a collective effort that engaged everyone equally. We believe that had smaller groups taken on the similar tasks, it is likely that different formulations would have resulted, rather than the common single NEMURO and NEMURO.FISH formulations used in these papers. Similarly, once the formulations were agreed to, the implementation and application of the common model to different regions and different times was done with the benefit of the collective understanding gained through the joint "bottom-up" effort of the researchers involved. In other words, through the team effort, everyone's cross-disciplinary awareness of the different issues and limitations was increased. The resulting contributions, even at the level of the individual papers, provide a broader perspective and integration of the results than would otherwise have occurred by groups working in isolation. It is safe to say that the effort resulting in the papers in the *Ecological Modelling* issue is greater that the sum of its parts, and even goes beyond the scientific content of the papers to how the scientists involved will approach new problems in the future.

The framework offered by the NEMURO model and its extensions provided the opportunity to examine the dynamics and variability of the North Pacific marine ecosystem. Although the complexity of the system demanded significant idealizations and approximations, important contributions resulted in several areas ranging from methodological, such as techniques for coupling across trophic levels and better parameter estimation, to process studies that provided better understanding of the factors controlling marine ecosystems. The next steps should include increased resolution (not just computational, but in the processes included) with the aim of providing projections of future states. There will continue to be a need for additional hindcast studies, but these will always be data-limited to some extent. It is important that models be used to identify where additional data need to be collected (e.g., through Observing System Simulation Experiments, Robinson and Lermusiaux, 2002) so that maximum advantage is taken of available resources and so that the data are collected optimally for integration with the models.

As we better quantify the observed variability in marine ecosystems and our predictive capacity increases, we will move closer to our goal of providing stewardship of our marine ecosystems (Runge et al., 2004). While our approaches so far are relatively simple, they represent important steps towards the integration of our understanding of climate variability and the responses of lower trophic levels and fish populations. As such, we have reason to be optimistic about models providing information needed to manage our oceanic resources. However, efforts of the magnitude required to take the next steps in the development of future marine ecosystem models cannot happen without sustained resources to train the next generation of scientists that will lead this charge.

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Appendix

Conferences/Symposia/Workshops

2006

Ito, S., Rose, K., Noguchi-Aita, M., Megrey, B.A., Yamanaka, Y., Werner, F.E., Kishi. M.J. Interannual response of fish growth of Pacific saury to the 3-D global NEMURO output with realistic atmospheric forcing. Presented at the Symposium on Climate variability and ecosystem impacts on the North Pacific: a basin-scale synthesis, April 19-21, 2006, Honolulu, HI.

Hay, D. Rose. K.A., Schweigert, J., and Megrey, B.A. Geographic variation in herring populations in the North Pacific: Understanding latitudinal response to climate change. Presented at the Symposium on Climate variability and ecosystem impacts on the North Pacific: a basin-scale synthesis, April 19-21, 2006, Honolulu, HI.

Rose, K.A., Megrey, B.A. Ito, S. Werner, F., Hay, D., Noguchi-Aita, M., Yamanaka, Y., Schweigert, J., Foster, M.B., Kishi, M.J., Ware, D., Eslinger, D., Klumb, R., and Smith, L.S. Fish Growth and Population Responses to Regime Shifts in the North Pacific: A Comparison of Herring and Saury Using Coupled Fish Bioenergetics and NPZ Models. Presented at the Symposium on Climate variability and ecosystem impacts on the North Pacific: a basin-scale synthesis, April 19-21, 2006, Honolulu, HI.

Werner, F., Rose, K.A., Megrey, B.A., Nouguchi-Aita, M., and Yamanaka, Y. Simulated Herring Growth Reponses in the Northeastern Pacific to Historic Temperature and Zooplankton Conditions Generated by the 3-Dimensional NEMURO NPZ Model. Presented at The Ocean Sciences meeting, February 24, 2006, Honolulu, HI.

2005

Megrey B.A., Rose, K.A., Klumb, R. Hay, D. Werner, F.E. Eslinger, D.L. and Smith, L.S. NEMURO.FISH - A fish bioenergetics and population dynamics model coupled to a lower trophic level NPZ model: Description, calibration, sensitivity analysis and application to climate research. Presented at FRA/APN/GLOBEC/PICES Joint Workshop “Global comparison of sardine, anchovy and other small pelagics – building towards a multi-species model”, November 14-17, 2005, Tokyo, Japan.

Rose, K.A., Megrey, B.A., Werner, F., Yamanaka, Y., Noguchi-Aita, M., Ito, S., and Kishi, M.J. Presented in Session 4, The comparative response of differing life history strategists to climate shifts. Interannual Response of Fish Growth to the 3-D Global NEMURO Output with Realistic Atmospheric Forcing. Part I: Latitudinal Differences in Pacific herring growth. PICES Annual Meeting, September 29-October 9, 2005, Vladivostok, Russia.

Ito, S., Rose, K.A., Noguchi-Aita, M., Megrey, B.A., Yamanaka, Y., Werner, F.E., and Kishi, M.J. Interannual response of fish growth to the 3-D global NEMURO output with realistic atmospheric forcing. Part II: Pacific saury growth. Presented at Session 4, The comparative response of differing life history strategists to climate shifts. PICES Annual Meeting, September 29-October 9, 2005, Vladivostok, Russia.

Megrey, B.A. and F.E. Werner. NEMURO.FISH: A NPZ-Fish Bioenergetics/Population Dynamics Model for Pacific Saury and Herring. Advances in Marine Ecosystem Modelling Research Symposium, June 27-30, 2005 Plymouth, UK.

Megrey, B.A. NEMURO: A multi-trophic level numerical simulation model of a marine ecosystem. Presented at the Workshop to Evaluate Ocean Circulation Models for the Bering Sea and Aleutian Island Regions, 3-4 February, 2005, Seattle, WA

Megrey, B.A. Review of NEMURO and NEMURO.FISH. Presented at the APN workshop on Climate Interactions and Marine Ecosystems, 10-13 Oct., 2005, Ala Moana Hotel, Honolulu, HI.

Werner, F. and Megrey, B.A. Climate change as a problem, relevance to APN, PICES, and GLOBEC, and a review of the APN proposal, objectives and goals. Presented at the APN workshop on Climate Interactions and Marine Ecosystems, 10-13 October 2005, Ala Moana Hotel, Honolulu, HI.

Ito, Shin-ichi, Michio J. Kishi, Daiki Mukai, Yukata Kurita, Yasuhiro Ueno, Yasuhiro Yamanaka, Bernard A. Megrey, and Francisco E. Werner. A study of interannual variability of Pacific saury using a simple 3-box model of NEMURO.FISH. Presented at the PICES XIII Annual Meeting, Session S10, Modeling approaches that integrate multiple spatial scales and trophic levels between shelf and open oceans. PICES Annual meeting, October 10-16, 2005, Honolulu, HI.

2004

Rose. K.A., B.A. Megrey, R. Klumb, D.E. Hay, D.M. Ware, S. Ito, D.L. Eslinger, Y. Yamanaka, F.E. Werner, and M.J. Kishi Linking climate change, water quality, and fish growth and population dynamics using bioenergetics: a case study in the North Pacific. Presented at the Annual AFS Meeting, Madison, WI. 2004

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Glossary of Terms

APN Asian Pacific Network
FAO Food and Agriculture Organization of the United Nations
GLOBEC Global Ocean Ecosystem Dynamics
HYCOM HYbrid Coordinate Ocean Model
IBM Individual-based modeling
ICES International Council for Exploration of the Sea
IGBP International Geosphere-Biosphere Programme
JGOFS Joint Global Ocean Flux Study
NCAR National Centre of Atmospheric Research
NEMURO North Pacific Ecosystem Model for Understanding Regional Oceanography
NEMURO.FISH NEMURO For Including Saury and Herring
NPZD Nutrient Phytoplankton Zooplankton Detritus
OGCM Ocean General Circulation Models
PICES North Pacific Marine Science Organization
POM Princeton Ocean Model
ROMS Regional Ocean Modeling System
SPACC Small Pelagic Fish and Climate Change

Abstracts

PICES XIIIth Annual Meeting, Honolulu, Hawaii, 2004, Session S10

Interdecadal variation of lower trophic ecosystems in the Northern Pacific between 1948 and 2002, using a 3-D physical-NEMURO coupled model

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Regime shifts, consisting of decadal-scale oscillation in atmosphere-ocean systems, have recently been the focus of many marine ecosystem studies. These "regime shifts" affect the sea surface temperature and Mixed Layer Depth (MLD), as well as overall changes the environment of marine ecosystems. We simulated changes in lower trophic marine ecosystems caused by interdecadal climate variability, using data from 1948 to 2002 using a global threedimensional physical-biological "3D-NEMURO" coupled

model. The results were consistent with observations. Comparing before and after the late 1970s regime shift, primary production and biomass of phytoplankton increased in the North Central Pacific region but decreased in the sub tropical zone in the Western and Eastern Northern Pacific after the regime shift. This corresponds to the Pacific Decadal Oscillation index (PDO) that indicates interdecadal climate variability in the sub-tropical and tropical Pacific. The biomass in the North Central Pacific correlates positively with PDO, while that in the East and West North Pacific correlates negatively with PDO.

A study for interannual variability of Pacific saury using a simple 3-box model of NEMURO.FISH

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A simple 3-box model of NEMURO.FISH (saury version: Ito *et al.* 2004) was forced by observed sea surface temperature (SST) from 1950 to 2002. In the model, fish wet weight is calculated according to a fish bioenergetics equation. The observed condition factor of Pacific saury showed quite large decadal variability with relatively large year-to-year variability. In the model, wet weight of Pacific saury also showed decadal and year-to-year variability, however the amplitude of decadal variability was much smaller than the observed. It may be due to the absence of a multi-species fish formulation in the model. Fishes like sardine which have large biomass and fluctuation, have the potential to affect to the zooplankton density in the saury migration region. We also investigate differences of interannual growth variability between spawning seasons. Since Pacific saury spawns from autumn to the folllowing spring, we set three seasonal (autumn, winter and spring) spawned cohorts in the model. The amplitude of growth variability is largest for the autumn spawned cohort and smallest in the spring spawned cohort. This difference is caused by the difference of life history of each spawned cohort. The spring spawned cohort spawns only once in the life, however other cohorts spawn twice in their life. The second spawning timing changed year-to year and it caused relatively large interannual variability in the autumn and winter spawned cohorts.

Modeling iterannual and decadal variability of Pacific saury

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Pacific saury, *Cololabis saira*, is mainly located in Northwest Pacific, and it is one of important commercial fisheries in Japan. Saury migrates widely in Northwest Pacific. Saury growth and stock vary widely from year to year, but the cause for these fluctuations is unclear due to paucity of data. A modeling approach is useful to investigate physical and biological processes responsible for variation of saury biomass and growth rate. This study focuses on interannual and decadal variability of physical and biological processes regulating Pacific saury growth. The saury model is linked with a 3-D lower trophic biological model consisting of multiple phytoplankton and zooplankton. The results show that the saury growth rate is higher during El Niño years, but lower in La Niña years. This is mainly due to the modeled interannual variability of zooplankton biomass in the mixed water region (Kuroshio-Oyashio interfrontal zone) and Oyashio regions where both young and adult saury feed. Also, the growth rate tends to be higher after the 1976/77 Pacific climate shift due to the modeled zooplankton biomass increase after the 1976/77 climate shift, which correlate well with the Pacific Decadal Oscillation (PDO). During the positive PDO phase, the mixed water region tends to be colder with deeper mixing during the winter and early spring. Therefore spring phytoplankton productivity is higher, which results in higher zooplankton biomass. The results show potential linkages between the physical variability and plankton dynamics with the Pacific saury growth and migration patterns.

Geographic variation in herring populations in the North Pacific: Understanding latitudinal responses to climate change

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Pacific herring (Clupea pallasi) occupy shelf waters (< 200 m depth) in all coastal areas in the northern Pacific, from the northern Bering Sea to California in the eastern Pacific, and to the Yellow Sea in the western Pacific. Within this range herring display both geographical (latitudinal) variation and location-specific climate variation (inter-annual climate variation). On both sides of the Pacific, the biological responses of herring to latitudinal variation are similar to those in many fish species. Compared to northern areas, in southern areas spawning time is earlier, duration of spawning time is longer, age and size of sexual maturity is younger, and asymptotic size ($L\infty$ and $W\infty$) is smaller. In contrast, latitudinal differences in length-weight relationships, egg size, size-specific fecundity and relative fecundity are relatively small when compared among widely separated locations. Other aspects of geographic and temporal variation are not well understood. In recent years some more trends in geographic differences are emerging. Population diversity varies less in the north where there are fewer, but larger populations. The territory occupied by individual herring populations in the north may exceed that in the south. There may be a latitudinal difference in mean density of the adult stock (g/m2) estimated as the ratio of spawning stock biomass to the estimated habitat used by the stock. Among North American populations there also appears to be a latitudinal difference in recruitment, and the factors affecting it. Specifically, trophic conditions during the juvenile stages, especially during the first winter, appear to have greater impact in northern areas, although this remains speculative. Understanding the impacts of climate change on herring requires that we also understand the extent of latitudinal variation in biological and ecological processes. This paper presents a summary and synthesis of such latitudinal variation in Pacific herring, examined in the context of climate change.

Geographic variation in fish growth and population responses to regime shifts in the North Pacific: A comparison of herring and saury using NEMURO.FISH, a coupled fish bioenergetics and NPZ model

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NEMURO.FISH consists of a fish bioenergetics model coupled to the NEMURO lower trophic model, and evolved as a central synthesis tool from the MODEL Task Team activities of the CCCC Program for performing cross-species and geographical comparisons of fish responses to climate variability. The

NEMURO component simulates the daily dynamics of the lower trophic levels by simulating the uptake and recycling dynamics of nitrogen and silicon, and the photosynthesis and grazing interactions of multiple functional groups of phytoplankton and zooplankton. The fish bioenergetics component simulates the daily numbers of individuals, and their mean weight, in each age class over multiple generations. Three zooplankton groups simulated in NEMURO provide the prey for the fish models. Analyses will be presented that illustrate the advantages of synthesis centered on a common set of quantitative models. The examples involve simulation of historical regime shift effects on a north-south progression of three herring populations in the eastern North Pacific, and comparison of herring responses in the east basin with saury responses in the west basin. All populations showed a late 1970's shift in growth, but the direction and magnitude of the responses differed within herring populations and between herring and saury populations. Responses were also predicted during other time periods for various combinations of the populations. We discuss the advantages and limitations of the coupled modeling approach, likely future directions of our collaborative effort, and progress and challenges in using simulation modeling tools for forecasting climate effects on fish populations.

Ocean Sciences Meeting 2006, Honolulu, Hawaii

Simulated Herring Growth Reponses in the Northeastern Pacific to Historic Temperature and Zooplankton Conditions Generated by the 3-Dimensional NEMURO NPZ Model

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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-D NEMURO lower trophic 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 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 NEMURO-3D 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 to 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 1970's. 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 1970's shift. Interannual variation in zooplankton densities caused the herring growth response for WCVI. Temperature and zooplankton densities affected the herring growth responses in both Alaskan locations, with zooplankton dominating

Conference/symposium/workshop reports

Report of the APN Workshop "Climate Interactions and Marine Ecosystems"

In: PICES Newsletter, 13(1), 2005

Report submitted by: Cisco Werner (University of North Carolina), Bernard A. Megrey (NMFS, Alaska Fisheries Science Center) and Kenneth A. Rose (Louisiana State University)

 *Cisco is a Professor and Chairman of the Marine Sciences Department at the University of North Carolina at Chapel Hill, USA and also chairs the GLOBEC Scientific Steering Committee. Originally from Venezuela, Cisco completed his graduate work in physical oceanography at the University of Washington in Seattle. His research includes the development of circulation of coastal ocean models and their coupling to trophodynamic inidvidual-based models of planktonic and early life stages of marine organisms.*	 *Bernard is a Research Fisheries Biologist with NOAA's Alaska Fisheries Science Center where he has worked since 1982. As the lead investigator for recruitment modeling studies for FOCI, he has over20 years of experience studying dynamics of exploited North Pacific fish populations, relationships of environment to recruitment variability, and application of computer technology to fisheries research and natural resource management. His recent research has focused on developing indices of ecosystems status and health, building simulation models of marine ecosystems, and performing comparative analyses of system level characteristics of similar marine ecosystems.*	 *Kenny is a Professor with a joint appointment in the Coastal Fisheries Insitute and the Department of Oceanography and Coastal Sciences at Louisiana State University. Kenny joined the faculty of Louisiana State University in 1998, after 11 years as a research scientist at Oak Ridge National Laboratory. Kenny's research interests focus on the development and application of quantitative methods to aquatic ecosystems and fish population and community dynamics. Recent projects have centered on using individual-based and matrix projection models for fisheries management and for linking habitat quality and quantity with population health and sustainability.*

A workshop on Climate Interactions and Marine Ecosystems was held in Honolulu, Hawaii from 10-13 October 2004. In attendance were scientists from Canada, the Peoples Republic of China, Russia, South Korea and the United States (Fig. 1). Funding for the workshop was provided by the Asia-Pacific Network for Global Change Research (APN; http://www.apn.gr.jp/) through the award "Effects of Climate on the Structure and Function of Marine Food-Webs and Implications for Marine Fish Production in the North Pacific Ocean and Marginal Seas". Additional support for some of the workshop participants was provided by PICES and GLOBEC. The workshop took place roughly midway through the APN award and as such the goals of the workshop were to assess achievements of the working team to date and to develop plans for the remaining six months of the project.

Figure 1. APN workshop participants. Back row (standing): Matt Foster (USA), Shin-ichi Ito (Japan), Skip McKinnell (PICES), Alexander Leonov (Russia), Bernard Megrey (USA), Chang Ik Zhang (South Korea), Jake Schweigert (Canada), Doug Hay (Canada), Dave Eslinger (USA). Front row: Hal Batchelder (PICES, CCCC), Wei Hao (PRC), Irina Ishmukova (Russia), Michio Kishi (Japan), Kenny Rose (USA), Cisco Werner (USA).

The project's overall hypothesis is that global climate change can alter both the structure and function of the marine ecosystem, causing changes in energy cycling, plankton composition and dynamics, and ultimately fish production. The objectives of the project include: *(i)* to use a common marine food-web and fisheries bioenergetics modeling approach, along with long-term area-specific oceanographic and fisheries data sets, to understand the propagation of climate change effects up the marine food-web, *(ii)* to quantify its effects on energy cycling and fish growth and production in distinct geographic regions in the North Pacific; and *(iii)* to initiate a discussion of how these results can be integrated into the decision and policy making process by fisheries and resource managers.

Using NEMURO.FISH as a modeling framework (PICES Scientific Report No. 20, pp. 77-176), we focused on selected sites of the North Pacific shelf and continental margin regions. With Pacific herring as the initial target fish species, the workshop sub-hypotheses and resulting action items to be undertaken over the remaining months of the project can be summarized as follows.

Hypothesis 1: geographic variations in fish growth can be explained by differences in environmental conditions and resulting differences in lower trophic conditions. To address this hypothesis the workshop participants:

- identified locations where data sets are available for calibration of lower trophic levels (LTLs);
- cross-referenced the LTL target list with locations that may have data on Pacific herring, sardines, anchovy, mackerel and other potential target species;
- developed a strategy for analysis of these data via a coupled LTL and fish model to address the hypothesis on geographic variability; and,
- agreed to compile the available datasets with final site and target species selection to be determined depending on the quality of the various data sets.

Hypothesis 2: synchronous (or asynchronous) changes in herring growth rates across locations may be accounted for by basin-wide decadal-scale changes in environmental conditions. The workshop participants were updated on the recent efforts of the PICES' Fisheries and Ecosystem Responses to Recent Regime Shifts (FERRRS) Study Group. In particular, our hypothesis was reinforced by the FERRRS formal recommendation that Regime Shifts be considered as a concept for inclusion in ecological and management practices. With full-basin scale solutions as targets for the study of regime shifts in the longer term, an agreed target for the next six months is to implement and study the response of point LTL and coupled LTL-fish models at selected sites in the North Pacific both before and after periods associated with "regime shifts". This will allow for a measure of the possible sensitivity of the models' biological parameters to the pre- and post-regime shift conditions.

Hypothesis 3: future climate/global change scenarios may affect fish production through changes in structure of the lower trophic levels. The study of this hypothesis requires a three-dimensional basin-scale approach that, beyond simple sensitivity studies, may fall beyond the present six-month goals of the project. Preliminary results of a basin-scale approach were presented at the PICES meeting (following the APN workshop) that suggested that simulations of future climate change scenarios may be available in one to two years time. At this stage however, and guided by the basin scale model results and other sources such as the IPCC reports, it was agreed that exploratory tests could be conducted by changing bulk parameters in the point model.

An example of calibrating NEMURO.FISH to the region off the west coast of Vancouver Island (WCVI) British Columbia is given in Figures 2 and 3. First, the lower trophic level (LTL) model without fishes was calibrated to primary and secondary production data from the region (Fig. 2). Once the LTL was calibrated, then fishes were added and dynamically linked to the prey resource provided by the LTL in such a way that consumption by fishes appeared as a mortality term for the prey species. Parameters of the fish bioenergetic model were calibrated to observed Pacific herring data. These data indicate that total biomass ranges from 2-5 g wet weight/m^2 (Fig. 3, upper panel), that a 10 year-old herring is about 200 g wet weight (Fig. 3, middle panel), and that size-at-age data, expressed in g wet weight from the model compare well to observed growth and size data (Fig. 3, lower panel). Workshop participants will be actively searching for useable data sets with which to perform similar calibrations of NEMURO.FISH to other regions of interest around the Pacific Rim. We can then effectively examine large-scale ecosystem response to climate change or regime shifts once the calibrated versions of the model are in place.

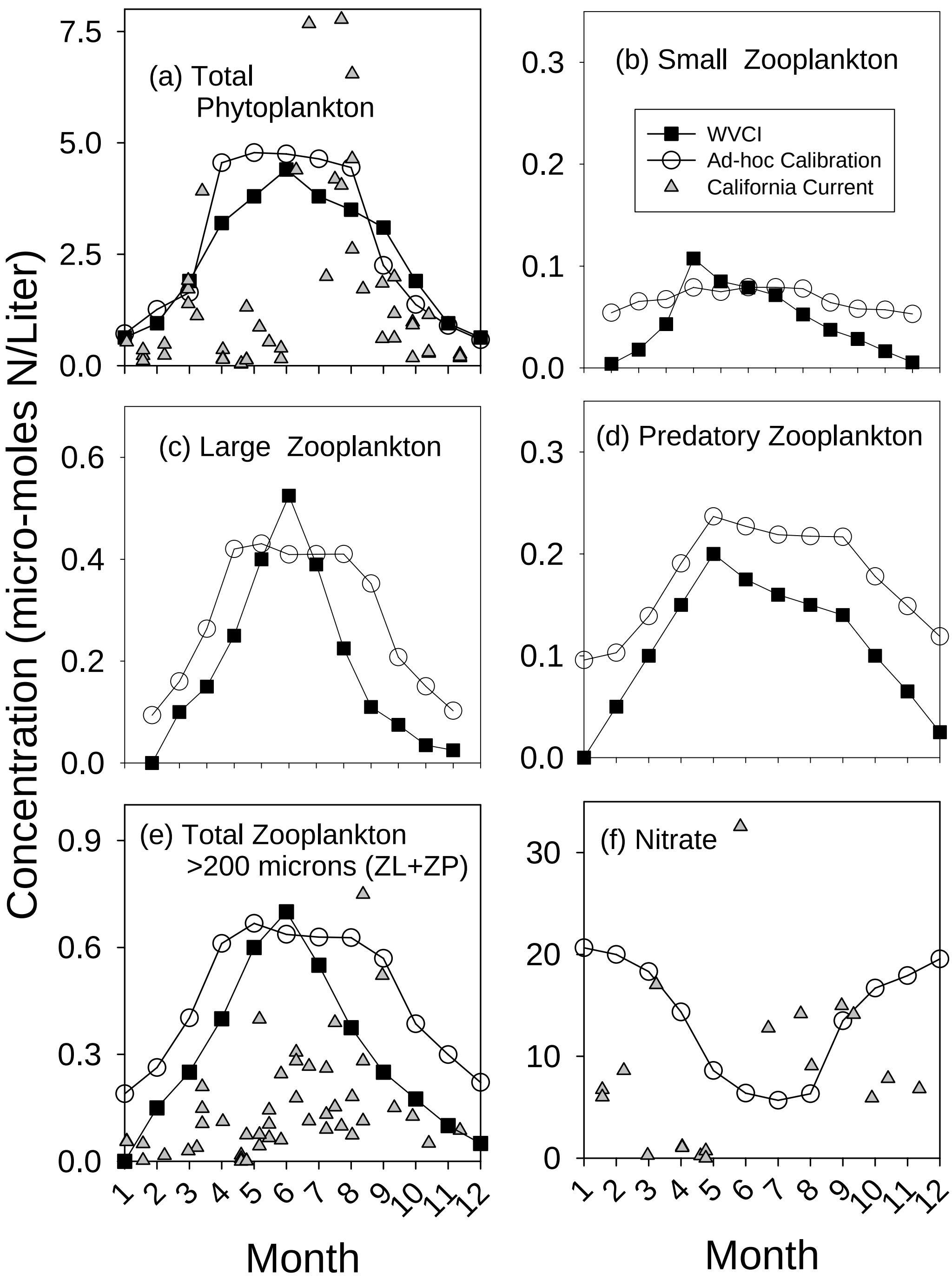

Figure 2. Idealized coastal data set for WVCI (solid square), field data reported for the California Current (grey triangles), and model predictions from the ad-hoc calibration (open circle). WVCI calibration data was not available for nitrate. California Current data was available for total phytoplankton, total zooplankton (greater than 200 microns), and nitrate. (a) total phytoplankton, (b) small zooplankton, (c) large zooplankton, ZL, (d) predatory zooplankton, ZP, (e) total zooplankton greater than 200 microns (ZL+ZP from NEMURO), (f) nitrate.

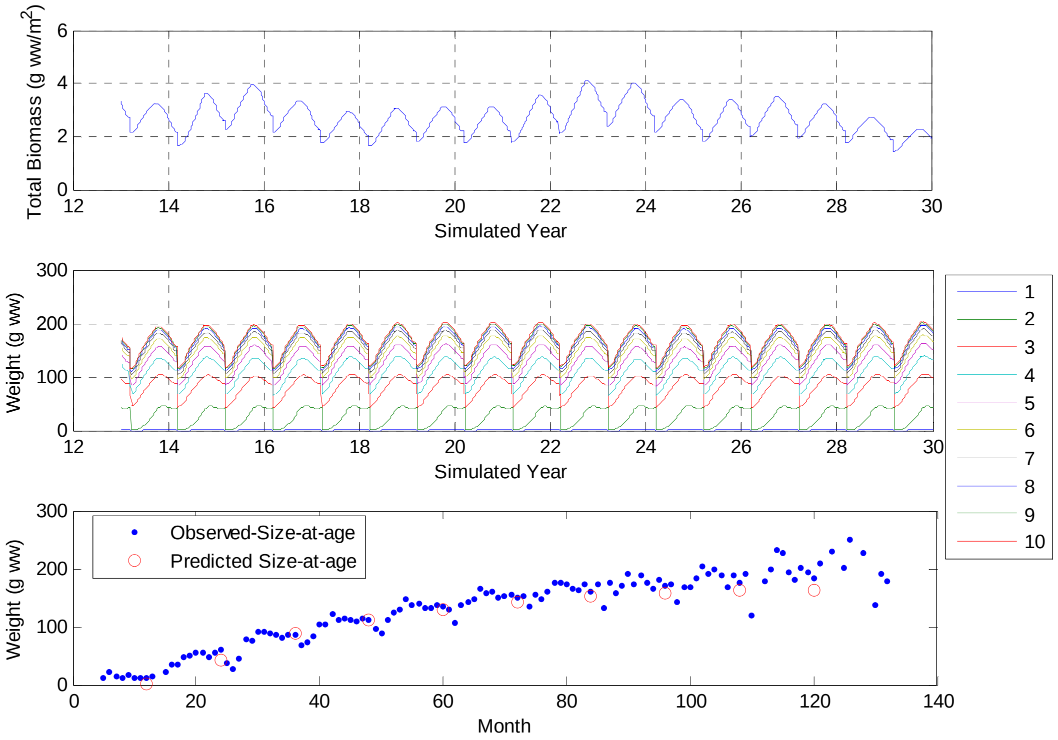

Figure 3. Results from the calibration NEMURO.FISH to Pacific herring data (simulating 10 year classes) from the west coast of Vancouver Island, British Columbia.

The workshop's success was not only in being able to address the above scientific hypotheses. The workshop also yielded significant results and insights in the areas or management – in particular as related to the communication of the present models' results to the managers – and in the area of capacity sharing.

Links to management. The discussions of the relevance of the present model products to management led to the following observations: *(i)* correlations between size-at-age and fish biomass (and their fluctuations) exist; *(ii)* providing information on the size-at-age of the target fish species is a useful indicator of population health; and *(iii)* size-at-age allows us to better understand fish mortality in the context of bottom up (fishing independent) factors.

Capacity sharing. The exchange of information among the workshop participants resulted in collective gains in the following areas: *(i)* preliminary model codes were explained and distributed; *(ii)* novel quantitative methods to study model sensitivity were discussed and adopted as part of the group's approach to studies in the coming months; and *(iii)* new fish target species (e.g., anchovy, sardines, etc.) were identified for future consideration and the associated data is to be made available.

Future communications. A portal will be set up to allow for ease of access of model code, data products and written material. The site will also serve as a repository of archival material.

To appear in PICES Newsletter (2007):

A seven year effort of the PICES CCCC MODEL Task Team culminates in a dedicated issue of *Ecological Modelling*

By Bernard A. Megrey, Francisco E. Werner, Michio J. Kishi and Shin-ichi Ito

A seven year effort of the PICES CCCC MODEL Task Team including planning, organizing, funding, and conducting 10 international workshops, will soon culminate with the publication of 19 peer-reviewed scientific papers on NEMURO (**N**orth Pacific **E**cosystem **M**odel for **U**nderstanding **R**egional **O**ceanography) and NEMURO.FISH (NEMURO **F**or **I**ncluding **S**aury and **H**erring) in a dedicated issue of *Ecological Modelling*. These contributions represent a rich set of case-studies and in-depth modeling studies using the NEMURO family of models focused on the North Pacific that address: oceanic biogeochemistry, regional and seasonal variability of phytoplankton and zooplankton, reconstruction of 40-50 years of plankton dynamics, effects of climate on herring and saury growth and population dynamics, the feasibility of automatic calibration methods, the sensitivity of the model to parameter values, and projections of future states of the ecosystem under scenarios of climate change.

NEMURO is a nutrient-phytoplankton-zooplankton (NPZ) model of the lower trophic level of the marine ecosystem dynamically coupled to a fish bioenergetics model (NEMURO.FISH). It was originally developed for Pacific saury and Pacific herring to study climate change impacts on important commercial species in the North Pacific basin. The model was named after the City of Nemuro that generously hosted the first model-buildup workshop in 2000 and several subsequent workshops. Under a separate project funded by PICES, Intra-American Institute (IAI), GLOBEC and the Asian Pacific Network (APN), NEMURO.FISH is now being extended to include species-to-species interactions via an implementation for anchovy and sardine populations (NEMURO.SAN) for regions that support important populations of small pelagic fish (California Current, Humboldt Current, Benguela Current, Oyashio/Kuroshio). NEMURO and NEMURO.FISH are among the few models that span and couple the processes from physics to populations of fish, include density-dependent ecosystem feedbacks, and potentially can be used to investigate the effects of climate change on populations of small pelagic fish.

Through the workshop process, the structure of NEMURO was developed in the course of discussions within a broad group of researchers from different fields including physics, biology and fisheries. Formulations and parameterizations were a result of a collective effort that engaged everyone equally. We believe that had smaller groups taken on similar tasks, it is likely that different formulations would have resulted, rather than the common single NEMURO and NEMURO.FISH formulations used in these papers. Similarly, once the formulations were agreed to, the implementation and application of the common model to different regions and different times was done with the benefit of the collective understanding gained through the joint “bottom-up” effort of the researchers involved. In other words, through the team effort, everyone’s cross-disciplinary awareness of the different issues and limitations was increased. The resulting contributions, even at the level of the individual papers, provide a broader perspective and integration of the results than would otherwise have occurred by groups working in isolation. It is safe to say that the effort resulting in the papers in the special *Ecological Modelling* issue is greater that the sum of its parts, and even goes beyond the scientific content of the papers to how the scientists involved will approach new problems in the future.

To achieve a long-term goal of a true common ecosystem model, the community of researchers needs to come to agreement on unique expressions of key biological traits. A grand challenge is to define unique empirical equations for marine ecosystems. For example, scientists working in one region of the ocean will formulate the temperature dependence of target organisms using the data from that region, while scientists at other sites will likely derive a different formulation. The MODEL Task Team’s effort in implementing NEMURO required the compilation of data from several locations in the North Pacific in order to set the model parameters. To make the data uniform and to be able to compare across sites, conversions needed to be applied. However, the factors themselves varied across sites and varied seasonally. The goal of constructing a “simple” ecosystem model for the North Pacific clearly showed that one of the most basic and important elements that can result from sustained international collaborations is the unification of observational methods, measurements and their interpretation. Such uniformity in approach will greatly help the definition of unique empirical equations for ecosystem modeling in general, and for their inclusion in a common NEMURO-like model.

Support from PICES and other agencies. Carrying out such ambitious objectives, among individuals coming from different countries and scientific cultures and backgrounds, was made difficult given that the work was conducted without the sustained support of a large well-funded international program. Fortunately, PICES provided a different approach. Working with PICES, the Co-Chairmen of the MODEL Task Team the four Co-Chairmen (who rotated over a seven year period) realized this difficulty and were able to secure funding from various sources [The Japan International Science and Technology Exchange Center (JISTEC, US$ 70,000), PICES (US$ 12,000), the City of Nemuro (US$ 40,000), Japan’s Fisheries Research Agency (FRA, US$ 60,000), the Heiwa-Nakajima foundation of Japan (US$ 30,000), GLOBEC (US$ 6,000), the Asian

Pacific Network (APN, US$ 45,000), and the Asian Pacific Network Capacity Building/Enhancement for Sustainable Development in Developing Countries Program (APN CAPaBLE, US$ 10,500)] to help fund the workshops that fostered model development.

PICES contributed significantly to the collaborative environment that was necessary to build our team by providing opportunities to meet at inter-sessional meetings and workshops, and by sponsoring special sessions at PICES Annual Meetings. This latter contribution helped keep the PICES community up-to-date on model developments as progress was reported, and basically kept the project on track. PICES has generously providing funding to help support new emerging scientists. It is important to note the capacity building component of this effort whereby many students were afforded the opportunity to be trained through the workshop process, with the tangible result that several papers in the *Ecological Modelling* volume resulted from MS and Ph.D. theses (including those by M. Fujii, D. Mukai, T. Hashioka and N. Yoshie). It bears re-iterating that the success of these efforts would not have been possible without the encouragement, support, coordination and funding enabled by PICES' commitment to the project.

Now that NEMURO and NEMURO.FISH have been tested and scrutinized by an international community, we thank PICES and the other agencies mentioned above for their support and we are pleased to publish the *Ecological Modelling* special issue which contains the latest papers describing the present status of NEMURO and/or NEMURO.FISH, as well as specific applications.

Summary. NEMURO was developed as a common ecosystem model for the North Pacific. However, ecosystem models are different from general ocean circulation models. Circulation models are derived from first principles, together with constraints imposed by temperature, salinity and mass conservation equations. Ecosystem models rely much more on empirical relations and the judgment of the developers as to what to include and what to ignore. Hence, developing a generalized ecosystem model involves additional challenges.

NEMURO is only one milestone in a long process toward achieving a common ecosystem formulation for use in the North Pacific. The framework offered by the NEMURO model and its extensions provide the opportunity to examine the dynamics and variability of the North Pacific marine ecosystem. Although the complexity of the system demands significant idealizations and approximations, important contributions resulted in several areas ranging from methodological, such as techniques for coupling across trophic levels and better parameter estimation, to process studies that provided better understanding of the factors controlling marine ecosystems. The next steps should include increased resolution (not just computational, but in the processes included) with the aim of providing projections of future states. There will continue to be a need for additional hindcast studies, but these will always be data-limited to some extent. It is important that models be used to identify where additional data need to be collected so that maximum advantage is taken of available resources, and so that the data are collected optimally for integration with the models.

As we better quantify the observed variability in marine ecosystems and our predictive capacity increases, we will move closer to our goal of providing stewardship of our marine ecosystems. While our approaches so far are relatively simple, they represent important steps towards the integration of our understanding of climate variability and the responses of lower trophic levels and fish populations. As such, we have reason to be optimistic about models providing information needed to manage our oceanic resources. However, efforts of the magnitude required to take the next steps in the development of future marine ecosystem models cannot happen without sustained resources to train the next generation of scientists who will lead this charge.

Personal Aspects of an International Collaboration

During the period of model development numerous investigators freely contributed untold amounts of energy, disciplinary perspective, and intellect towards the creation, testing and application of these models. This often required working extra hours planning for the workshop, long hours criss-crossing the international dateline, writing computer code in hotel rooms or while riding buses and trains, gathering in the lobby of a hotel after a late dinner to continue pursuing an interesting line of scientific thought, and then polishing these thoughts by working at home after the workshop. We are proud to report that the work was done in a true international team setting of cooperation and in a highly collegial manner of open scientific sharing. The code for the NEMURO and NEMURO.FISH is or soon will be posted on the PICES web site. The inter-personal collaborative aspect of the group's endeavor was as important as its scientific contributions. One outcome has been the growth of deep personal friendships among the participants and, in many situations, opportunities to exchange visits to each others houses and for families to meet each other. The photographs at the end of this article were taken on an excursion to Mt. Rainier National Park, during one such meeting in Seattle.

Dedication. We acknowledge the important contributions to NEMURO and NEMURO.FISH made by our colleague, mentor and friend Dr. Daniel Ware who sadly passed away in 2005. Dan's many insights and encyclopedic knowledge into the workings of marine ecosystems and detailed knowledge about fish biology and population dynamics greatly enhanced NEMURO and NEMURO.FISH. All of the MODEL Task Team members who collaborated with Dan feel privileged to have worked with him. In recognition of Dan's contribution, we dedicated the special issue of *Ecological Modelling* to him.

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