On the interannual variability of the growth of Pacific saury (*Cololabis saira*): A simple 3-box model using NEMURO.FISH

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ABSTRACT

To elucidate the interannual response of Pacific saury growth to climate variability, a simple 3-box model of NEMURO.FISH was forced by observed sea surface temperature (SST) from 1950 to 2002. In the model, fish wet weight is calculated according to a fish bioenergetics equation. The observed condition factor of Pacific saury showed large decadal variability with significant year-to-year variability. In the model, wet weight of Pacific saury also showed decadal and year-to-year variability, however the amplitude of decadal variability was much smaller than observed. The cause of the model failure is suggested to be the absence of a multi-species fish formulation in the model. The Japanese sardine population, which has a large biomass that exhibits great decadal fluctuations, is proposed as potentially affecting zooplankton density in the saury migration region. We also investigated differences of interannual growth variability between spawning seasons. Since Pacific saury spawns from autumn to the following spring, we consider three seasonal (autumn, winter and spring) cohorts in the model. The amplitude of growth variability is largest for the spring-spawned cohort and smallest in the winter-spawned cohort. This difference is caused by the difference of life history of each spawned cohort. The spring-spawned cohort spawns only once in their life-cycle, however other cohorts spawn twice. During the (autumn) fishery season, age 1 spring-spawned cohort has not yet spawned, while the other cohorts have spawned once. As a result, the spring-spawned cohorts retain the memory of the environmental influence during the early life stages while the other cohorts, through their spawning, have erased that memory. Hence, the spring-spawned cohort shows a larger fluctuation in wet weight than other cohorts.

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1. Introduction

Pacific saury (*Cololabis saira*) is a typical pelagic inhabitant of the North Pacific and is widely distributed (Hubbs and Wisner, 1980). Its biomass was estimated as 2.8 million tonnes (t) in the North Pacific (Tohoku National Fisheries Research Institute, 2005) based on a basin-wide mid-water trawl sampling in 2002 early summer (Ueno et al., 2004). The total number of Pacific saury was estimated as 56.1 billion. The biomass west of 162°E, which is speculated to migrate to Japan's coastal region, is also large and it was about 0.9 and 1.3 million tonnes in 2001 and 2002, respectively. As such, Pacific saury is one of the most important commercial fish in the northwestern Pacific with an average total yearly catch of about 0.25 million tonnes. Yearly landings in Japan have fluctuated between 575,000 and 52,000 tonnes depending on the stock size. Body size and weight of landed saury also fluctuate interannually and are important factors in determining their price (Watanabe et al., 1997). However, because of the complex life history and wide distribution of saury, the cause of their fluctuation remains undetermined.

In the northwestern Pacific, saury spawning starts in autumn in the mixed water region (MW), in the Kuroshio–Oyashio interfrontal zone. In winter the saury spawning area moves to the subtropical region of the Kuroshio area (KR), and returns to the mixed water region in spring (Odate, 1977; Watanabe and Lo, 1989; Watanabe et al., 1997). Larvae are advected to the Kuroshio extension region, where they grow to juveniles, and then migrate to the subarctic Oyashio area (OY), crossing MW for feeding. After sufficient feeding they migrate back to MW and KR to spawn. During their southward migration, they are fished in the Japanese coastal zone. Saury's knob length (KL) (nearly the same as body length) reaches 30 cm in adults and their life span is about 2 years (Kurita et al., 2004).

A fish bioenergetics model, coupled with an ecosystem model North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO; Kishi et al., 2007), was developed to reproduce the growth of Pacific saury (Ito et al., 2004). The NEMURO.FISH (NEMURO for Including Saury and Herring) formulation is described in Megrey et al. (2007), while the parameters and implementation specific to saury are contained in Ito et al. (2004) and Mukai et al. (2007). Our model covers three different oceanographic spatial domains corresponding to KR, MW, and OY. The timing of spawning and migration between the KR, MW, and OY were defined by fixed calendar dates in Ito et al. (2004). However, Mukai et al. (2007) improved the timing of spawning and migration to fluctuate from the fixed calendar date assumption of Ito et al. (2004) to depend on the size of the saury and water temperature. Model results of Mukai et al. (2007) reproduced appropriate Pacific saury growth rates and growth rate differences between different seasonal spawned cohorts.

In this manuscript, the saury version of NEMURO.FISH was integrated with observed sea surface temperature (SST) for the decades from 1950 to 2002 and the interannual response was investigated. The present paper extends the Ito et al. (2004) and Mukai et al. (2007) contributions that focused on the seasonal variation of the saury growth. The objectives of
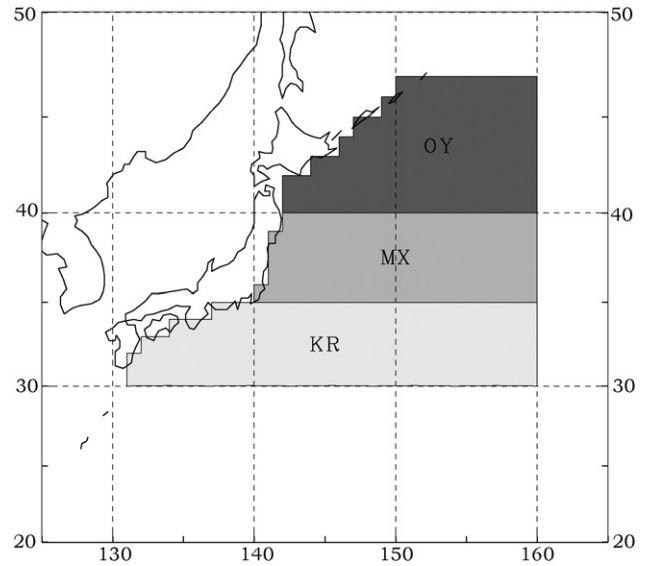

Fig. 1 – Schematic view of the three oceanic spatial domains where SST data was averaged and simulated in the model. The three domains correspond to the Kuroshio (KR), mixed water (MW), and Oyashio regions (OY).

this study are: (1) to test the performance of a simple, vertically averaged NEMURO.FISH to reproduce the interannual variation of Pacific saury growth and (2) elucidate the mechanisms that induce interannual variability of Pacific saury wet weight.
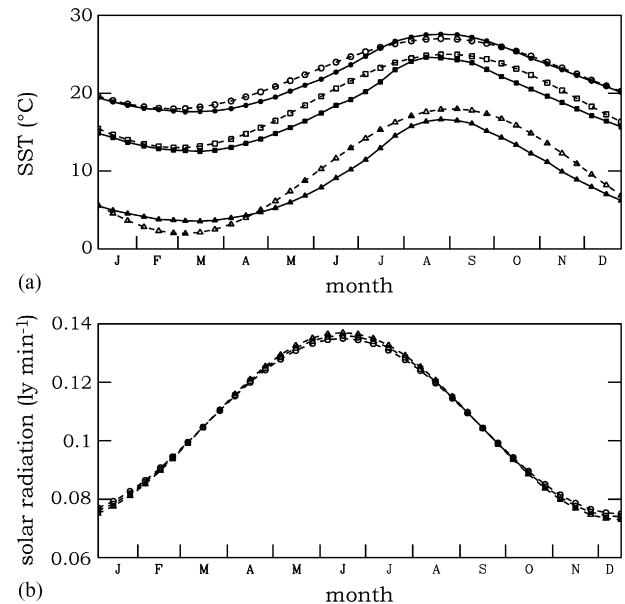

Fig. 2 – Forcing of the model in the control run: (a) seasonal SST (°C) forcing (circles: Kuroshio area, rectangles: mixed water region, triangles: Oyashio area) for NEMURO.FISH in this study (solid lines) and in Mukai et al. (2007) and Ito et al. (2004) (broken lines); (b) light intensity (ly min⁻¹) at the surface (circles: Kuroshio area, rectangles: mixed water region, triangles: Oyashio area).

2. Methods

2.1. Fish bioenergetics/ecosystem coupled model

The basic modeling concept is the same as that presented by Ito et al. (2004). A vertically averaged box model version of NEMURO was developed for the three (KR, MW and OY) regions. Saury migrate between these three boxes according to their life stages. The equations and the parameters are the same as those of Mukai et al. (2007) except for the forcing. The idealized seasonal solar radiation is the same as that of Mukai et al. (2007). However, the SST was estimated by averaging the observed values over KR, MW, and OY regions, respectively. The source of observed SST is from Japan Meteorological Agency (JMA) products (http://www.goos.kishou.go.jp) with the horizontal resolution of 1° in latitude and longitude and a temporal resolution of about 10 days from 1950 to 2002. The regions in which SST was averaged for KR, MW, and OY are shown in Fig. 1.

2.2. Simulations

2.2.1. Control run

As a control run, the saury bioenergetics/ecosystem NEMURO.FISH coupled model was driven by climatological values for SST sampled three times per month in each region (Fig. 2a) and by idealized seasonal solar radiation as described above (see Fig. 2b). The climatological seasonal variations of SST in KR and MW are close to those of Ito et al. (2004) and Mukai et al. (2007). Also note that, in comparison to Ito et al. (2004) and Mukai et al. (2007), the OY region's SST has a weaker amplitude and the SST is colder in KR and MW from March to July. The boundary conditions at the bottom of mixed layer were exactly same as those of Mukai et al. (2007).
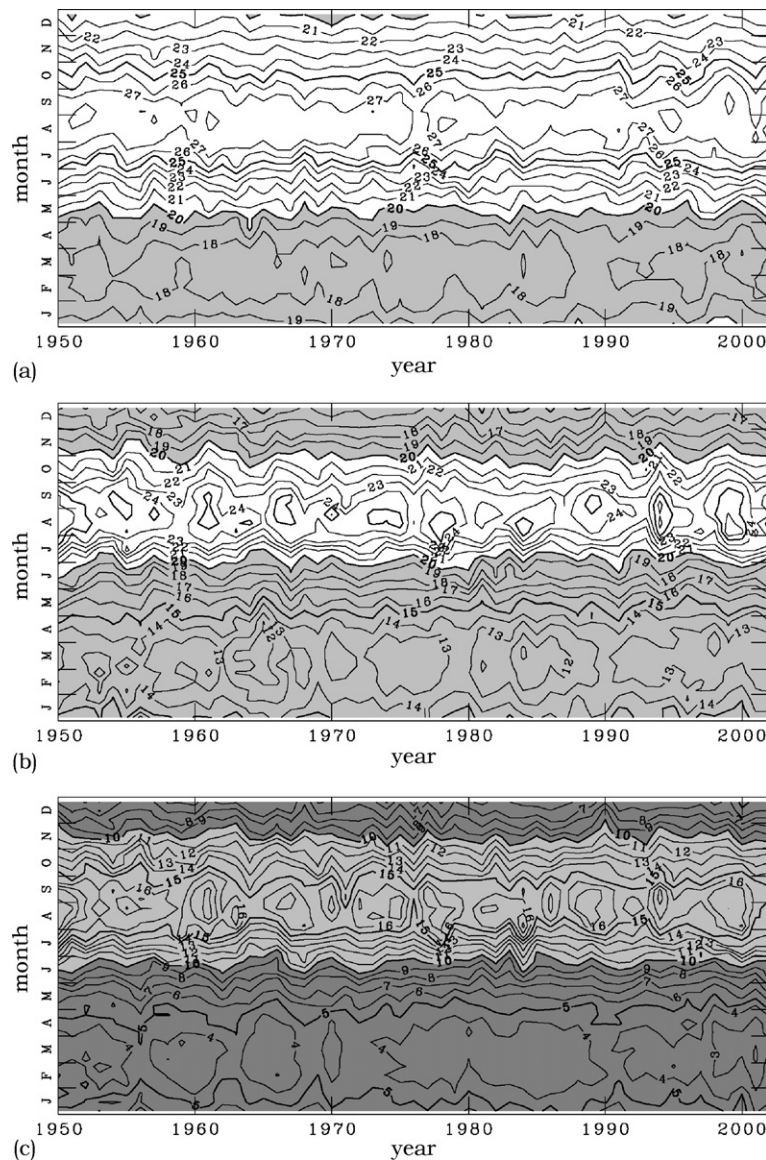

Fig. 3 – Sea surface temperature (°C) used to force the interannual run: (a) Kuroshio area, (b) mixed water region, and (c) Oyashio area. The contour interval is 1 °C and the temperatures lower than 20 °C are lightly shaded and temperature below 10 °C are darkly shaded.

2.2.2. Interannual run

To consider interannual variability, the saury version of NEMURO.FISH was forced by the observed SST (from 1950 to 2002) averaged over KR, MW, and OY regions (Fig. 3). On the other hand, the same idealized seasonal solar radiation pattern was prescribed (Fig. 2b).

2.2.3. Sensitivity runs

To elucidate the influence of SST variations on saury growth in each region, three additional experiments were performed considering only the winter-spawned cohort. First, only the SST in KR was allowed to fluctuate interannually, while the SSTs in the other regions were kept at their climatological values (hereafter denote this experiment as EX-KR). Similarly, interannual variability was only prescribed for SST in MW in EX-MW and for OY in EX-OY.

3. Results

3.1. Control run and typical saury growth

Since the spring SST in MW is colder than the one of Mukai et al. (2006), the migration from KR to MW was delayed in this control run (see Table 1). Also since the OY SST is colder than the one of Mukai et al. (2007) in summer, the migration of small size fish (which corresponds to spring-spawned cohort) from MW to OY was delayed in this control run (Table 1). In contrast, migrations from OY to MW and from MW to KR were advanced because of colder SST in OY and MW in autumn.

As a result, while most of the distinctive characteristics of saury growth are the same as those of Mukai et al. (2007), all cohorts show a little lower growth in this control run. Despite these differences: (1) winter-spawned cohort shows the highest growth in the earlier stages, (2) winter-spawned cohorts catch up with autumn-spawned cohorts in wet weight and KL by the first winter, (3) spring-spawned cohorts catch up with autumn and winter-spawned cohorts in wet weight and KL by the second early summer, and (4) spring-spawned cohorts spawn only in the second winter while autumn and winter-
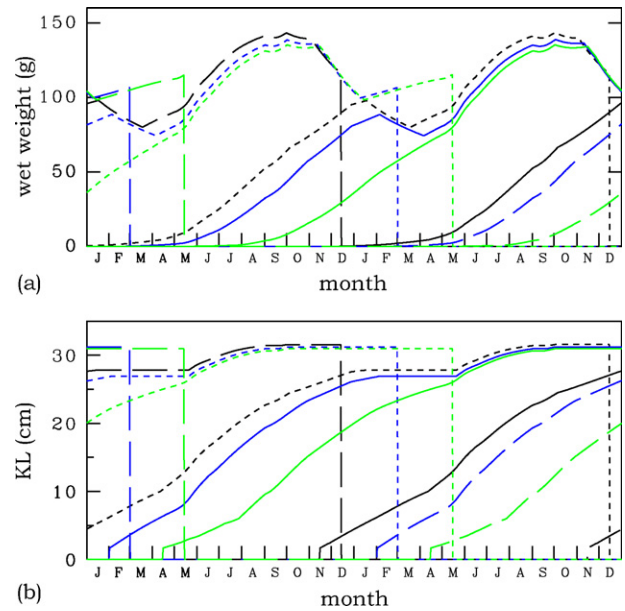

Fig. 4 – Seasonal variation of: (a) the wet weight (g) and (b) the knob length (cm) of Pacific saury derived in the control run (black lines: autumn-spawned cohort, blue lines: winter-spawned cohort, green lines: spring-spawned cohort). Since the life span of the Pacific saury is assumed to be 2 years, the pattern is repeated for every 2 years for each cohort and solid lines and dashes lines represent different year cohorts.

spawned cohorts spawn both in the first and second winter (Fig. 4).

3.2. Interannual run and differences in wet weight between seasonal spawned cohorts

Since the mixed layer depth in the model is estimated using the temperature difference between the surface and bottom, the thickness of the mixed layer is deeper in severe winter years and shallower in warmer winter years (Fig. 5). As a result,

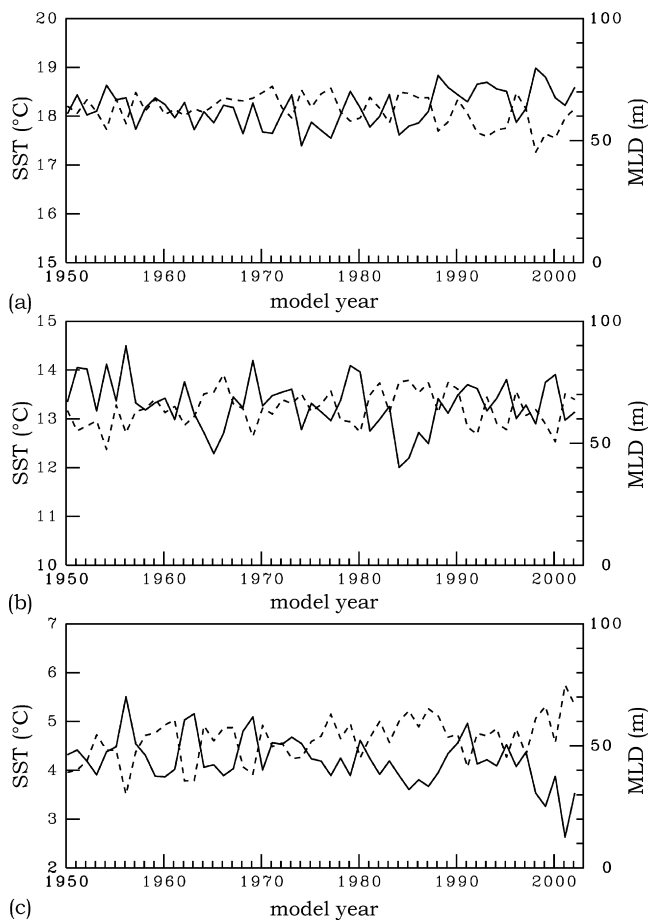| Table 1 – Migration timing for autumn-, winter-, and spring-spawned saury cohorts in this study and in Mukai et al. (2007) | | | | | | |
|---|---|---|---|---|---|
| Migration | Autumn-spawned cohorts | | Winter-spawned cohorts | | Spring-spawned cohorts | |
| | This study | Mukai et al. | This study | Mukai et al. | This study | Mukai et al. |
| Spawning | 15 November (MW) | 15 November (MW) | 1 February (KR) | 1 February (KR) | 15 April (MW) | 15 April (MW) |
| MW to KR | 30 November | 30 November | | | | |
| KR to MW | 8 May | 19 April | 8 May | 18 April | | |
| MW to OY | 15 June | 15 June | 15 June | 15 June | 9 July | 26 June |
| OY to MW | 5 October | 20 October | 30 October | 29 October | 30 October | 11 November |
| MW to KR | 28 December | 5 January | 28 December | 5 January | 12 February | 4 March |
| KR to MW | 8 May | 19 April | 8 May | 19 April | 8 May | 19 April |
| MW to OY | 15 June | 15 June | 15 June | 15 June | 15 June | 15 June |
| OY to MW | 1 October | 1 October | 1 October | 1 October | 1 October | 1 October |
| MW to KR | | | 26 November | 9 December | 26 November | 9 December |
| KR to MW | | | | | 8 May | 19 April |
| Death | 15 December | 15 December | 28 February | 28 February | 15 May | 15 May |

Fig. 5 – Winter SST (°C) used to force the interannual run (solid lines) and the resulting mixed layer depth (m) (broken lines): (a) Kuroshio area, (b) mixed water region, and (c) Oyashio area. The winter values were averaged from January to March.

Fig. 6 – Winter SST (°C) used to force the interannual run (solid lines) and the resulting zooplankton density (μmolN l^{-1}) (broken and dotted-dashed lines): (a) Kuroshio area with ZS (broken line) and ZP (dotted-dashed line), (b) mixed water region with ZL (broken line) and ZP (dotted-dashed line), and (c) Oyashio area with ZL (broken line) and ZP (dotted-dashed line). The winter SST was averaged from January to March. The durations of zooplankton density averaging are noted in the figure.

zooplankton density depends on the mixed layer thickness, and hence on the variation in SST. In KR, although the density of the small zooplankton (ZS) and predatory zooplankton (ZP) showed no significant interannual variability, they showed relatively high values in severe winter years because nutrient-rich water was entrained into the mixed layer through the process of deepening of the mixed layer (not shown). Years with severe winters also allowed a delay in the timing of the spring bloom. In average years both ZS and ZP show maximum values in May. Hence, in years with warmer winters, the April zooplankton density shows relatively high values (Fig. 6a), although the amplitude of the variation is still small.

In MW and OY, the density of the large zooplankton (ZL) and ZP were negatively correlated with the winter SST (Fig. 6b and c) and related to the nutrient supply from the deeper layer. The timing of the spring bloom is also delayed in the severe winter years in MW and OY, with maximum values of ZL and ZP occurring during May–June.

In NEMURO.FISH, saury growth depends on their ability to prey on three zooplankton classes (ZS, ZL and ZP) and thus their growth rate strongly depends on zooplankton density. As a result, saury basically showed high growth rates in years
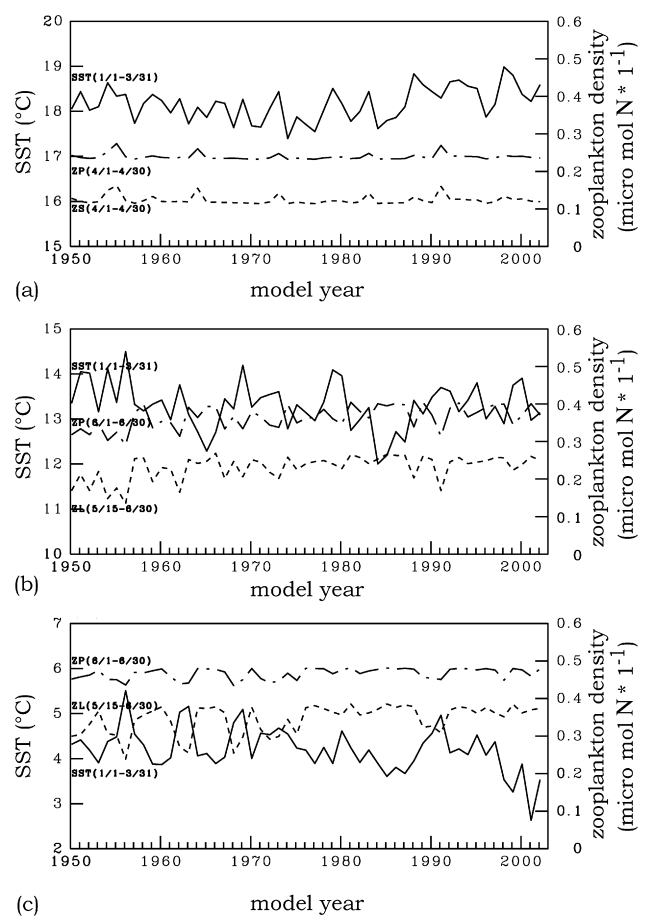
with severe winters because the deeper convection sustained higher production of phytoplankton, and hence higher zooplankton densities in subsequent springs. However, since the SST and hence zooplankton density shows different patterns in KR, MW and OY, the response of saury is complicated. To focus on the wet weight and KL during the fishing season, values in early September were selected (Fig. 7). Although the average wet weights of adults is the highest in the autumn-spawned cohort and the lowest in the spring-spawned cohort, the difference is about 10 g (Table 2), corresponding to a difference in KL of less than 1 cm. The condition factor is defined as

$$CF = \frac{1000.0W}{KL^3}, \tag{1}$$

where CF is the condition factor, W the wet weight (g), and KL is the knob length (cm). Condition factor is an indicator for fatness of fish. However, since KL is calculated from the wet

weight using a model assumption

$$KL = 6.13W^{0.33},\tag{2}$$

the model condition factor becomes

$$CF = \frac{1000.0}{6.13^3}W^{0.01}$$

(Ito et al., 2004) and does not deviate far from

$$\frac{1000.0}{6.13^3} = 4.13.$$

The standard deviation of the spring-spawned cohort shows the highest value both for the wet weight and KL. Since the autumn and winter-spawned cohorts spawn in their first winter, their wet weight decreases during spawning and they do not retain some of their growth achieved in their early stages (Fig. 4). Therefore, changes of the wet weight and KL are smoothed out for the autumn and winter-spawned cohorts. On the other hand, since the spring-spawned cohort is able to conserve the memory of the growth in their early stages, it shows large fluctuations in both wet weight and KL.

Regarding the KL composition in the autumn fishery season, the mode (and sharpness) of the large saury fluctuation is reported from observations. Since model results show large KL fluctuations in the spring-spawned cohort, the spring-spawned cohort seems to be the key factor determining the mode of KL composition and the sharpness of the mode. However, to compare the results with observations, information on the population is needed. However, the model does not calculate the number of fish at this stage although approaches such as that of Rose et al. (in press) and Megrey et al. (2007) should be considered.

3.3. Sensitivity runs and effects of each region

To clarify the influence of SST in each region on saury growth, sensitivity runs were conducted where a lagged correlation was estimated between the saury wet weight on 5 September and SST lagged from 0 to 2 years. When SST fluctuated only in KR, the wet weight showed positive correlation with winter SSTs in the current and previous year (Fig. 8a). Because zooplankton densities do not show large interannual variation in
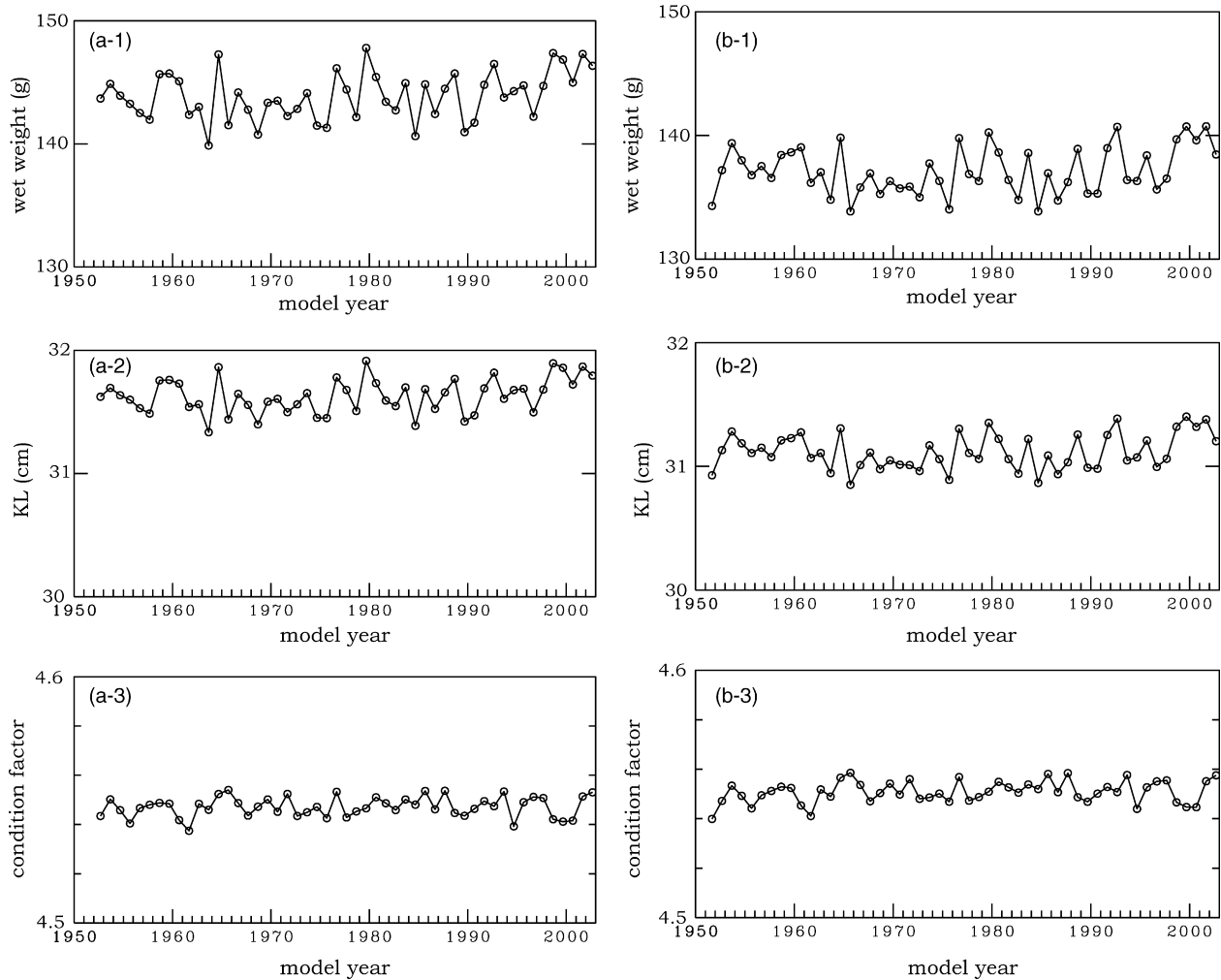

Fig. 7 – (a) Simulated interannual variation of wet weight (upper), knob length KL (middle) and condition factor CF (lower) on 5 September of the autumn-spawned cohort. (b) Simulated interannual variation of wet weight (upper), knob length KL (middle) and condition factor CF (lower) on 5 September of the winter-spawned cohort. (c) Simulated interannual variation of wet weight (upper), knob length KL (middle) and condition factor CF (lower) on 5 September of the spring-spawned cohort.
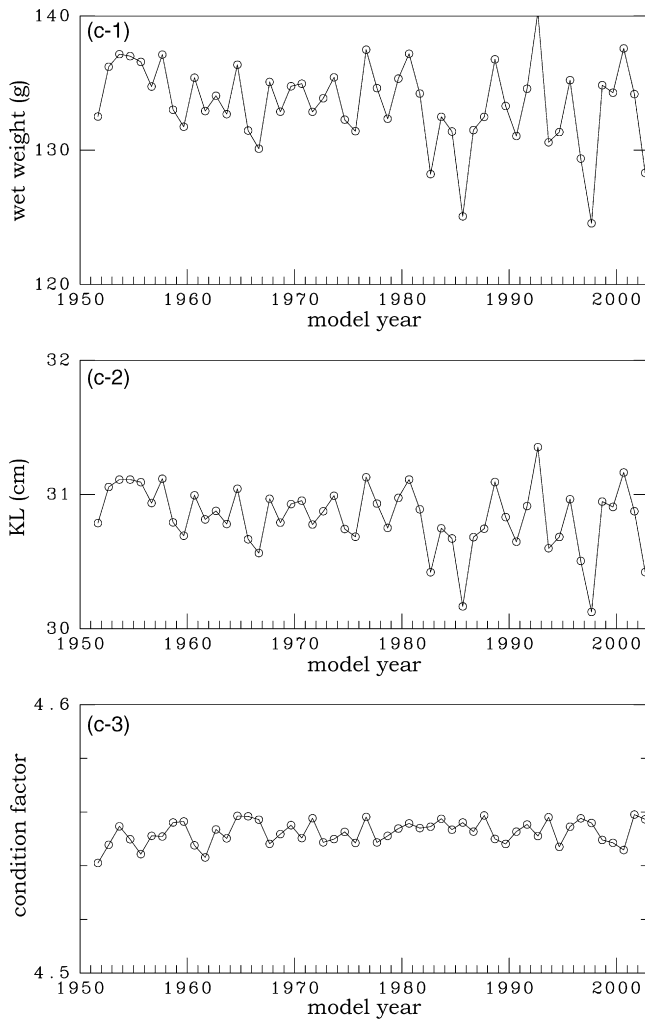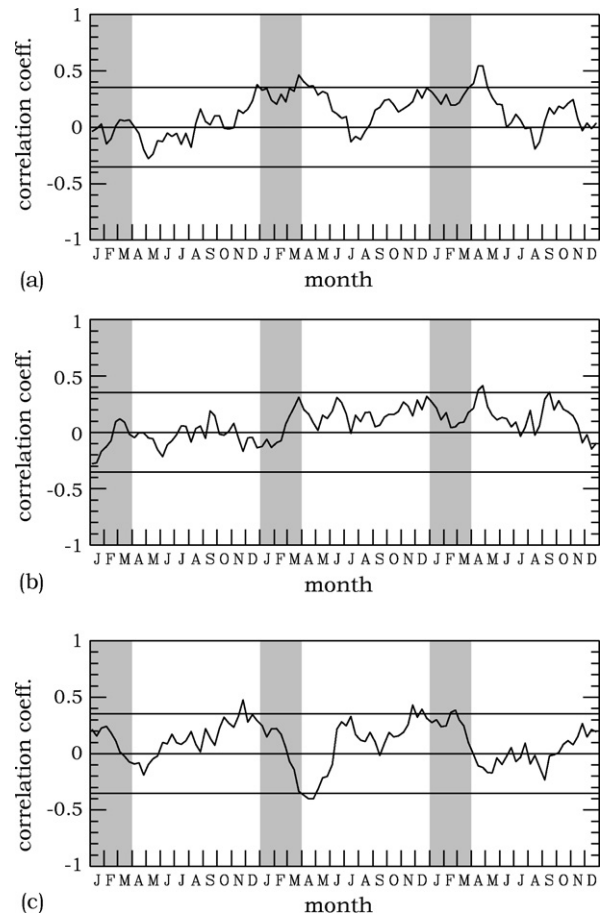
Fig. 7 – (*Continued*).

Fig. 8 – Lagged correlation between the simulated wet weight of Pacific saury: (a) in EX-KR and KR SST, (b) in EX-MW and MW SST and (c) in EX-OY and OY SST. Shaded regions show the winter season. The lagged correlation was calculated from the current year to 2 years before. The horizontal lines show the range of 99% significant levels of correlation.

KR (Fig. 6a), it is considered that warmer SSTs in KR provide higher consumption through the temperature dependence of the consumption rate.

However, EX-MW wet weight (Fig. 8b) showed weak negative correlations with winter SST in the previous year and negative correlations with the winter SST 2 years earlier. It is suggested that severe winters enhance productivity of the lower trophic level through deepening of the mixed layer (Fig. 6b) and therefore saury grow at high rates using high densities of zooplankton in MW.

On the other hand, wet weight showed negative correlations with the April SST and showed positive correlations with SST in late autumn to early winter in EX-OY (Fig. 8c). We infer that the delay of spring bloom, resulting from the colder spring SST, causes high zooplankton densities during the saury migration through the OY region, and results in higher growth rates.

4. Discussion

4.1. Comparison with observation

In the previous section, we presented the response of modeled saury growth to realistic SST forcing. In this section, the results are compared with observations. For Pacific saury, although there are no historical wet weight data, the time series of CF (condition factor) is available for analysis (Tohoku National Fisheries Research Institute, 2005). As noted previously, CF in the model was almost stably constrained by Eqs. (1) and (2).
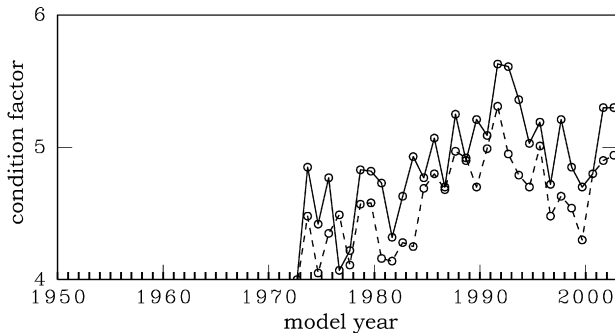
Table 2 – Average and standard deviation (STD) of saury wet weight (g), knob length (cm) and condition factor on 5 September derived from the NEMURO.FISH interannual run

Cohort	Wet weight		KL		Condition factor	
	Average	STD	Average	STD	Average	STD
Autumn	143.9	2.0	31.6	0.1	4.6	0.41E−2
Winter	137.1	1.9	31.1	0.1	4.6	0.45E−2
Spring	133.5	3.1	30.8	0.2	4.6	0.44E−2

Fig. 9 – Time series of observed Pacific saury condition factor in early September (solid line: large saury, broken line: small saury).

Therefore, wet weight in the model is suitable for comparison with the observed CF. The interannual variation of the model wet weight (Fig. 7) does not show variations similar with the observed saury CF (Fig. 9).

To investigate the cause of the inconsistency between the modeled wet weight and the observed CF, correlations between the averaged SSTs in each region and CF of Pacific saury, which was observed in early September, were compared. Focusing on winter, when the mixed layer depth reaches its maximum thickness and the entrainment of nutrients from deeper layer is determined, the SST in KR shows positive correlations with CF while the SST in MW and OY shows negative correlations in the current year, the previous year and two previous years (Fig. 10). Therefore, from the standpoint of nutrient supply, the increase of nutrients in MW and OY seems to bring increased saury growth. On the other hand, nutrient supply in KR seems to have no relationship with growth of saury.

Correlations with SSTs are consistent between the modeled wet weight and the observed CF in KR and MW: with winter SST in KR correlations are positive in the current and previous year, while with winter MW SST correlations are weakly negative with the previous year, and negatively correlated with the two previous years (Fig. 8a and b). However, the relationship between the modeled wet weight and the OY SST is different from that observed between CF and the OY SST (Fig. 8c and

Fig. 10). Two possible mechanisms for this inconsistency follow. One is a salinity effect and the other is the effect of sardine predatory pressure on zooplankton. In the subtropical region, the vertical temperature profile is the dominant factor determining mixed layer depth. However, the salinity effect is as important as temperature in the (cold water) subarctic region including the OY because of the nonlinear effect of temperature and salinity on water density. Since the effect of salinity is not included in this study, it may because of the failure of the model to simulate realistic relationships between the saury wet weight and the OY SST. Unfortunately there are no long time series (e.g., of more than 50 years) of salinity in OY, pointing to the need for further investigation of the effect of salinity in future studies. The second possibility, the effect of sardine population's predation on zooplankton will be investigated in the next subsection.

4.2. Sardine predatory effects on saury zooplankton prey

In this study, we only treated a single species fish growth model. However, in real oceanic situations, there are multiple species that interact with each other. In the northwestern Pacific, Japanese sardine (*Sardinops melanostictus*) shows dramatic fluctuations in the standing stock. Wada and Jacobson (1998) and Tadokoro et al. (2005) pointed out that the standing stock of Japanese sardine exhibited an inverse relation to the biomass of *Neocalanus* copepods, an important prey of Japanese sardine, and hence to the total mesozooplankton biomass during the summer.

To elucidate the effect of sardine predatory pressure on the saury zooplankton prey, another numerical experiment was performed (EX-S). In EX-S, the predatory pressure of sardine on the large zooplankton ZL was included. The predatory pressure was assumed to be 2.5% of the total sardine biomass in the model according to the observationally based estimates of 2–3% of Noguchi et al. (1990). The Japanese sardine biomass data were derived from Wada and Jacobson (1998), Yatsu et al. (2005) and the recent unpublished Japanese stock assessment (Japanese Fisheries Research Agency), and was prescribed in the model. The predatory pressure from sardine on ZL was assumed to be limited from 1 July to 1 September roughly corresponding to the timing migration of Japanese sardine. The biomass of sardine was converted to density divided by the model mixed layer depth and area of 125,000 km^2 (this size roughly corresponds to the area of sardine distribution in summer during high biomass periods; from 40 to 45°N and from the Japan coast to 155°E). Then, the predatory pressure from sardine P_{ZL} on ZL was defined as

$$P_{ZL}\,(\mathrm{gww\,m^{-3}}) = 0.025\,\frac{B_S}{125,000 \times 10^6 \times D}$$

in the EX-S, where B_S is the biomass of sardine (gww) and D is the model mixed layer depth (m).

The result of ZL in EX-S is shown in Fig. 11 together with that of the interannual run and the observational value derived from Odate (1994) and its extension (Sugisaki, 2006). To compare the ZL density with the observational value, the
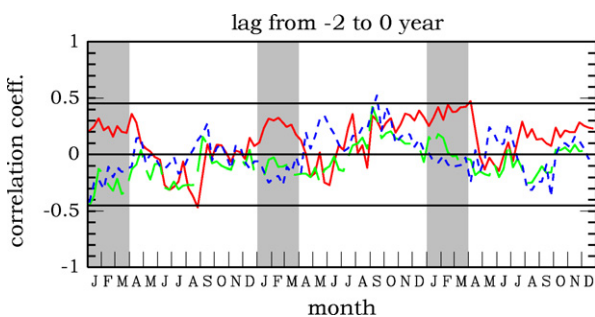

Fig. 10 – Lagged correlation between the observed Pacific saury condition factor (CF) and SST in KR (red line), MW (green line) and OY (blue line). Shaded regions show the winter season.
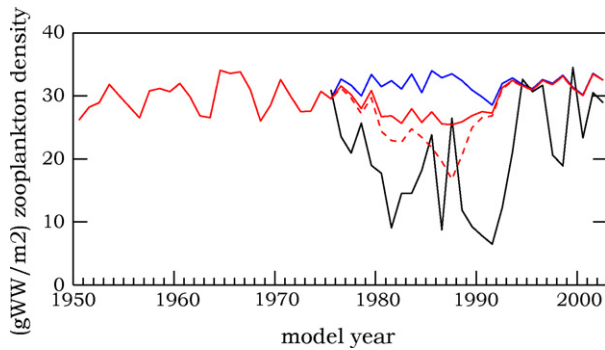
Fig. 11 – Density of large zooplankton ZL in the interannual run (blue line) and in EX-S (red solid line), and observed zooplankton density (black) in the Oyashio area OY. In EX-S, the predatory pressure of Japanese sardine on ZL is assumed to be 2.5% of sardine biomass and changed to 3.3% (red broken line) for the sensitivity analysis.

ZL density unit was converted from $\mu MN\,l^{-1}$ to $gww\,m^{-3}$ by multiplying the factors:

$$14\left(\frac{\mu gN}{\mu MN}\right)\times 10^{-6}\left(\frac{g}{\mu g}\right)\times\frac{1}{0.07}\left(\frac{gdw}{gN}\right)\times\frac{1}{0.2}\left(\frac{gww}{gdw}\right)$$

$$\times 10^{3}\left(\frac{l}{m^{3}}\right)=1.0\left(\frac{gww\,m^{-3}}{\mu MN\,l^{-1}}\right),$$

and it was converted to $gww\,m^{-2}$ by multiplied by 150 m, the vertical towed depth of the zooplankton net.

The observational zooplankton density shows a distinctive decrease in 1980s. The decrease in 1980s was reproduced in EX-S although the amplitude of the decrease is about half of the observed value. The amplitude of the decrease depends on the ratio of sardine prey consumption to the biomass. When the ratio is increased from 2.5 to 3.3%, the amplitude was doubled (Fig. 11). Moreover, the decrease in 1980s was not achieved in the interannual run. This result suggests the predatory pressure of Japanese sardine on ZL can be significant for overall zooplankton abundance, especially on decadal time scales. Therefore, even for a single species like Pacific saury, the competitive effect of Japanese sardine can be important and should be taken into account.

5. Conclusion

A simple 3-box model of NEMURO.FISH (saury version, Ito et al., 2004) was forced by observed SST to elucidate the mechanism of Pacific saury growth in response to interannual variability. A control run of NEMURO.FISH driven by climatological SST (averaged for 1950–2002) showed realistic growth of saury and captured the realistic difference in growth between cohorts spawned in different seasons.

For the interannual run, the model was forced by observed SST from 1950 to 2002. Basically zooplankton density showed a negative relationship with winter SST. It reflects the model mechanism that colder SST increases the mixed layer depth, enhances uptake of nutrients from deeper layers, increases primarily production and hence, increases the zooplankton prey density. However, since saury populations migrate widely from KR (subtropical) to OY (subarctic), the growth response of saury becomes complicated. Focusing on the fishing season of Pacific saury, the wet weight and KL standard deviation of the spring-spawned cohort is higher than those of the other two cohorts. This was caused by the difference in spawning times. The spring-spawned saury cohort is able to retain the growth from early life stages because they do not spawn in the first year. Saury of the autumn and winter-spawned cohorts cannot since they spawn in the first winter, decrease their wet weight in the spawning season and completely lose the growth of the early stages.

Compared to the observed saury CF, the model derived saury wet weight showed smaller decadal variability. The relationship between observed CF and SST was compared with that between model-derived wet weight and SST. The relationships showed consistent correlations for SSTs in KR and MW but not for OY SST. Two possibilities of this lack of correspondence were discussed. One is the effect of salinity stratification and the other is predatory pressure of Japanese sardine on zooplankton prey. The experiment including the effect of sardine showed the possible importance of the competition with other species.

In future studies, a multi-species fish formulation model needs to be established and applied to growth of the target species in the presence of multiple (competing) fish species. Similarly, studies of this type can be expected to add to our comprehensive understanding of the mechanisms causing the switches in dominant small pelagic fish on decadal time scales.

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