

# Spatial and temporal migration modeling for stock of Pacific saury *Cololabis saira* (Brevoort), incorporating effect of sea surface temperature

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**ABSTRACT:** A model is proposed that expresses the spatial and temporal migration pattern for stock of Pacific saury *Cololabis saira* (Brevoort), in order to investigate the effect of sea surface temperature (SST) on migration rates. Two factors are considered: (i) Saury emigrate to waters of an optimal SST zone; and (ii) saury immigrate from water zone that is extremely cold for saury. Parameters of migration and initial levels of stock are estimated with a maximum likelihood method based on catch per unit effort (CPUE) data for 1995–2001. The best model was selected using Akaike's information criteria. The results suggested that the emigration rate to southern adjacent regions is dependent on the coverage proportion of their waters under some threshold temperatures; 20°C to Doutou and Sanriku, 23°C to Joban and Izu.

**KEY WORDS:** migration, population dynamics, saury, sea condition, spatial and temporal model.

## INTRODUCTION

Pacific saury *Cololabis saira* (Brevoort) is one of the important fishery stocks and is widely distributed in the North Pacific,<sup>1</sup> and seasonally migrates. In the western part of the North Pacific, saury move northwards from the southern waters off Japan in spring, stay in the Oyashio region during summer, and start their southward migration from autumn to winter.<sup>2,3</sup> The Japanese commercial fishery exploits the stock of saury using stick-held dip nets (lift net fishery) from mid-August to mid-December. Fishing operations of the fisheries begin in August off the Pacific side of the Kuril Islands, after which the fishing ground there closes and shifts south to the regions off the Sanriku and Joban coasts.<sup>4</sup> The operations usually decrease in mid-December. Therefore, the span of operations is approximately 140 days. Aggregations of saury are found in the Oyashio waters along the oceanic front between the Oyashio cold water and warm waters that originated from Kuroshio warm-core

rings, warm streamers or the Tsugaru warm waters.<sup>5,6</sup> Therefore the geographic distribution of sea water temperature impacts on the distribution of the stock.

In terms of planning of fishing operations, the prediction of the annual catch is one of the important issues for the fishery, because the stock and catch of the saury have widely fluctuated from year to year.<sup>2,3,7</sup> Some models to forecast the amount of catch have been presented.<sup>8,9</sup> These models are used to predict the catch in each region using the past records of the catch, location of fishing and/or sea conditions, and these might be useful to predict the catch. However, these models are not sufficient to express the monthly and regional changes in the catch because they do not incorporate basic models of the population dynamics. Models for the tagged populations have been presented,<sup>10</sup> in order to express temporal and spatial dynamics incorporating the effects of mortality and movement into dynamic models. However, the investigation using tagged saury is so difficult that the recapture rate was extremely low and the longest record of time at liberty was only for a few days in the past experiments.<sup>11</sup> In addition, the movement of saury depends on the oceanic condition in their migratory corridor. Therefore, the model incorporating the oceanic condition as an

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Received 20 March 2006. Accepted 7 June 2006.

explanatory variable is preferable and the sea water temperature (SST) represents the condition.

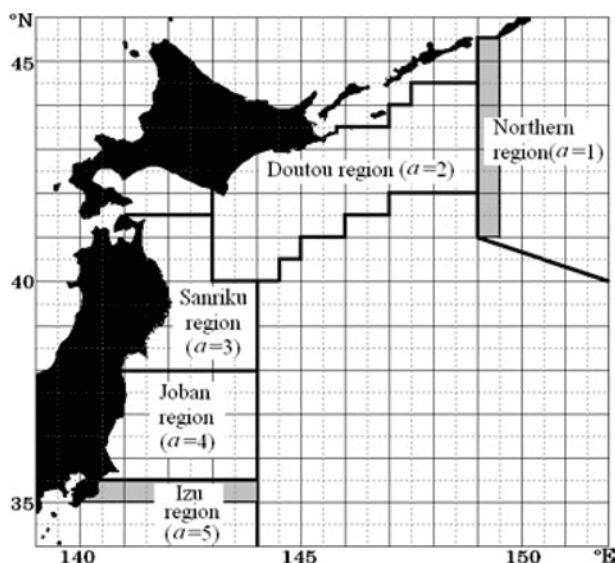
This paper proposes a model expressing the spatial and temporal dynamics for the stock of Pacific saury in order to investigate the effect of SST on migration rates. The model was applied to CPUE data of the saury fishery for 1995–2001 and the results are discussed.

## MODELS AND METHODS

### Basic model of stock dynamics

Figure 1 shows the whole of the fishing ground. For the sake of modeling purposes, the fishing ground was divided into five regions: (i) Northern region ( $a=1$ ); (ii) Doutou region ( $a=2$ ); (iii) Sanriku region ( $a=3$ ); (iv) Joban region ( $a=4$ ); and (v) Izu region ( $a=5$ ). The whole fishing season from early August to mid-December was divided into 14 periods, each with a duration of 10 days except for the last intervals in August and October, which have a duration of 11 days.

The fishing grounds move from the north toward the south through the five regions. Therefore, most fish move from the north toward the south. For these reasons, it is supposed that: (i) a part of the schools of saury in region  $a$  in period  $k$  ( $=1, 2, \dots, 14$ ) emigrate to  $a+1$  in  $k+1$ , and the other schools stay in region  $a$  in  $k+1$ ; and (ii) no movement occurred from or into any of the other than the five regions.



**Fig. 1** Division of fishing grounds. Shaded areas are used for the area of calculating index of sea surface temperature.

Fishing operations of the fisheries begin off the Pacific side of the Kuril Islands, but fishermen rarely operate in region 1. Hence, it is assumed that: (i) the whole stock is distributed in region 1 at the beginning of the fishing season; and (ii) the amount of catch in region 1 is negligible. Moreover, it is assumed that: (iii) the natural mortality coefficient, that is,  $M$  (per period), is constant through the whole season over all the regions; and (iv) the individual growth can be ignored, because the duration of each period is not so long.

The stock in weight in region  $a$ , period  $k$  and year  $y$  is studied here. The stock size in region  $a$  increases by the immigration from region  $a-1$ , while it decreases by catch and natural mortality, as well as the emigration, to region  $a+1$ . Let  $N_{a,t,y}$  and  $C_{a,t,y}$  be the stock in weight (tons) and the catch (tons) in region  $a$ , time  $t$  and year  $y$ , respectively. Mathematical models for  $N_{a,t,y}$  and  $C_{a,t,y}$  for time interval  $k \leq t \leq k+1$  are expressed by

$$\frac{dN_{a,t,y}}{dt} = -Z'_{a,t,y}N_{a,t,y} + h_{a-1,t,y}N_{a-1,t,y} \quad (1)$$

$$Z'_{a,t,y} = F_{a,t,y} + M + h_{a,t,y} \quad (2)$$

$$F_{a,t,y} = \begin{cases} 0 & (a=1) \\ q_{a,k,y}X_{a,k,y} & (a>1, k \leq t < k+1) \end{cases} \quad (3)$$

$$C_{a,k,y} = \int_k^{k+1} F_{a,t,y}N_{a,t,y}dt \quad (4)$$

where  $F_{a,k,y}$ ,  $h_{a,k,y}$ ,  $q_{a,k,y}$  and  $X_{a,k,y}$  indicate the fishing mortality coefficient (per period) in region  $a$ , period  $k$  and year  $y$ , the emigration coefficient to southern adjacent regions (per period), the catchability coefficient (per haul), and the effort (hauls per period), respectively. Here,  $h_{0,k,y} = 0$  (for  $k=1, 2, \dots, 14$ ) is assumed. Detailed solutions of  $N_{a,k,y}$  and  $C_{a,k,y}$  are shown in the Appendix I.

### Model of $h_{a,k,y}$

Two possible factors of the movement incorporated effect of SST are considered:

- 1 Saury emigrate to waters of an optimal SST zone, and the fishing grounds expand with the increasing coverage of the optimal SST waters.<sup>12</sup> From this nature, it is supposed that the emigration coefficient to southern adjacent regions ( $h_{a,k,y}$ ) increases the coverage proportion of the optimal SST waters in the southern adjacent region.
- 2 Saury immigrate from water zone that is extremely cold for saury. Due to the consideration,

it is supposed that the emigration coefficient to southern adjacent regions ( $h_{a,k,y}$ ) increases the coverage proportion of the extremely cold water in the present region. In addition, one possible factor of the movement free from the influence of SST is considered.

### 3 Saury emigrate to southern adjacent regions at a fixed rate, free from to the influence of SST.

From the above consideration, six types of models were made assuming a linear structure for  $h_{a,k,y}$  as follows:

$$\text{Model 1: } h_{a,k,y} = \delta''_{a+1} \quad (5A)$$

$$\text{Model 2: } h_{a,k,y} = \delta_{a+1} T_{a+1,k,y} \quad (5B)$$

$$\text{Model 3: } h_{a,k,y} = \delta_{a+1} T_{a+1,k,y} + \delta'' \quad (5C)$$

$$\text{Model 4: } h_{a,k,y} = \delta' T_{Low\ a,k,y} + \delta'' \quad (5D)$$

$$\text{Model 5: } h_{a,k,y} = \delta_{a+1} T_{a+1,k,y} + \delta' T_{Low\ a,k,y} \quad (5E)$$

$$\text{Model 6: } h_{a,k,y} = \delta_{a+1} T_{a+1,k,y} + \delta' T_{Low\ a,k,y} + \delta'' \quad (5F)$$

where  $T_{a+1,k,y}$  ( $0 \leq T_{a+1,k,y} \leq 1$ ) and  $T_{Low\ a,k,y}$  ( $0 \leq T_{Low\ a,k,y} \leq 1$ ) are the coverage proportion of the optimal SST waters on the whole, and the coverage proportion of the extremely cold SST waters on the whole, respectively. Parameter  $\delta'$  is a proportional coefficient related to the emigration coefficient to southern adjacent regions (per period).  $\delta'$  is assumed to be constant through the season over all the regions.  $\delta_a''$  and  $\delta''$  are the emigration coefficients free from the influence of SST (per period).

In regions 4 and 5, it is assumed that the optimal SST for calculating  $T_{a,k,y}$  is the same, and the proportional coefficients are the same ( $\delta_4 = \delta_5$ ) for two reasons as follows: (i) there is little information for estimating parameter ( $\delta_5$ ) in the Izu region; and (ii) locations of saury fishing grounds are related to the distribution of the Kuroshio water which is distributed across both the Joban and the Izu regions.

Sea surface temperature below 10°C was used as the threshold temperature of the extremely cold SST water (calculating  $T_{Low\ a,k,y}$ ), because the expansion of the water below 10°C correlates closely with the closure of the fishing season.<sup>13</sup> Let  $SST_{Low\ a}$  (°C) be the threshold temperature for calculating  $T_{Low\ a,k,y}$  in region  $a$ .

$$SST_{Low\ a} \leq 10 \quad (6)$$

### Model of $q_{a,k,y}$

The catchability coefficient is assumed to be inversely proportional to the size of the habitat area, and the size of habitat area in each region seasonally fluctuates. The model for  $q_{a,k,y}$  used in this paper is expressed by

$$q_{a,k,y} = \kappa s / A_{Temp\ a,k,y} \quad (7)$$

where  $s$ ,  $\kappa$  and  $A_{Temp\ a,k,y}$  show the swept area by a unit operation, gear efficiency and the size of habitat area, respectively. It is supposed that the habitat area ( $A_{Temp\ a,k,y}$ ) is the area that fishermen are able to operate. Let  $SST_{low\ a}$  (°C) and  $SST_{up\ a}$  (°C) be lower bound and upper bound of temperature for calculating  $A_{Temp\ a,k,y}$  in region  $a$ , respectively. Below 10°C as  $SST_{low\ a}$  was used because the expansion of the water below 10°C correlates closely with closure of the fishing season.<sup>13</sup>

$$SST_{low\ a} \leq 10 \quad (8)$$

It was assumed that  $SST_{up\ a}$  were equal to the upper bound of SST at the operating positions. The frequencies of SST at operating positions reported by fishermen to decide the upper bound of the SST were used.

### Estimation of parameters

Let  $u_{a,k,y}$  and  $u'_{a,k,y}$  be the theoretical value and data of the CPUE in region  $a$ , period  $k$  and year  $y$  (=1995, 1996, ..., 2001), respectively. The model of  $u'_{a,k,y}$  is the following multiplicative measurement error model:

$$\ln(u'_{a,k,y}) = \ln(u_{a,k,y}) + \varepsilon_{a,k,y} \quad (9)$$

$$\varepsilon_{a,k,y} \sim N(0, \sigma^2) \quad (10)$$

where  $\varepsilon_{a,k,y}$  are independent and identical normal variables with a mean of zero and variance  $\sigma^2$ . Models of  $u_{a,k,y}$  can be expressed by

$$\ln(u_{a,k,y}) = \ln(q_{a,k,y}) + \ln(\bar{N}_{a,k,y}) \quad (11)$$

$$\bar{N}_{a,k,y} \equiv C_{a,k,y} / F_{a,k,y} \quad (12)$$

where  $\bar{N}_{a,k,y}$  and  $C_{a,k,y}$  denote the theoretical values of average stock over a period, and that of catch.

The value of  $u'_{a,k,y}$  was calculated by:

$$u'_{a,k,y} = \frac{C'_{a,k,y}}{X_{a,k,y}} \quad (13)$$

where  $C'_{a,k,y}$  is the observed catch. The value of  $M$  (per period) was calculated by:

$$M = 2.5/\lambda = (2.5/1.35) \times (1/36) \equiv 0.0514 \quad (14)$$

where  $\lambda$  is the span of life (years) and assumed that  $\lambda$  is 1.35 years.<sup>14</sup>

The likelihood function to be maximized is

$$l = -\frac{1}{2} \sum_y \sum_k \sum_a \left[ \ln(2\pi\sigma^2) + \frac{\{\ln(u'_{a,k,y}) - \ln(u_{a,k,y})\}^2}{\sigma^2} \right] \quad (15)$$

The parameters to be estimated are  $N_{1,0,y}$  ( $y = 1995, \dots, 2001$ ),  $\kappa s$ ,  $\delta_a$  ( $a = 2, 3, 4$ ),  $\delta'_a$ ,  $\delta''_a$ ,  $\delta'''_a$  and  $\sigma$ . The quasi-Newton method was used for numerically searching the maximum likelihood estimates of these parameters. Variances of the parameter estimates in log-scale were estimated using an inverse of the observed Fisher information:

$$\hat{V}[\hat{\theta}] = -\left[ \frac{\partial^2 l}{\partial \theta_i \partial \theta_j} \Big|_{\hat{\theta}} \right]^{-1} \quad (16)$$

where  $\theta_i (i = 1, \dots, m)$  and  $\hat{\theta}$  denote the unknown parameter in a log-scale and the vector of maximum likelihood estimators, respectively. The best model was selected using Akaike's information criteria (AIC).

$$AIC = -2l + 2N \quad (17)$$

where  $N$  is the number of estimated parameters.

For the selected model, the 95% confidence interval for the original parameter  $\phi_i = \exp(\theta_i)$  was calculated using the following equation:

$$\exp(\hat{\theta}_i - 1.96\hat{\sigma}_i) \leq \phi_i \leq \exp(\hat{\theta}_i + 1.96\hat{\sigma}_i) \quad (18)$$

Here  $\hat{\sigma}_i$  is the estimate of standard error of  $\hat{\theta}_i$ .

Candidates of the threshold temperatures for calculating  $T_{a,k,y}$  ranged from 18 to 24°C. In selection of the threshold temperatures, an additional rule was introduced that the threshold temperature in a region is equal to or lower than that in the adjacent southern region, for example, such as 18, 19, 19 and 22°C for regions 2, 3, 4 and 5, respectively. The optimal model was statistically selected by comparing the likelihood value from 84 scenarios (model 1 and 3 are only one model). Let  $SSTT_{a+1}$  (°C) be the threshold temperature for calculating  $T_{a+1,k,y}$  in region  $a$ .

$$SSTT_{a+1} \leq 18, 19, 20, 21, 22, 23 \text{ or } 24 \quad (19A)$$

$$SSTT_2 \leq SSTT_3 \leq SSTT_4 = SSTT_5 \quad (19B)$$

The best model was statistically selected using AIC from the six optimal models. Sensitivity tests for different values of  $M$  were carried out to assess the effect on the best model.

## DATA

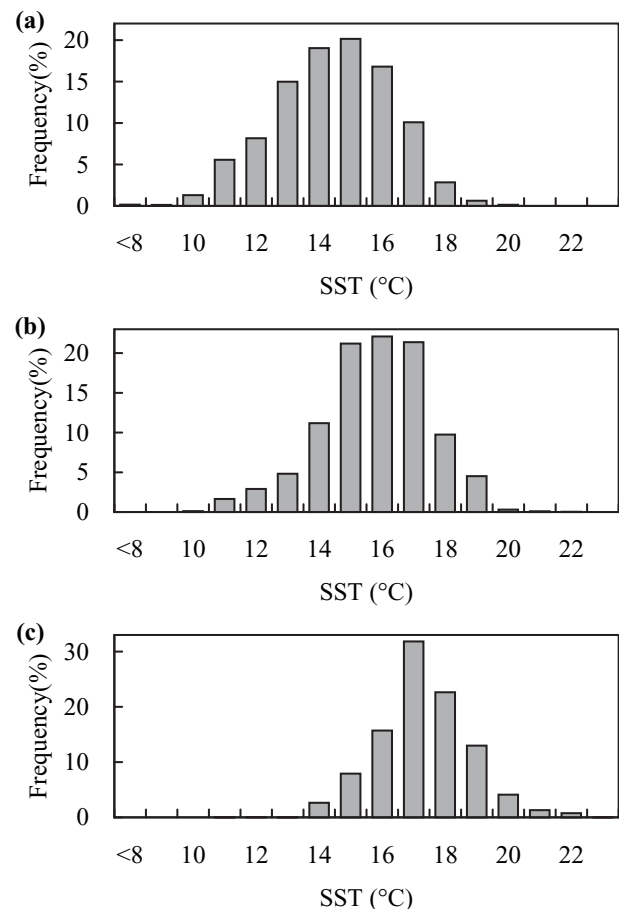
Data used in the estimation are the statistics of the catch and effort by the stick-help dip nets fishery in the Pacific Ocean off Japan (except for the Ohot-

suku Sea), submitted to the Japan Fisheries Agency by fishermen. These data contain the position of the operating area, SST, daily fishing effort (number of hauls) and daily catch of saury by boat. Only the data for boats of gross tonnages greater than 50 tons was used in order to minimize differences of fishing power due to the size of the boats. For calculating  $T_{a+1,k,y}$ ,  $T_{Low a,k,y}$  and  $A_{Temp a,k,y}$ , the grid data of SST by 2' made from SST counters map published by Japan Fisheries Information Service Center was used.

## RESULTS

### Selection of SST zone for calculating $A_{Temp a,k,y}$

Figure 2 shows the frequency of SST in the operating sites where catch was recorded in regions 2–4. The figure indicates that the SST at the mode in the



**Fig. 2** Frequency distribution of sea surface temperature (SST) in fishing sites for 1995–2001. (a) Doutou region ( $a = 2$ ); (b) Sanriku region ( $a = 3$ ); (c) Joban region ( $a = 4$ ).



northern region was lower than that in the southern one, such as 15°C in region 2, 16°C in region 3, and 17°C in region 4. The upper bound of the SST was 20°C in region 2, 21°C in region 3, and 22°C in region 4. Therefore,  $SSTupA_{Tempa,k}$  (°C) was used as follows:

$$SSTupA_{Tempa} \leq \begin{cases} 20 & (a=2) \\ 21 & (a=2) \\ 22 & (a=3) \end{cases} \quad (20)$$

### Selection of model of $h_{a,k,y}$

Table 1 lists the values of  $AIC$  on the optimal model and some candidates. The best model was model 3, which included the effect of the optimal SST waters and free from the influence of SST, while the full model (model 5) resulted in the second best model. The models that included  $T_{a,k,y}$  (models 2, 3, 5, 6) were better than the model free from the influence of SST (model 1). The model included the factor of the extremely cold SST water, and free from the influence of SST (model 4) turned out to be worse than the model free from the influence of SST (model 1).

### Estimation of parameters

Table 2 lists the values of  $AIC$  on the optimal model and some candidates on the model 3 as an example. The optimal model was one when  $SSTT_2$  and  $SSTT_3$  were below 20°C and  $SSTT_4$  and  $SSTT_5$  were below 23°C, and then  $AIC = 353.96$ . Table 2 shows that, in cases when SST in regions 4 and 5 are the same, the value of  $AIC$  using below 20°C for  $SSTT_2$  and  $SSTT_3$  is lower than that using the other com-

binations of SST. Figure 3 illustrates the value of  $AIC$  using below 20°C for  $SSTT_2$  and  $SSTT_3$  against  $SSTT_4$  and  $SSTT_5$ . In the figure, the value of  $AIC$  suddenly decreased as  $SSTT_2$  and  $SSTT_3$  were increased from 21 to 22°C, and then the shape of the value of  $AIC$  curve was almost flat in the domain ranged from 22 to 24°C.

Figure 4 compares the observed CPUE with the theoretical one in 1998 as a typical example. The figure supports that most of the theoretical CPUE values agree well with the observed ones, but some show disagreement, for example early September in region 2.

Table 3 tabulates the estimates of parameters in the best model with the confidence intervals. Using the variance-covariance matrix, the estimates of  $N_{1,0,y}$  are negatively correlated to that of  $\kappa$  ( $r$ -values ranged from -0.88 to -0.94) and hence the values between two estimates of  $N_{1,0,y}$  were positively correlated to each other ( $r$ -values ranged from 0.81 to 0.90). Figure 5 shows the annual changes in the estimates of initial stock, and indicates that the estimated stock rapidly decreased in 1998 and gradually increased in 2001. This trend in the stock is approximately consistent with the results of stock assessment published by the Japan Fisheries Agency,<sup>15</sup> though the absolute values are smaller than the results by the Japan Fisheries Agency. The estimate of  $\delta_4$  was greater than that of  $\delta_2$  or  $\delta_3$ , and this result suggests that emigration to regions 4 and 5 is rapid.

From the results of the sensitivity test using 90% of  $M$ , estimates of  $N_{1,0,y}$  were decreased at the rate of 10–12% of the originals (Table 3). Even though the value of  $M$  changed, the value of the estimated parameters except for  $N_{1,0,y}$  did not change very much.

**Table 1** Estimate of parameters and Akaike's information criteria using the optimal model

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
$AIC$	358.6	357.9	354.0	384.0	358.3	355.8
$N_{1,0,1995}$ (1000t)	508.7	926.3	542.0	473.0	539.2	551.7
$N_{1,0,1996}$ (1000t)	442.3	827.3	482.9	437.7	473.4	492.9
$N_{1,0,1997}$ (1000t)	723.5	1482.6	773.2	623.4	735.6	777.2
$N_{1,0,1998}$ (1000t)	155.0	268.5	176.5	165.8	168.0	180.3
$N_{1,0,1999}$ (1000t)	198.0	401.9	195.5	160.1	203.7	198.7
$N_{1,0,2000}$ (1000t)	247.1	464.6	271.3	268.6	262.0	274.9
$N_{1,0,2001}$ (1000t)	436.2	884.3	475.6	460.7	461.9	482.9
$\kappa$ (area per haul)	0.2442	0.2358	0.2114	0.3210	0.2149	0.2033
$\delta_2$ (per unit time)	0.2762	0.0909	0.2577	—	0.2709	0.2601
$\delta_3$ (per unit time)	0.3079	0.1886	0.2095	—	0.2552	0.2006
$\delta_4$ (per unit time)	0.4439	0.4331	0.3539	—	0.4522	0.3664
$\delta'$ (per unit time)	—	—	—	0.0025	0.1622	0.0564
$\delta''$ (per unit time)	—	—	0.0326	0.1562	—	0.0293
$\phi$	0.5381	0.5330	0.5266	0.5890	0.5341	0.5262

$AIC$ , Akaike's information criteria.

**Table 2** Value of Akaike's information criteria by combining  $SST_2$  and  $SST_3$ 

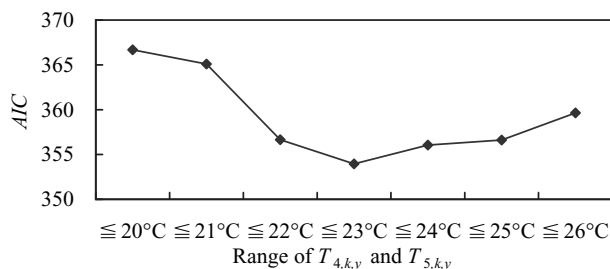
$SST_3$		$\leq 18^\circ\text{C}$	$\leq 19^\circ\text{C}$	$\leq 20^\circ\text{C}$	$\leq 21^\circ\text{C}$	$\leq 22^\circ\text{C}$	$\leq 23^\circ\text{C}$	$\leq 24^\circ\text{C}$
(a)								
$SST_2$	$\leq 22^\circ\text{C}$	—	—	—	—	364.73		
	$\leq 21^\circ\text{C}$	—	—	—	361.01	364.81		
	$\leq 20^\circ\text{C}$	—	—	356.65	361.62	365.27		
	$\leq 19^\circ\text{C}$	—	360.06	358.34	362.97	366.26		
	$\leq 18^\circ\text{C}$	365.93	362.44	360.90	365.00	367.80		
(b)								
$SST_2$	$\leq 23^\circ\text{C}$	—	—	—	—	—	365.06	
	$\leq 22^\circ\text{C}$	—	—	—	—	362.29	364.50	
	$\leq 21^\circ\text{C}$	—	—	—	358.13	362.43	364.60	
	$\leq 20^\circ\text{C}$	—	—	353.96	358.83	362.99	365.10	
	$\leq 19^\circ\text{C}$	—	358.30	355.73	360.39	364.21	366.10	
	$\leq 18^\circ\text{C}$	365.09	360.76	358.46	362.72	366.04	367.67	
(c)								
$SST_2$	$\leq 24^\circ\text{C}$	—	—	—	—	—	—	368.62
	$\leq 23^\circ\text{C}$	—	—	—	—	—	366.56	368.22
	$\leq 22^\circ\text{C}$	—	—	—	—	363.87	366.00	367.62
	$\leq 21^\circ\text{C}$	—	—	—	359.90	363.99	366.10	367.66
	$\leq 20^\circ\text{C}$	—	—	356.06	360.55	364.53	366.58	368.07
	$\leq 19^\circ\text{C}$	—	360.39	357.72	362.04	365.70	367.54	368.84
	$\leq 18^\circ\text{C}$	367.14	362.77	360.38	364.33	367.51	369.09	370.14

(a)  $SST_4$  and  $SST_5$  are fixed below  $22^\circ\text{C}$ . (b)  $SST_4$  and  $SST_5$  are fixed below  $23^\circ\text{C}$ . (c)  $SST_4$  and  $SST_5$  are fixed below  $24^\circ\text{C}$ .

**Table 3** Estimate of parameters using the best model

	Point estimate	95% confidence intervals		90% of $M$ Point estimate
		Lower	Upper	
$N_{1,0,1995}$ (1000t)	542.0	448.0	655.7	496.5
$N_{1,0,1996}$ (1000t)	482.9	385.7	604.6	441.7
$N_{1,0,1997}$ (1000t)	773.2	596.9	1001.6	705.1
$N_{1,0,1998}$ (1000t)	176.5	131.3	237.4	160.0
$N_{1,0,1999}$ (1000t)	195.5	166.0	230.3	179.6
$N_{1,0,2000}$ (1000t)	271.3	227.4	323.6	248.7
$N_{1,0,2001}$ (1000t)	475.6	394.5	573.4	437.3
$\kappa$ (area per haul)	0.2114	0.1397	0.3198	0.2229
$\delta_2$ (per unit time)	0.2577	0.2195	0.3025	0.2695
$\delta_3$ (per unit time)	0.2095	0.1855	0.2366	0.2078
$\delta_4$ (per unit time)	0.3539	0.3314	0.3778	0.3524
$\delta'$ (per unit time)	0.0326	0.0197	0.0538	0.0323
$\phi$	0.5266	0.5232	0.5300	0.5271

90% of  $M$  (per period) shows estimating of parameters using  $M = (2.5/\lambda) \times 0.9 = (2.5/1.35) \times (1/36) \times 0.9 = 0.0463$ .  $\lambda$  is the span of life (years).

**Fig. 3** Akaike's information criteria (AIC) against the range of  $T_{4,k,y}$  and  $T_{5,k,y}$ . The threshold water temperature in  $a=2$  and  $a=3$  are fixed below  $20^\circ\text{C}$ .

Calculated values of  $q_{a,k}$  in 1998 are shown in Table 4 as an example. The values in region 2 are much smaller than those in the other regions.

### Seasonal changes of $T_{a,k,y}$ and $N_{a,k,y}$

Figure 6 shows seasonal changes in  $T_{a,k,y}$  and estimated  $N_{a,k,y}$  in 1998 and 1999. In 1998,  $N_{1,k,1998}$  decreased with time in the Northern region and peaks of the stock occurred in late September in Doutou, in late October or early November in

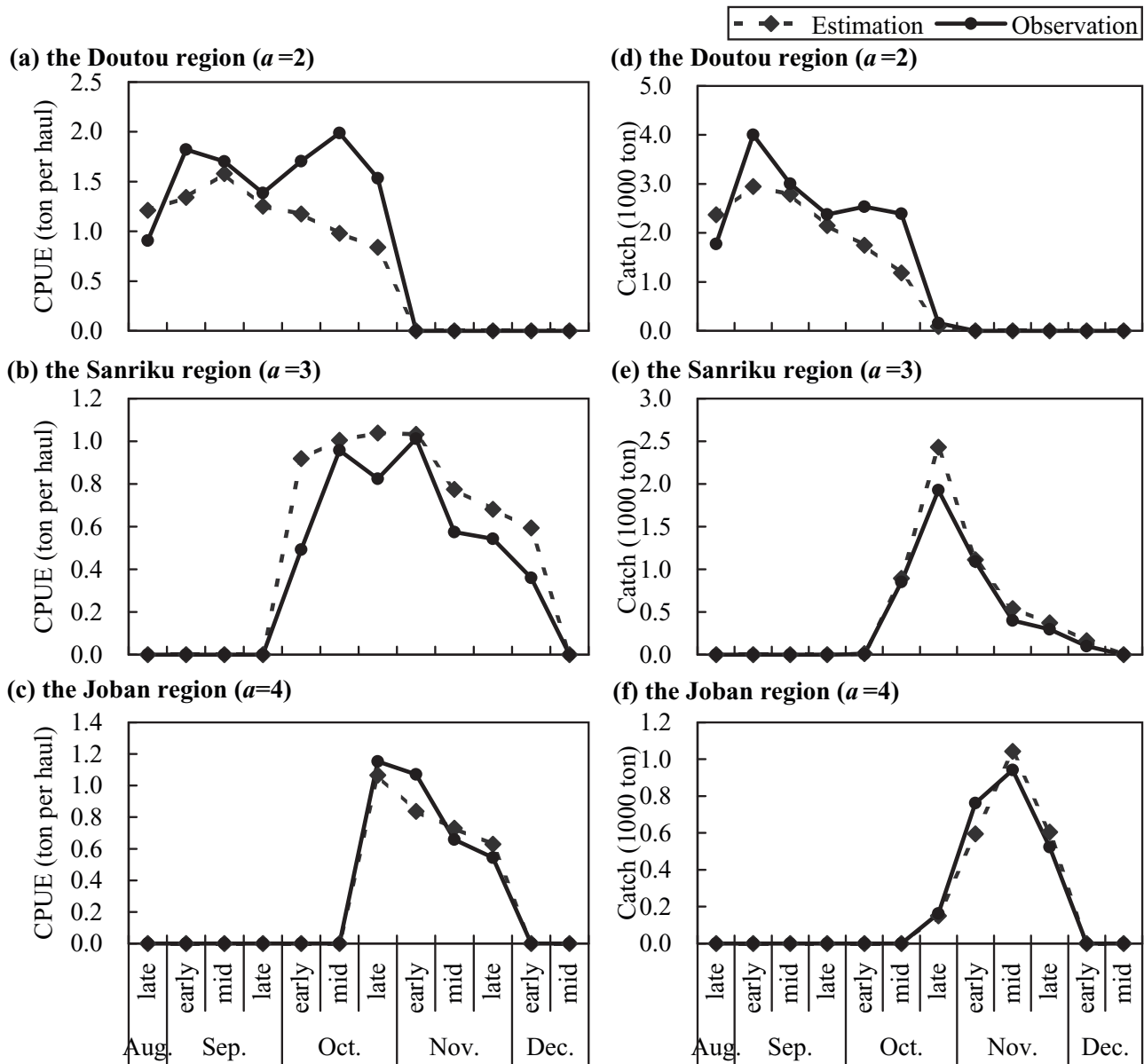


Fig. 4 Comparison of estimates of CPUE and catch with observation of those in 1998 using the optimal model.

Sanriku, and in early December in Joban. In 1999, the increase of  $T_{a,k,1999}$  was slow in comparison with those in 1998. Although the estimate of initial stock in 1999 was higher than in 1998, the size of migratory stock in Sanriku and Joban were similar to the stock values in 1998 because the influx of immigrating fish was late.

## DISCUSSION

The values of  $AIC$  of the models, including the factor of the optimal SST waters, were smaller than the values of  $AIC$  of the model free from the effect

of SST; therefore this suggests that the factor of the optimal SST waters is effective for the saury migration. Consequently, it shows that the timing of the migration for saury was influenced by the annual change of the coverage proportion of optimal SST waters. However, the models included the factor of the extremely cold water, and were not the best models. The difference of the values of  $AIC$  between the best model (model 3) and the full model (model 6) was approximately 1.8, which is a very slight figure. When  $T_{low\ a,k,y}$  is large, especially in region 2 after November, the amount of CPUE data in region 2 for estimating the parameter is insufficient. Therefore, the number of data for

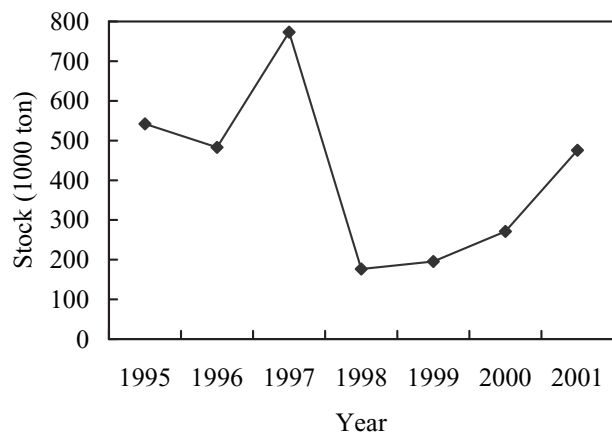
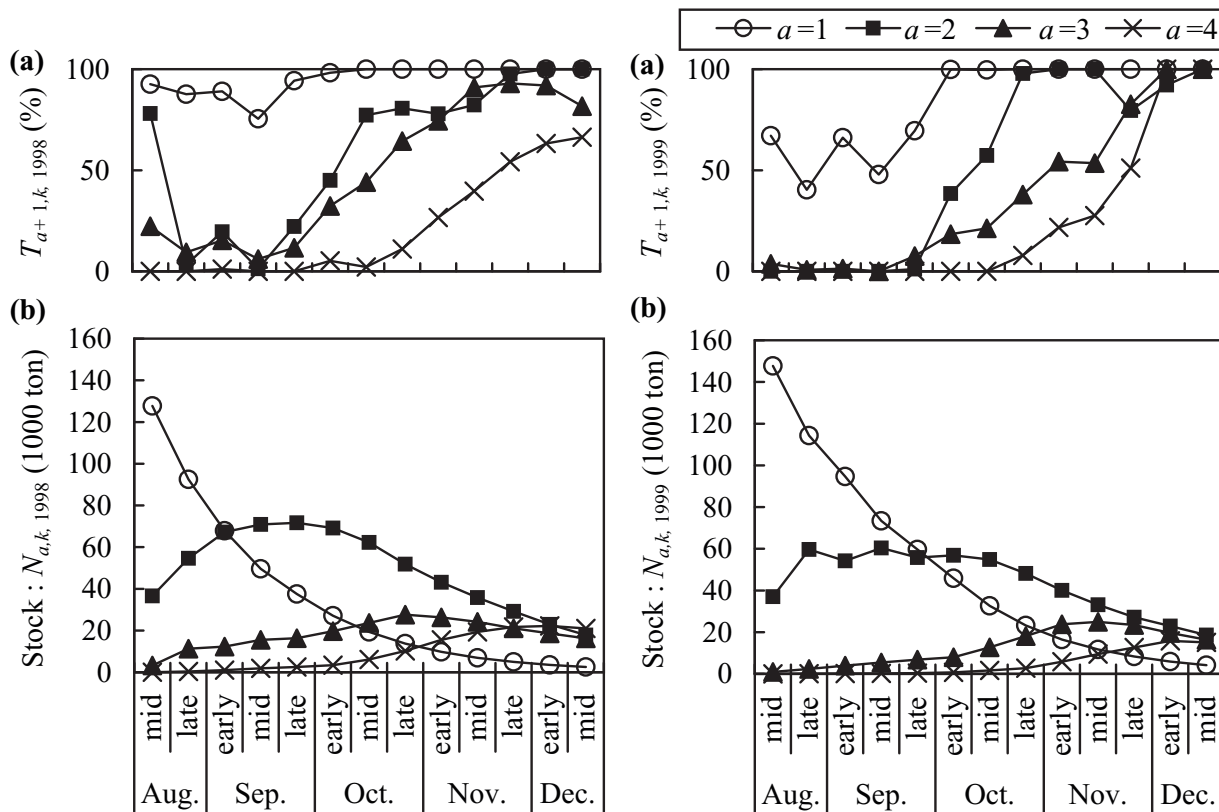


Fig. 5 Annual variation of estimated  $N_{1,0,y}$ .

**Table 4** Estimate of  $q_{a,k,1998}$  ( $10^{-5}$  per haul) in 1998 using the best model when fishermen catch Pacific saury *Cololabis saira* (Brevoort)

		$a = 2$	$a = 3$	$a = 4$
August	Late	0.20	–	–
	September	0.19	–	–
	Mid	0.22	–	–
October	Late	0.18	–	–
	Early	0.18	0.42	–
	Mid	0.17	0.39	–
November	Late	0.18	0.38	0.68
	Early	–	0.41	0.43
	Mid	–	0.34	0.33
December	Late	–	0.34	0.27
	Early	–	0.34	–
	Mid	–	–	–



**Fig. 6** Change in the coverage proportion of the optimal sea surface temperature (SST) waters to the whole (a) and comparison of among regions about stock in weight ( $N_{a,k,y}$ ) using the optimal model (b) from early August to mid December. Left and right panels are changes in 1998 and 1999.

estimated the parameter might not be sufficient. More data and more analysis are required to state whether the factor of the extremely cold water is effective for the saury migration.

The selected  $SSTT_{a+1}$  (threshold temperature for calculating  $T_{a,k,y}$ ) was below 20°C in the Doutou

and Sanriku regions, and below 23°C in Joban region. Although  $T_{a,k,y}$  relates to the emigration rate, the SST zone, defined by  $T_{a,k,y}$  was consistent with most of the operating sites where some catch occurs (see Fig. 2). The present model shows that the saury emigrate to the adjacent southern region



when SST in the adjacent region falls below that threshold temperature (20°C in the Doutou and Sanriku regions and 23°C in Joban region). Therefore, it can be said that extremely warm water plays a role of a hard barrier that blocks the southward migration of the saury. The result of the model corresponds to the fact that the operating sites are formed in the Oyashio water, along the oceanic front between the Oyashio cold water and warm waters originated from the Kuroshio.<sup>5,16</sup>

Figure 7 illustrates the changes in the stock by region and period. Comparing the changes, the difference of the stock in Sanriku region and Joban region between 1996 and 1999 was noted. In San-

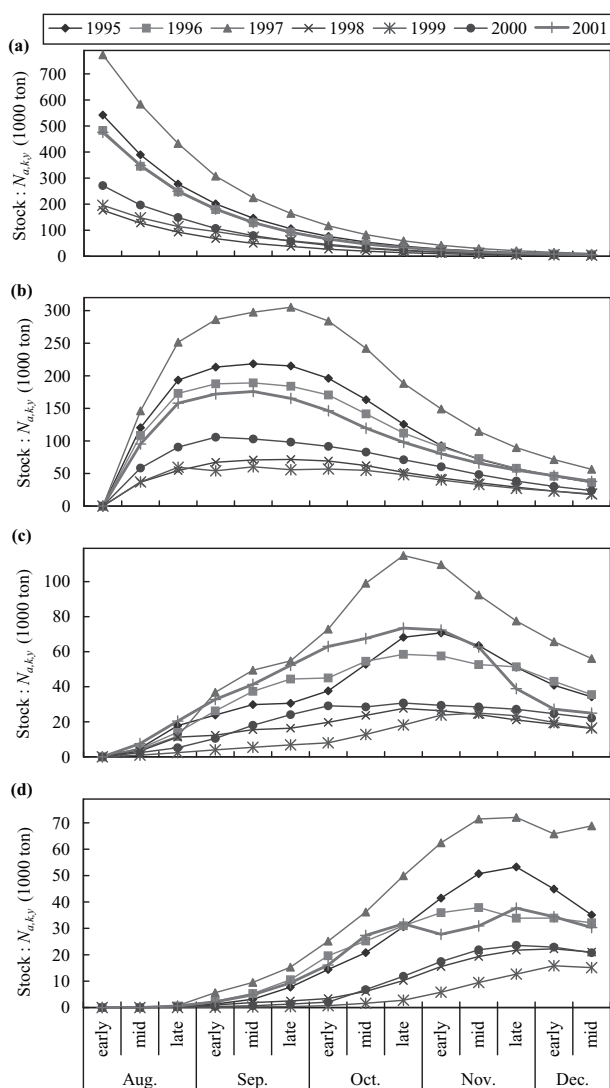
riku, the present study's model shows that the stock in 1996 begins to increase in mid and late August, but in 1999 begins to increase in early and mid October. The result of the model approximately corresponds to the fact that the first day of fishing in Sanriku was on 22 August 1996 and on 6 October 1999.<sup>17</sup> Regarding the Joban region, the present model shows that the stock in 1996 begins to increase in mid and late September, but that in 1999 begins to increase in mid October. The result of the model was supported by the fact that the first day of fishing in Joban was on 28 September 1996 and 7 October 1999.<sup>17</sup>

Although, the estimation showed that a certain extent of stock exists in Doutou for the periods after early November, as shown in Figures 6 and 7, the estimates of  $N_{a,k,y}$  for the periods might be larger than the actual stock, because the fishing operations in Doutou usually cease from early November. In November, the fishermen have two choices of operation, one is to exploit the saury stock in Sanriku which might immigrate from Doutou and consist of fish of small or middle length, and the other is to exploit the stock of large or middle saury in the southern regions. Expectation of the catch amounts in the southern regions is greater than that in Sanriku, and most of fishermen prefer operations in southern regions because of their profitability. Further examinations such as analyzing operating conditions, including price of fish and size of fish to be exploited, will be needed to see whether a stock exists in Doutou.

Trend of relative changes in estimates of  $N_{1,0,y}$  is almost the same with the stock assessment published by the Japan Fisheries Agency,<sup>15</sup> but the absolute values are different. Three reasons might explain this: (i) that the values of  $M$  might not be the same with the stock assessment published by the Japan Fisheries Agency; (ii) the difference of data between the selected data used in the study and the full data causes the discrepancy; and (iii) is that our estimates are made for exploitable stocks, but the other estimates are done for the whole stock. This should be investigated by examining the data of fish size in various data sources in the near future.

In this present study, it was assumed that the catchability coefficient was inversely proportional to the size of the habitat area. Models were made to assume the catchability coefficient was constant, but in many of those models the estimate of parameters were not found. There is the relationship between  $q_{a,k,y}$  and  $N_{1,0,y}$ , and it might be one of the reasons.

The estimated values of  $q_{a,k,y}$  ranged from 0.000017 to 0.000068 during the fishing seasons, and some of those values were much smaller than



**Fig. 7** Estimation results of stock in weight at  $t=0$  ( $N_{a,k,y}$ ) using the optimal model from early August to mid December for 1995–2001. (a) Northern region ( $a=1$ ), (b) Doutou region ( $a=2$ ), (c) Sanriku region ( $a=3$ ), (d) Joban region ( $a=4$ ).

the past estimate (0.00028).<sup>18,19</sup> Annual exploitation rates calculated from the catch and estimated initial stock were not low (0.139–0.363) and therefore the present estimates were not considered to be too low. The past estimate is not comparable because it was made from data for years different from the period used in this study. The difference may be explained by annual changes in  $q_{a,k,y}$  because a part of the present estimates was close to the past one. To obtain more precise estimates requires the incorporation of other effects into the model of catchability, for example, the effects of seasonal and regional differences of fish behavior to the fishing lamp.

Recently, some questions have arisen regarding the effectiveness of the use of CPUE as an index of stock size because fishermen have begun to use fish sorting machines<sup>20</sup> in order to land only high-grade saury. If the effect of the use of fish sorting machines turns out to be too significant to be ignored, a new index of stock size instead of CPUE should be introduced, and further investigation may be necessary.

In this study, it is supposed that no movement occurred from or into any of the areas other than the five regions. However, depending on the sea conditions, this assumption may be invalid. Further investigation into the influence and timing of various sea conditions is needed.

The multiplicative measurement error model was used, assuming normal distribution in this study. A better model using other models might be found.

The present model can be useful for planning fishing operations at the start of the fishing season, if the initial stock in the year is calculated by some direct estimation using a trawl survey,<sup>15</sup> and the water temperature is predicted by time series analysis.<sup>21</sup> Annual demand of saury in Japan has been estimated to be constant. Therefore, the issue for the saury fishers is to minimize the cost necessary to achieve that demand, avoiding waste due to lack of knowledge of stock density of the region and period using information in the model. This model can be modified for other migratory stocks such as sardine and mackerel, and this is an issue to be resolved in the near future.

## ACKNOWLEDGMENTS

The authors are grateful to Mr Hiroshi Shyono, Mr Hirotune Yamaguchi and Dr Sunao Kosaka for their helpful comments and suggestion for improving this study. The statistics data of the catch and effort were collected by a stock assessment project from the Japan Fisheries Agency.

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## APPENDIX I: DERIVATION OF CATCH EQUATION

### Solution of $N_{a,k,y}$

Solution for  $N_{a,k,y}$  differential equations from 1 to 3.  $N_{a,k,y}$  is expressed by the following formula.

$$N_{1,k+1,y} = N_{1,k,y} \exp(-M - h_{1,k,y}) \quad (\text{A1})$$

$$N_{2,k+1,y} = \begin{cases} N_{2,k,y} \exp(-Z'_{2,k,y}) + N_{1,k,y} h_{1,k,y} \frac{\{\exp(-Z'_{2,k,y}) - \exp(-Z'_{1,k,y})\}}{Z'_{1,k,y} - Z'_{2,k,y}} & (Z'_{1,k,y} \neq Z'_{2,k,y}) \\ N_{2,k,y} \exp(-Z'_{2,k,y}) + h_{1,k,y} N_{1,k,y} \exp(-Z'_{2,k,y}) & (Z'_{1,k,y} = Z'_{2,k,y}) \end{cases} \quad (\text{A2})$$

$$N_{3,k+1,y} = \begin{cases} N_{3,k,y} \exp(-Z'_{3,k,y}) + N_{2,k,y} h_{2,k,y} \frac{\{\exp(-Z'_{3,k,y}) - \exp(-Z'_{2,k,y})\}}{Z'_{2,k,y} - Z'_{3,k,y}} \\ \quad + N_{1,k,y} h_{1,k,y} h_{2,k,y} \left[ \frac{\exp(-Z'_{1,k,y})}{(Z'_{2,k,y} - Z'_{1,k,y})(Z'_{3,k,y} - Z'_{1,k,y})} + \frac{\exp(-Z'_{2,k,y})}{(Z'_{1,k,y} - Z'_{2,k,y})(Z'_{3,k,y} - Z'_{2,k,y})} \right. \\ \quad \left. + \frac{\exp(-Z'_{3,k,y})}{(Z'_{1,k,y} - Z'_{3,k,y})(Z'_{2,k,y} - Z'_{3,k,y})} \right] & (Z'_{1,k,y} \neq Z'_{2,k,y} \neq Z'_{3,k,y}) \\ N_{3,k,y} \exp(-Z'_{3,k,y}) + h_{2,k,y} \left[ N_{2,k,y} + \frac{h_{1,k,y}}{Z'_{1,k,y} - Z'_{3,k,y}} N_{1,k,y} \right] \exp(-Z'_{3,k,y}) \\ \quad + h_{1,k,y} h_{2,k,y} N_{1,k,y} \left[ \frac{\exp(-Z'_{3,k,y})}{(Z'_{1,k,y} - Z'_{3,k,y})(Z'_{2,k,y} - Z'_{1,k,y})} + \frac{\exp(-Z'_{1,k,y})}{(Z'_{2,k,y} - Z'_{1,k,y})(Z'_{3,k,y} - Z'_{1,k,y})} \right] & (Z'_{1,k,y} \neq Z'_{2,k,y} = Z'_{3,k,y}) \\ N_{3,k,y} \exp(-Z'_{3,k,y}) + \frac{h_{2,k,y} N_{2,k,y}}{Z'_{2,k,y} - Z'_{3,k,y}} [\exp(-Z'_{3,k,y}) - \exp(-Z'_{2,k,y})] & (Z'_{1,k,y} = Z'_{2,k,y} \neq Z'_{3,k,y}) \end{cases} \quad (\text{A3})$$

$$N_{4,k+1,y} = \begin{cases} N_{4,k,y} \exp(-Z'_{4,k,y}) + N_{3,k,y} h_{3,k,y} \frac{\{\exp(-Z'_{4,k,y}) - \exp(-Z'_{3,k,y})\}}{Z'_{3,k,y} - Z'_{4,k,y}} \\ + N_{2,k,y} h_{2,k,y} h_{3,k,y} \left[ \frac{\exp(-Z'_{2,k,y})}{(Z'_{3,k,y} - Z'_{2,k,y})(Z'_{4,k,y} - Z'_{2,k,y})} + \frac{\exp(-Z'_{3,k,y})}{(Z'_{2,k,y} - Z'_{3,k,y})(Z'_{4,k,y} - Z'_{3,k,y})} \right. \\ \left. + \frac{\exp(-Z'_{4,k,y})}{(Z'_{2,k,y} - Z'_{4,k,y})(Z'_{3,k,y} - Z'_{4,k,y})} \right] \\ + N_{1,k,y} h_{1,k,y} h_{2,k,y} h_{3,k,y} \sum_{i=1}^4 \exp(-Z'_{i,k,y}) \prod_{j \neq i} \frac{1}{(Z'_{j,k,y} - Z'_{i,k,y})} \quad (Z'_{3,k,y} \neq Z'_{4,k,y}) \\ N_{4,k,y} \exp(-Z'_{4,k,y}) + h_{3,k,y} N_{3,k,y} \exp(-Z'_{4,k,y}) \quad (Z'_{3,k,y} = Z'_{4,k,y}) \end{cases} \quad (A4)$$

About second section of (A2), we can express by the following formula.

$$\begin{aligned} & \int_0^1 N_{1,k,y} \exp(-Z'_{1,k,y}t) \times h_{1,k,y} \exp(-Z'_{2,k,y}(1-t)) dt \\ &= N_{1,k,y} h_{1,k,y} \exp(-Z'_{2,k,y}) \int_0^1 \exp(Z'_{2,k,y} - Z'_{1,k,y}) t dt \\ &= N_{1,k,y} h_{1,k,y} \frac{\{\exp(-Z'_{2,k,y}) - \exp(-Z'_{1,k,y})\}}{Z'_{1,k,y} - Z'_{2,k,y}} \end{aligned} \quad (A5)$$

### Solution of $C_{a,k,y}$

Solution for  $C_{a,k,y}$  differential equations from 1 to 4.  $C_{a,k,y}$  is expressed by the following formula.

$$C_{1,k,y} = 0 \quad (A6)$$

$$E_{a,k,y} = \frac{F_{a,k,y}}{Z'_{a,k,y}} \{1 - \exp(-Z'_{a,k,y})\} \quad (A7)$$

$$C_{2,k,y} = \begin{cases} N_{2,k,y} E_{2,k,y} + N_{1,k,y} F_{2,k,y} h_{1,k,y} \left[ \frac{1 - \exp(-Z'_{2,k,y})}{Z'_{2,k,y}(Z'_{1,k,y} - Z'_{2,k,y})} + \frac{1 - \exp(-Z'_{1,k,y})}{Z'_{1,k,y}(Z'_{2,k,y} - Z'_{1,k,y})} \right] \\ N_{2,k,y} E_{2,k,y} + N_{1,k,y} F_{2,k,y} h_{1,k,y} \left[ \frac{1 - (1 + Z'_{2,k,y}) \exp(-Z'_{2,k,y})}{Z'_{2,k,y} \times Z'_{2,k,y}} \right] \end{cases} \quad \begin{matrix} (Z'_{1,k,y} \neq Z'_{2,k,y}) \\ (Z'_{1,k,y} = Z'_{2,k,y}) \end{matrix} \quad (A8)$$

$$C_{3,k,y} = \begin{cases} N_{3,k,y} E_{3,k,y} + N_{2,k,y} F_{3,k,y} h_{2,k,y} \left[ \frac{1 - \exp(-Z'_{3,k,y})}{Z'_{3,k,y}(Z'_{2,k,y} - Z'_{3,k,y})} + \frac{1 - \exp(-Z'_{2,k,y})}{Z'_{2,k,y}(Z'_{3,k,y} - Z'_{2,k,y})} \right] \\ + N_{1,k,y} F_{3,k,y} h_{1,k,y} h_{2,k,y} \left[ \frac{1 - \exp(-Z'_{3,k,y})}{Z'_{3,k,y}(Z'_{1,k,y} - Z'_{3,k,y})(Z'_{2,k,y} - Z'_{3,k,y})} \right. \\ \left. + \frac{1 - \exp(-Z'_{2,k,y})}{Z'_{2,k,y}(Z'_{1,k,y} - Z'_{2,k,y})(Z'_{3,k,y} - Z'_{2,k,y})} + \frac{1 - \exp(-Z'_{1,k,y})}{Z'_{1,k,y}(Z'_{2,k,y} - Z'_{1,k,y})(Z'_{3,k,y} - Z'_{1,k,y})} \right] \\ N_{3,k,y} E_{3,k,y} + N_{2,k,y} F_{3,k,y} h_{2,k,y} \left[ \frac{1 - \exp(-Z'_{3,k,y})}{Z'_{3,k,y}(Z'_{2,k,y} - Z'_{3,k,y})} + \frac{1 - \exp(-Z'_{2,k,y})}{Z'_{2,k,y}(Z'_{3,k,y} - Z'_{2,k,y})} \right] \end{cases} \quad \begin{matrix} (Z'_{1,k,y} \neq Z'_{2,k,y}) \\ (Z'_{1,k,y} = Z'_{2,k,y}) \end{matrix} \quad (A9)$$

$$\begin{aligned}
C_{4,k,y} = & N_{4,k,y}E_{4,k,y} + N_{3,k,y}F_{4,k,y}h_{3,k,y} \left[ \frac{1 - \exp(-Z'_{4,k,y})}{Z'_{4,k,y}(Z'_{3,k,y} - Z'_{4,k,y})} + \frac{1 - \exp(-Z'_{3,k,y})}{Z'_{3,k,y}(Z'_{4,k,y} - Z'_{3,k,y})} \right] \\
& + N_{2,k,y}F_{4,k,y}h_{2,k,y}h_{3,k,y} \left[ \frac{1 - \exp(-Z'_{4,k,y})}{Z'_{4,k,y}(Z'_{2,k,y} - Z'_{4,k,y})(Z'_{3,k,y} - Z'_{4,k,y})} \right. \\
& \quad \left. + \frac{1 - \exp(-Z'_{3,k,y})}{Z'_{3,k,y}(Z'_{2,k,y} - Z'_{3,k,y})(Z'_{4,k,y} - Z'_{3,k,y})} + \frac{1 - \exp(-Z'_{2,k,y})}{Z'_{2,k,y}(Z'_{3,k,y} - Z'_{2,k,y})(Z'_{4,k,y} - Z'_{2,k,y})} \right] \\
& + N_{1,k,y}F_{4,k,y}h_{1,k,y}h_{2,k,y}h_{3,k,y} \sum_{i=1}^4 \frac{1 - \exp(-Z'_{i,k,y})}{Z'_{i,k,y}} \prod_{j \neq 1} \frac{1}{Z'_{j,k,y} - Z'_{i,k,y}}
\end{aligned} \tag{A10}$$