

Modeling the influence of oceanic-climatic changes on the dynamics of Pacific saury in the northwestern Pacific using a life cycle model

YONGJUN TIAN^{1,2,*}, TATSURO AKAMINE¹
AND MAKI SUDA¹

¹National Research Institute of Fisheries Science, Fisheries Research Agency (FRA), Kanazawa, Yokohama 236-8648, Japan

²Present address: Japan Sea National Fisheries Research Institute, Fisheries Research Agency (FRA), Suido-cho, Niigata 951-8121, Japan

ABSTRACT

A life cycle model for Pacific saury (*Cololabis saira*) was developed to clarify the possible causes of interannual and decadal variability in its abundance. In the model, the population of saury is composed of two spawning cohorts: one spawned in the Kuroshio region during autumn–winter and the other spawned in the Kuroshio-Oyashio Transition Zone during winter–spring. The life cycle of saury was divided into six stages: namely egg, larval, juvenile, young, immature and adult stages. The life cycle model combines growth, survival, fishing and reproductive processes, in which the effects of sea surface temperature (SST) in the Kuroshio region and El Niño-Southern Oscillation (ENSO) events on the winter-spawning cohorts, the effects of SST in the Oyashio region on the spring-spawning cohorts, and the effects of fishing on the two spawning cohorts are taken into account. Results of basic modeling, in which environments are assumed stable and the stock is affected by fishing only, shows that the interannual fluctuations in the abundance are small and could hardly explain the observed large annual changes in abundance. On the contrary, results of modeling incorporating the effects of oceanic-climatic changes corresponded well with actual interannual-decadal variations in abundance. These results suggest the following environmental effects: (1) SST in the Kuroshio region affects decadal changes in abundance; (2) ENSO events influence the survival of the winter spawning cohort and result in large inter-

annual variations in the abundance. It is concluded that large-scale climatic and oceanic changes strongly affect the abundance of saury.

Key words: Climate change, El Niño-Southern Oscillation, Kuroshio, life-cycle model, Pacific saury, population dynamics, sea surface temperature

INTRODUCTION

Pacific saury (*Cololabis saira*) is one of the most commercially important pelagic species in the Northwest Pacific along with Japanese sardine (*Sardinops melanostictus*) and anchovy (*Engraulis japonica*). However, Pacific saury exhibits immense interannual variations both in abundance and size composition (Fukushima, 1979; Kosaka, 2000; Tian *et al.*, 2002a, 2003). Annual catches of saury in Japan have fluctuated from 572 000 metric tonnes (t) in 1958 to 63 000 t in 1969 with an annual average of about 257 800 t over the last half century (Tian *et al.*, 2003). In fact, despite a descending trend in fishing effort in the 1990s, both the catch and Catch Per Unit Effort (CPUE) of saury experienced an abrupt decline in 1998 from an abundant period, indicating a strong influence of environmental factors on the trend in abundance (Ebisawa and Sunou, 1999; Tian *et al.*, 2003).

Understanding fluctuations in marine fish stocks is important for the management of fisheries, but the causes of the large variations in the abundance of saury are poorly understood. Matsumiya and Tanaka (1978) pointed out that the abundance of saury is significantly affected by reproductive success or failure, and drastic population decline does not result from overfishing. Variability in oceanic conditions is believed to contribute to the large fluctuations in recruitment success, distribution and migration pattern of saury (Sablin and Pavlychev, 1982; Gong, 1984; Yasuda and Watanabe, 1994), although there are no acceptable answers to explain the mechanisms of stock fluctuation for Pacific saury. Recently, increasing evidence has demonstrated that the population dynamics of fishes are linked to oceanographic and climatic variability (e.g. Francis

*Correspondence. e-mail: yjtian@fra.affrc.go.jp

et al., 1998; Beamish et al., 1999; Zhang et al., 2000; Attrill and Power, 2002; Finney et al., 2002). Using historical time series data of catch and climatic indices, Tian et al. (2002a) examined the relationship between saury abundance and environment factors, and revealed that long-term variability in the abundance of saury was largely affected by oceanic and climatic changes. Furthermore, Tian et al. (2003) deduced that El Niño-Southern Oscillation (ENSO) events in the previous year and sea surface temperatures (SST) in the Kuroshio region in winter correlated significantly with abundance of the large size group saury, whereas abundance of the medium size group saury showed high correlations with SST in the Kuroshio-Oyashio Transition Zone (TZ) and in the Oyashio region, suggesting that the two size groups reflecting the winter- and spring-spawning cohorts are affected by different oceanic systems. Accordingly, a possible mechanism for the variability of saury was proposed, in which the winter- and spring-spawning cohorts are affected by the subtropical and subarctic oceanic systems, respectively, and interannual-decadal variations of saury largely resulted from the effect of ENSO and SST on survival processes during the early life stage of winter-spawning cohorts (Tian et al., 2002b, 2003).

However, lack of information on the age composition and population structure, and the complex life history characteristics increase the difficulty in understanding the causes and mechanisms of fluctuations in the saury stock. Pacific saury makes extensive migrations from the subtropical to the subarctic region throughout the TZ (Fukushima, 1979; Gong, 1984). Pacific saury start their northward migration in spring,

feed on the plentiful food in the Oyashio region during summer and are fished during their southward migration off the northeast coast of Japan (Fig. 1). Pacific saury have a long spawning season continuing from autumn through spring, shifting spawning grounds from the TZ to the Kuroshio region (Fukushima et al., 1990; Watanabe et al., 1997). Larval growth and survival rates of saury largely vary with spawning cohorts, suggesting strong effects of oceanic conditions (Watanabe et al., 1997). Recent studies suggested that winter-spawning cohorts play an important role in recruitment success (Kurita, 2001; Tian et al., 2002b). As different spawning cohorts are affected by different oceanic systems from the subtropical to the subarctic region throughout the TZ during their life history, recruitment, and factors determining the recruit success of each spawning cohort are different. It is important to identify critical factors affecting survival and growth during each life stage and to evaluate their contributions to the population dynamics of saury.

Undoubtedly, modeling approaches incorporating life history parameters and impacts of environmental factors are useful in exploring the causes and mechanisms of fluctuations in fish stocks (Kimura et al., 1992; Hermann et al., 1996; Kishida and Suda, 1998; Willette et al., 2001). However, because Pacific saury is a large-scale migratory pelagic fish as are sardines and anchovies, their abundance is largely affected by environmental factors in various time scales (Tian et al., 2002a, 2003); hence it is difficult to predict the trend in the abundance using traditional stock-recruitment models. Tian and Shimizu (1999) developed a life cycle model for the cockle *Fulvia mutica*, in

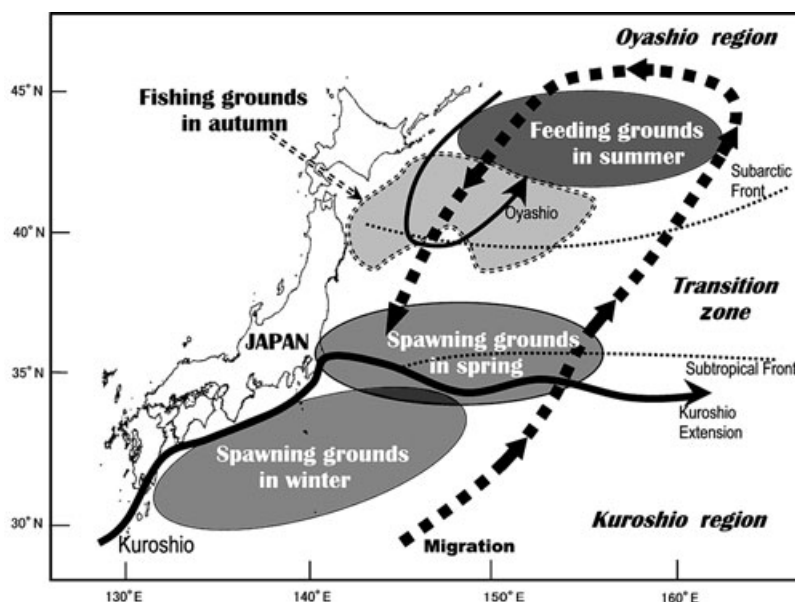


Figure 1. Schematic diagram showing the life history and migration pattern of Pacific saury, and oceanographic structures along the Pacific coast of Japan.

which mortality and growth at different life stages are affected by different environmental factors, suggested that a life cycle model is an effective tool to investigate the impacts of fishing and environment on the dynamics of fish populations. In the present study, based on the possible mechanisms of stock fluctuations proposed by Tian *et al.* (2003), we developed a life cycle model for Pacific saury incorporating its life history characteristics and the effects of oceanic-climatic variability. We run this model with possible scenarios to determine quantitatively the impacts of fishing and oceanic-climatic changes on the population dynamics of saury, and to verify linkages between fluctuations in the saury stock and oceanic-climatic variability. We also attempt to reveal the structure in age and population, and to discuss their contributions to the population dynamics of Pacific saury.

METHODS

Life cycle stages

Based on Odate (1977) and Kosaka (2000), our model divides the life cycle of saury into six stages: egg, larval, juvenile, young, immature and adult (Fig. 2). In

Figure 2. Life stages for Pacific saury. Age and length ranges at each stage [from Kosaka (2000)] and survival processes are shown.

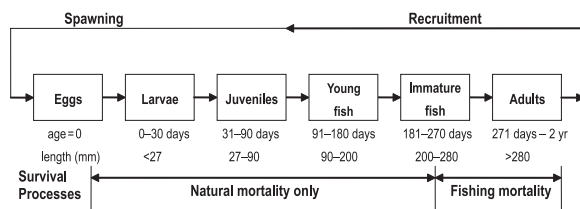
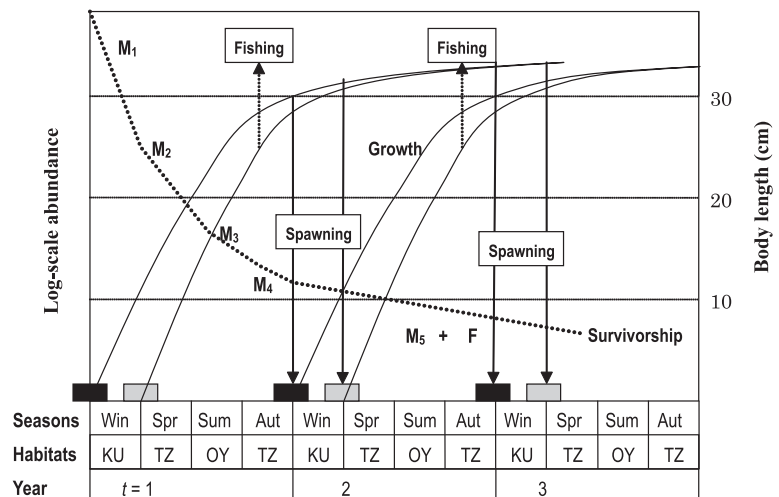


Figure 3. Schematic diagram showing the structure of the life cycle model for Pacific saury. The black and gray rectangles indicate the winter- and spring-spawning cohorts, respectively. The solid and dotted arrows indicate spawning and fishing respectively. For clarity, only one survival curve for the winter-spawning cohort is drawn as a dotted line. M_1 – M_5 represent natural mortality coefficients from larvae to adult stages. Win, Spr, Sum and Aut indicate winter, spring, summer and autumn, respectively. KU, TZ and OY indicate the Kuroshio region, the Kuroshio-Oyashio Transition Zone and the Oyashio region, respectively.



general these divisions not only correspond to developmental stages, but also represent changes in prey and habitats during their growth and migrations (Odate, 1977; Kosaka, 2000). According to this division of the life cycle, and growth estimated from Watanabe *et al.* (1988) and Kurita *et al.* (2004), juveniles of saury grow to about 90 mm within 3 months, and grow to 280 mm adults within 10 months when they recruit to the fishery.

The model structure and equations

The life cycle model for Pacific saury is composed of two spawning cohorts, one spawns in the Kuroshio region during autumn–winter and the other spawns in the TZ during winter–spring (Fig. 3). This life cycle model is an extension and modification of Tian and Shimizu (1999), in which only a single spawning cohort was considered. For the winter-spawning cohort, spawning is assumed to occur on Jan. 1 in the Kuroshio region, the larvae and juveniles stay in the Kuroshio region during winter, and migrate to the TZ during the young stage in spring. They then migrate to the Oyashio region to feed on the plentiful prey during the immature stage in summer. While growing to adults, they start their southward migration homing to the Kuroshio region and they are fished in the TZ in autumn (also see Fig. 1). During autumn to winter, most of the adults mature and become ready for first spawning (Kosaka, 2000; Kurita, 2001). Spawning of the spring cohort is assumed to occur on April 1 in the TZ; accordingly the spring-spawning cohort seems to trace the same migration pattern as the winter-spawning cohort just with a 3-month time lag. In the model, all individuals of each cohort spawn at the same time four

times (once each winter, and once each spring) during their life of 2 yr (Fig. 3).

The life cycle model combines growth, survival, fishing, and reproductive processes (Tian and Shimizu, 1999). Basic equations of the model are as follows:

$$\text{Growth } \frac{dL_{t,j}}{dt} = G_{t,j}L_{t,j} \quad (1)$$

$$W_{t,j} = aL_{t,j}^b$$

$$\text{Survival } \frac{dN_{t,i,j}}{dt} = -(M_{t,i,j} + F_{t,i,j})N_{t,i,j} \quad (2)$$

$$\text{Catch } \frac{dC_{t,i,j}}{dt} = F_{t,i,j}N_{t,i,j} \quad (3)$$

$$P_t = \frac{\sum_{i=1}^2 \sum_{j=4}^5 (C_{t,i,j}W_{t,j})}{X_t}$$

$$\text{Reproduction } E_t = \sum_{i=1}^2 \sum_{j=4}^5 (N_{t,i,j}h_ir) \quad (4)$$

Definitions of variables and symbols are shown in Table 1.

The growth process of saury is modeled using the Gompertz growth curve described in Watanabe *et al.* (1988), which is generally consistent with Kurita *et al.* (2004) for growth of 0+ Pacific saury. In our model, Pacific saury grows fast and reaches about 30 cm within 1 yr, then the growth rate slows rapidly with maturation; there is little growth during the second year (see Fig. 3). Growth rates for the two spawning cohorts are assumed to be the same and not to vary between years, in contrast to the survival processes in which mortality varies with spawning cohort and year.

Survival is driven by natural and fishing mortality. Natural mortality is assumed to be different at different life stages and is affected by oceanic and climatic changes, while fishing mortality is a function of fishing

Symbol	Definition	Value	Unit	Note
<i>L</i>	Body length	–	mm	Variable
<i>W</i>	Body weight	–	g	Variable
<i>N</i>	Stock size	–	number	Variable
<i>C</i>	Catch	–	number	Variable
<i>P</i>	Relative abundance index (CPUE)	–	tonnes haul ⁻¹	Variable
<i>E</i>	Egg production	–	number	Variable
<i>t</i>	Time (year)	–	–	
<i>i</i>	Number of spawning cohort	1: winter 2: spring	–	
<i>j</i>	Number of life stages	1–5	–	
<i>G</i>	Growth rate	–	–	Watanabe <i>et al.</i> (1988)
<i>a</i>	Correlation constant	1.49·10 ⁻³	–	Kosaka (2000)
<i>b</i>	Correlation constant	3.32	–	Kosaka (2000)
<i>M</i>	Natural mortality coefficient	Larva: 42.0 Juvenile: 24.2 Young: 5.6 Immature: 4.0 Adult: 1.5	yr ⁻¹	Baseline simulation
<i>F</i>	Fishing mortality coefficient	–	month ⁻¹	
<i>X</i>	Fishing effort	–	hauls month ⁻¹	
<i>h</i>	Fecundity	–	number of eggs	Kurita (2001)
<i>r</i>	Sex ratio	0.5	–	
<i>q</i>	Catchability coefficient	1.5·10 ⁻⁶	haul ⁻¹	

Table 1. Definitions of variables and parameter values used in the baseline simulation.

effort. The CPUE calculated from the catch model (Eqn 3) is used as a relative abundance index of the model output to compare with the observed CPUE. In the reproductive model, total egg production is calculated using fecundity per female based on field survey data (Kurita, 2001).

Estimation of natural mortality

Natural mortality (M) at a specific life stage can be defined as follows:

$$M = M_c + M_e \quad (5)$$

where M_c is a constant representing the stable or average environment conditions, and M_e is mortality resulting from environmental variability (Tian and Shimizu, 1999).

Tian *et al.* (2003) demonstrated that the abundance of large size saury corresponds well with the ENSO and SST in the Kuroshio region, while the abundance of medium size saury shows a close relation to SST in the TZ and in the Oyashio region (Fig. 4). There are significant correlations between the Southern Oscillation Index (SOI), winter SST in the

Kuroshio region (SST1), and the abundance index of large size saury (AIL), and between the abundance index of medium size saury (AIM) and SST in the Oyashio region (SST2) in July (Tian *et al.*, 2003).

$$AIL_t = -1.805 \cdot SOI_{t-1} + 5.532 (r=0.42, P<0.01) \quad (6)$$

$$AIL_t = 7.104 \cdot SST1_t - 126.8 (r=0.46, P<0.01) \quad (7)$$

$$AIM_t = 3.484 \cdot SST2_t - 34.17 (r=0.38, P<0.01) \quad (8)$$

Where the SOI is an index of ENSO, the extreme negative (positive) values represent El Niño (La Niña) events (Trenberth, 1990). The SOI used here is the average for the periods June–December of each year, and the SST are area-averaged values for the Kuroshio region (28–35°N, 128–145°E) and for the Oyashio region (40–45°N, 140–160°E) from the original 1° grid SST data set (Tian *et al.*, 2003). According to the life history and migration pattern stated above, the ENSO and SST in the Kuroshio region influence the survival of juveniles for the winter-spawning cohort, and SST in the Oyashio region in early summer affect the young stage of the spring-spawning cohort. We apply a logarithmic function to estimate mortality resulting from the environmental variability (M_e) as described in Tian and Shimizu (1999) (Fig. 5):

$$M_e = \ln(f(V_t)/f(V_0)) \quad (9)$$

where V_t represents an environmental factor such as SOI and SST in year t , V_0 represents the mean of V_t for the period of the model run, and f represents the correlation equations (6–8).

According to the above functions, a strong El Niño with a value of -2 for SOI and a negative anomaly of 1° in the winter SST in the Kuroshio region will lead to a 0.4 decrease and 1.5 increase in the natural mortality coefficient, respectively (Fig. 5).

Estimation of fishing mortality

The fishing mortality coefficient (F) was calculated using the following equation:

$$F = q \cdot Q \cdot X \quad (10)$$

where q is the catchability coefficient, Q is the selectivity of the fishing gear with a 50% selection length of 200 mm (Fig. 6), and X is the fishing effort. Pacific saury are fished off the northeast coast of Japan using stick-held dip-nets; the fishing season is from August through December with a peak during September to November (Fukushima, 1979). The numbers of hauls

Figure 4. Time series in (a) the Southern Oscillation Index (SOI), (b) sea surface temperature anomalies in the Kuroshio region in winter (solid line) and in the Oyashio region in July (dotted line), (c) anomalies in the abundance index for the large (solid line) and medium (dotted line) size group saury during 1951–2000.

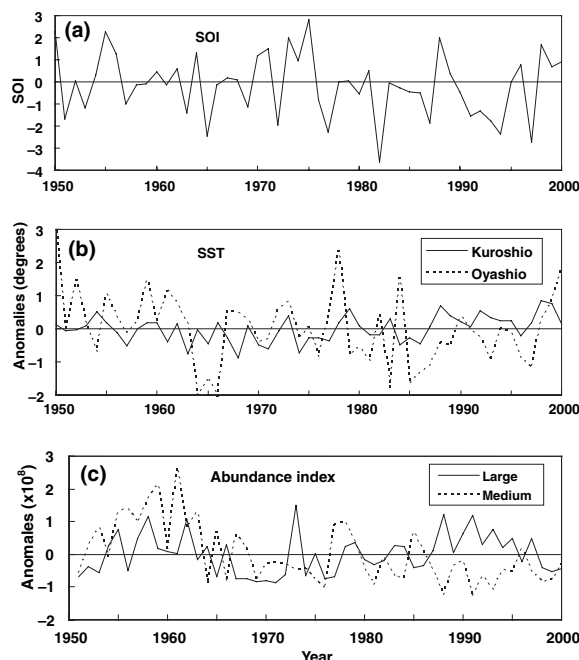
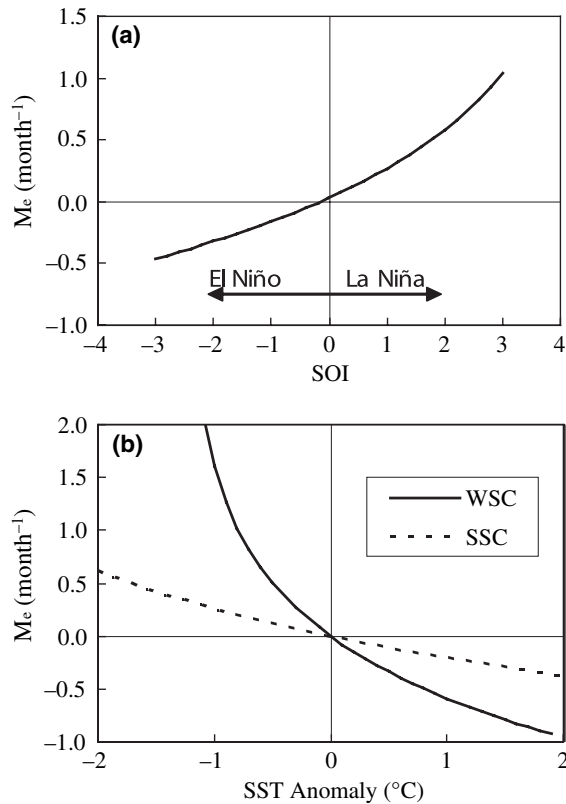


Figure 5. Function curves for natural mortality coefficient (M_e) based on environmental factors as defined by Eqn (9). (a) Effect of ENSO on the winter-spawning cohort. (b) Effects of SST anomalies in the Kuroshio region and in the Oyashio region on the winter- (WSC) and spring-spawning cohort (SSC), respectively.



are used as the fishing effort. Monthly fishing effort data during the fishing seasons from 1971 to 2000 were provided from the Tohoku National Fisheries Research Institute of Japan. The observed CPUE data are used as the abundance index for model validation.

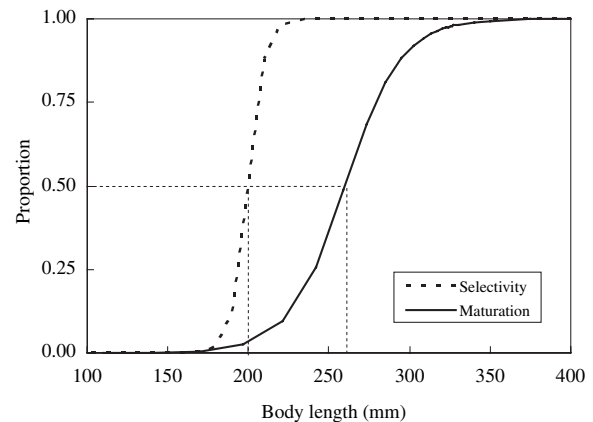
Reproductive process

Field survey data showed that batch fecundity for Pacific saury in the winter is higher than in spring (Kurita, 2001). We estimated fecundity (h) of mature female fish (larger than 30 cm) as 42 000 and 36 000 during the winter and spring spawning seasons respectively, and a simple sigmoid curve is applied to represent the proportion of maturation depending on the body length in which half of 250 mm fish and more than 80% of 280 mm fish are assumed to be mature (Fig. 6).

Initial parameters, simulation scenarios and conditions

The life cycle model is sensitive to the mortality coefficients of early life stages (Tian and Shimizu,

Figure 6. Selectivity and maturation curves for Pacific saury. The 50% body length for selectivity of gear and maturation are shown by thin dotted lines.



1999). Initial mortality coefficients at larval and juvenile stages are mainly referred from Watanabe *et al.* (1997) and Oozeki and Watanabe (2000). Catchability and natural mortality coefficients for immature and adult fishes are according to Doi (1958).

We simulated several scenarios to investigate the impacts of different environmental factors at the different life stages on the dynamics of saury. Table 2

Table 2. Simulation scenarios and conditions for model runs.

Scenario	Fishing effort	SST-KU ENSO SST-TZ			Note
		Fishing for WSC	events for SSC		
1	–	–	–	–	Baseline simulation
2	+	–	–	–	Effect of fishing
3	+	+	–	–	Effect of SST on WSC
4	+	–	+	–	Effect of ENSO on WSC
5	+	+	+	+	Effect of SST on SSC
6	–	+	+	+	Effect of environment only

+, Impacts were included; –, impacts were excluded; SST-KU, sea surface temperature in the Kuroshio region in winter; SST-TZ, sea surface temperature in the Oyashio region in July; WSC, winter spawning cohort; SSC, spring spawning cohort.

shows the scenarios and conditions for model runs. First, a baseline simulation was run to test the sensitivity of the initial parameters and the stability of the model. In the baseline simulation, all of the parameters including fishing mortality were assumed to be constant and were tuned so that the output of the model (hereafter it is referred to as the relative abundance index) reached stability during a 30-yr run. The final parameters used in the baseline simulation after tuning are shown in Table 1. Our second scenario was to investigate the impact of fishing, using the observed data of fishing effort in which only fishing mortality at the immature and adult stages is considered. Scenarios 3–4 were to assess the effects of SST in the Kuroshio region and ENSO events on the winter-spawning cohorts, whereas scenario 5 also included effects of SST in the Oyashio region on the spring-spawning cohort. The final simulation was to investigate the effects of environmental changes only, supposing fishing mortality was constant.

All simulations except scenario 6 are run for 30 yr during 1971–2000 when fishing effort data are available.

RESULTS

Baseline simulation and the effect of fishing

Here the calculated CPUE is referred to as the relative abundance index of the model output to compare with the observed CPUE. The output of the baseline simulation was set to around 1.4 (ton haul⁻¹), close to the annual average of observed CPUE during 1971–2000. The abundance index from scenario 2 (Fig. 7) varied from 0.6 to 1.4, showed a descending trend with small interannual variations during 1971–87, and tended to increase after 1989, generally corresponding

to the actual trend in fishing effort. Because of the intense fishing effort until late the 1980s, the abundance index was lower than the baseline for all of the 30-yr runs, suggesting a slow recovery from the population decline under regime of increasing fishing effort. The maximum CPUE from the simulation is about twice the minimum; fairly small compared with the approximately 10-fold difference between the maximum and minimum values in the observed CPUE data. This suggested that although fishing has considerable impact in the trend in abundance, the large observed interannual variability in abundance of saury seems to result from factors other than fishing.

Effect of SST and ENSO

The abundance index estimated from scenario 3 varied from 0.17 in 1986 to 1.84 in 1999 (Fig. 7). The difference between the maximum and minimum is about 10 times, almost the same as that in the observed CPUE. This simulation showed a long ascending trend since the late 1980s with evident interannual variations compared with scenario 2. However, it seems that the winter SST in the Kuroshio region largely affected decadal-scale variations rather than interannual variations, reflecting the decadal variation pattern and the regime shift in SST in the Kuroshio region which occurred at the end of the 1980s (see Fig. 4). On the contrary, the simulation of scenario 4 closely corresponds to observations both on decadal and interannual scales (Correlation coefficient r between calculation and observation for 1971–97 is 0.68, $P < 0.001$), suggesting that previous ENSO events largely affect survival of the juveniles from the winter-spawning cohort and determine the variability in abundance of saury. The dominant years in 1973, 1977, 1983 and 1988, and the high abundance period during early 1990s seem associated with strong El Niño events. As regarding to scenario 5, in which the effects of the SST in the Oyashio region on the spring-spawning cohorts are included together with the effects of ENSO and SST in the Kuroshio region on the winter-spawning cohorts, it generally agreed with scenario 4, but it is lower in the 1980s and extremely higher after 1998. This resulted from the lower SST trend both in the Kuroshio and Oyashio regions in the 1980s, and from the positive anomalies of SST both in the Kuroshio and Oyashio, and the positive effects of the El Niño trend after 1988, respectively.

In scenario 6, the model was run for 50 yrs from 1951 to 2000 in which environmental time series data are available, assuming that fishing effort was constant (average value during 1971–2000), to investigate the effects of environmental changes only (Fig. 8).

Figure 7. Simulation results of baseline and scenario 2–5 in comparison with observed Catch Per Unit Effort data from 1971 to 2000. See Table 2 for details of simulation scenarios.

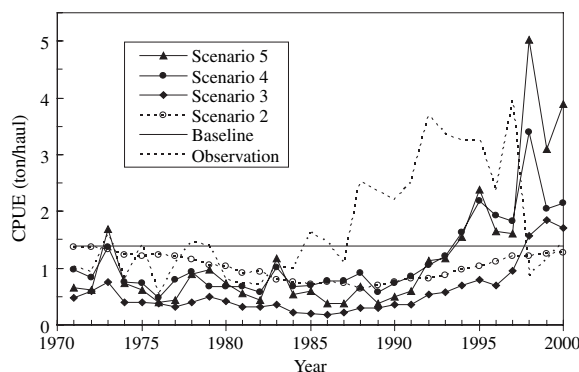
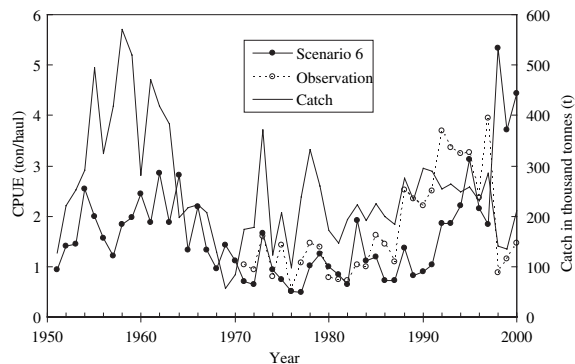


Figure 8. Simulation results of scenario 6 in comparison with observed catch and Catch Per Unit Effort (CPUE) data from 1951 to 2000 (CPUE is from 1971 to 2000). See Table 2 for the details of simulation scenarios.



Although the simulation is higher than the observations after 1998 resulting from the combined positive effects of SST and ENSO, the high periods of simulated abundance during the mid-1950s to mid-1960s and during the 1990s, and the low period during the 1970s to 1980s, are generally consistent with the trends both in the observed catch and CPUE. This suggests that, compared to variation in fishing efforts, oceanic and climatic changes have larger impacts on the variability in saury abundance at both long-term and interannual time scales.

Population structure

In our model, the population of Pacific saury is composed of four year (age) classes: two year classes for each spawning cohort. Figure 9 shows the monthly changes in abundance with age structure from scenario 5 in which all factors including fishing and environment are incorporated. Both the winter- and spring-spawning cohorts experienced sharp decreases during the larval and juvenile stages. The stock size of the 1+ year class seems to depend largely on the recruitment success of juveniles. The winter-spawning cohort shows larger variations (with C.V. of 133% and 144% for 0+ and 1+ on October 1) than the spring-spawning cohort (with C.V. of 107% and 88.7% for 0+ and 1+ on October 1) during the 30 years of the model run, representing the combined effects of ENSO and SST in the Kuroshio region on the early survival of the winter spawning cohort.

There is large interannual variation not only in abundance but also in size composition. Figure 10 shows the yearly changes in abundance and its proportion by year (age) class estimated from scenario 5 during the fishing season. These four year classes are equal to 0.5, 0.75, 1.5 and 1.75 yr in age on October 1 with theoretical lengths of 19.7, 28.0, 32.8 and 33.0 cm, respectively. More than 80% are 0+ year classes in most years, suggesting that the population is dominated by recruitment success of both the

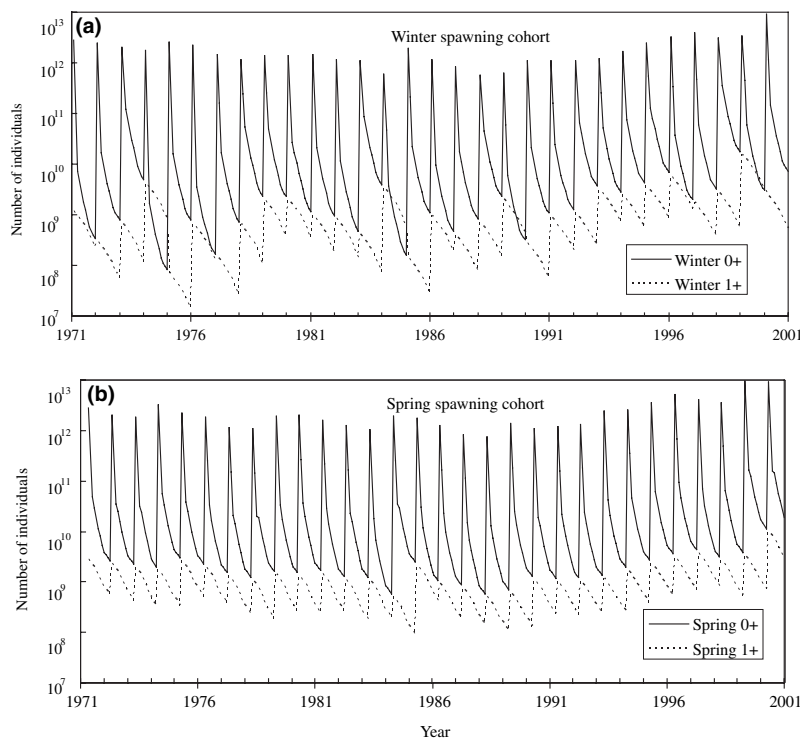


Figure 9. Monthly changes in abundance with age structure by spawning cohort from January 1971 to December 2000 estimated from the simulation of scenario 5.

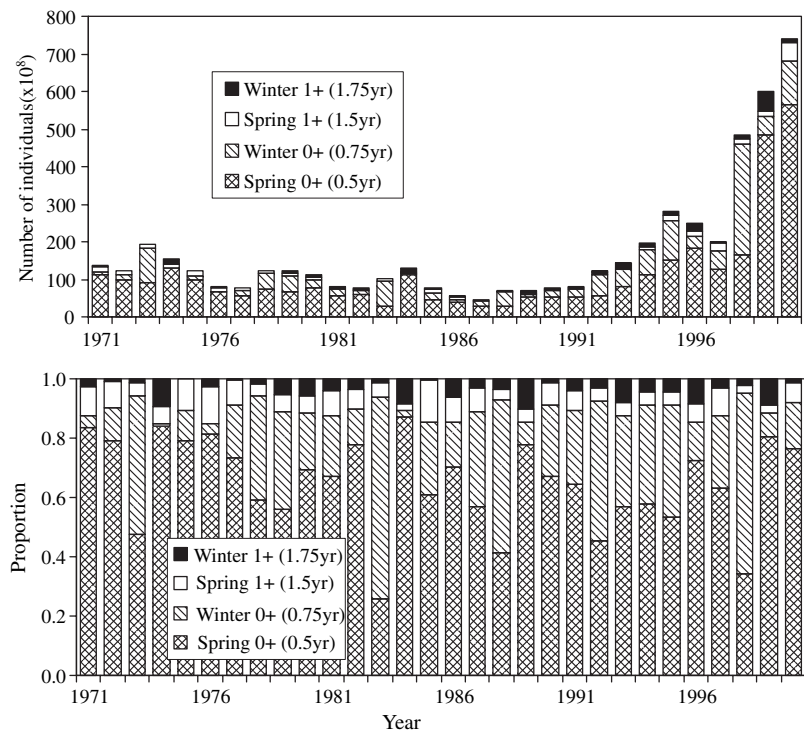


Figure 10. Yearly changes in age structure, by abundance (top panel) and proportion (bottom panel), on October 1 from 1971 to 2000 estimated from the simulation of scenario 5.

winter- and spring-spawning cohorts each year. There is only a small difference in the lengths of the fish more than 1 yr old (see Fig. 3), therefore the three older year classes, except the 0+ of the spring-spawning cohort, can be regarded as the same group with similar length compositions (>28 cm) during the fishing season, which is different than the 0+ year class of the spring-spawning cohort in size composition (with a length range 20–28 cm). These results suggest that the population structure of saury is composed of four classes in age composition but approximately only two groups appear in the size composition during the fishing season. Furthermore, a fish of 20-cm length is about 31 g in weight, which is only 1/3 the weight of 28 cm fish, implying that the biomass of the 0+ year class of the spring-spawning cohort is smaller than that of the winter-spawning cohort.

DISCUSSION

It is widely accepted that large fluctuations in fish stocks result from recruitment success during the early life stages (Houde, 2002). However it is difficult to extract the critical factors determining growth and survival of saury during the early life stages among the various biological and physical factors. Although some specific factors such as water temperature and prey density are known to affect early growth and survival rates of Pacific saury (Oozeki and Watanabe, 2000;

Oozeki *et al.*, 2004), it is not possible to quantitatively assess their contributions to recruitment and reproduction throughout the life time. The life cycle model for saury, however, has a strong advantage in elucidating mechanisms affecting stock variability which are the integrated consequences of various factors on growth and survival at different life stages.

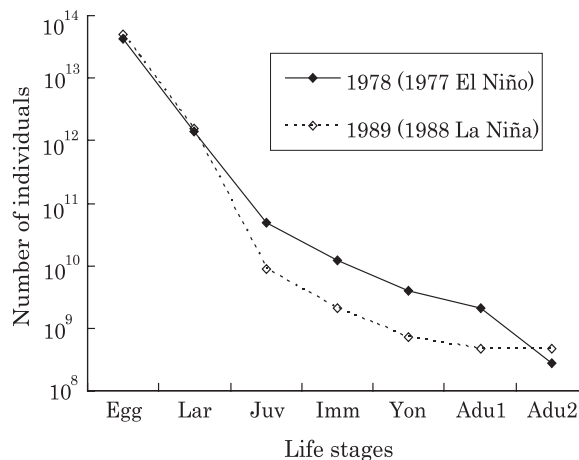
From several scenarios, our simulations strongly indicate that population dynamics of saury are forced by oceanic-climatic variability rather than by fishing, verifying the hypothesis that variation in abundance is linked to climate changes as described in Tian *et al.* (2003). The simulation for the effect of fishing (scenario 2) showed that fishing has some influence on the trend in abundance but it is not essential to cause the observed large interannual variations (Fig. 7). Previous studies have pointed out that the decline in catch is not attributable to increased fishing intensity but to a decline in the abundance caused by non-fishing factors (Matsumiya and Tanaka, 1978; Sablin and Pavlychev, 1982). This is also supported by our simulation of scenario 6, which indicated that the long-term trend in abundance of saury can be explained generally by environmental variability alone (Fig. 8). Fishing mortality is dependent on fishing effort. Using 10-day CPUE data during fishing season, Kimura (1960) estimated that the fishing mortality coefficient (F) from 1949 to 1957 had a range of 0.01–0.05 (per 10 days). Assuming the fishing seasons

extended about 4 months (from September to December), F is estimated as $0.12\text{--}0.60$ (yr^{-1}), which is approximately consistent with the range of our estimation from Eqn (3) ($0.11\text{--}0.40$), implying small contributions to total mortality compared with natural mortality in the adult stage.

Our simulations indicate that effects of ENSO and SST in the Kuroshio region on saury abundance are evident but at different time scales (Fig. 7). SST approximately reproduced effect of the regime shift that occurred at the end of the 1980s, while ENSO explained the large amount of interannual variation. This is important in understanding the effects of environmental factors at different time scales. Pacific saury shows cycles around 4–7 and 16–17 yr responding to ENSO-scale and decadal-scale SST variations, respectively (Tian *et al.*, 2002a). It is well documented that regime shifts in atmospheric and oceanic conditions in the North Pacific occurred in 1976/77, 1989/90 and possibly around 1998 (Beamish *et al.*, 1999; Watanabe and Nitta, 1999; McFarlane *et al.*, 2000; Zhang *et al.*, 2000). The abrupt changes in the abundance of saury which occurred around 1963/64, 1976/77, 1987/88 and 1997/98 are thought to be consequences of climatic regime shifts (Zhang *et al.*, 2000; Tian *et al.*, 2003). Our results demonstrate that the regime shift for saury occurred around 1987/88 was a consequence of the regime shift in SST in the Kuroshio region, while the shifts in 1976/77 and 1997/98 seem associated with ENSO events (see Figs 4 and 7).

Tian *et al.* (2003) showed that the abundance index of the large size group saury during El Niño years is about three times higher than that during La Niña years, and demonstrated that El Niño (La Niña) events have positive (negative) effects on winter-spawning cohorts. Figure 11 shows survival curves during typical El Niño and La Niña years for the winter-spawning cohort estimated from scenario 4 as an example. It is explicit that the large differences in recruitment result from the effect of ENSO on survival of juveniles, although the survival of adults is dependent on fishing. The dominant year classes in 1973, 1978, 1983 and 1988, and the abundant period during the early 1990s in the abundance of saury (Fig. 7) seem associated with strong El Niño events. Climatic forcing (ENSO) is consistently the most important parameter explaining variation in size composition, recruitment and abundance of saury by affecting the early survival of the winter-spawning cohort. A possible mechanism for the effect of ENSO is the differential in the SST fields in the subtropical northwestern Pacific which forms an important

Figure 11. Survival curves for the winter-spawning cohort showing the difference after typical El Niño and La Niña years estimated from the simulation of scenario 4. Egg, Lar, Juv, Imm, Yon Adu1 and Adu2 indicate egg, larval, immature, young, 1 yr and 2 yr adult stages, respectively.



spawning and nursery ground for saury (Hong *et al.*, 2001; Tian *et al.*, 2002b). This teleconnection effect of ENSO has also been found in other pelagic species such as Japanese eel, anchovy and mackerel which inhabit the subtropical northwestern Pacific (Tsai *et al.*, 1997; Kim and Kang, 2000; Kimura *et al.*, 2001; Sugimoto *et al.*, 2001).

Abrupt changes in the trend in abundance of the large size group saury was largely associated with switching of the ENSO phase such as in 1976–77, 1987–88 and 1997–98 (Tian *et al.*, 2003). However the causes of the abrupt decline in abundance which occurred in 1998 may also be related to conditions in SST field. SST anomalies in the Kuroshio region in winter were positive in the 1990s (except the small negative value in 1996), while SST in the TZ and Oyashio region was cooler until 1998 (see Fig. 4). Spring-spawning cohorts are largely dependent on the SST fields in the subarctic region (Tian *et al.*, 2003). As the size composition in 1998 was dominated by the large size group, it seems that the abrupt decline in 1998 resulted from unfavorable oceanic conditions for the spring-spawning cohort. Different oceanic–climatic systems affecting the two spawning cohorts have contributed to the complexity in the dynamics of saury (Tian *et al.*, 2002b, 2003).

Because of the difficulty in age determination of older fish, the age composition and population structure for saury is not well understood (Kosaka, 2000), increasing the uncertainty of stock assessment and management. Our simulations indicate that the population structure of saury is composed of four classes in

age composition but approximately only two groups appear in the size composition during the fishing season. The population is dominated by the 0+ year class of the two spawning cohorts (Figs 9 and 10). This is important in understanding the mechanisms of fluctuations in size composition and population dynamics of saury. Length frequency analysis showed that the catch of saury can be divided into two size groups (Matsumiya and Tanaka, 1974), and the two size groups are believed to be different age groups (Kimura, 1960; Fukushima *et al.*, 1990). Our results indicate that the two size groups are almost all 0+ year class of the winter- and spring-spawning cohorts, although the large size group contains a very small proportion of 1+ year classes. The estimated large proportion of the large size group in our simulation of 1973, 1983, 1988 and in 1990s (Fig. 10) generally agrees with the size composition of the catch (Fukushima *et al.*, 1990; Kosaka, 2000).

Biological effects such as prey and predation on growth and mortality of saury are not considered in our model because of lack of information, although larval growth rates are affected by prey density (Oozeki *et al.*, 2004). Pacific saury are typically zooplanktivores during their whole life, although the size and species composition of prey is different according to their size and migration route (Odate, 1977; Kosaka, 2000). Saury are also preyed on by a number of large piscivorous fishes such as pomfret (*Brama japonica*) and sharks, and marine mammals (Brodeur, 1988; Spring *et al.*, 1999). It is difficult to estimate quantitatively what biological effects such as prey–predator relationships have on the abundance of saury. Since in some years, Pacific saury are the most important prey species for minke whales (*Balaenoptera acutorostrata*) in the northwestern North Pacific in summer (Tamura *et al.*, 1998), mortality during the adult stage may also be affected by predation such as by whales. Kosaka (2000) pointed out that prey density may have some influence on mortality of juveniles, but survival at the other life stages is not affected by prey density, although variation in size composition may result from the effect of prey availability on growth. Biomass of small copepods, which are the main prey of saury during the early life stages in winter, is related to oceanographic conditions in the Kuroshio Current (Nakata *et al.*, 2001). Effects of SST on the juvenile stage in our model can imply the effects of prey indirectly. Density-dependent growth and mortality during the early life stages also is widely known for many fishes (Houde, 2002). However, condition factors of saury by size group correlated positively with the abundance index and SST (Hara, 1986; Tian *et al.*, 2004) indicating that the density-

dependent effect is weak, and that growth is affected by oceanic conditions.

CONCLUSIONS

In summary, the following conclusions may be drawn.

1. A life cycle model incorporating the effect of the oceanic–climate system and life history information is useful to explore the mechanisms of population dynamics for Pacific saury, and it well reproduced the interannual–decadal variations in abundance. Given oceanic and climatic data, this model can also predict future variations in abundance of Pacific saury.
2. Although fishing has considerable impact on the trend in abundance, large variations both in abundance and size composition do not result from fishing, but are forced by environmental factors.
3. The ENSO events have marked impacts on interannual variation, while SST in the Kuroshio region is largely associated with decadal regime shifts in abundance of saury. Possible mechanisms of ENSO and SST are their contributions to the survival of juveniles spawned in the Kuroshio region in winter. SST in the subarctic region also affected the young fish of the spring-spawning cohort. Different systems affecting the two spawning cohorts have contributed to the complexity in the population dynamics of saury.
4. The population structure of saury is composed of four classes in age composition but of two groups in size composition, and the population is dominated by the 0+ classes of the two spawning cohorts. This is important in understanding the mechanisms of fluctuations in size composition and population dynamics of saury.

ACKNOWLEDGEMENTS

We thank Drs Y. Ueno, Y. Kurita, and H. Sugisaki of TNFRI for their valuable comments on an early version of the manuscript and for their collaborations. We are grateful to Dr S. Suyama of TNFRI for his collaboration and discussions in conducting this work. We also thank all researchers of the VENFISH project for providing data and for their discussions. Comments from two reviewers helped to improve this manuscript. This study was partially supported by grants from the VENFISH project of the Japanese Minister of Agriculture, Forestry and Fisheries. This is a contribution of NRIFS.

REFERENCES

- Attrill, M.J. and Power, M. (2002) Climatic influence on a marine fish assemblage. *Nature* **417**:275–278.

- Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V. and Kurashov, V. (1999) The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* **56**:516–526.
- Brodeur, R.D. (1988) Zoogeography and trophic ecology of the dominant epipelagic fishes in the northern North Pacific. *Bull. Ocean. Res. Inst. Univ. Tokyo* **26**:1–27.
- Doi, T. (1958) A trial on estimating the abundance of population of the Pacific saury *Cololabis saira* (BREVOORT). *Bull. Jap. Soc. Sci. Fish.* **24**:608–612 (in Japanese with English abstract).
- Ebisawa, Y. and Sunou, H. (1999) Influence of variation of the Kuroshio water on catch fluctuations of saury, *Cololabis saira*, in the waters off northeastern Japan. *Bull. Ibaraki Pref. Fish. Exp. Stn.* **37**:29–36 (in Japanese).
- Finney, B., Gregory-Eaves, I., Douglas, M.S.V. and Smol, J.P. (2002) Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature* **416**:729–733.
- Francis, R.C., Hare, S.R., Hollowed, A.B. and Wooster, W.S. (1998) Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr.* **7**:1–21.
- Fukushima, S. (1979) Synoptic analysis of migration and fishing conditions of saury in the northwestern Pacific Ocean. *Bull. Tohoku Reg. Fish. Res. Lab.* **41**:1–70 (in Japanese with English abstract).
- Fukushima, S., Watanabe, Y. and Ogawa, Y. (1990). Correspondence of spawned seasons to large, medium, and small size Pacific saury exploited in the Northwestern Pacific Ocean. *Bull. Tohoku Reg. Fish. Res. Lab.* **52**:17–27 (in Japanese with English abstract).
- Gong, Y. (1984) Distribution and movements of Pacific saury, *Cololabis saira* (BREVOORT), in relation to oceanographic conditions in waters off Korea. *Bull. Fish. Res. Dev. Agency* **33**:59–172.
- Hara, M. (1986) Changes in the fatness coefficient and catch of Pacific saury *Cololabis saira* during southward migration. *Bull. Tohoku Reg. Fish. Res. Lab.* **48**:1–12 (in Japanese with English abstract).
- Hermann, A.J., Hinckley, S., Megrey, B.A. and Stabeno, P.J. (1996) Interannual variability of the early life history of walleye Pollock near Shelikof Strait as inferred from a spatially explicit, individual-based model. *Fish. Oceanogr.* **5**(Suppl. 1):39–57.
- Hong, C.-H., Cho, K.-D. and Kim, H.-J. (2001) The relationship between ENSO events and sea surface temperature in the East (Japan) Sea. *Prog. Oceanogr.* **49**:21–40.
- Houde, E.D. (2002) Mortality. In: *Fishery Science: The Unique Contributions of Early Life Stages*. L.A. Fuiman & R.G. Werner (eds) Oxford: Blackwell, pp. 64–87.
- Kim, S. and Kang, S. (2000) Ecological variations and El Niño effects off the southern coast of the Korean Peninsula during the last three decades. *Fish. Oceanogr.* **9**:239–247.
- Kimura, K. (1960) A population study on autumn Pacific saury (*Cololabis saira*) in the north-eastern sea of Honshu, Japan. *Bull. Tohoku Reg. Fish. Res. Lab.* **14**:1–82 (in Japanese with English abstract).
- Kimura, S., Kishi, M., Nakata, H. and Yamashita, Y. (1992) A numerical analysis of population dynamics of the sand lance (*Ammodytes personatus*) in the eastern Seto Inland Sea, Japan. *Fish. Oceanogr.* **1**:321–332.
- Kimura, S., Inoue, T. and Sugimoto, T. (2001) Fluctuation in the distribution of low-salinity water in the North Equatorial Current and its effect on the larval transport of the Japanese eel. *Fish. Oceanogr.* **10**:51–60.
- Kishida, T. and Suda, M. (1998) Analysis of the cause of stock fluctuation in the Japanese sardine, *Sardinops melanostictus*, using a population dynamics model. *Bull. Natl. Res. Inst. Fish. Sci.* **11**:37–64.
- Kosaka, S. (2000) Life history of Pacific saury *Cololabis saira* in the Northwest Pacific and consideration of resource fluctuation based on it. *Bull. Tohoku Natl. Fish. Res. Inst.* **63**:1–96 (in Japanese with English abstract).
- Kurita, Y. (2001) *Seasonal Changes in Spawning Grounds and the Abundance of Egg-laying of Pacific saury*. Tohoku National Fisheries Research Institute. Annual report of the research meeting on saury resource No. 49. Aomori, pp. 203–205 (in Japanese).
- Kurita, Y., Nemoto, Y., Oozeki, Y., Hayashizaki, K. and Ida, H. (2004) Variations in patterns of daily changes in otolith increment widths of 0+ Pacific saury, *Cololabis saira*, off Japan by hatch date in relation to the northward feeding migration during spring and summer. *Fish. Oceanogr.* **13**(Suppl. 1): 54–62.
- Matsumiya, Y. and Tanaka, S. (1974) Considerations on the so-called large- and intermediated-sized fish of saury on the basis of the analysis of the length composition. *Bull. Tohoku Reg. Fish. Res. Lab.* **33**:1–18 (in Japanese with English abstract).
- Matsumiya, Y. and Tanaka, S. (1978) Dynamics of the saury population in the Pacific Ocean off northern Japan-III Reproductive relations of large and medium sized fish. *Bull. Jpn. Soc. Sci. Fish.* **44**:451–455.
- McFarlane, G.A., King, J.R. and Beamish, R.J. (2000) Have there been recent changes in climate? Ask the fish. *Prog. Oceanogr.* **47**:147–169.
- Nakata, K., Koyama, S. and Matsukawa, Y. (2001) Interannual variation in spring biomass and gut content composition of copepods in the Kuroshio Current, 1971–89. *Fish. Oceanogr.* **10**:329–334.
- Odate, K. (1977) On the feeding habits of the Pacific saury, *Cololabis saira* (Brevoort). *Bull. Tohoku Reg. Fish. Res. Lab.* **38**:75–88 (in Japanese with English abstract).
- 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. *Mar. Bio.* **236**:349–359.
- Oozeki, Y., Watanabe, Y. and Kitagawa, D. (2004) Environmental factors affecting larval growth of Pacific saury, *Cololabis saira*, in the northwestern Pacific Ocean. *Fish. Oceanogr.* **13**(Suppl. 1): 44–53.
- Sablin, V.V. and Pavlychev, V.P. (1982) Dependence of migration and catch of Pacific saury upon thermal conditions. *Bull. Tohoku Reg. Fish. Res. Lab.* **44**:109–117.
- Spring, A.M., Piatt, J.F., Shuntov, V.P. et al. (1999) Marine birds and mammals of the Pacific Subarctic Gyres. *Prog. Oceanogr.* **43**:443–487.
- Sugimoto, T., Kimura, S. and Tadokoro, K. (2001) Impacts of El Niño events and climate regime shifts on living resources in the western North Pacific. *Prog. Oceanogr.* **49**:13–127.
- Tamura, T., Fujise, Y. and Shimazaki, K. (1998) Diet of minke whales *Balaenoptera acutorostrata* in the northwestern part of the North Pacific in summer, 1994 and 1995. *Fish. Sci.* **64**:71–76.
- Tian, Y. and Shimizu, M. (1999) Analysis of population dynamics of the cockle *Fulvia mutica* using a life cycle model incorporating the environmental factors. *Bull. Jpn. Soc. Fish. Oceanogr.* **63**:30–37 (in Japanese with English abstract).

- Tian Y., Akamine, T. and Suda, M. (2002a) Long-term variability in the abundance of Pacific saury in the northwestern Pacific ocean and climate changes during the last century. *Bull. Jpn. Soc. Fish. Oceanogr.* **66**:16–25 (in Japanese with English abstract).
- Tian Y., Ueno, Y., Suda, M. and Akamine, T. (2002b) Climate-ocean variability and the response of Pacific saury (*Cololabis saira*) in the northwestern Pacific during the last half century. *Fish. Sci.* **68**(Suppl. 1): 158–161.
- Tian Y., Akamine, T. and Suda, M. (2003) Variations in the abundance of Pacific saury (*Cololabis saira*) from the northwestern Pacific in relation to oceanic-climate changes. *Fish. Res.* **60**:439–454.
- Tian Y., Ueno, Y., Suda, M. and Akamine, T. (2004) Decadal variability in the abundance of Pacific saury and its response to climatic/oceanic regime shifts in the northwestern subtropical Pacific during the last half century. *J. Mar. Syst.* (submitted).
- Trenberth, K.E. (1990) Recent observed interdecadal climate changes in the Northern Hemisphere. *Bull. Amer. Meteor. Soc.* **71**:988–993.
- Tsai, C.F., Chen, P.Y., Chen, C.P., Lee, M.A., Shian, G.Y. and Lee, K.T. (1997) Fluctuation in abundance of larval anchovy and environmental conditions in coastal waters off southwestern Taiwan as associated with the El Niño-Southern Oscillation. *Fish. Oceanogr.* **6**:238–249.
- Watanabe, M. and Nitta, T. (1999) Decadal changes in the atmospheric circulation and associated surface climate variations in the Northern Hemisphere. *J. Climate.* **12**:494–510.
- Watanabe, Y., Butler, J.L. and Mori, T. (1988) Growth of Pacific saury, *Cololabis saira*, in the northeastern and northwestern Pacific Ocean. *Fish. Bull. U.S.* **86**:489–498.
- Watanabe, Y., Oozeki, Y. and Kitagawa, D. (1997) Larval parameters determining preschooling juvenile production of Pacific saury (*Cololabis saira*) in the northwestern Pacific. *Can. J. Fish. Aquat. Sci.* **54**:1067–1076.
- Willette, T.M., Cooney, R.T., Patrick, V., Mason, D.M., Thomas, G.L. and Scheel, D. (2001) Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. *Fish. Oceanogr.* **10**(Suppl. 1): 14–41.
- Yasuda, I. and Watanabe, Y. (1994) On the relationship between the Oyashio front and saury fishing grounds in the north-western Pacific: a forecasting method for fishing ground locations. *Fish. Oceanogr.* **3**:172–181.
- Zhang, C.I., Lee, J.B., Kim, S. and Oh, J.H. (2000) Climatic regime shifts and their impacts on marine ecosystems and fisheries resources in Korean waters. *Prog. Oceanogr.* **47**:171–190.