



Modelling ecological responses of Pacific saury (*Cololabis saira*) to future climate change and its uncertainty

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An ecosystem-based bioenergetics model was used to investigate the responses of Pacific saury (*Cololabis saira*) to global warming. The model was forced by the projected sea surface temperature (SST) generated by climate models that formed the bases for the Intergovernmental Panel on Climate Change fourth Assessment Report (IPCC-AR4). Twelve climate models, which reproduced the Pacific Decadal Oscillation well compared with observations, were selected and B1, A1B, and A2 emissions scenarios were used. In total, 33 ensemble simulations were conducted, of which 24 (73%) showed a decrease in wet weight of Pacific saury. The migration pattern was modified in 11 (33%) cases. In these cases, higher SST and size reduction under global warming prevented or delayed the southern migration of saury in winter. As a result, egg production was enhanced by the higher availability of prey plankton in the modified spawning region. A case study to separate the direct temperature effects was conducted, in which prey plankton density was assumed to be the same as the control run. The results suggest that an SST increase will directly reduce juvenile growth, whereas a prey plankton density decrease has an influence on the growth of adults and migration pattern, and hence egg production.

Keywords: CMIP3, SST, ecosystem model, egg production, fish growth, fish migration, global warming, Pacific saury, uncertainty.

Introduction

Pacific saury (*Cololabis saira*) is one of the dominant small pelagic fish in the western North Pacific and is widely distributed in the North Pacific (Hubbs and Wisner, 1980). Biomass estimates from early summer, basin-wide, midwater trawl surveys decreased from 8.0 million tonnes in 2004 to 2.2 million tonnes in 2010 in the North Pacific (Ueno *et al.*, 2004; Fisheries Agency and Fisheries Research Agency, 2009). The total number of Pacific saury has fluctuated between 12.4 and 48.5 billion during 2002–2008. Saury west of 162°E represent fish that presumably migrate to Japan's coastal region. The abundance in this region is also large and has fluctuated between ~0.3 and 2.5 million tonnes during 2003–2009. Commercial catch of Pacific saury fluctuated between 0.17 and 0.60 million tonnes during 1980–2008 and the share of the total catch by Japan has decreased from 83.3% in 1980 to 56.9% in 2008 (Figure 1). Body size and weight of landed saury also fluctuated

interannually and are important factors in determining the price in Japan (Watanabe *et al.*, 1997).

In the western North Pacific, saury spawn from autumn to the next spring with the peak spawning in winter. The spawning region is formed in the mixed water (MW) region, which corresponds to the Kuroshio–Oyashio interfrontal zone, in autumn and spring and in the subtropical region of the Kuroshio (KR) area in winter (Watanabe and Lo, 1989; Watanabe *et al.*, 1997). Eggs and larvae are advected to the KR extension region (Iwahashi *et al.*, 2006), where they grow to juveniles, then migrate to the Subarctic Oyashio (OY) area, crossing MW for feeding. After sufficient feeding, they migrate back to MW and KR to spawn (Ito *et al.*, 2004a). Their lifespan is ~2 years (Kurita *et al.*, 2004; Suyama *et al.*, 2006) and they make this extensive migration twice within their life. The Knob length (KL; nearly the same as the body length) of Pacific saury reaches ca. 30 cm in adults.

A fish bioenergetics model NEMURO.FISH [North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) for Including Saury and Herring; Ito *et al.*, 2004b, 2007; Megrey *et al.*, 2007; Mukai *et al.*, 2007], coupled with an ecosystem model NEMURO (Kishi *et al.*, 2007), was developed to investigate the mechanism controlling the growth of Pacific saury. Ito *et al.* (2004b) reproduced saury growth reasonably using NEMURO.FISH, and Mukai *et al.* (2007) reproduced the growth rate differences between different seasonally spawned cohorts of saury. Additionally, Ito *et al.* (2007) reproduced the interannual fluctuation of saury growth reasonably except for the 1980s. In the 1980s, the standing stock of Japanese sardine reached a maximum and the predation pressure on the planktonic biomass from Japanese sardine seems to have reduced the prey density in the western North Pacific and hence the wet weight of Pacific saury (Ito *et al.*, 2007). From this series of studies, NEMURO.FISH seems to be able to appropriately reproduce Pacific saury growth in regard to single fish response to climate forcing.

Ito *et al.* (2010a) integrated NEMURO.FISH under a global warming scenario. The sea surface temperature (SST) forcing was determined from an atmosphere–ocean coupled general circulation model (AOGCM) of CCSR/NIES/FRCGC (Center for Climate System Research, University of Tokyo/ National Institute of Environmental Studies/ Frontier Research Center for Global Change) with the A2 carbon emission scenario (IPCC, 2000). The model projected that the weight and the KL of saury will decrease by ~ 10 g and 1 cm, respectively, under the global warming scenario. The reduction in length and weight occurs in response to the projected reduction in prey (zooplankton density) resulting from the shallower mixed layer. Although the higher SST will enhance primary production by a temperature-dependence effect, the decrease in nutrient supply from the subsurface layer to the surface due to weaker cooling in winter will surpass this effect. Therefore,

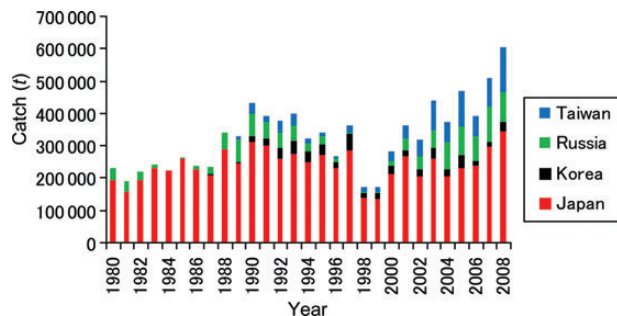


Figure 1. Catch of Pacific saury in Japan, Korea, Russia, and Taiwan.

the model projects a decrease in both the primary and the secondary production. In addition, the metabolic energy loss of saury increases because of the higher temperature. As a result, the growth of adult saury slows down under the global warming scenario.

Projected reductions in weight (or KL) trigger a change in migration patterns. In the model, the timing of feeding migration was assumed to depend on temperature and KL (Mukai *et al.*, 2007). For example, larger saury were able to migrate to the north earlier than smaller fish for feeding, since larger fish can enter colder temperature water (Kosaka, 2000). When the temperature falls below the critical temperature, saury start to migrate southwards for spawning, but the critical temperature is higher for larger fish and lower for smaller fish. Therefore, larger fish migrate southwards earlier than smaller ones, from autumn to winter. Since the temperature in the MW was high enough under the global warming scenario for saury to inhabit, age-0 saury did not migrate to the south and age-1 saury migration was delayed. Since the prey density in the MW is much higher than the KR, saury growth under global warming caught up to produce sizes consistent with the current values by February and saury start to spawn. Egg production of saury was increased under global warming because of the higher food availability. As a conclusion, the projection suggested that saury will become smaller but the number of individuals is likely to increase (Ito *et al.*, 2010a).

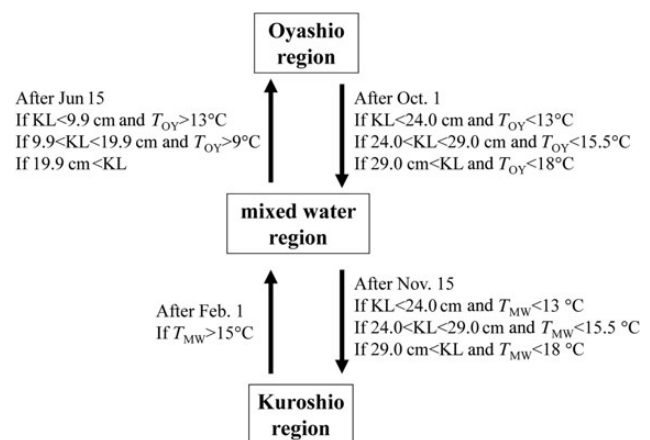


Figure 2. Schematic of the migration of Pacific saury assumed in this study. Northward feeding migration is regulated by the water temperature in the northern ocean domain and southward spawning migration is regulated by the water temperature in the ocean domain in which saury are located. KL denotes the knob length of Pacific saury and T_{OY} and T_{MW} denote the water temperatures in the OY and MW regions, respectively.

Table 1. List of coupled atmosphere–ocean models from which SST products were used for forcing of NEMURO.FISH.

IPCC ID	Code name	Country	Atmosphere resolution	Ocean resolution
CCSM3	CCSM3	USA	$1.4 \times 1.4^\circ \text{L26}$	$(0.3 - 1.0^\circ) \times 1.0^\circ \text{L40}$
CGCM3.1(T47)	CGCM-T47	Canada	$3.75 \times 3.7^\circ \text{L31}$	$1.9 \times 1.9^\circ \text{L29}$
CGCM3.1 (T63)	CGCM-T63	Canada	$2.8 \times 2.8^\circ \text{L31}$	$1.4 \times 0.9^\circ \text{L29}$
ECHAM5/ MPI-OM	ECHAM5	Germany	$1.875 \times 1.865^\circ \text{L31}$	$1.5 \times 1.5^\circ \text{L40}$
GFDL-CM2.0	GFDL2.0	USA	$2.5 \times 2.0^\circ \text{L24}$	$1 \times 1^\circ \text{L50}$
GFDL-CM2.1	GFDL2.1	USA	$2.5 \times 2.0^\circ \text{L24}$	$1 \times 1^\circ \text{L50}$
MIROC3.2 (hires)	MIROC(h)	Japan	$1.125 \times 1.12^\circ \text{L56}$	$0.28 \times 0.188^\circ \text{L47}$
MIROC3.2 (medres)	MIROC(m)	Japan	$2.8 \times 2.8^\circ \text{L20}$	$(0.5 - 1.4^\circ) \times 1.4^\circ \text{L44}$
ECHO-G (MIUB)	ECHO-G	Germany/Korea	$3.75 \times 3.7^\circ \text{L19}$	$(0.5 - 2.8^\circ) \times 2.8^\circ \text{L20}$
MRI-CGCM2.3.2	MRI	Japan	$2.8 \times 2.8^\circ \text{L30}$	$(0.5 - 2.5^\circ) \times 2^\circ \text{L23}$
PCM	PCM1	USA	$2.8 \times 2.8^\circ \text{L18}$	$(0.5 - 0.7^\circ) \times 0.7^\circ \text{L32}$
UKMO-HadCM3	HadCM3	UK	$3.75 \times 2.5^\circ \text{L15}$	$1.02 \times 1.25^\circ \text{L20}$

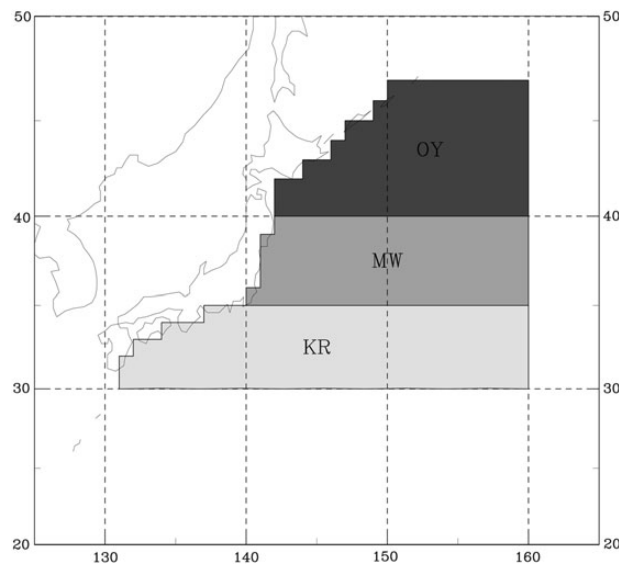


Figure 3. Schematic view of the three oceanic spatial domains where SST data were averaged and simulated in the model. The three domains correspond to the KR, MW, and OY regions. After Ito et al. (2007).

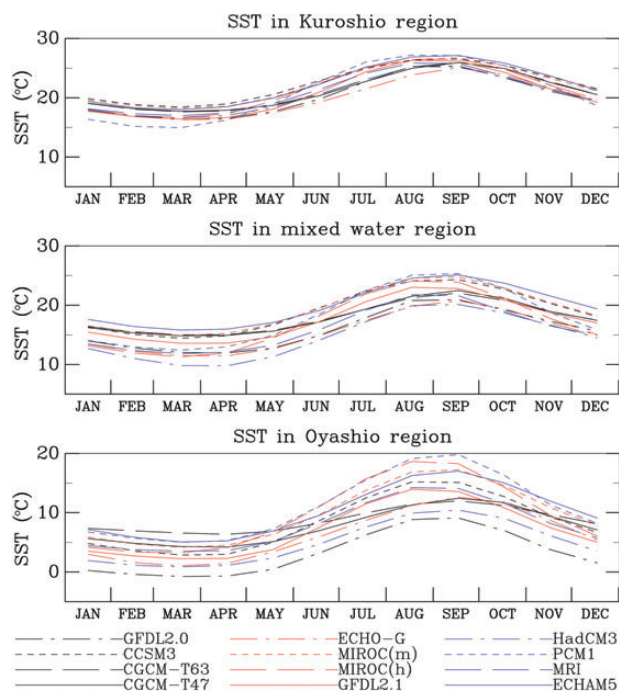


Figure 4. Climatological SST from 1950 to 1999 in each ocean domain for the 12 climate models.

The results described above were derived from a very simplified model and always model predictions have uncertainties. The uncertainty could be caused by forcing and deficiency of physical, lower-trophic-level ecosystem, fish growth, and fish migration models. In the Intergovernmental Panel on Climate Change fourth Assessment Report (IPCC-AR4), ensemble simulation approaches were conducted and evaluated the uncertainty and robustness of the future climate projections. Ito et al. (2010a) only used the NEMURO.FISH model and one forcing SST produced by the

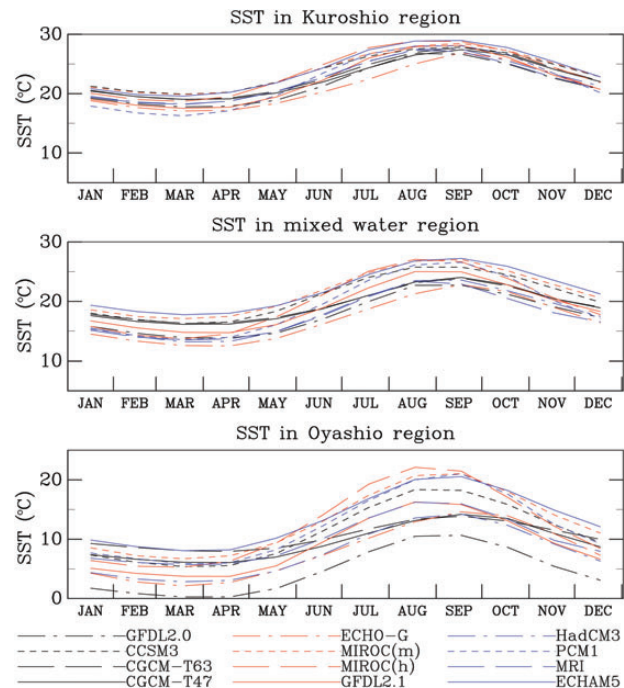


Figure 5. Climatological SST from 2045 to 2055 in each ocean domain for the 12 climate models with the A1B carbon emission scenario.

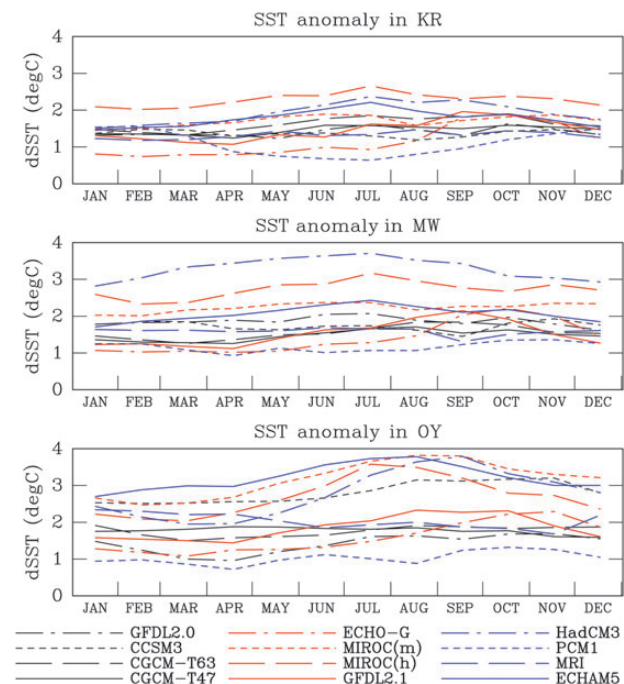


Figure 6. SST anomaly between 2045–2055 climatology (A1B scenario) and 1950–1999 climatology in each ocean domain for the 12 climate models.

MIROC (Model for Interdisciplinary Research on Climate). SST projections produced by IPCC-AR4 climate models with several emissions scenarios are available. Therefore, as a first step, we evaluated the uncertainty of the saury future projection caused by forcing SST in this study. The objective of this study is (i) to test the

robustness of future projections of Pacific saury response and (ii) to elucidate the mechanisms that will cause change in wet weight and egg production of Pacific saury under global warming.

Method

Model configuration

We used the same model as Ito *et al.* (2007). The model covers three different oceanographic spatial domains corresponding to KR, MW, and OY. In each ocean domain, the mixed layer depth fluctuates according to the difference between SST and the temperature at the bottom of the mixed layer (BLT), which is set to be constant as the bottom boundary condition (19.1°C for KR, 14.7°C for MW, and 4.58°C for OY). The thickness of the mixed layer increases (decreases) when the SST is lower (higher) than BLT. The exchange rate of NO_3 and Si(OH)_4 between the mixed layer and the bottom layer is modelled as a function of the stability defined by the

difference of temperature between SST and BLT. NEMURO is driven by the SST forcing and light intensity at the surface. Zooplankton densities and seawater temperature derived from NEMURO are coupled with the Pacific saury bioenergetics model.

The timing of spawning and migration between the KR, MW, and OY were defined as a function of the size of the saury and water temperature (Figure 2). Northward migration is controlled by SST in the northern ocean domain. After 1 February, if SST in MW is higher than 15°C, saury migrate to MW. After 15 June, saury of KL larger than 19.9 cm migrate to OY, whereas saury of KL between 9.9 and 19.9 cm remain until SST in OY becomes higher than 9°C and saury of KL smaller than 9.9 cm remain until SST in OY becomes higher than 13°C. On the contrary, southward migration was defined by SST in the ocean domain where saury occur. After 1 October, saury of KL larger than 29.0 cm migrate to MW if SST in OY becomes lower than 18°C.

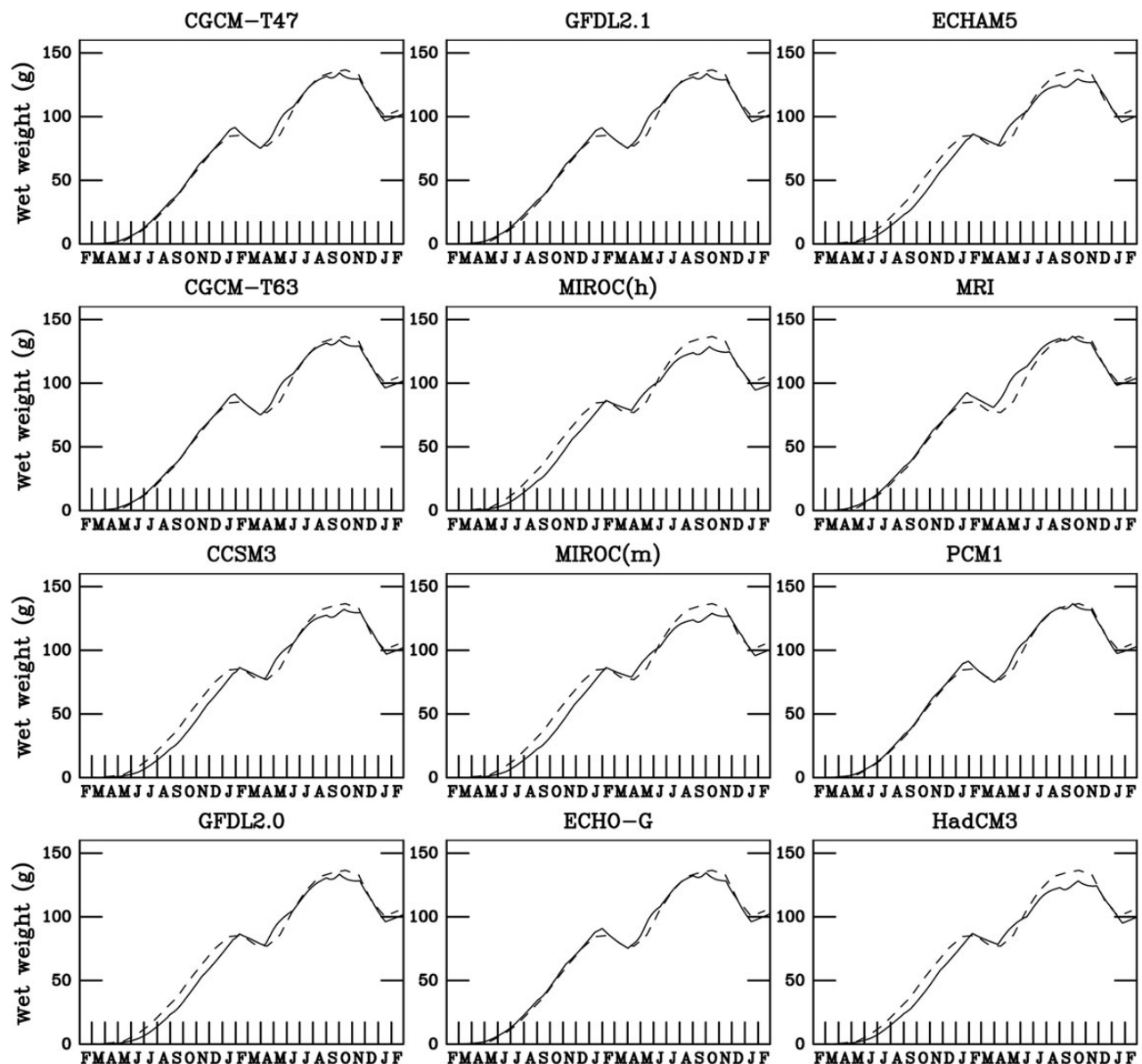


Figure 7. Modelled wet weight growth of Pacific saury under observational 1950–1999 climatological SST (broken lines) and 2045–2055 SST (A1B scenario) of the 12 climate models (solid lines).

Saury of KL between 24.0 and 29.0 cm remain until SST in OY becomes cooler than 15.5°C. Saury of KL smaller than 24.0 remain until SST becomes lower than 13°C. The migration to KR is similarly defined except that the migration is permitted after 15 November.

Ensemble experiments

NEMURO.FISH is driven by light and SST. Idealized seasonal light intensity was assumed the same as Ito *et al.* (2007). For SST, we used IPCC-AR4 model outputs. Wang *et al.* (2010) investigated the performance of model simulated SST over the North Pacific region and concluded only 12 models reasonably reproduced the Pacific Decadal Oscillation (PDO) when compared with the observation. Since PDO is a leading mode variability in the North Pacific SST, only these 12 models were used in the current study (Table 1). Additionally, the projected SST depends on emissions scenarios. Therefore, we used three types of scenarios: A2 (relatively high), A1B (moderate), B1 (relatively low) (IPCC, 2000). Although several simulations were conducted in each IPCC-AR4 climate model, we used only one simulation from each model in this study because of computational limitations. Not all the 12 models submitted their simulations under all three emission scenarios. As a result, 33 future SSTs were prepared (10 for A2, 12 for A1B, and 11 for B1).

The SST was monthly averaged in each ocean domain (Figure 3). The monthly averaged SST was averaged from 1950 to 1999 and climatological SST for the late 20th century was made (Figure 4). Likewise, climatological SST for the middle of the 21st century was computed by averaging from 2045 to 2055 (Figure 5). To remove the potential model bias, the SST increase anomaly was calculated by subtracting SST in the late 20th century from that in the middle of 21st century (Figure 6). Although the SST anomalies are positive in all models for all three regions, their variability is not negligible especially in MW and OY. The SST anomaly was added to the observational SST climatology to reproduce the future SST field. We used the same observational SST climatology with Ito *et al.* (2007) to make the comparison easier. The source of observed SST is from Japan Meteorological Agency (JMA) data (<http://www.goos.kishou.go.jp>) from 1950 to 2002. NEMURO.FISH was first integrated by the climatological SST of the late 20th century as a control run. NEMURO.FISH was also integrated by the future SST field as a projection of the saury response under global warming.

Case studies

Future SST anomaly directly impacts on the growth of Pacific saury through metabolism and their migration timing. On the other hand, the future SST will affect the prey plankton density and will indirectly impact the growth of Pacific saury. To separate the influence of SST and prey plankton, as a case study, we integrated NEMURO.FISH by the future SST with the A1B scenario but the prey plankton density was kept the same as the control run.

Results

Pacific saury responses under the A1B scenario

Wet weight of Pacific saury under the A1B scenario varied in response to SST projections (Figure 7). The wet weight changes can be categorized into three groups comparing with the results of the control run. Group 1 showed a decrease in wet weight in both age-0 and age-1 [CCSM3, GFDL2.0, MIROC(h), MIROC(m),

Table 2. SST anomaly in each of the ocean domains.

Change of wet weight of saury	Climate model	KR	MW	OY	Average
Decrease in age-0 and age-1	CCSM3	1.36	1.73 ^a	2.80 ^b	1.97 ^a
	GFDL2.0	1.41 ^a	1.86 ^a	1.41	1.56
	MIROC(h)	2.28 ^b	2.73 ^b	2.70 ^a	2.57 ^b
	MIROC(m)	1.71 ^b	2.24 ^b	3.16 ^b	2.37 ^b
	ECHAM5	1.78 ^b	2.07 ^b	3.22 ^b	2.35 ^b
	HadCM3	1.93 ^b	3.30 ^b	2.78 ^b	2.67 ^b
Decrease in age-1	CGCM-T47	1.46 ^a	1.48	1.77 ^a	1.57
	CGCM-T63	1.63 ^a	1.55 ^a	1.75	1.65 ^a
	GFDL2.1	1.46 ^a	1.53	1.85 ^a	1.61 ^a
	ECHO-G	1.14	1.41	1.58	1.38
	PCM1	1.10	1.17	1.03	1.10
No decrease	MRI	1.32	1.59 ^a	2.04 ^a	1.65 ^a

KR, Kuroshio area; MW, mixed water region; OY, Oyashio area and averaged in three ocean domains (average) for the A1B scenario.

^aMiddle four.

^bHighest four.

ECHAM5, and HadCM3]. Group 2 showed a decrease in wet weight only in age-1 (CGCM-T47, CGCM-T63, GFDL2.1, and ECHO-G). Group 3 showed no decrease or increase in wet weight (MRI and PCM1). There is a tendency that a higher anomaly of SST causes a greater decrease in weight (Table 2). But the decrease in weight is not in order of the SST anomaly. For example, SST of MRI showed a relatively higher anomaly in MW and OY; however, there was no change in the wet weight of saury. The responses seem complex depending on the timing, threshold, and combination with prey availability.

On the other hand, egg production increased in seven cases [CCSM3, GFDL2.0, MIROC(h), MIROC(m), ECHAM5, MRI, and HadCM3] and was unchanged in the other five cases (Figure 8). In the case egg production is increased, the migration pattern of saury was modified as shown in Ito *et al.* (2010a).

Pacific saury responses under the A2 scenario

Wet weight of Pacific saury under the A2 scenario varied based on SST and the changes can be categorized to the similar groups (Figure 9). Group 1, which showed a decrease in wet weight in both age-0 and age-1, consisted of MIROC(m), ECHO-G, and HadCM3. Group 2, which showed a decrease in wet weight only in age-1, consisted of CGCM-T47, CCSM3, ECHAM5, and MRI. Group 3, which showed no decrease or increase in wet weight, consisted of GFDL2.0, GFDL2.1, and PCM1. There is a tendency that the higher anomaly of SST causes a greater decrease in weight; however, again the decrease in weight is not in order of the SST anomaly (not shown). Egg production change is similar to the A1B scenario (not shown). Egg production increased in three cases [MIROC(m), ECHO-G, and HadCM3] with migration pattern change and was unchanged in the other cases.

Pacific saury responses under the B1 scenario

Projected wet weight of Pacific saury under the B1 scenario varied based on SST and the changes were categorized to the similar groups (Figure 10). Group 1, which showed a decrease in wet weight in both age-0 and age-1, consisted of MIROC(h) and HadCM3. Group 2, which showed a decrease in wet weight only in age-1, consisted of CCSM3, GFDL2.1, MIROC(m), ECHO-G, and MRI. Group 3, which showed no decrease or increase in wet weight,

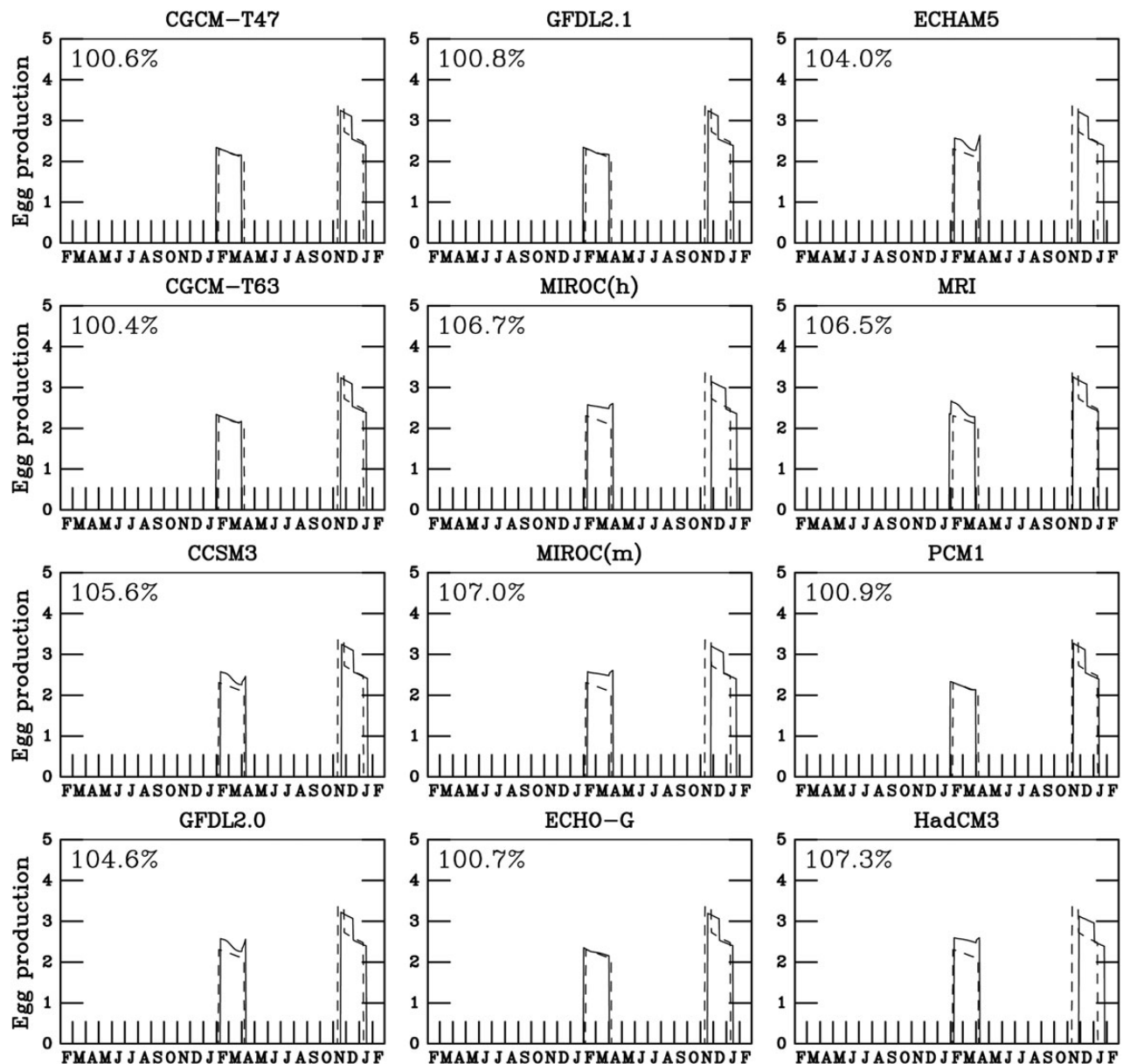


Figure 8. Modelled egg production of Pacific saury under observational 1950–1999 climatological SST (broken lines) and 2045–2055 SST (A1B scenario) of the 12 climate models (solid lines). The number in the left-up corner represents ratio of the total egg production for 2045–2055 SST to one for 1950–1999 SST.

consisted of CGCM-T47, CGCM-T63, ECHAM5, and PCM1. The tendency that a higher anomaly of SST causes a greater decrease in wet weight became rather clear in this case (not shown). This is because the increase in SST is moderate and seems not to be more than critical values which influence their migration. Indeed egg production was increased only for HadCM3 SST which showed the highest SST increase (not shown). Only for this case, the migration pattern of saury was modified.

As a whole, 24 of the 33 cases (73%) showed a decrease in wet weight of saury (Table 3). Eleven of the 33 cases (33%) showed a decrease in wet weight in both age-0 and age-1. Thirteen of the 33 cases (39%) showed a decrease in wet weight only in age-1. Therefore, the decrease in age-1 wet weight, which is most sensitive for the price of landings, seems robust regarding the future SST forcing.

Case studies: direct effect of SST

The case study in which SST was changed but the prey plankton density was kept as the same as the control run also showed variability in wet weight in response to projected SST. However, in this case, no ensemble member showed a decrease in wet weight of saury in age-1 (Figure 11). Moreover, the egg production was not increased in any ensemble member (not shown). Therefore, it can be concluded that the decrease in wet weight in age-1 was caused by the prey density decrease under the global warming condition, then it resulted in a modification of the migration pattern and egg production.

The wet weight changes can be categorized to two groups (Figure 11). Group 1 showed a decrease in wet weight of saury in age-0 [CCSM3, GFDL2.0, MIROC(h), MIROC(m), ECHAM5, and HadCM3] Group 2 showed no decrease or increase in wet

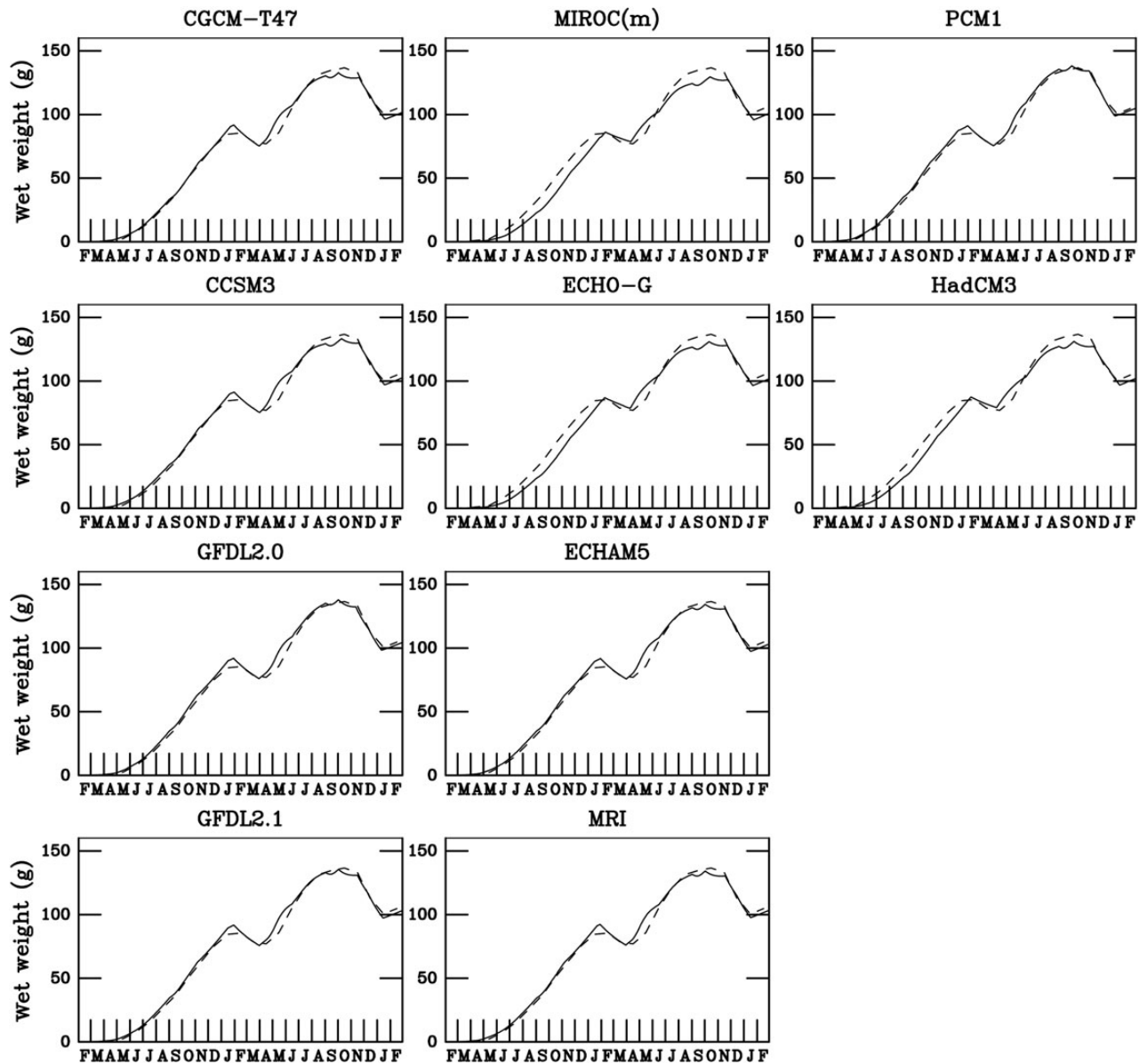


Figure 9. Modelled wet weight growth of Pacific saury under observational 1950–1999 climatological SST (broken lines) and 2045–2055 SST (A2 scenario) of the ten climate models (solid lines).

weight of saury (CGCM-T47, CGCM-T63, GFDL2.1, ECHO-G, PCM1, and MRI). In this case, the tendency that a higher anomaly of SST causes a greater decrease in weight became clear (Table 4). Especially, the response of saury wet weight highly depends on SST in MW. Therefore, it can be concluded that SST directly influenced wet weight in age-0 and SST in MW is the most important factor to control age-0 weight.

Summary and discussion

Although Ito *et al.* (2010a) showed the possibility of a decrease in wet weight of Pacific saury and an increase in population numbers under global warming using one SST output of a climate model, ensemble experiments using 33 set of SST from IPCC-AR4 climate models showed the range of potential outcomes caused by different SST scenarios. Seventy-three per cent indicated a size reduction in Pacific saury under global warming; 33% showed a decrease in

wet weight in both age-0 and age-1; and 39% showed a decrease in wet weight only in age-1. Therefore, the decrease in age-1 wet weight seems robust regarding the future SST forcing. The price of age-1 is higher than that of age-0 and large age-1 are highly valued. Therefore, the size reduction in age-1 under global warming will have a large influence on fisheries.

On the other hand, only 33% of the models showed an increase in egg production; therefore, the increase in egg production does not seem robust. Additionally, even if the egg production is increased, the survival rate must be considered. Oozeki and Watanabe (2000) showed that the growth rate of Pacific saury is higher for higher water temperatures. Watanabe *et al.* (2003) estimated the survival rate of larvae and juveniles of Pacific saury and showed a higher survival rate of juveniles for higher water temperature. This information suggests a possibility that higher temperatures result in higher growth and hence higher survival of Pacific saury juveniles.

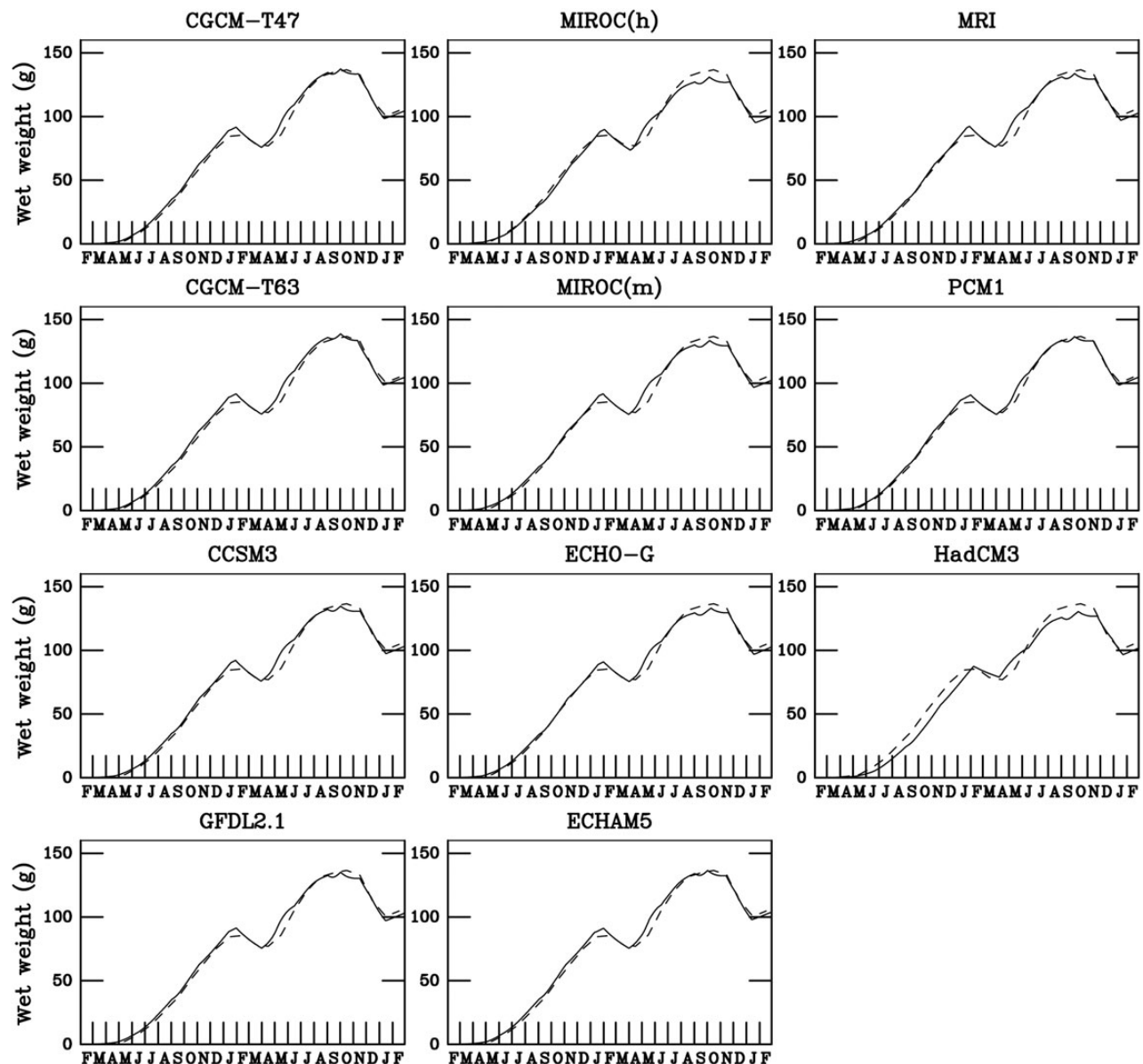


Figure 10. Modelled wet weight growth of Pacific saury under observational 1950 – 1999 climatological SST (broken lines) and 2045 – 2055 SST (B1 scenario) of the 11 climate models (solid lines).

Indeed, [Watanabe \(2007\)](#) projected higher production of Pacific saury juveniles based on the above estimations. Together with the egg production and the survival rate, the number of saury may increase under global warming.

Another important issue is how the fishing fleets will respond to shifts in the distribution of saury. In our model, the southward migration was delayed in 11 cases (33%) under global warming. [Kuwahara et al. \(2006\)](#) also pointed out the possibility of a northward shift of saury fishing grounds and a delay of fishing ground formation around Japan. Saury is traditionally fished in fall in Japan and the fishing season is closely related to Japanese culinary culture. Additionally, saury caught early in the fishing season sell at high prices. If it becomes difficult to catch these higher-priced early saury in the Japanese economic waters, that will be a serious problem for Japanese fisheries. Therefore, it is important to carefully estimate saury migration timing under global warming.

This study has identified many uncertainties associated with future projections of fish responses to climate change. In this study, we evaluated the impact of different forcing SSTs on the weight, migration, and abundance of Pacific saury. Uncertainty could be also caused by the deficiency of each model component (physical, lower-trophic-level ecosystem, fish growth, and fish migration models). In this study, the physical model configuration itself was largely oversimplified. The mixed layer depth was only controlled by SST and the influence of salinity was neglected in this study. A study projected enhancement of KR ([Sakamoto et al., 2005](#)) and offshore transport of fish larvae; however, this study did not consider the horizontal advection. Each ocean domain was considered as homogeneous, and eddies and mesoscale variability was ignored in this study. Uncertainty associated with these more complex physical processes were not considered in our study. However, recently, eddy permitted climate models have

Table 3. Changes in the wet weight of saury for three carbon emission scenarios (A2, A1B, and B1) and SST products.

Climate model	A2	A1B	B1
HadCM3	Decrease in age-0 and age-1	Decrease in age-0 and age-1	Decrease in age-0 and age-1
MIROC(h)	–	Decrease in age-0 and age-1	Decrease in age-0 and age-1
MIROC(m)	Decrease in age-0 and age-1	Decrease in age-0 and age-1	Decrease in age-1
CCSM3	Decrease in age-1	Decrease in age-0 and age-1	Decrease in age-1
ECHAM5	Decrease in age-1	Decrease in age-0 and age-1	No decrease
GFDL2.0	No decrease	Decrease in age-0 and age-1	–
ECHO-G	Decrease in age-0 and age-1	Decrease in age-1	Decrease in age-1
CGCM-T63	–	Decrease in age-1	No decrease
CGCM-T47	Decrease in age-1	Decrease in age-1	No decrease
GFDL2.1	No decrease	Decrease in age-1	Decrease in age-1
MRI	Decrease in age-1	No decrease	Decrease in age-1
PCM1	No decrease	No decrease	No decrease

“–” means the climate model projection was not available for the emission scenario.

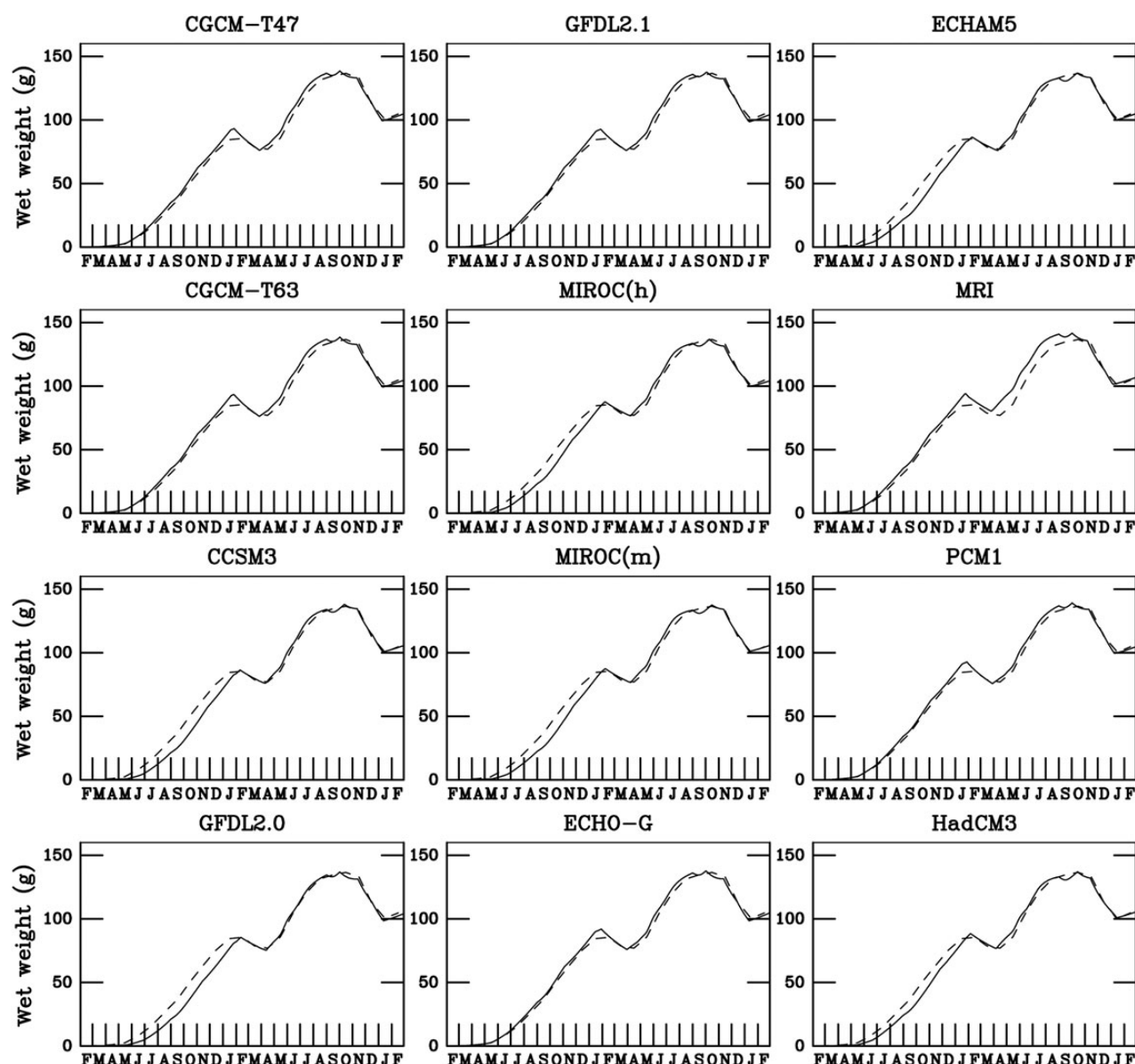
**Figure 11.** Modelled wet weight growth of Pacific saury under observational 1950–1999 climatological SST (broken lines) and 2045–2055 SST (A1B scenario) of 12 climate models with keeping the prey density the same as the control run (solid lines).

Table 4. SST anomaly in each ocean domain.

	KR	MW	OY	Average
Decrease in age-0 and age-1				
CCSM3	1.36	1.73 ^a	2.80 ^b	1.97 ^a
GFDL2.0	1.41 ^a	1.86 ^a	1.41	1.56
MIROC(h)	2.28 ^b	2.73 ^b	2.70 ^a	2.57 ^b
MIROC(m)	1.71 ^b	2.24 ^b	3.16 ^b	2.37 ^b
ECHAM5	1.78 ^b	2.07 ^b	3.22 ^b	2.35 ^b
HadCM3	1.93 ^b	3.30 ^b	2.78 ^b	2.67 ^b
No decrease or increase				
CGCM-T47	1.46 ^a	1.48	1.77 ^a	1.57
CGCM-T63	1.63 ^a	1.55 ^a	1.75	1.65 ^a
GFDL2.1	1.46 ^a	1.53	1.85 ^a	1.61 ^a
ECHO-G	1.14	1.41	1.58	1.38
PCM1	1.10	1.17	1.03	1.10
MRI	1.32	1.59 ^a	2.04 ^a	1.65 ^a

KR, Kuroshio area; MW, mixed water region; OY, Oyashio area and averaged for the three ocean domains (average) for the A1B scenario and only SST changed case.

^aMiddle four.

^bHighest four.

been developed (e.g. Sakamoto *et al.*, 2005) and downscaling techniques have been developed. Therefore, it will be possible to conduct projections using such physical model tools in the future.

Uncertainty in prey plankton models is attributed to process errors related to the selection of the functional form and parameterization of models. For phytoplankton, global data are available from satellite observations. Therefore, the validation of phytoplankton biomass and production has been conducted and the predictability has been improved. However, for zooplankton, data availability is limited in both space and time. Moreover, many lower trophic level ecosystem models added zooplankton compartments as closure terms of the models. Therefore, the validation or the evaluation of zooplankton parts has been limited or not conducted carefully. As a result, we have much uncertainty in zooplankton projection and it is an urgent task to improve zooplankton mechanical models. Optimal parameter estimations of zooplankton models using data assimilation methods (e.g. Ito *et al.*, 2010b) are also effective to improve the accuracy of zooplankton models.

We used NEMURO.FISH in this study. However, several parameters of the bioenergetics model could not be determined by observational or laboratory experimental approaches. These parameters were approximated from other fish species. To fill the information gap, laboratory experiments are continuing (e.g. Nakaya *et al.*, 2010). Especially, adaptation mechanisms of fish are a big issue for projections under global warming. Laboratory experiments to investigate adaptation mechanisms are important, although they take several years.

The migration model used in this study was based on a retrospective analysis of seasonal movements of fishers, and there are no data directly observing saury movements. This is because Pacific saury is a fragile fish and is easily damaged by handling; therefore, it is impossible to conduct catch and tag release observations. Development of the technology to enable direct measurements of Pacific saury (and other small pelagic fish) movements is needed.

Our model conditioned movement on size and temperature. Tu *et al.* (2012) applied an algorithm to Japanese anchovy in which fish migrate along the current then change to swimming towards their optimal spawning temperature. This simple algorithm successfully simulated the realistic spawning migration of Japanese anchovy. For Japanese sardine, Okunishi *et al.* (2009) modelled feeding

migration by a fitness algorithm (e.g. Bertignac *et al.*, 1998) in which fish migrate towards regions enabling optimal growth and modelled the spawning migration by an artificial neural network with a genetic algorithm (e.g. Huse and Fiksen, 2010). Humston *et al.* (2004) applied a kinesis model for a coastal fish movement in which fish alter the speed and frequency of directional change depending on their habitat condition. Okunishi *et al.* (2012a) proposed an extended kinesis algorithm to simulate realistic feeding migration of Japanese sardine which is an improved version of a kinesis algorithm. Such migration algorithms should be improved together with direct measurements of fish movement and applied to evaluate fish responses to climate change as Okunishi *et al.* (2012b) conducted.

Most of challenging issues are interactions between other species (competitors and predators). For Pacific saury, especially competition with Japanese sardine cannot be ignored (Tadokoro *et al.*, 2005; Ito *et al.*, 2007). During the high stock period of Japanese sardine, their feeding pressure on prey plankton is quite large, leading to a decrease in prey plankton density and hence influence on growth of Pacific saury (Ito *et al.*, 2007). On the other hand, Pacific saury are important prey of whales (e.g. Tamura and Fujise, 2002). Therefore, ecosystem responses must be considered in the future. End-to-end modelling approaches (e.g. Travers *et al.*, 2007) are needed to make projections of ecosystems.

The goal of this study was quantify the range of possible outcomes stemming from changes in ocean ecosystems under different climate forcing. The biophysical projections revealed the implications of climate change on future shifts in size distribution and abundance of Pacific saury. We separated the SST direct impacts and prey plankton impacts in the case study. The model results suggested that an SST increase (especially in MW) directly reduces juvenile growth, and a prey decrease influences the growth of adults and the migration pattern, hence egg production. This kind of information is important to plan observations and laboratory experiments. Additionally, the simple model enables ensemble experiments with reasonable computational costs. Therefore, we are able to estimate the uncertainty caused by SST products and the probability of the results. Approaches combining simple theoretical models with models incorporating realistic processes and conditions are desirable to enable a more comprehensive understanding of fish responses to climate change.

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References

Bertignac, M., Lehodey, P., and Hampton, J. 1998. A spatial population dynamics simulation model of tropical tunas using a habitat index

- based on environmental parameters. *Fisheries Oceanography*, 7: 326–334.
- Fisheries Agency and Fisheries Research Agency. 2009. Marine fisheries stock assessment and evaluation for Japanese waters (fiscal years 2008/2009). Tokyo, pp. 1–229 (in Japanese).
- Hubbs, C. L., and Wisner, R. L. 1980. Revision of the sauries (Pisces, Scomberesocidae) with descriptions of two new genera and one new species. *Fishery Bulletin US*, 77: 521–566.
- Humston, R., Olson, D. B., and Ault, J. S. 2004. Behavioral assumptions in models of fish movement and their influence on population dynamics. *Transactions of the American Fisheries Society*, 133: 1304–1328.
- Huse, G., and Fiksen, Ø. 2010. Modelling encounter rates and distribution of mobile predators and prey. *Progress in Oceanography*, 84: 93–104.
- IPCC. 2000. Special report on emissions scenarios: a special report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge. 570 pp.
- Ito, S., Kishi, M. J., Kurita, Y., Oozeki, Y., Yamanaka, Y., Megrey, B. A., and Werner, F. E. 2004b. Initial design for a fish bioenergetics model of Pacific saury coupled to a lower trophic ecosystem model. *Fisheries Oceanography*, 13(Suppl. 1): 111–124.
- Ito, S., Megrey, B. A., Kishi, M. J., Mukai, D., Kurita, Y., Ueno, Y., and Yamanaka, Y. 2007. On the interannual variability of the growth of Pacific saury (*Cololabis saira*): a simple 3-box model using NEMURO.FISH. *Ecological Modelling*, 202: 174–183.
- Ito, S., Rose, K. A., Miller, A. J., Drinkwater, K., Brander, K. M., Overland, J. E., Sundby, S., et al. 2010a. Ocean ecosystem responses to future global change scenarios: a way forward. In *Global Change and Marine Ecosystems*, pp. 287–322. Ed. by M. Barange, J. G. Field, R. H. Harris, E. Hofmann, R. I. Perry, and F. Werner. Oxford University Press. 440 pp.
- Ito, S., Sugisaki, H., Tsuda, A., Yamamura, O., and Okuda, K. 2004a. Contributions of the VENFISH program: meso-zooplankton, Pacific saury (*Cololabis saira*) and walleye pollock (*Theragra chalcogramma*) in the northwestern Pacific. *Fisheries Oceanography*, 13(Suppl. 1): 1–9.
- Ito, S., Yoshie, N., Okunishi, T., Ono, T., Okazaki, Y., Kuwata, A., Hashioka, T., et al. 2010b. Application of an automatic approach to calibrate the NEMURO nutrient-phytoplankton-zooplankton food web model in the Oyashio region. *Progress in Oceanography*, 87: 186–200.
- Iwahashi, M., Isoda, Y., Ito, S., Oozeki, Y., and Suyama, S. 2006. Estimation of seasonal spawning ground locations and ambient sea surface temperatures for eggs and larvae of Pacific saury (*Cololabis saira*) in the western North Pacific. *Fisheries Oceanography*, 15: 125–138.
- Kishi, M. J., Kashiwai, M., Ware, D. M., Megrey, B. A., Eslinger, D. L., Werner, F. E., Aita-Noguchi, M. N., et al. 2007. NEMURO - a lower trophic level model for the North Pacific marine ecosystem. *Ecological Modelling*, 202: 12–25.
- Kosaka, S. 2000. Life history of the Pacific saury *Cololabis saira* in the northwest Pacific and consideration on resource fluctuations based on it. *Bulletin of the Tohoku National Fisheries Research Institute*, 63: 1–96 (in Japanese with English abstract).
- Kurita, Y., Nemoto, Y., Oozeki, Y., Hayashizaki, K., and Ida, H. 2004. Variations in patterns of daily changes in otolith increment width of 0+ Pacific saury, *Cololabis saira*, off Japan by hatch date in relation to the northward feeding migration during spring and summer. *Fisheries Oceanography*, 13(Suppl. 1): 54–62.
- Kuwahara, H., Aketa, S., Kobayashi, S., Takeshita, A., Yamashita, Y., and Shiroto, K. 2006. Prediction of habitat change of Japanese fisheries target species by global warming. *Chikyu Kankyo*, 11: 49–57 (in Japanese).
- Megrey, B. A., Rose, K. A., Klumb, R. A., Hay, D. E., Werner, F. E., Eslinger, D. L., and Smith, S. L. 2007. A bioenergetics-based population dynamics model of Pacific herring (*Clupea harengus pallasii*) coupled to a lower trophic level nutrient-phytoplankton-zooplankton model: description, calibration and sensitivity analysis. *Ecological Modelling*, 202: 144–164.
- Mukai, D., Kishi, M. J., Ito, S., and Kurita, Y. 2007. The importance of spawning season on growth of Pacific saury: a model-based study using NEMURO.FISH. *Ecological Modelling*, 202: 165–173.
- Nakaya, M., Morioka, T., Fukunaga, K., Murakami, N., Ichikawa, T., Sekiya, S., and Suyama, S. 2010. Growth and maturation of Pacific saury *Cololabis saira* under laboratory conditions. *Fisheries Science*, 76: 45–53.
- Okunishi, T., Ito, S., Ambe, D., Takasuka, A., Kameda, T., Tadokoro, K., Setou, T., et al. 2012a. A modeling approach to evaluate growth and movement for recruitment success of Japanese sardine (*Sardinops melanostictus*) in the western Pacific. *Fisheries Oceanography*, 21: 44–57.
- Okunishi, T., Ito, S., Hashioka, T., Sakamoto, T. T., Yoshie, N., Sumata, H., Yara, Y., et al. 2012b. Impacts of climate change on growth, migration and recruitment success of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific. *Climatic Change*, 3–4: 485–503.
- Okunishi, T., Yamanaka, Y., and Ito, S. 2009. A simulation model for Japanese sardine (*Sardinops melanostictus*) migrations in the western North Pacific. *Ecological Modelling*, 220: 462–479.
- Oozeki, Y., and Watanabe, Y. 2000. Comparison of somatic growth and otolith increment growth in laboratory-reared larvae of Pacific saury, *Cololabis saira*, under different temperature conditions. *Marine Biology*, 136: 349–359.
- Sakamoto, T. T., Hasumi, H., Ishii, M., Emori, S., Suzuki, T., Nishimura, T., and Sumi, A. 2005. Responses of the Kuroshio and the Kuroshio Extension to global warming in a high-resolution climate model. *Geophysical Research Letter*, 32: L14617.
- Suyama, S., Kurita, Y., and Ueno, Y. 2006. Age structure of Pacific saury *Cololabis saira* based on observations of the hyaline zones in the otolith and length frequency distributions. *Fisheries Science*, 72: 742–749.
- Tadokoro, K., Chiba, S., Ono, T., Midorikawa, T., and Saino, T. 2005. Interannual variation in *Neocalanus* biomass in the Oyashio waters of the western North Pacific. *Fisheries Oceanography*, 14: 210–222.
- Tamura, T., and Fujise, Y. 2002. Geographical and seasonal changes of the prey species of minke whale in the Northwestern Pacific. *ICES Journal of Marine Science*, 59: 516–528.
- Travers, M., Shin, Y. J., Jennings, S., and Cury, P. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Progress in Oceanography*, 75: 751–770.
- Tu, C. Y., Tseng, Y. H., Chiu, T. S., Shen, M. L., and Hsieh, C. H. 2012. Using coupled of fish behavior-hydrodynamic model to investigate spawning migration of Japanese anchovy, *Engraulis japonicus*, from the East China Sea to Taiwan. *Fisheries Oceanography*, 21: 255–268.
- Ueno, Y., Suyama, S., Kurita, Y., and Kumazawa, T. 2004. Design and operation methods of a mid-water trawl for quantitative sampling of a surface pelagic fish, Pacific saury (*Cololabis saira*). *Fisheries Research*, 66: 3–17.
- Wang, M., Overland, J. E., and Bond, N. A. 2010. Climate projections for selected large marine ecosystems. *Journal of Marine Systems*, 79: 258–266.
- Watanabe, Y. 2007. Global warming and saury recruitment. *Kaiyo Monthly*, 39: 309–313 (in Japanese).
- Watanabe, Y., Kurita, Y., Noto, M., Oozeki, Y., and Kitagawa, D. 2003. Growth and survival of Pacific saury *Cololabis saira* in the Kuroshio-Oyashio transitional waters. *Journal of Oceanography*, 59: 403–414.
- Watanabe, Y., and Lo, N. C. H. 1989. Larval production and mortality of Pacific saury, *Cololabis saira*, in the northwestern Pacific Ocean. *Fishery Bulletin US*, 87: 601–613.
- Watanabe, Y., Oozeki, Y., and Kitagawa, D. 1997. Larval parameters determining preschooling juvenile production of Pacific saury (*Cololabis saira*) in the northwestern Pacific. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 1067–1076.