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Initial design for a fish bioenergetics model of Pacific saury coupled to a lower trophic ecosystem model

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ABSTRACT

A fish bioenergetics model coupled with an ecosystem model was developed to reproduce the growth of Pacific saury. The model spatially covers three different oceanographic spatial domains corresponding to the Kuroshio, Oyashio, and interfrontal (mixed water) regions. In this coupled model, three (small, large, and predatory) zooplankton densities which were derived from the lower trophic level ecosystem model were input to the bioenergetics model of saury as the prey densities. Although certain model parameters were imposed from other species' bioenergetics, several model parameters were estimated from observational data specific to Pacific saury. The integrated model results reproduced appropriate growth rates of Pacific saury. Model sensitivities to water temperature and prey density are examined and observational methods to evaluate the model parameters are discussed.

Key words: fish/ecosystem coupled model, Kuroshio-Oyashio region, Pacific saury

INTRODUCTION

Pacific saury (*Cololabis saira*) is an important pelagic commercial fish in the northwestern Pacific with an average total yearly catch of about 250 000 tonnes (t). Landings in Japan have fluctuated from year to year depending on stock size. Body size and weight, which have fluctuated greatly from year to year (Watanabe *et al.*, 1997) are important factors in the price of saury. However, the causes of these fluctuations remain undetermined.

Pacific saury is widely distributed in the North Pacific (Hubbs and Wisner, 1980) and life history observations are limited. Similarly, experimental information has been limited, since saury are difficult to rear in laboratory settings (Hotta, 1958). Under these conditions of uncertain (or incomplete) information, modeling approaches are important tools to identify information and data gaps. Model sensitivity analyses can show which parameters are the most important to determine and can help guide and prioritize future field and laboratory research.

To investigate the mechanisms affecting variability in saury growth, abundance, and biomass, a model which is able to reveal the effect of environmental and feeding conditions is required. In this study, and as a first step, a fish bioenergetics model was coupled with a lower trophic level ecosystem model, to investigate the relationship between sea surface temperature (SST), prey zooplankton density and growth of saury. Although many model parameters were imposed from other species' bioenergetics, several model parameters were estimated from observational data specific to Pacific saury. Model sensitivities to water temperature and prey density are examined and observational methods to evaluate the model parameters are discussed. Megrey and Kishi (2002) already recommended and pointed out the possibility of extending such a fish bioenergetics/ecosystem coupled model to a

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*Correspondence. e-mail: goito@affrc.go.jp population level model. This kind of population dynamics including a fish bioenergetics/ecosystem coupled model will hopefully contribute to fisheries management of saury and other fishes.

Life history

In the northwestern Pacific, saury spawning starts in the mixed water region (the Kuroshio-Oyashio interfrontal zone) in autumn, moves to the Kuroshio area (the subtropical region) in winter and then returns to the mixed water region in spring (Odate, 1977; Watanabe and Lo, 1989; Watanabe *et al.*, 1997). Juveniles are advected to the Kuroshio extension region, where they grow, and migrate to the Oyashio region (the subarctic region) crossing the mixed water region for feeding. After sufficient feeding they migrate back in winter to the Kuroshio region to spawn. During their southward migration, they are fished in the Japanese coastal zone. During the last half century the total yearly catch of saury has fluctuated between 575 000 and 52 000 t with the size composition also varying considerably (Watanabe *et al.*, 1997).

Saury's knob length (KnL) (nearly the same as body length) reaches 30 cm in adults and many studies have been conducted to estimate saury growth rate using otolith analyses. For saury larvae and juveniles, Watanabe *et al.* (1997) and Oozeki and Watanabe (2000) estimated growth rate using geographically extensive field data in the northwestern Pacific during 1990–1997. They also estimated survival rate and production of juveniles in each season and suggested that juvenile production is stable in winter and that wintertime juvenile production might contribute to stable recruitment and fisheries landings of medium size (24.0–28.9 cm) saury in autumn. Also, using larval catch data during 1973–1986, Watanabe and Lo (1989) pointed out that winter was the most active spawning season.

It is very difficult however, to estimate the growth rate of adults, as a hyaline zone occurs in the otolith of adult saury which obscures accurate counting of growth increment there. This problem makes it difficult to determine the life span of saury. For example, Watanabe *et al.* (1988) estimated that saury grow up to 30 cm within 1 yr in the western Pacific whereas Suyama *et al.* (1996) estimated that it took about 560–690 days to grow to 31.5 cm.

Recently Kurita *et al.* (2004) developed a new method to estimate the hatch date from the age at which the otolith increment width reached a maximum for the second time. It has become possible to estimate the age of saury using this method even if there is a hyaline zone. They estimated the hatch date of large saury and suggested a new scenario of the life history of Pacific saury incorporating information on growth of saury with no hyaline zone (Okuda, 2002). According to this scenario, saury which hatch earlier in the season spawn in their first winter and also in their second winter. However, those that hatch later in the season do not spawn in their first year but spawn only in their second year. The complex life history of Pacific saury makes it difficult to identify the mechanisms causing variations in its biomass and size composition.

To identify environmental effects on the hatching of eggs, Oozeki and Watanabe (2000) conducted a laboratory incubation experiment on eggs of saury. They reared the same age larvae in three different temperatures and observed growth rates in the laboratory. Experiments were conducted for larvae of three different ages (9, 20, 30 days) and the dependence of growth rate as a function of age was tested. The results showed that growth rate increased linearly with temperature and also increased with larval age. They also analyzed the relationship between incremental growth of otolith and somatic growth of larvae in the laboratory. The results showed the possibility of estimating the growth rate of saury juveniles from otolith field data. Oozeki *et al.* (2004) estimated the instantaneous growth rate from field otolith data and analyzed the relationship between recent growth rate and the oceanic environment. Their results showed that SST and food density affected larval growth during the early stages, with SST and chlorophyll becoming more important in later larval stages. However, environmental influences on young and adult saury have not been quantified as saury are easily damaged during laboratory rearing.

THE FISH BIOENERGETICS/ECOSYSTEM COUPLED MODEL

The basic fish bioenergetics/ecosystem coupled model is the 'North Pacific Ecosystem Model for Understanding Regional Oceanography For Including Saury and Herring' (NEMURO.FISH). NEMURO.FISH was developed by the North Pacific Marine Science Organization (PICES) Model Task Team (Megrey and Kishi, 2002). NEMURO.FISH is composed of a lower trophic level ecosystem model (NEMURO) and a fish bioenergetics model.

The NEMURO includes 11 compartments (Eslinger *et al.*, 2000; Kishi and Megrey, 2001). Three are zooplankton compartments: small zooplankton (ZS), large zooplankton (ZL) and predatory zooplankton (ZP); two are for phytoplankton: small phytoplankton (PS) and large phytoplankton (PL); three are for nutrients: nitrate (NO_3), ammonium (NH_4) and silicate [$Si(OH)_4$] and others are for particulate organic nitrogen (PON), dissolved organic nitrogen (DON) and particulate organic silicate (Opal). We applied this lower trophic level ecosystem model, NEMURO, to three oceanographically different spatial areas representing the Kuroshio, mixed water and Oyashio regions (Fig. 1). In each area, SST is specified as both the surface boundary condition and the mixed layer temperature. The temperature at the bottom of the mixed layer (BLT) is set to be constant (World Ocean Atlas 1998: Antonov *et al.*, 1998) and is given as the bottom boundary condition (Table 1). The thickness of the mixed layer is assumed to increase to 150 m with a time scale of 100 days when the SST is lower than BLT. It is restored to 30-m depth with a time scale of 5 days when the SST is higher than BLT. The exchange rate of NO_3 and $Si(OH)_4$ between the mixed layer and the bottom layer is changed as a function of stability defined by the difference in temperature between the SST and the BLT. Light intensity is prescribed at the surface to integrate phytoplankton growth in NEMURO. Zooplankton densities and sea water temperature derived from NEMURO are used as inputs to the Pacific saury bioenergetics model.

The bioenergetics model is based on a model for Atlantic herring (*Clupea harengus*) proposed by Rudstam (1988). The growth rate of an individual Pacific saury is represented by the weight increment per unit of wet weight per time and is defined as:

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

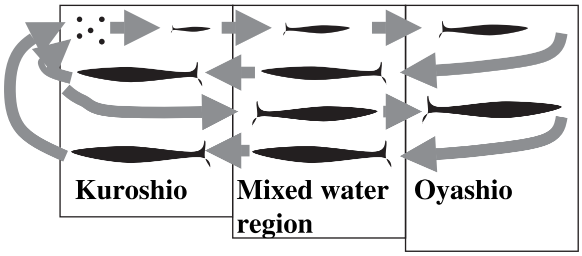
where W is wet weight of the fish (g), t is time (days), C is consumption (g prey g fish^{-1} day^{-1}), R is respiration or losses through metabolism (g prey g fish^{-1} day^{-1}), S is specific dynamic action or losses because of energy costs of digesting food (g prey g fish^{-1} day^{-1}), F is egestion or losses because of feces (g prey g fish^{-1} day^{-1}), E is excretion or losses of nitrogenous excretory wastes (g prey g fish^{-1} day^{-1}) and P is egg production or losses because of reproduction (g prey g fish^{-1} day^{-1}). CAL_z and CAL_f are caloric equivalents of zooplankton (cal g zooplankton^{-1}) and fish (cal g fish^{-1}) respectively. The formulations for these terms are the same as those of Megrey and Kishi (2002) except for egg production and are listed in the Appendix; values for constants are given in Table 2. Egg production is defined as a constant proportion as follows:

$$P = a_P \cdot C. \quad (2)$$

Table 1. Bottom boundary conditions for temperature and nutrients in NEMURO.

Bottom boundary condition	Kuroshio	Mixed water region	Oyashio
Water temperature (°C)	19.10	14.70	4.58
Nitrate (molN L^{-1})	6.0×10^{-6}	18.0×10^{-6}	25.0×10^{-6}
Silicate (molSi L^{-1})	6.0×10^{-6}	25.0×10^{-6}	30.0×10^{-6}

Figure 1. Schematic meridional view of the three oceanic spatial domains simulated in the model. The three oceanographically domains correspond to the Kuroshio, mixed water, and Oyashio regions. Eggs of Pacific saury (black dots) are assumed to be spawned in the Kuroshio region on 1 February. The saury (black fish shaped symbols, size of symbols indicate size of saury) migrate into the mixed water and Oyashio regions for feeding, then move southward for spawning during late autumn to winter, and repeat the migration in the next year. The saury life span is assumed to be 2 yrs.



PARAMETERS IN THE BIOENERGETICS MODEL

Odate (1977) and Kosaka (2000) divided the Pacific saury life history into six stages based on KnL. However, their divisions are not sufficient for adults since they migrate widely from the Kuroshio region to the Oyashio region. Herein, we divided the life history into nine stages, i.e. three stages in the Kuroshio region, four in the mixed water region and two in the Oyashio region (Table 3). We assume Pacific saury spawn in the Kuroshio region on 1 February, migrate into the mixed water and Oyashio regions for feeding, move southward for spawning, and then repeat the cycle (Fig. 1). The whole life span was assumed to be 2 years and our investigation concentrated on the winter-spawned saury.

Although many of the historical studies and data on Pacific saury are mainly classified by KnL, wet weight W is used as an indicator of saury growth in the bioenergetics model. Therefore, it was required to convert KnL to wet weight. Kosaka (2000) proposed five kinds of allometric functions for wet weight versus KnL

Table 2. Summary of parameter values used in the saury bioenergetics model.

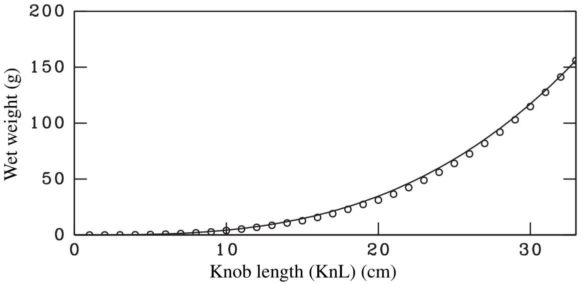
Symbol	Parameter description	Value
Consumption, C_{MAX}		
a_C	Intercept for C_{MAX} at $(te1 + te3)/2$	0.8
b_C	Coefficient for C_{MAX} versus weight	−0.340
te1	Temperature for *xk1* (in°C)	5
te2	Temperature for *xk2* (in°C)	20*, 16†
te3	Temperature for *xk3* (in°C)	26*, 20†
te4	Temperature for *xk4* (in°C)	30
xk1	Proportion of C_{MAX} at *te1*	0.10
xk2	Proportion of C_{MAX} at *te2*	0.98
xk3	Proportion of C_{MAX} at *te3*	0.98
xk4	Proportion of C_{MAX} at *te4*	0.5
Metabolism, *R*		
a_R	Intercept for *R*	0.0033
b_R	Coefficient for *R* versus weight	−0.227
c_R	Coefficient for *R* versus temperature	0.020
d_R	Coefficient for *R* versus swimming speed	0.026
S	Coefficient for specific dynamic action	0.150*, 0.175†
Swimming speed, *U*		
a_A	Intercept *U* (<12°C) (in cm s^{-1})	2.0
a_A	Intercept *U* (=12°C) (in cm s^{-1})	12.3
b_A	Coefficient *U* versus weight	0.33
c_A	Coefficient *U* versus temperature (<12°C)	0.149
c_A	Coefficient *U* versus temperature (=12°C)	0.0
Egestion and excretion, *F* and *E*		
a_F	Proportion of consumed food egested	0.16
a_E	Proportion of consumed food excreted	0.10

*values for stage 1 saury.
†values for stage 2 and higher saury.

Table 3. Life stages of Pacific saury in the saury bioenergetics model.

Stage	Age (days)	Period	Region
Larva	1–28	February 1–28	Kuroshio
Juvenile and young	29–150	March 1–June 30	Mixed
Small	151–273	July 1–October 31	Oyashio
Adult	274–317	November 1–December 14	Mixed
Adult mature	318–393	December 15–February 28	Kuroshio
Adult	394–499	March 1–June 14	Mixed
Adult	500–638	June 15–October 31	Oyashio
Adult	639–682	November 1–December 14	Mixed
Adult mature	683–730	December 15–January 31	Kuroshio

Figure 2. Wet weight (g) versus knob length (KnL) (cm) relationship of Kosaka (2000) (white circles) and the one used in the saury bioenergetics model (black line).



based on life stage. However, we adopted the following simple equation for all stages:

$$W = (KnL/6.13)^3. \tag{3}$$

The wet weight versus KnL curves of Eqn 5 and Kosaka's equations shown in Fig. 2 demonstrate a close fit.

Consumption

To estimate the maximum consumption curve, it is necessary to conduct rearing experiments with excess appropriate prey, at optimal temperatures. However, saury are easily damaged during laboratory rearing and are difficult to keep in non-stressed conditions. Therefore, there is no experimental data for the maximum consumption rate except for Hotta (1958). His analysis was limited to small saury with wet weight <18 g. Field data showed the annual average rations of Pacific saury are 4.3 (gww day^{-1} $individual^{-1}$) for 23–25 cm, 4.7 for 24–27 cm, 5.7 for 29–31 cm, 6.6 for 31–33 cm and 8.4 for 33–35 cm fish (Kurita and Sugisaki, 2004). They also estimated the rations of Pacific saury in the Oyashio region and the values are 6.1 (gww day^{-1} $individual^{-1}$) for 23–25 cm, 7.3 for 24–27 cm, 9.1 for 29–31 cm, 10.3 for 31–33 cm and 13.2 for 33–35 cm fish. These values are converted to consumption rate (g prey g $fish^{-1}$ day^{-1}) by dividing by the wet weight as calculated by Eqn 5 (Fig. 3). The field data is considerably lower than the maximum consumption rate (about 20–50%), as the prey density is not usually sufficient to achieve feeding satiation

Figure 3. C_{MAX} curve (black line) and observed Pacific saury ration per unit wet weight. Shown are the observed annual average values (open circles) and the average values in the summer season in the Oyashio region (black squares).

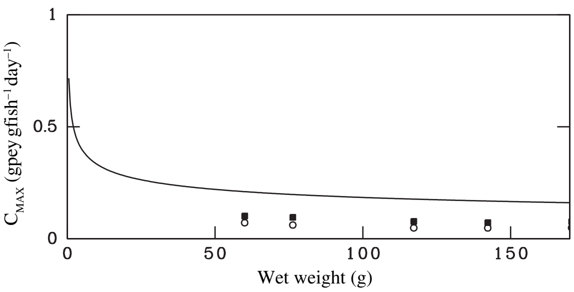
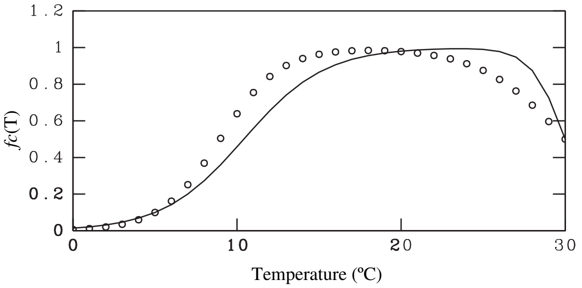


Figure 4. Dependence of consumption on temperature for Pacific saury, for life stage 1 (black line), and for other stages (open circles).



and not all temperatures are optimal (Hotta, 1958). Moreover, the maximum consumption values only restrict the upper limit of consumption in this model. Therefore, we set the maximum consumption value to be twice the observed field values to avoid underestimating consumption in the model. The adopted maximum consumption rate curve is also shown in Fig. 3. Consumption depends both on the maximum consumption rate and the half-saturation constants. The half-saturation constants (Table 4) were adjusted to provide the best fit between the growth of saury predicted from the model and observed growth.

Although Oozeki and Watanabe (2000) measured growth rate but did not measure the consumption rate directly, their results showed that larval growth increased linearly with temperature between 14 and 22°C and did not show any significant difference between 20 and 24°C. Therefore, we assumed that consumption during the larval stage has the highest values between 20 and 24°C. The adopted temperature function of the consumption rate of stage-1 saury is shown in Fig. 4. Although there is no experimental data on the dependence of consumption rate on temperature for adult saury, the habitat temperature is between 16 and 20°C. Thus we set the temperature dependence function to have a higher value within this habitat temperature range for stages 2 and higher (Fig. 4).

Vulnerability

For vulnerability of fish feeding on three prey zooplankton species, we assumed values according to the results of the feeding habits of Pacific saury (Odate, 1994; Sugisaki and Kurita, 2004). The adopted values are listed in Table 5.

Table 4. Half-saturation constants K_{ij} for the saury bioenergetics model. Values were adjusted to provide the best fit between model-predicted growth and observed growth.

		Half-saturation constants for each zooplankton compartment		
Stage	Region	ZS	ZL	ZP
1	Kuroshio	0.30	–	–
2	Mixed water	0.30	0.30	–
3	Oyashio	–	0.45	0.45
4	Mixed water	–	0.45	0.45
5	Kuroshio	0.45	–	0.45
6	Mixed water	–	0.45	0.45
7	Oyashio	–	0.45	0.45
8	Mixed water	–	0.45	0.45
9	Kuroshio	0.45	–	0.45

ZS, small zooplankton; ZL, large zooplankton; ZP, predatory zooplankton.

Table 5. Vulnerability coefficients v_{ij} for the saury bioenergetics model.

		Vulnerability coefficients for each zooplankton compartment		
Stage	Region	ZS	ZL	ZP
1	Kuroshio	1.0	0.0	0.0
2	Mixed water	1.0	1.0	0.0
3	Oyashio	0.0	1.0	1.0
4	Mixed water	0.0	1.0	1.0
5	Kuroshio	1.0	0.0	1.0
6	Mixed water	0.0	1.0	1.0
7	Oyashio	0.0	1.0	1.0
8	Mixed water	0.0	1.0	1.0
9	Kuroshio	1.0	0.0	1.0

ZS, small zooplankton; ZL, large zooplankton; ZP, predatory zooplankton.

Respiration

Respiration (gO$_2$ g fish^{-1} day^{-1}) of adult fishes generally scales negatively with weight (g fish) ranging from −0.25 to −0.15 (Winberg, 1956). Atlantic menhaden *Brevoortia tyrannus* has range from −0.19 to −0.28 (Hettler, 1976), alewife *Alosa pseudoharengus* has −0.125 (Stewart and Binkowski, 1986), Atlantic herring shows −0.227 (de Silva and Balbontin, 1974), and a mesopelagic planktivore, *Maurolicus muelleri* has −0.15 (Ikeda, 1996). There are no data for respiration of saury. As saury and herring are both pelagic fish and planktivores, we will assume as a first approximation that the values for intercept a_R and slope b_R of the allometric mass function for respiration for saury (see Appendix) are the same as the values for Atlantic herring used by Rudstam (1988). For the dependence of temperature and swimming speed on respiration, it can be easily speculated that these dependencies are lower for saury than for herring because of the differences of ambient habitat temperature and body shape between them. We adapted lower values for dependence parameter of temperature c_R and swimming speed d_R for respiration (see Appendix) than those for herring.

Swimming speed

For swimming speed, there are no actual laboratory values for Pacific saury. Generally other small pelagic fish swim at speeds of two to three times their body length per second, although herring and salmon swim three to four times their body length per second (Blaxter, 1967). We assumed that the normal swimming speed is two times the KnL per second:

$$U = 2.0 \cdot KnL. \tag{4}$$

By substituting Eqn 3 into Eqn 4, the following allometric equation was derived:

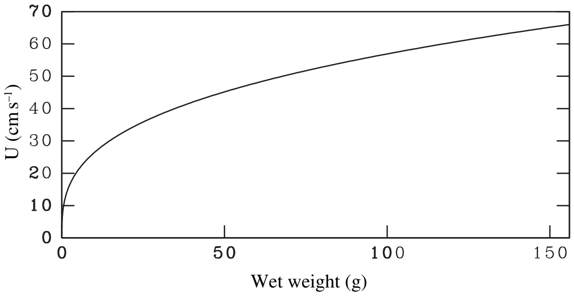
$$U = 12.3 \cdot W^{0.33}. \tag{5}$$

We adopted this equation when temperature is higher than 12°C (Fig. 5), while a slower swimming speed was assumed for temperatures lower than 12°C (Table 2).

Egg production

For egg production of Pacific saury, Kurita (2004) estimated that about 35% of the total assimilated energy was allocated to winter egg production in the Kuroshio region. Based on his estimate we set 0.35 for a_P. For specific dynamic action, egestion, and excretion, and as a first approximation, we assumed the same values as those for Atlantic herring.

Figure 5. Swimming speed dependence on wet weight in the case of higher temperature (=12°C).



Caloric equivalent

Although the energy density of zooplankton shows seasonal variability, the average energy density of copepoda was estimated as 2580 (J g zooplankton^{-1}) (Laurence, 1976) and we used 617 (cal g zooplankton^{-1}) for the caloric equivalent of zooplankton. Kurita and Ueno (2003) estimated the seasonal variability of lipid and protein content in Pacific saury. The lipid content showed high seasonal variability while protein showed stable values. The lipid and protein content was converted to energy by multiplying by 9500 (cal g lipid^{-1}) and 5000 (cal g protein^{-1}) (Beamish *et al.*, 1975) respectively and the caloric equivalent was estimated. The seasonal variability of the caloric equivalent of Pacific saury was quite large, the maximum was 14449 (cal g fish^{-1}) in summer and the minimum was 4924 (cal g fish^{-1}) in winter. We used an annual average value 9541 (cal g fish^{-1}) herein.

CONTROL RUN

In a control run, the saury bioenergetics/ecosystem coupled model was driven by idealized seasonal forcing. The idealized seasonal change of solar radiation (Fig. 6a) was determined from the dataset of Oberhuber (1988) and that of SST (Fig. 6b) was determined from the World Ocean Atlas 1998 (Antonov *et al.*, 1998). Under this idealized forcing, the mixed layer thickness showed a clear seasonal variation in response to the SST seasonal change (Fig. 6c). The mixed layer depth showed a maximum in winter. The actual maximum value is generally deeper in the north and shallower in the south. However, south of the Kuroshio Extension, the actual mixed layer depth shows a maximum even in the Subtropical region. Therefore, the spatial difference in the actual mixed layer depth is not as significant when the regional average is considered and it is consistent with the model result. The

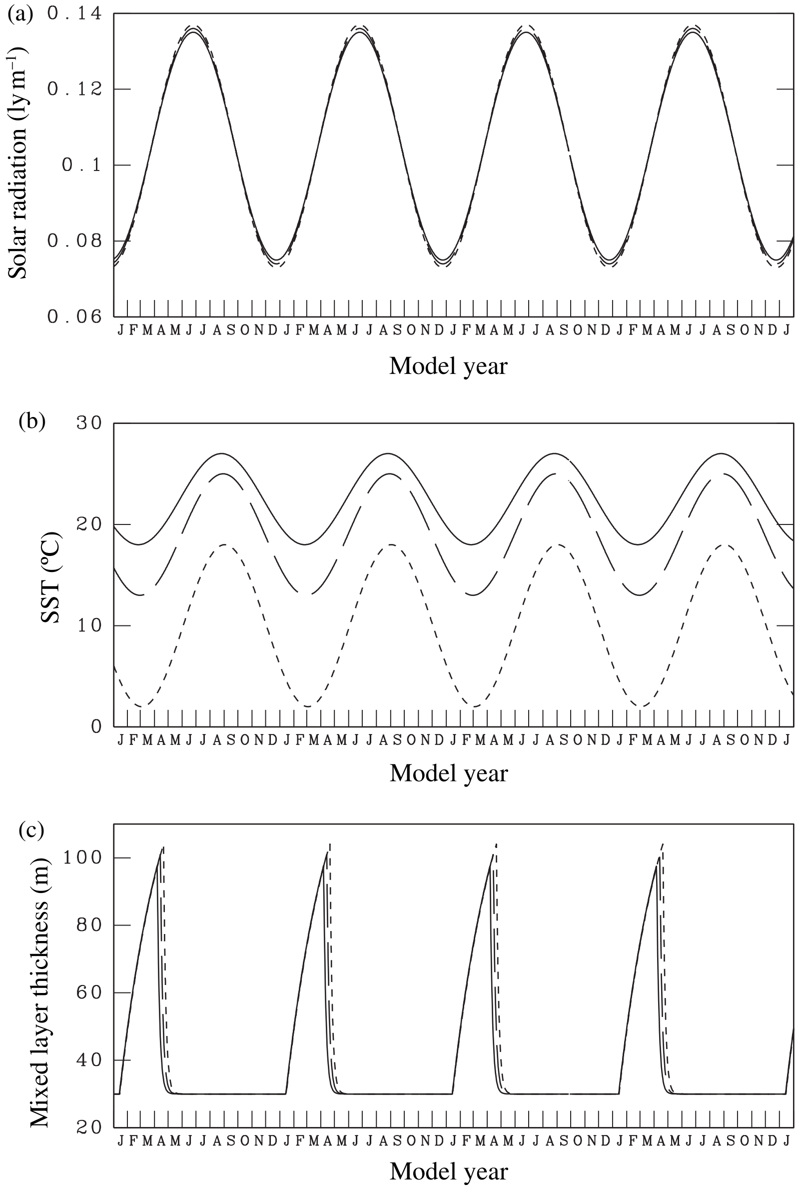


Figure 6. Idealized seasonal change in (a) solar radiation and (b) sea surface temperature which is used as the surface boundary condition and (c) simulated seasonal variation in the mixed layer thickness in the control run for the Kuroshio (solid line), mixed water (broken line) and Oyashio regions (dotted line).

actual mixed layer depth in winter is about 100–150 m. Although the actual mixed layer is at a minimum in spring and increases in thickness until autumn, we do not model this. Rather, in this model the exchange between the mixed layer and bottom layer occurs only when the water column becomes thermally unstable. In our model, the mixed layer depth is restored to 30 m on a time scale of 5 days following a return to thermally stable conditions, and therefore, it shows a stable value around 30 m. Although this does not resemble the actual ocean, it is reasonable from the point of nutrient supply.

Nutrients are supplied from the bottom layer in winter and are consumed by the phytoplankton for photosynthesis under solar radiation forcing in other seasons. The biomass of zooplankton varies because of the biomass change of phytoplankton. Further, the seasonal vertical ontogenetic migration of ZL enhances the seasonal variation of phytoplankton and other zooplankton biomass (Fig. 7). The total density of ZS and ZL (small and large zooplankton) shows a minimum in March (0.08 μmolN L^{-1}) and a maximum in May (0.62 μmolN L^{-1}) in the Oyashio region and is consistent with observational results of Saito *et al.* (2002): a minimum in January (0.08 ± 0.05 μmol N L^{-1}) and a maximum in May or June–July (1.36 ± 1.17 μmolN L^{-1}). The seasonal variability of zooplankton density in the three regions is

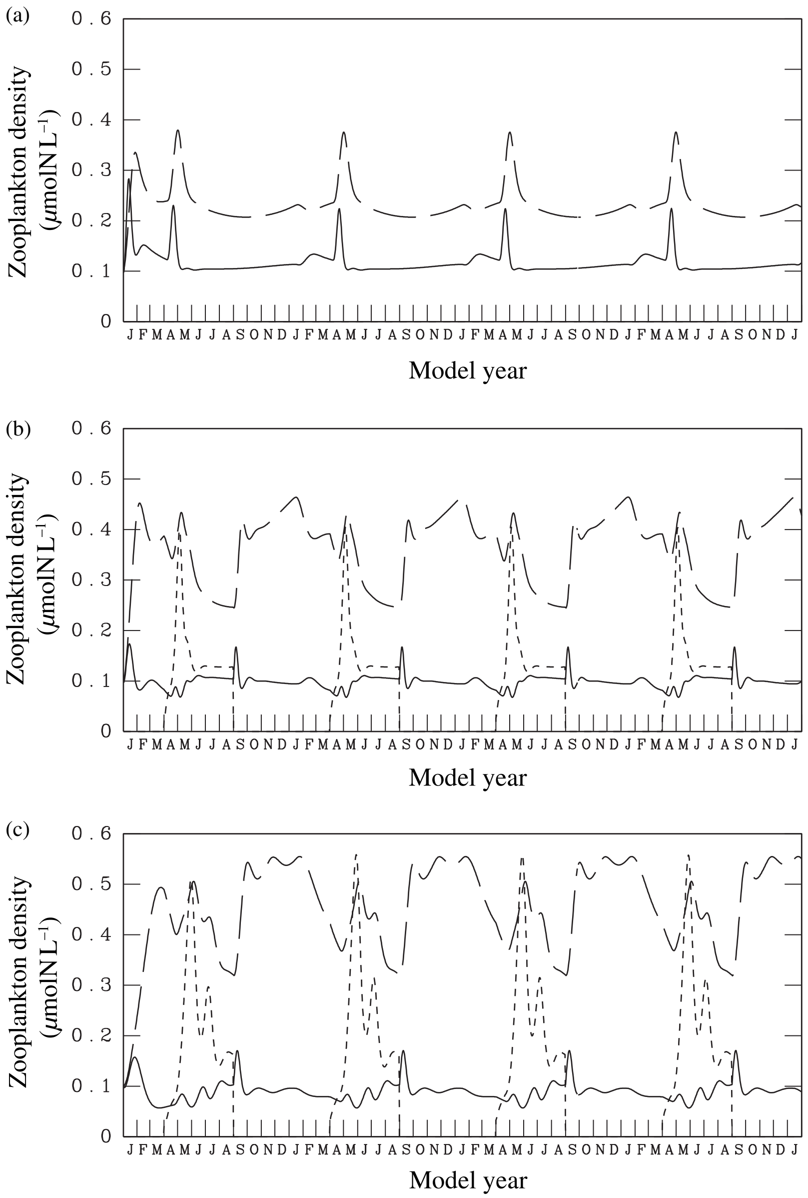


Figure 7. Simulated seasonal variation of zooplankton biomass in the control run for the (a) Kuroshio, (b) mixed water and (c) Oyashio regions. Solid lines shows small zooplankton, dotted lines shows large zooplankton and broken line shows predatory zooplankton.

quantitatively consistent with observational data of Odate (1994).

Using zooplankton as prey, saury growth results from the bioenergetics model as shown in Fig. 8a. The wet weight continuously increases through the larval and juvenile stages in the Kuroshio region to the Oyashio region and it reaches its first maximum of about 75 g in late autumn of the first year of life. Although weight decreases in the Kuroshio region, it again increases in the mixed water and Oyashio region during the second spring and summer. It reaches a second maximum of about 140 g during summer in the Oyashio region and a third maximum of about 150 g during late autumn in the mixed water region. After that, it decreases rapidly because of egg production until it reaches about 120 g in the Kuroshio region.

In Fig. 8, observed growth of Pacific saury (Okuda, 2002), which is estimated using the method of Kurita *et al.* (2004), is also plotted. As noted in the previous section, because of the absence of data, the half-saturation constants of fish feeding on zooplankton prey were adjusted to provide correspondence between modeled and observed growth. As a result, the simulated results showed good agreement. Fig. 8b shows the individual terms of the bioenergetics equation. Consumption is the most important term and respiration is the second leading

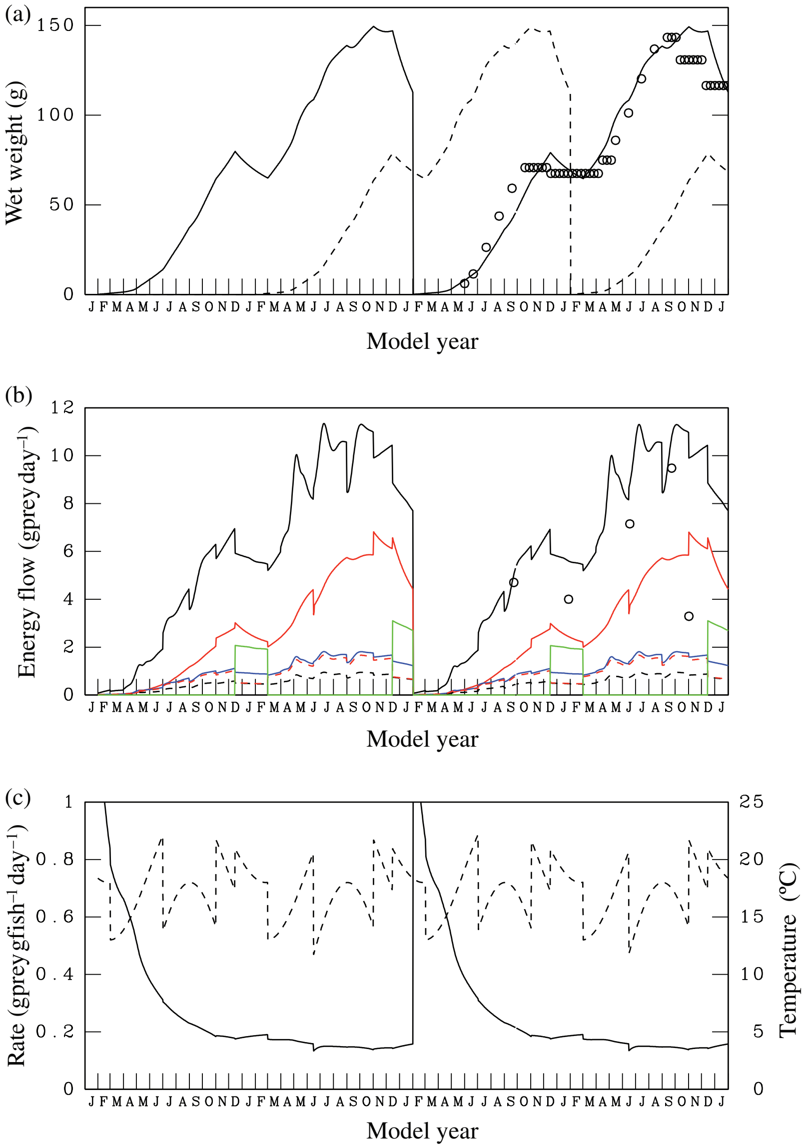


Figure 8. Results of control run of the bioenergetics/ecosystem coupled model, and observed values of some parameters. (a) Simulated wet weight change of individual saury. In the model, there are two cohorts. The solid line represents the first cohort and the dashed line represents the second cohort. Also shown is observed growth (open circles), which is estimated using the method of Kurita *et al.* (2004). (b) Simulated time trajectory of individual terms of the bioenergetics equation for the first cohort in Fig. 8a (black solid: consumption, red solid: respiration, blue solid: egestion, black dashed: excretion, red dashed: specific dynamic action, green: egg production). All values are multiplied by fish weight. Also shown is the observed consumption by Kurita and Sugisaki (2004) for appropriate KnL (open circles). (c) Variation in the maximum consumption rate multiplied by the temperature function (solid line) and water temperature (dashed line).

term and it shows similar seasonal variation to that of consumption. Both terms strongly depend on the wet weight of saury. The maximum consumption rate depends only on wet weight (cf. Eqn A4). Its effect is very strong and the variation (the time scale approximates the life span of saury) of consumption was basically determined by the dependency on weight. Temperature does not play an important role in the variation of consumption except during the early stages of life (Fig. 8c). Consumption also depends strongly on zooplankton prey density, and intra-seasonal to seasonal variation in consumptions are strongly affected by prey density variation. Respiration shows a rapid response to temperature change, increasing when temperature rises. High temperature in the Kuroshio region leads to high energy flow through the respiration term of the bioenergetics equation. Moreover, energy expended on egg production in the Kuroshio region is evident. As a result, the wet weight of saury decreases rapidly in the Kuroshio region during the spawning season.

MODEL SENSITIVITY

In the previous section, NEMURO.FISH successfully reproduced the observed growth of Pacific saury. However, the model parameters were not all determined from field-derived results or laboratory experiments. For example, the half-saturation constants of fish feeding on zooplankton prey were selected to fit modeled growth to observed values. In this case, the most important aspect is whether the model reproduced appropriate consumption or not. In Fig. 8b, observed consumption values are plotted. The model results show similar consumption values during spring to summer, although they showed higher values during autumn to winter. As Pacific saury starts egg production in autumn and migrates southward, the assimilation and consumption of energy may change in those seasons. More investigations on these parameters are needed in future.

The leading term of the bioenergetics model was the consumption term and it depends on both water temperature and prey density. To investigate the sensitivity of the model to water temperature and prey density, two other experiments were performed. In Experiment 1 (EX1), water temperature was fixed at 17°C only in the bioenergetics model (Fig. 9c), whereas the seasonal variation of SST was prescribed as the surface boundary condition in the lower trophic model (NEMURO). In Experiment 2 (EX2), prey densities were fixed to 0.10, 0.15, and 0.30 μmolN L^{-1} for ZS, ZL, and ZP, respectively, and the effects of ontogenetic vertical migration of ZL were included.

In EX1, respiration became higher than in the control run (Fig. 9b), according to Eqn (A15). However, consumption increased in EX1 (Fig. 9b), according to the definition of temperature dependence (Fig. 4). As a result, the growth of Pacific saury slightly increased in EX1 (Fig. 9a). Although intra-seasonal variability of respiration was smoothed out in EX1, variability in consumption remained.

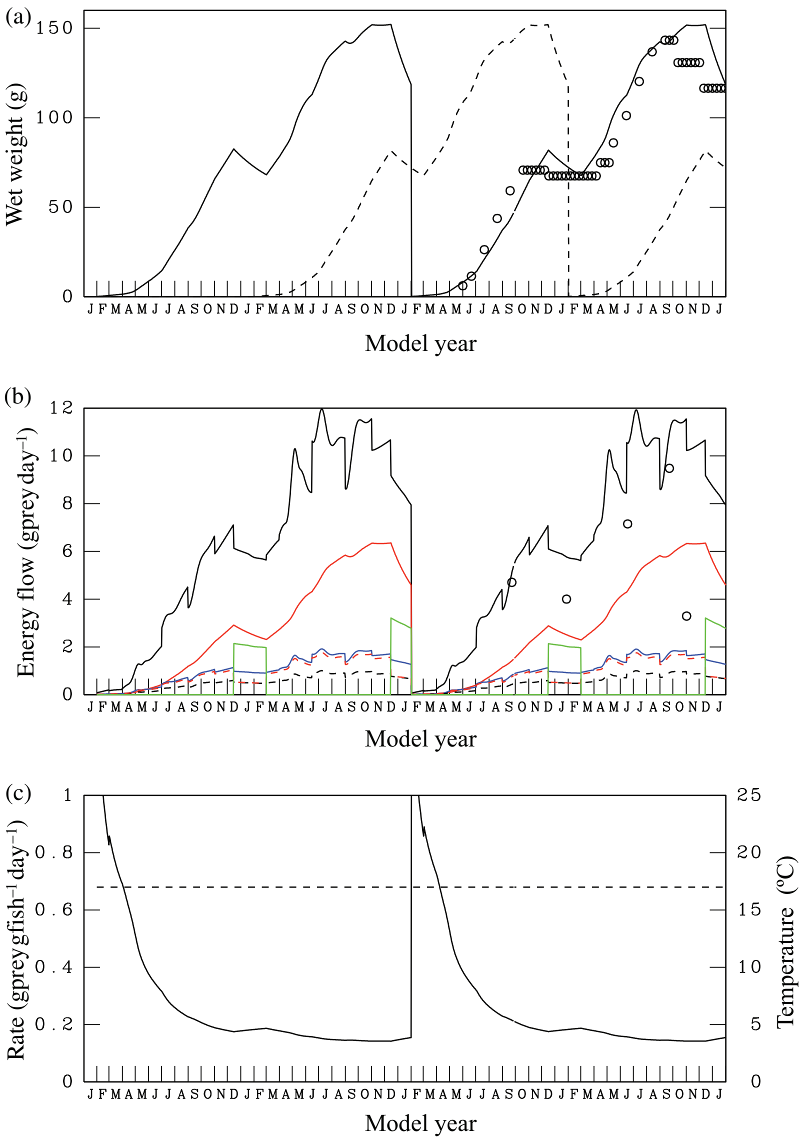


Figure 9. The same as Fig. 8 but for Experiment 1.

In EX2, prey density was set at non-bloom levels. Therefore, saury growth was reduced significantly. Seasonal variability of ZP consumption was suppressed in EX2, as ZP increase did not occur from autumn to winter. Intra-seasonal variability in consumption was also reduced in all zooplankton compartments in EX2, as the spring bloom and intra-seasonal variability of zooplankton was eliminated. From these results, it is noted that prey density has dominant effects on the intra-seasonal to seasonal variability of saury growth in this model (Fig. 10).

CONCLUSION AND DISCUSSION

An initial design of a fish bioenergetics model coupled with an ecosystem model was developed to investigate growth of Pacific saury. We adapted NEMURO.FISH to the coupled model and expanded it to three oceanic spatial domains corresponding to the Kuroshio, Oyashio, and interfrontal (mixed water) regions. In each spatial domain model, the difference between SST and the bottom layer temperature determined the mixed layer depth and the exchange rate with the bottom layer. As the bottom layer temperature was fixed, the

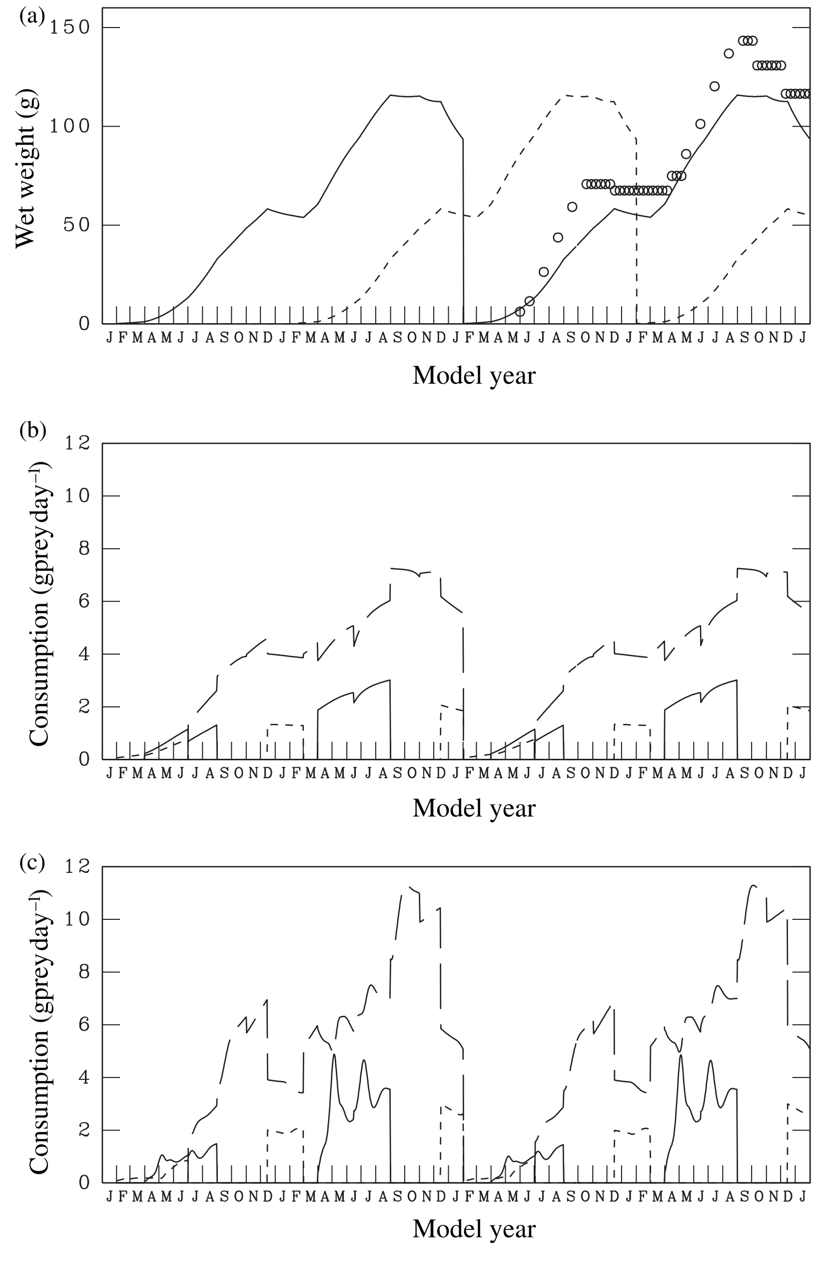


Figure 10. (a) The same as Fig. 8a but for Experiment 2 (EX2). (b) Consumption of saury on small zooplankton (dashed line), large zooplankton (solid line), and predatory zooplankton (broken line) in EX2. All values are multiplied by fish weight. (c) The same as Fig. 10b but for the control run.

SST determined lower trophic level ecosystem variation.

The parameters in the bioenergetics model were examined and applied to Pacific saury. Only the half-saturation constants of fish feeding on prey zooplankton were selected/tuned to fit modeled saury growth to observed growth values. As a result, the model reproduced observed saury growth. Results of the control run showed the importance of temperature on respiration rate. It also showed the importance of egg production energy losses. Results of sensitivity experiments showed strong sensitivity of respiration on water temperature and of consumption on prey zooplankton density.

The NEMURO.FISH type models are useful in analyzing the mechanisms of changes in fish growth. For example, it is straightforward to run a multi-decadal simulation with realistic atmospheric forcing and analyze the mechanisms affecting interannual variability in saury growth. However, the determination of parameters is not complete. Especially for Pacific saury, the difficulty of rearing them in the laboratory is an obstruction to improvements in the model parameters. However, this does not fatally weaken the results or negate the relevance of the modeling study. Despite the assumptions we have had to make in this model study, we have been able to identify data gaps and priorities of parameters to be determined by field observations or laboratory experiments. The prey vulnerability, half-saturation constants for prey zooplankton, and temperature effects on consumption are the most important factors in this model. Laboratory experiments on larvae (KnL < 2.5 cm) and juveniles (2.5 ≤ KnL < 6.0 cm) aimed at estimating consumption and respiration parameters will be essential to improving the model. Also, incubation laboratory experiments on young and adult saury are recommended. From observational aspects, information of young saury (6.0 ≤ KnL < 15.0 cm) is insufficient. We recommend greater efforts to collect information regarding small and young saury. To seek these parameters, more hydrographic observations and zooplankton sampling collected simultaneously with Pacific saury samples is required.

In this study, only winter-spawned saury were considered. In future efforts, the effect of spawning season should be investigated. In addition, to investigate variability of Pacific saury biomass, variation in the number of Pacific saury must also be considered. Megrey and Kishi (2002) already recommended and pointed out the possibility of extending NEMURO.FISH to a population level model. Tian *et al.* (2000) analyzed the relationship between the abundance of Pacific saury and climatic indicators using historical data. They pointed out that longer-period abundance variations in Pacific saury of large size is closely related to SST variation in the Kuroshio Extension region and that of medium size saury is closely related to SST north of the mixed water region. However, the mechanisms underlying the variations in abundance remain undetermined. Population dynamics models including a fish bioenergetics/ecosystem coupled model will greatly contribute to investigating the mechanisms and those have potential to bring better guidance to fisheries management of saury and other fishes.

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APPENDIX: MODEL FORMULATIONS

A multispecies consumption formulation is defined as follows (Rose *et al.*, 1999):

$$C = C_r \cdot f_C(T), \tag{A1}$$

$$C_r = \sum_{j=1}^{n} C_j, \tag{A2}$$

$$C_j = \frac{C_{MAX} \cdot \frac{PD_{ij} \cdot v_{ij}}{K_{ij}}}{1 + \sum_{k=1}^{n} \frac{PD_{ik} \cdot v_{ik}}{K_{ik}}}, \tag{A3}$$

$$C_{MAX} = a_C \cdot W^{b_C}, \tag{A4}$$

where C_r is total available consumption rate without temperature effects, $f_C(T)$ is a temperature dependent function for consumption, T is sea water temperature (°C). j and k denote the prey type, i denotes predator type (life stage of saury), n is the total number of prey types, C_{MAX} is the maximum consumption rate (g prey g fish^{-1} day^{-1}), PD_{ij} is the density of prey type

j (g prey m^{-3}), v_{ij} is the vulnerability of prey type j to predator i (dimensionless), and K_{ij} is the half-saturation constant (g prey m^{-3}) for individual predator type i feeding on prey type k. a_C is the intercept of the allometric mass function and b_C is the slope of the allometric mass function for consumption.

Consumption shows a non-linear dependency on weight, prey zooplankton density and temperature according to Eqs A4, A3, A1 respectively. Temperature dependency is given by

$$f_C(T) = gcta \cdot gctb, \tag{A5}$$

where

$$tt5 = \frac{1}{(te2 - te1)}, \tag{A6}$$

$$t5 = tt5 \cdot a\log\left[0.98 \cdot \frac{(1.0 - xk1)}{(0.02 \cdot xk1)}\right], \tag{A7}$$

$$t4 = e^{[t5 \cdot (T - te1)]}, \tag{A8}$$

$$tt7 = \frac{1}{(te4 - te3)}, \tag{A9}$$

$$t7 = tt7 \cdot a\log\left[0.98 \cdot \frac{(1.0 - xk4)}{(0.02 \cdot xk4)}\right], \tag{A10}$$

$$t6 = e^{[t7 \cdot (te4 - T)]}, \tag{A11}$$

$$gcta = \frac{(xk1 \cdot t4)}{[1.0 + xk1 \cdot (t4 - 1.0)]}, \tag{A12}$$

$$gctb = \frac{(xk4 \cdot t6)}{[1.0 + xk4 \cdot (t6 - 1.0)]}. \tag{A13}$$

This function was proposed to represent the temperature dependence for cool and cold water species by Thornton and Lessem (1978). The function is the multiplication of two sigmoid curves. One denotes the increasing portion of the temperature dependence function (*gcta*) and the other denotes the decreasing portion (*gctb*). For the increasing part of the curve, *te1* is the lower temperature at which temperature dependence is a small fraction *xk1* of the maximum rate and *te2* is the water temperature corresponding to *xk2* of the maximum consumption rate. For the decreasing portion of the curve, *te3* is the water temperature (=*te2*) at which dependence is *xk3* of the maximum and *te4* is the temperature at which dependence is a reduced fraction *xk4* of the maximum rate.

The respiration rate or energy loss because of routine metabolism is defined as follows after Stewart and Binkowski (1986):

$$R = a_R \cdot W^{b_R} \cdot f_R(T) \cdot activity \cdot 0.59, \tag{A14}$$

$$f_R(T) = e^{(c_R \cdot T)}, \tag{A15}$$

$$\text{activity} = e^{(d_R \cdot U)}, \tag{A16}$$

$$U = a_A \cdot W^{b_A} \cdot e^{(c_A \cdot T)} \tag{A17}$$

where a_R is the intercept of the allometric mass function and represents the specific weight of oxygen consumption rate of a 1 g fish at 0°C with no activity (gO^2 g fish^{-1} day^{-1}), b_R is the slope of the allometric mass function for standard metabolism, f_R *(T)* is the temperature dependence function for respiration, c_R approximates the Q_{10} (the rate at which the function increases over relatively low water temperatures), and activity is the activity multiplier. U is the swimming speed (cm s^{-1}) and d_R is a coefficient relating swimming speed to the metabolism. a_A is the intercept of allometric mass function, b_A is the slope of the allometric mass function for standard swimming speed, and c_A is the coefficients for temperature dependence of the swimming speed. The coefficient 0.59 converts g O$_2$ g fish^{-1} day^{-1} into g prey g fish^{-1} day^{-1} using the conversion

$$\frac{13\,560\,\text{joules}}{\text{gO}_2} \cdot \frac{1\,\text{cal}}{4.18\,\text{joules}} \cdot \frac{1\,\text{gwetweight}}{5533\,\text{cal}} = 0.59. \tag{A18}$$

While respiration depends on activity and non-linearly depends on weight and temperature, activity also non-linearly depends on weight and temperature. This brings a high non-linear effect of weight and temperature on respiration.

The specific dynamic action is defined as the proportion of residual difference between consumption and egestion rate F (g prey g fish^{-1} day^{-1}) like

$$SDA = S \cdot (C - F), \tag{A19}$$

where S is a constant coefficient after Stewart and Binkowski (1986).

Egestion (F, fecal waste) and excretion (E, nitrogenous waste) are also defined as the constant proportions:

$$F = a_F \cdot (C - P), \tag{A20}$$

$$E = a_E \cdot (C - P - F), \tag{A21}$$

following formulations suggested by Stewart and Binkowski (1986).

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