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REVIEW

A review of the NEMURO and NEMURO.FISH models and their application to marine ecosystem investigations

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Abstract The evolution of the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) family of models to study marine ecosystems is reviewed. Applications throughout the North Pacific have shown the models to be robust and to be able to reproduce 1D, 2D and 3D components of nutrient, carbon cycle and biogeochemical cycles as well as aspects of the lower trophic levels ecosystem (phyto- and zooplankton). NEMURO For Including Saury and Herring, an extension that includes higher trophic levels, can be run uncoupled or coupled to NEMURO. In the uncoupled mode, the growth and weight of an individual fish is computed using plankton densities simulated by NEMURO but with no feedback between fish consumption and plankton mortality. In the coupled mode, the feeding, growth and weight of a representative fish are computed, and prey removals due to feeding by fish appear as mortality terms on the prey. The NEMURO family of models continues to evolve, including effects of the microbial loop and iron limitation at lower trophic levels, and full life cycle, multi-species and multi-generational simulations at higher trophic levels. We outline perspectives for future end-to-end modeling efforts that can be used to study marine ecosystems in response to global environmental change.

Keywords NEMURO · Marine ecosystem model · North Pacific · PICES

1 Introduction

Climate change has come to the public's attention for its effects on the structure and function of oceanic ecosystems, and for its impact on fisheries resources. Terms such as

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global warming, El Niño and sea-level rise are now familiar to the general public. From a scientific perspective, a critical next step for addressing climate change-related issues is the construction and testing of models that can be widely applied and used to forecast the responses of oceanic ecosystems, including higher trophic levels, to climate change and variability.

To date, models of marine ecosystems have generally either focused on the physics (hydrodynamics) and lower trophic levels [nutrients, phytoplankton, zooplankton (NPZ)] or the higher trophic levels (e.g., fish); few "end-to-end" models exist, i.e., that simultaneously consider physical processes and dynamics of fish populations (Fulton 2010). For example, PlankTOM5 is an ocean ecosystem and carbon-cycle model that represents five plankton functional groups: the calcifiers, silicifiers, and mixed phytoplankton types, and the proto- and mesozooplankton types (Aumont et al. 2003). PlankTOM5 is a biomass-based ecosystem model that builds on the formulations proposed by Fasham (1993) and others, and is representative of many NPZ models that have been successfully used in the study of biogeochemical cycling (Le Quéré et al. 2005) and carbon budgets (e.g., Zahariev et al. 2008).

Modeling higher trophic levels has proceeded somewhat independently of the physics–NPZ approaches (Travers et al. 2007). Fish population dynamics has been emphasized because of its importance to stock assessment and management of harvest. Often, structured approaches, in which the population is divided into age- or stage-classes (e.g., Tuljapurkar and Caswell 1997), are used to allow for growth, mortality, and reproduction rates to vary as individuals go through their life cycle. In many higher trophic level models, the physics and lower trophic level dynamics are either ignored or idealized (Latour et al. 2003), the focus being on the population dynamics of the higher trophic level organism itself. Such structured models have also been developed for zooplankton, but for specific zooplankton species rather than the total zooplankton community (e.g., Carlotti et al. 2000; Moll and Stegert 2007). Multi-species models for the higher trophic levels exist, but these also tend to use simplified physics and lower trophic dynamics, and are considered exploratory because of data limitations in parameterization and testing (Rose and Sable 2009).

The PICES MODEL Task Team undertook a group effort to develop and link NPZ models to higher trophic levels (e.g., fish) to investigate climate effects on marine ecosystems in the North Pacific (Batchelder and Kashiwai 2007). The ultimate, long-term goal was to develop an end-to-end modeling framework that could be applied to a variety of locations. The PICES MODEL Task Team held a series of workshops and constructed a prototype lower-trophic ecosystem model named "NEMURO" (North Pacific Ecosystem Model for Understanding Regional Oceanography) (Fig. 1; Kishi et al. 2007a). Following the development of NEMURO, the Task Team developed a fish growth bioenergetics model designed to use as input the plankton densities generated by the NEMURO model. The resulting "NEMURO.FISH" (NEMURO For Including Saury and Herring) model, and its one- and two-way coupled implementations, is described for herring (Megrey et al. 2007a, b; Rose et al. 2007a, 2008) and Pacific saury (Ito et al. 2004, 2007). With NEMURO and NEMURO.FISH as the basis, the MODEL Task Team and others then modified these basic models for their specific systems and questions. We refer to this suite of models as the NEMURO family of models. NEMURO, NEMURO.FISH, and the first wave of these further applications were published in a special issue of *Ecological Modelling* (Kishi et al. 2007b), which served as a benchmark for the NEMURO effort.

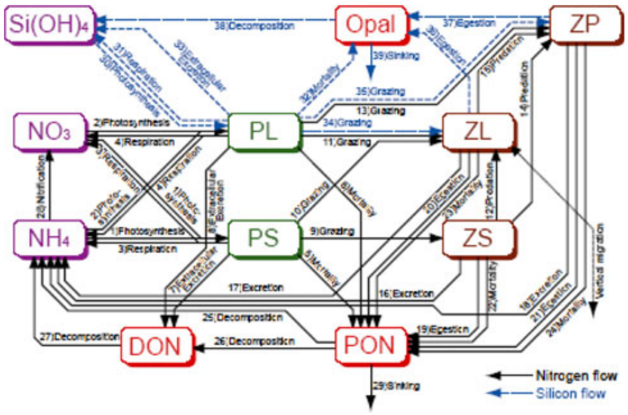
Si(OH)4
Opal
ZP
38)Decomposition
37)Egestion
36)Egestion
39)Sinking
31)Respiration
30)Photosynthesis
33)Extracellular Excretion
32)Mortality
35)Grazing
13)Grazing
34)Grazing
11)Grazing
15)Predation
14)Predation
NO3
PL
ZL
2)Photosynthesis
4)Respiration
3)Respiration
4)Respiration
2)Photosynthesis
1)Photosynthesis
8)Extracellular Excretion
10)Grazing
6)Mortality
20)Egestion
23)Mortality
12)Predation
20)Nitrification
NH4
PS
ZS
1)Photosynthesis
3)Respiration
9)Grazing
7)Extracellular Excretion
5)Mortality
17)Excretion
16)Excretion
22)Mortality
18)Excretion
21)Egestion
24)Mortality
Vertical migration
25)Decomposition
27)Decomposition
DON
26)Decomposition
PON
19)Egestion
29)Sinking
Nitrogen flow
Silicon flow

Fig. 1 Schematic view of the NEMURO flow chart

NEMURO and NEMURO.FISH have proven to be solid foundations for the development of versions applicable to other locations, new species and community types, and a broad range of questions related to climate change and variability. Since 2000, the year of the first NEMURO workshop, an extensive dialog between modelers, plankton biologists, oceanographers, and fisheries scientists has taken place producing over 30 NEMURO-related papers in peer-reviewed scientific journals. Many of these were conducted for distinct geographic regions and specific marine organisms. It is timely to pause and look retrospectively at the collection of the papers that have resulted. In this paper, we highlight the results based on the NEMURO family of models to date, discuss ongoing and next steps in the continued evolution of NEMURO towards the ultimate goal of an end-to-end modeling framework, and offer some observations concerning our experience with an international, multidisciplinary research effort.

2 NEMURO lower trophic model

NEMURO was initially developed for the North Pacific ecosystem and process formulations were agreed to during the initial MODEL Task Team workshops. Phytoplankton was represented by two functional groups [small (flagellates) and large (diatoms)] and zooplankton by three functional groups (small, large, predatory). The currency in the model was nitrogen, and many of the process equations were similar to other existing NPZ models (Fig. 1). A one-box version was developed, coded, and extensively exercised, both during and between workshops. Once the set of governing equations was agreed upon, participants in the workshops took the NEMURO set of equations and developed versions for their systems and questions. Below, we highlight NEMURO applications to carbon cycle/biogeochemical and ecosystem applications (see also Table 1). NEMURO special volume (*Ecological Modelling*, vol. 202) was published in 2002. We roughly review the papers in this volume and add the updated new papers related with NEMURO.

2.1 Carbon and biogeochemical cycling

Fujii et al. (2002) added a carbon cycle to the basic NEMURO model, embedded it within a vertical one-dimensional physical model, and applied it to Station KNOT (Kyodo North Pacific Ocean Time series; 44°N, 155°E). Observed seasonal cycles of ecosystem dynamics at Station KNOT, including surface nutrient concentration and column-integrated chlorophyll-*a*, were successfully reproduced by the model. The diatom bloom appeared about 1 month too soon, and while the simulated seasonality of total primary production was realistic, its magnitude was almost 50% higher than observed values during the summer period. Yoshie et al. (2003) used a one-

Table 1 Evolution of the NEMURO model

Paper	Spatial resolution	Location	Category	Contribution	Position in Fig. 3
Aita et al. (2003)	3D	North Pacific	Application	Influence of ontogenetic seasonal migration of large copepods	C
Fujii et al. (2002)	1D	Station KNOT	Application	New biogeochemical cycle (carbon)	A
Kuroda and Kishi (2004)	1D	Station A7	Data assimilation/ calibration	Used adjoint method to assimilate data	A
Yoshie et al. (2003)	1D	Western subarctic Pacific	Application	Addition of new biogeochemical cycle (carbon)	A
Yamanaka et al. (2004)	1D	Station A7	Application	Examination of biological processes equations	A
Smith et al. (2005)	1D	Hawaii	Application	Addition of microbial food web	E
Kishi et al. (2004)	1D	Station A7	Development/ methods	Framework and description of the lower trophic level NEMURO model	A
Kishi et al. (2007a)	3D	Western North Pacific	Application	Comparison of several NPZ models including NEMURO	C
Fujii et al. (2007)	1D	Station A7 and KNOT	Application	Spatial differences in seasonal dynamics	A
Wainright et al. (2007)	2D	California current	Application	Local response in seasonal dynamics	B
Hashioka and Yamanaka (2007a)	3D	Western North Pacific	Application	Relative roles of top-down versus bottom control	C
Komatsu et al. (2007)	3D	Kuroshio extension	Application	Role of advection and local production on plankton dynamics	D
Aita et al. (2007)	3D	North Pacific	Application	Retrospective decadal simulation and impact of regime shifts	C
Hashioka and Yamanaka (2007b)	3D	North Pacific	Application	Effects of global warming	C
Rose et al. (2007b)	1D	Station Papa	Data assimilation/ calibration	Use PEST to calibrate parameters	A
Yoshie et al. (2007a)	1D	Station A7 and Station Papa	Data assimilation/ calibration	Used Monte Carlo sensitivity analysis to examine parameter sensitivity	A
Lee and Chang (2008)	1D	East China Sea	Data assimilation/ calibration	Used ad hoc parameter manipulation to calibrate model to observed chlorophyll data	A

dimensional vertical model with NEMURO plus the addition of a carbon cycle to investigate the processes relevant to the spring diatom bloom in the western subarctic Pacific. The diatom bloom plays an important role in the biogeochemical cycles in this region. The 1991 conditions were repeated for 10 years, after which the actual forcing for 1991 through 1998 was applied. Their analysis concluded that deep mixing significantly affected the amplitude of the spring diatom bloom not only through increased supply of nutrients but also through dilution of zooplankton which, in turn, significantly reduced grazing pressure. Yamanaka et al. (2004) applied a one-dimensional version of NEMURO that included the carbon cycle to data from Station A7 off Hokkaido Island (41.5°N, 145.5°E), Japan. The model successfully simulated the observed diatom spring bloom, seasonal variations in nitrate and silicic acid concentrations in the surface water, and inter-annual variations in chlorophyll-*a*. Smith et al. (2005) added a microbial food web to NEMURO and used a one-dimensional version to simulate primary production, recycling, and export of organic matter at a location near Hawaii. They compared model predictions with and without the cycling of dissolved organic matter (DON) via the microbial food web, and were able to match the observed mean DOC vertical profiles near the station by tuning only the parameter that determined the fraction of overflow DOC that was labile within their model. The simulated bulk C:N re-mineralization ratio from the microbial model agreed well with observed estimates for the North Pacific subtropical gyre. They concluded that overflow production and the microbial food web were needed to reconcile biogeochemical and primary production measurements at this oligotrophic site. Fujii et al. (2007) described a 1D (vertical) version of NEMURO that was applied to Stations A7 and KNOT in the subarctic western North Pacific and to Station PAPA (50°N, 145°W) in the subarctic eastern North Pacific. Model results show significant west–east differences in seasonal dynamics, including larger seasonal amplitudes in sea surface temperature, mixed layer depth, surface nutrients, chlorophyll and partial pressure of CO_2 at the sea surface (pCO_2), and higher primary productivity at Stations A7 and KNOT than at Station PAPA. Two measures of productivity were compared: the e-ratio defined as the ratio of the export production (downward PON flux across 100 m depth) to net community production above 100 m depth, and the f-ratio defined as a ratio of new production (NO_3 uptake) to net community production (uptake of NO_3 and NH_4) above 100 m depth. The modeled annual-mean e-ratios were higher at Stations A7 and KNOT than at Station PAPA due to higher plankton biomass and mortality in the western North Pacific. Modeled annual-mean f-ratios were systematically higher than e-ratios due to the effect of nitrification, and f-ratios were lower at Stations A7 and KNOT than at Station PAPA because of higher ammonium concentrations in the western North Pacific. Fujii et al. concluded that detailed information on winds and pCO_2 values was necessary to reduce the uncertainty in estimating air–sea CO_2 flux, and that the west versus east differences in the biogeochemistry were primarily caused by differences in the physical and environmental conditions.

The original NEMURO process equation that describe the preferential uptake of NH_4 over NO_3 can at times show formulation inconsistencies (Vallina and Le Quéré 2008) for certain combination of parameter values. While we are aware of this problem, we believe all applications of NEMURO described here use parameter values that provide credible values of this process equation (i.e., they range between 0 and 1.0). We note this result to alert potential users of NEMURO to check these process equations for proper outcomes or consider the alternative formulation proposed by Vallina and Le Quéré (2008).

2.2 Lower trophic ecosystem results

Aita et al. (2003) developed a global three-dimensional version of NEMURO (3D-NEMURO) for the North Pacific. They compared simulations with and without ontogenetic seasonal vertical migration of the large zooplankton group (ZL). In the northwestern Pacific, they found that primary production was higher when vertical migration was included, that large phytoplankton dominated, and that the presence of large zooplankton throughout the year reduced primary production of the large phytoplankton. The effect was greatest for the spring bloom period. This is a very important point in NEMURO products and this is the reason why ontogenetic vertical migration of copepods is included in NEMURO.

A 2D cross-shelf formulation was used by Wainright et al. (2007) to simulate the lower trophic level dynamics of the near-shore pelagic zone of the California Current System. They simplified the basic NEMURO structure by grouping certain parameters related to density-dependent mortality rates, grazing rates, and Ivlev constants, and by eliminating the seasonal vertical migration of the large zooplankton group. The model predicted low and constant phytoplankton biomass during the upwelling season, which closely fit the low values observed in the early-summer and fall, but model predictions underestimated phytoplankton biomass during the mid-summer period. Kamezawa et al. (2007) also noted that NEMURO model predictions of zooplankton densities were low, and they used a correction factor based on field data to adjust the simulated zooplankton biomass when they used the results in a salmon bioenergetics model in the northern Pacific.

Hashioka and Yamanaka (2007a) used a version of 3D-NEMURO focused on the western North Pacific to study the seasonal and horizontal variation in phytoplankton and their relation to top–down and bottom–up control. Consistent with observations, their results showed that the annually averaged biomass of diatoms (large phytoplankton), represented as a percentage of total phytoplankton, was 50–60% in the subarctic region and <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. Diatom biomass at the Kuroshio and subarctic sites was dominant during the winter, and then decreased from the spring bloom to the summer due to return of the copepods from the deep waters and low silicate concentrations. At the subtropical site, the dominance of diatoms was mostly controlled by nutrient availability.

Also focusing on the western Pacific region, Komatsu et al. (2007) analyzed a 3D implementation of NEMURO focused on the role of advection in affecting plankton biomass in the frontal region of the Kuroshio and its extension. 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, plankton biomass was controlled mostly by advective processes. Local maxima were predicted in convergence zones associated with meander ridges, which was also pointed out by Yoshimori (1994). Outside the frontal zone and meanders, plankton biomasses were greatly influenced by in situ biological growth.

Aita et al. (2007) used 3D-NEMURO to perform a retrospective simulation from 1948 to 2002 for the North Pacific to investigate the effects of regime shifts on phytoplankton and zooplankton dynamics. They found that the model results showed changes in phytoplankton biomass, zooplankton biomass, and primary production in the central North Pacific consistent with the known regime shift in the late 1970s, and that these changes correlated with the Pacific decadal oscillation (PDO; Hare and Mantua 2000). Aita et al. (2007) hypothesized that additional top–down predation on phytoplankton, presently missing from the model, may explain the discrepancy between model results and observations at the Bering Sea site. Hashioka and Yamanaka (2007b) also used 3D-NEMURO to examine potential global warming impacts on the lower trophic level in the western North Pacific. They used the results of Hashioka and Yamanaka (2007a) as present-day conditions. They then used the projected conditions in 1990–2100 from a climate model as boundary conditions for their physical model. Model simulations showed that global warming increased vertical stratification associated with rising temperatures, and resulted in decreased surface nutrient and chlorophyll concentrations by the end of the twenty-first century.

Sumata et al. (2010) made eddy-permitting ocean general circulation model and embedded NEMURO-like model. Although their model is not the same as NEMURO because many parameter values were modified and excluded ontogenetic vertical migration of copepods, the structure of ecosystem model was based on NEMURO. And they discussed the role of meso-scale eddies on primary production, concluding that horizontal advection due to seasonal and eddy fluctuations plays an important role in the redistribution process, in addition to that effected by temporal-mean advection.

2.3 Model parameter sensitivity studies

Kuroda and Kishi (2004) applied a data assimilation technique to estimate NEMURO's biological parameter values. They used a Monte Carlo method and selected eight parameters (of the over 70 parameters in NEMURO) that most impacted the simulated values of interest. They then used an adjoint method, with biological and chemical data from Station A7 (east of Japan), to estimate values for the eight parameters. Twin experiments were conducted to determine how well the data constrained the values of the eight parameters. Model predictions using the optimum parameter values determined with data assimilation agreed more closely with the seasonal changes of observations than predictions made based on set of parameter values subjectively determined based on the known dynamics at Station A7. Specifically, assimilation resulted in an increased maximum photosynthetic ratio of small phytoplankton, a decreased maximum photosynthetic ratio of large phytoplankton, and an increased maximum grazing ratio of predatory zooplankton. Kishi et al. (2004) compared NEMURO with several other lower trophic level models in the northern North Pacific. The different models were each embedded in a common three-dimensional physical model, and the simulated vertical flux of PON and the biomass dynamics of phytoplankton were compared among NPZ models. In their study, all original parameter values were used except the maximum photosynthetic ratio for the coastal model (KKYS: Kawamiya et al. 1997). All the models reproduced primary production well, even though none of them explicitly included iron limitation effects. On the whole, NEMURO gave a satisfactory simulation of the vertical flux of PON in the northern North Pacific.

Ito et al. (2010) carried out the calibration of NEMURO.FISH parameters using PEST (model-independent Parameter ESTimation) program. The PEST-estimated parameter values generated spatial maps that were similar to the satellite data for the Kuroshio Extension during

January and March and for the subarctic ocean from May to November. With non-linear problems, such as vertical migration, PEST should be used with caution because parameter estimates can be sensitive to how the data are prepared and to the values used for the searching parameters of PEST.

Other sensitivity studies of NEMURO's parameters include automatic calibration methods (Rose et al. 2007b), Monte Carlo sensitivity analysis (Yoshie et al. 2007a), and an implementation in the north East China Sea (Lee and Chang 2008).

3 Higher trophic model (NEMURO.FISH and others)

The initial extension of NEMURO to include higher trophic levels, namely fish, was fully described in Megrey et al. (2007a) using herring as the fish species. A NEMURO.FISH version for saury was developed using the herring version as a template. The bioenergetics component of the saury version of NEMURO.FISH was described by Ito et al. (2004).

NEMURO.FISH was designed to run in two modes: uncoupled or coupled to NEMURO. In the uncoupled mode, the growth and weight of an individual fish is computed using plankton densities simulated by NEMURO but there is no feedback between fish consumption and plankton mortality. In the coupled mode, the growth and weight of a representative fish is also computed, but in addition, the numbers of individual fish in each age-class are also followed. This enables the total consumption by the fish of prey to be included as a mortality term on the plankton groups, and the potential for density-dependent growth of the fish if predation mortality sufficiently exceeds the productivity of the plankton as predicted by NEMURO. In the coupled mode, excretion and egestion by the fish are also used to contribute to the ammonium and particulate organic nitrogen compartments of NEMURO. The coupled mode used a standard age-structured approach and was used for multi-year simulations. To ensure a complete set of age classes were present, newly entering individuals must be added to the population each year (recruitment of age-1). Two approaches were included within the coupled mode: one approach was to simply assume constant recruitment (same number of age-1 individual enter each year), and the other approach was to use a spawner–recruit relationship to dynamically generate the new age-1 individuals added to the population every year. The spawner–recruit approach allows the dynamics of the model to affect spawning biomass (reproduction), which in turn, affects subsequent recruitment of young.

The bioenergetics component of NEMURO.FISH simulates the daily growth rate of an individual fish and is an implementation of the Wisconsin type of fish bioenergetics model. Wisconsin style bioenergetics models have been developed since the late 1970s and are widely used for modeling individual fish growth rates (Brandt and Hartman 1993). NEMURO.FISH used the same formulations for consumption, respiration, excretion, and egestion as used in many of these earlier applications (Hanson et al. 1997).

One-way NEMURO.FISH differs from the classical Wisconsin bioenergetics model is in how daily consumption is determined. In the Wisconsin approach, prey is not explicitly modeled but rather prey availability is calibrated by determining by iteration the daily consumption rate (as a fraction of maximum consumption, called *p* value) that is needed for a fish to grow from a known initial weight to a known final weight over some time period. Model results are then used to determine how much prey is needed is to support the observed growth, without having to know the dynamics of the prey. In NEMURO.FISH, we wanted to simulate daily fish growth using prey densities generated from NEMURO so we followed the approach of Rose et al. (1999) and replaced the iterative calibration of the *p* value with a Type-2 multispecies functional response. The functional response uses the same maximum consumption rate as the *p* value approach but uses prey densities to then determine daily consumption. In essence, prey densities are used to predict the *p* value and thus daily growth rate. A summary of NEMURO.FISH studies follows below (also see Table 2).

3.1 Applications to Pacific herring and basin scale considerations

Megrey et al. (2007a) documented the basic NEMURO.FISH model. The bioenergetics, linkage to NEMURO, and uncoupled and coupled modes were described using the well-studied herring population off the West Coast Vancouver Island. Thirty-year simulations were performed, and total population biomass, weights-at-age, and zooplankton densities were compared between uncoupled and coupled versions to demonstrate the potential effects of density-dependent growth. Within the coupled version, both constant recruitment and dynamic recruitment (spawner–recruit relationship) approaches were illustrated. Sensitivity of NEMURO parameters were also discussed, and weight at age-5 and total biomass were most sensitive to consumption-related parameters of herring, when fish parameters were held constant.

Rose et al. (2007a) used output from Aita et al.'s (2007) basin-scale 3D-NEMURO simulations as input to NEMURO.FISH in the uncoupled mode. Rose et al. (2007a) simulated the daily growth of herring from 1948 to 2000 at three northeastern Pacific locations (West Coast Vancouver Island, Prince William Sound, and Bering Sea).

Table 2 Evolution of the NEMURO.FISH model

Paper	Species	Resolution	Physical environment	Migration	Feedback to LTL	Population	Category	Contribution	Position in Fig. 3
Ito et al. (2004)	Saury	3-box	Online	Calendar date	Static link	–	Development/ methods	Initial framework for a fish bioenergetics model	G
Megrey et al. (2007a)	Herring	1-box	Online	–	Dynamic link	Constant mortality	Development/ methods	Final framework for the fish bioenergetics model which dynamically linked the lower trophic level NEMURO to a higher trophic level fisheries population dynamics and bioenergetics model	F
Mukai et al. (2007)	Saury	3-box	Online	Size-dependent	Static link	–	Application	Impact of time of spawning to growth dynamics	G
Ito et al. (2007)	Saury	3-box	Offline	Size-dependent	From sardine	–	Application	Effects of sardine zooplankton predation on saury growth dynamics	G
Rose et al. (2007a)	Herring	1-box	Offline	–	Static link	Constant mortality	Application	Impact of historical temperature and zooplankton conditions on herring growth	F
Rose et al. (2007b)	Herring	1-box	Offline	–	Dynamic link	Constant mortality	Data assimilation/ calibration	Model calibration application using PEST	F
Megrey et al. (2007b)	Herring and saury	3-box	Offline	Size-dependent	Static link	Constant mortality	Application	Examination of basin-scale response to climate change	G
Rose et al. (2008)	Herring	1-box	Online	–	Static link	Constant mortality	Application	Impact of climate regime effects on herring growth	F
Kamezawa et al. (2007)	Salmon	Multi-box	Offline	Calendar date	–	–	Application	Impact of climate on growth of chum salmon using a 1D LTL	H
Kishi et al. (2009)	Squid	Multi-box	Offline	Calendar date	Static link	Constant mortality	Application	Impact of climate on growth of squid	H
Okunishi et al. (2009)	Sardine	¼°	Offline	Fitness + ANN	Static link	Constant mortality	Application	Individual-based fish model including a bioenergetics model, a Lagrangian transport model and an artificial neural network system to evaluate influence of food and the environment on fish migration	I
Kishi et al. (2010)	Salmon	Multi-box	Offline	Calendar date	Static link	Constant mortality	Application	Impact of climate on growth of chum salmon using a 3D LTL	H

Model predicted weights-at-age, and annual averaged temperature and zooplankton concentrations, were then analyzed statistically to identify specific regime periods. All three populations showed a shift corresponding to the known regime shift in the late 1970s, with herring growth decreasing in West Coast Vancouver Island and Prince William Sound and increasing in the Bering Sea. Rose et al. (2008) expanded on earlier NEMURO.FISH analyses of herring for the West Coast Vancouver Island location by using the coupled version to examine the growth and population dynamics of herring during historical climate regime periods. The coupled models simulated the nutrients, plankton, and herring growth and population dynamics in a single well-mixed spatial box configured for the coastal upwelling area off Vancouver Island that serves as the summer feeding grounds of southern British Columbia herring. Model simulations (41 years) were performed to isolate the effects of each of four documented climate regimes (1962–1976, 1977–1988, 1998–1999, 1998–2002) on herring growth and weight-at-age. Climate regimes differed in the environmental variables used in the spawner–recruit relationship, and the daily water temperature, mixed layer depth, and nutrient flux input into NEMURO. A historical simulation (1962–2002) and simulations that used repeated conditions for each regime (extended to cover 41 years) were performed. Model-predicted weights-at-age, recruitment, and spawning stock biomass were highest in Regime 1, intermediate in Regime 2, and lowest in Regime 3. Additional simulations with various combinations of the regime-specific environmental effects on recruitment and the environmental variables for NEMURO turned on and off showed that the regime effect on weight-at-age was a mix of recruitment and lower trophic level (NEMURO) effects that varied in direction and magnitude among the four regimes.

3.2 Applications to Pacific saury and migration considerations

In the initial saury application of NEMURO.FISH, Ito et al. (2004) simulated saury growth using NEMURO-generated zooplankton densities for three spatial boxes (Kuroshio, Oyashio, and inter-frontal zone or mixed water region). Weight of an individual saury was followed from larvae to age-2, and was started at two different times during the year to represent the two major cohorts from spawning. The individual fish was moved among the boxes using fixed rules to mimic their known migration patterns between the feeding grounds and spawning areas. Environmental conditions were repeated each year in short (4 years) simulations. Simulated weight per individual over time agreed well with observed growth patterns, and additional simulations demonstrated the sensitivity of growth to variation in temperature and prey densities.

Mukai et al. (2007) used NEMURO.FISH in the uncoupled mode to consider how spawning timing affected saury growth. They used a similar 3-spatial-box configuration as Ito et al. (2004), and examined the growth (wet weight) of an individual fish for 2 years that originated in winter in the Kuroshio box, in spring in the mixed water box, and in autumn in the mixed water box. 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 showed the fastest growth). Mukai et al. (2007) suggested that the different growth rates from the three spawning events could help explain the bimodal size distribution of the fishery catch.

Ito et al. (2007) also used the 3-box saury version of NEMURO.FISH in the uncoupled mode to examine how temperature affected saury growth. Observed sea surface temperatures for each spatial box for 1950–2002 were used as input to NEMURO and the saury bioenergetics model. Simulations using three spawning times (spring, winter, autumn) under climatological temperature and the historical temperatures showed that differences in observed growth variability were suggested to be related to differences in the life histories among the autumn, winter, and spring cohorts of saury. On longer time-scales, Ito et al. (2007) found that modeled wet weight of Pacific saury showed decadal variability consistent with long-term observations in the Kuroshio and mixed water regions.

3.3 Comparisons between herring and saury

Megrey et al. (2007b) used NEMURO.FISH to compare growth of both Pacific saury and herring at locations off Japan and California. Their approach, as in Rose et al. (2007a), was to use 3D-NEMURO output to force an uncoupled NEMURO.FISH model. The study of Megrey et al. (2007b) considered how the different life histories of herring and saury interacted with the different environmental conditions between Japan and California to influence their growth responses to regime periods during 1948–2002. They found consistent shifts in 3D-NEMURO generated temperature and zooplankton densities and in NEMURO.FISH predicted growth rates for both fish species in both areas that roughly matched the known regime shifts in 1976–1977 and 1988–1989, although not all variables responded to the same degree in exactly the same year. Megrey et al. (2007b) also noted that the simulated weights-at-age of herring and saury were sometimes synchronous and other times were out of phase.

3.4 Applications to other species: salmon, squid, sardine

Following the publication of the *Ecological Modelling* special issue in 2007 focusing on saury and herring for the upper trophic levels, NEMURO.FISH has been used in the study of other upper trophic levels. In the uncoupled mode (bioenergetics growth only), NEMURO.FISH has been applied to chum salmon, *Oncorhynchus keta* (Kamezawa et al. 2007; Kishi et al. 2010), Japanese common squid, *Todarodes pacificus* (Kishi et al. 2009), and Japanese sardine (Okunishi et al. 2009).

Aydin et al. (2005) used NEMURO coupled with food web model (Ecopath/Ecosim) for pink salmon (*Oncorhynchus gorbuscha*). The linked approach shows the importance of seasonal and ontogenetic prey switching for zooplanktivorous pink salmon, and illustrates the critical role played by lipid-rich forage species, especially the gonatid squid *Berryteuthis anonychus*, in connecting zooplankton to upper trophic level production in the subarctic North Pacific. They varied the timing and input levels of coastal salmon production to examine effects of density-dependent coastal processes on ocean feeding; coastal processes that place relatively minor limitations on salmon growth may delay the seasonal timing of ontogenetic diet shifts and thus have a magnified effect on overall salmon growth rates.

Kamezawa et al. (2007) and Kishi et al. (2010) applied the bioenergetics approach of NEMURO.FISH to chum salmon. They assumed that SST and prey zooplankton density were the main factors influencing the observed variations in chum salmon body size. The zooplankton densities (specifically the large zooplankton group) from Aita et al. (2007) were too low compared with observations, so Kamezawa et al. (2007) adjusted the zooplankton densities from 3D-NEMURO based on the observed data. Using the SST and adjusted large zooplankton densities from the 3D-NEMURO, simulated salmon growth was compared for the 1972 and 1991 year classes. Modeled growth was faster for the 1972 year class than for the 1991 year class, in agreement with observations.

Kishi et al. (2009) applied the same uncoupled NEMURO.FISH approach to Japanese common squid, *Todarodes pacificus*, which migrates in the North Pacific and the Japan Sea. Daily values of temperature and zooplankton densities for a 1-year period were interpolated from the present-day and global warming simulations reported in Hashioka and Yamanaka (2007b) for the western Pacific. Daily values were obtained for a 2D spatial grid by averaging the 3D NEMURO output over the top 50 m for temperature and the top 20 m for zooplankton densities. Weight of an individual squid was then simulated for a 1-year period using the interpolated temperature and zooplankton densities they experienced as they migrated and moved around on the 2D grid. Movement was simulated using migration routes derived from passive particle simulation results and field data information. Predicted growth of the squid was compared between two groups that differed in their season of spawning and in their migration routes. Results showed that differences in the growth rates of the groups could be explained by differences in temperature and prey experienced on their migration routes, and that global warming could result in slowed growth due to temperature exceeding optimal values.

Okunishi et al. (2009) developed a two-dimensional individual-based version of the uncoupled NEMURO.FISH model to investigate the early life stage growth of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific. The sardine model was much expanded from the basic NEMURO.FISH in that the age-structure was replaced by following individuals and movement was predicted rather than using fixed rules as in the saury and squid versions of NEMURO.FISH. Sardine was assumed to start as hatched larvae and their growth, survival, and movement followed. In the model, feeding migration was assumed to be governed by search for local optimal habitats, which was estimated by expected growth as predicted by the bioenergetics model. Spawning migration was modeled by an artificial neural network (ANN) with an input layer composed of five neurons that receive environmental information (surface temperature, temperature change experienced, current speed, day length and distance from land). The ANN parameters were optimized using a genetic algorithm (Huse and Giske 1998). Okunishi et al. (2009) successfully reproduced realistic migration of Japanese sardine, and showed that prey density may be important in determining the feeding migration route, whereas temperature and day-length appear dominant in controlling spawning migration routes.

4 Current state of the NEMURO family of models

NEMURO, and the various versions of NEMURO.FISH, have been applied to a variety of coastal and marine ecosystems (Fig. 2; Tables 1 and 2) and have spanned a wide range of temporal, spatial, and biological scales (Fig. 3). While the original focus was on the North Pacific, the application of NEMURO and NEMURO.FISH to the other locations and species described earlier suggests that the underlying modeling approach is flexible and robust. Figure 3 shows the positions of various NEMURO and

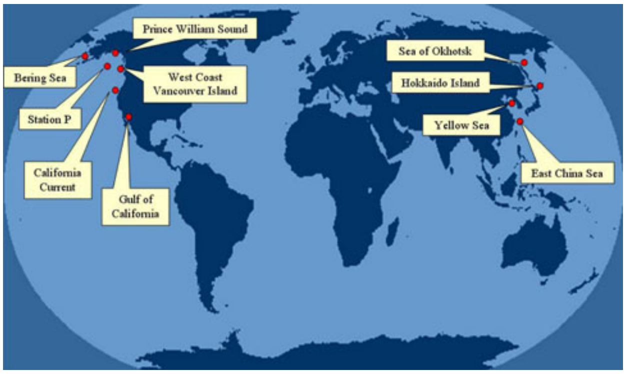

Fig. 2 Regions where NEMURO and/or NEMURO.FISH have been applied

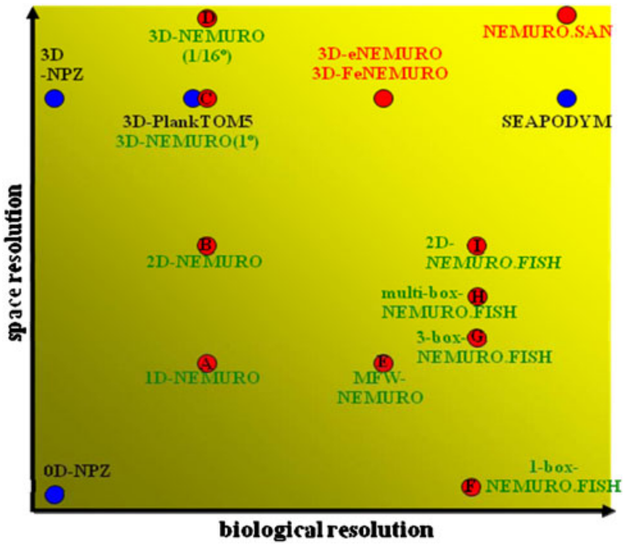

Fig. 3 NEMURO family features on a space-biological resolution plane (*red circles*). *Green legends* are NEMRO family models listed in Tables 1 and 2, and the *uppercase letters* in the *red circles* show corresponding references listed in Tables 1 and 2. *Red legends* are NEMURO family models on developing. Several other ecosystem models (*blue circles*) are also plotted for reference. SEAPODYM (Spatial Environmental Population Dynamics Model; Lehodey et al. 2003) is a multi-species model for tunas

NEMURO.FISH models on a space-biological resolution plane. We also included several other ecosystem models for reference. Some of the NEMURO-based models shown were not described in this paper because they are still under development or unavailable in English. Examples are: extended NEMURO (e-NEMURO) which includes subtropical plankton species (no-chain-forming diatom and pico-phytoplankton) in addition to the traditional subarctic plankton of NEMURO (Yoshie et al. 2007b, English version is in preparation); Fe-NEMURO, which adds iron limitation to NEMURO; NEMURO.SAN, a coupled, spatially explicit, individual-based, multispecies version; and NEMUROMS.SAN that embeds a multi-species formulation use the ROMS physical circulation model of Haidvogel et al. (2008) as a description of the physical setting. Indeed, NEMUROMS.SAN is approaching the end-to-end model stated as the ultimate long-term goal of this effort.

The NEMURO lower trophic level model appears to be a sound approach for simulating nutrient–phytoplankton–zooplankton dynamics. As NEMURO has its roots in the long tradition of NPZ modeling (Le Quéré et al. 2005; Franks 2009), this is not surprising but it is reassuring. Several analyses to date have included model to data comparisons that suggest NEMURO is a reasonable representation of lower trophic level dynamics for the open ocean (e.g., Fujii et al. 2002; Yoshie et al. 2003; Kishi et al. 2007a, b), as well as for coastal regions (e.g., Lee and Chang 2008). At the same time, there were many examples where NEMURO predictions differed from observed values. For example, Aita et al. (2007) noted that their 3D-NEMURO simulation underestimated zooplankton concentrations in the open ocean compared with observations. Kamezawa et al. (2007) noted consistent biases in simulated values from NEMURO compared to field data, and made adjustments to the values generated by NEMURO for use in their versions of NEMURO.FISH. They increased the simulated predatory plankton biomass by a factor of 1.9 to better agree with the observations. In NEMURO, the predatory zooplankton (ZP) is the highest trophic level in the ecosystem model, and includes the effects of other large predatory organisms, not explicitly included in the model, partly explaining why the simulated biomass of ZP is smaller than the one observed one.

NEMURO adopted a functional group approach to represent the phytoplankton and zooplankton communities. While changes in parameter values related to growth and mortality can accommodate the dominant plankton in many locations, the functional group approach has limitations. NEMURO followed two phytoplankton and three zooplankton groups, which is considered complex compared to other NPZ models (e.g., see Friedrichs et al. 2007), but yet is quite limited when the community-level shifts in the plankton are of interest or the NPZ model output is used to provide prey for a fish model that includes ontogenetic shifts in fish diets. At a recent workshop on end-to-end modeling, the idea of the traditional functional group approach to lower trophic modeling was questioned as being appropriate for linkage to fish and other upper trophic level organisms (Rose et al. 2010). The linkage to fish has shifted the purpose of the NPZ modeling from simulating biogeochemical cycling to providing realistic fluxes of the appropriate sizes and types of prey eaten by fish.

NEMURO was able to simulate the major temporal patterns in nutrients and plankton on interannual scales, but only moderately so for seasonal and daily time scales. NEMURO reproduced reasonable interannual dynamics compared with observations (e.g., Aita et al. 2007; Yamanaka et al. 2004), but had difficulty in some applications with seasonal timing of dominant groups. In general, NEMURO reproduced the well-defined peak of the spring bloom of diatoms (e.g., Kishi et al. 2007a, b; Yoshie et al. 2003; Yamanaka et al. 2004), but this was partly due to the forced vertical migration of the large zooplankton that terminated the bloom when they reappeared in the model in late spring. NEMURO performed more poorly when viewed at finer time scales than seasonal. As pointed out by Wainright et al. (2007), NEMURO used density-dependent mortality rates that were proportional to the square of plankton density. This type of mortality term is very effective in stabilizing biomass in the model, but also tends to suppress short time scale variation (day to a few days). However, short time scale variation in nutrients and plankton concentrations was reasonably reproduced in the Kuroshio Extension region (e.g., Komatsu et al. 2007). Caution should be used in relying on the short-term variation generated by NEMURO without careful evaluation of whether the variation is realistic enough for the particular system and application.

Judging how well NEMURO was able to reproduce key spatial dynamics is more difficult to ascertain. First, quantitatively comparing spatial variation and patterns between model predictions and observations is difficult (Rose et al. 2009). Second, the spatial variation generated by NEMURO depended on the resolution of skill of the physical model within which NEMURO was embedded. These physical models differed in their formulation, resolution, and domain across applications of spatially explicit versions of NEMURO, so a quantitative comparison of performance is not possible. Qualitatively, NEMURO appeared to be capable of generating broad-scale (100s of km or more) spatial features, and we suspect can generate meso-scale (10s of km) features if coupled to an appropriate physical model.

NEMURO.FISH offers a viable approach for linking the lower trophic levels to fish growth. The initial applications of NEMURO.FISH to herring and saury demonstrated that such linkages are possible and offers a way forward to addressing questions related to climate effects on fish. Promising results include the ability of NEMURO.FISH to reproduce regional differences in herring growth (Rose et al. 2007a; Megrey et al. 2007b) and in Japanese common squid (Kishi et al. 2009), and interannual differences related to climate (Rose et al. 2008; Ito et al. 2007; Kamezawa et al. 2007) and among cohorts spawned in different seasons (Mukai et al. 2007). NEMURO.FISH is a viable approach for clarifying single species responses to climate variability. Whether the functional group approach can continue to be expanded to accommodate the needs of the upper trophic organisms is unclear; the functional group approach generally gets unwieldy with more than 3–4 zooplankton groups. Others have proposed a size-based approach for lower trophic level modeling in order to provide realistic prey fields for the upper trophic levels (e.g., Maury et al. 2007).

In addition to being single-species, all of the versions of NEMURO.FISH either simulated multiple generations (i.e., full life cycle) in a very simplified spatial representation (one or a few spatial boxes), or simulated the dynamics of only a portion of the life cycle. The full life cycle versions also ignored the early life stages (eggs and larvae) and closed the life cycle via spawner–recruit relationships (eggs directly to age-1). Furthermore, movement beyond fixed rules has only been investigated in the sardine version (Okunishi et al. 2009). While the current set of NEMURO.FISH versions to date provides the components needed for an end-to-end model, no published version has combined all of these features into an operational end-to-end model.

We also point out that one danger to the continued evolution of models applied to new species is the ease of using parameter values from earlier species for the new species (Ney 1993). Such a situation can easily occur with NEMURO.FISH because the approach is to modify the basic NEMURO.FISH model when applying it to new species. Care must be taken to ensure that all model parameters are realistic for the new species because it is difficult to anticipate which parameters may become important in new applications.

5 Toward the future

The modeling approach to end-to-end food-web research has been well reviewed and proposed by Travers et al. (2007), Carlotti and Poggiale (2010), or Fulton (2010). As Fulton (2010) pointed out, no one approach defines end-to-end ecosystem modeling or there is no best model. Consequently, we have reviewed in this paper the Northern Pacific example based on NEMURO and its families. The NEMURO and NEMURO.FISH models continue to evolve. NEMURO was developed initially for a single spatial box model, and has been extended to one, two, and three spatial dimensions. The 3D-NEMURO used in many analyses has similar spatial and biological resolution as PlankTOM5. Komatsu et al. (2007) implemented a higher spatial resolution NEMURO (1°/16°) by coupling NEMURO with the CHOPE physical circulation model, and NEMURO is now also available as one of several NPZ model options in the publicly available version of ROMS (http://www.myroms.org/).

NEMURO has also evolved in its biological complexity. Initially, NEMURO tracked 11 state valuables involving silica, nitrogen, and functional groups of phytoplankton and zooplankton. In subsequent applications, NEMURO was extended to include the carbon cycle and the microbial food web, and ongoing efforts involve the inclusion of iron limitation (called Fe-NEMURO) and an extended set of plankton functional groups for subtropical plankton communities (called e-NEMURO). The functional group approach is commonly used in NPZ models, and the merits of the functional group approach and deciding on the number and types of functional groups continues to be a topic of discussion and some debate (Anderson 2005; Hood et al. 2006).

Further development of NEMURO.FISH involves continued use and expansion of existing versions, and the major step of combining aspects of the various versions into a single end-to-end model. NEMURO.FISH started with herring and saury, and was extended to simulate salmon, squid, sardine, and anchovy. Most applications of NEMURO.FISH used the uncoupled version and focused on specific life stages of the fish's life cycle. New versions of NEMURO.FISH are under development that simulate the entire life cycle so that multi-generational runs can be performed in which the long-term effects of climate change on population dynamics can be assessed. Effort is also focused on simulating multiple species so that competition and predation among the fish species can be explicitly represented. We are switching from an age-structured approach for the population dynamics to simulating individuals using an updated version of the super-individual method originally proposed by Scheffer et al. (1995). How to represent movement in three dimensions, adequately calibrate and validate model predictions of long-term fish community dynamics, and the numerical aspects of super-individuals eating super-individuals, closing the life cycle by representing eggs and larvae, and efficiently solving the coupled models so that runtime is reasonable, will all be formidable but surmountable challenges. None of the NEMURO models have dealt with acclimation and adaptation, detailed aspects of macroinvertebrates beyond the predatory zooplankton group (e.g., jellyfish, salps), and humans as active members of the upper trophic level community, all of which were identified at the recent end-to-end modeling workshop has important issues (Rose et al. 2010). With some additional work on these remaining issues, the basic ingredients are available from the various versions of NEMURO.FISH and other modeling efforts for constructing an end-to-end model, and we are optimistic we can achieve our ultimate goal of an operational end-to-end model within the next few years.

6 Concluding remarks

The NEMURO and NEMURO.FISH models greatly benefited from the international collaboration started as part of the MODEL Task Team of PICES. The variety of opinions and diversity of applications resulted in a better set of models. Our effort is a good example of an intensive international group effort involving a variety of disciplines. Our approach is one among many such efforts, and multidisciplinary collaborations will continue to increase into the future (Barabási 2005). We found that there is no substitute for face-to-face meetings despite the continued promise of remote meeting technology and the temptation to use email for interactive discussions. The result is that these efforts can seem inefficient in the beginning because the logistics and expense of face-to-face meetings results in only 1–2 meetings per year, and some time is needed to develop trust and effective communication among the team's members. Our effort was possible because of sufficient travel support and we gratefully acknowledge the agencies and programs that helped in this endeavor. The undertaking resulted in a well-tested and widely applied set of models and with many students gaining knowledge in marine ecosystem and fisheries modeling. Our experience was that, after a spin-up period, progress and applications accelerated and greatly surpassed the productivity likely obtained with an effort based on a smaller, more localized research team. A critical aspect was that at each step of the models' development there were cores of individuals within the broader group who devoted significant time and effort on the analyses between the meetings. Efforts, such as the development of NEMURO and NEMURO.FISH, should be encouraged because the product benefits from the diversity of the participants, and such efforts should be planned as long-term collaborations to ensure that the full benefits are realized.

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