

Abstract—Annual mean fork length (FL) of the Pacific stock of chub mackerel (*Scomber japonicus*) was examined for the period of 1970–97. Fork length at age 0 (6 months old) was negatively correlated with year-class strength which fluctuated between 0.2 and 14 billion in number for age-0 fish. Total stock biomass was correlated with FL at age but was not a significant factor. Sea surface temperature (SST) between 38–40°N and 141–143°E during April–June was also negatively correlated with FL at age 0. A modified von Bertalanffy growth model that incorporated the effects of population density and SST on growth was well fitted to the observed FL at ages. The relative FL at age 0 for any given year class was maintained throughout the life span. The variability in size at age in the Pacific stock of chub mackerel is largely attributable to growth during the first six months after hatching.

Effects of density-dependence and sea surface temperature on interannual variation in length-at-age of chub mackerel (*Scomber japonicus*) in the Kuroshio-Oyashio area during 1970–1997

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Variability in growth of marine fishes has been attributed to the effects of density-dependence or environmental factors such as water temperature, or to the effects of both factors (e.g. Moyle and Cech, 2002). Size-at-age data are crucial because they are necessary for stock assessment methods such as virtual population analysis, yield per recruit, and spawning-per-recruit analyses (Pauly, 1987; Mace and Sissenwine, 1993; Haddon, 2001) and are possibly useful for detecting regime shifts as well (Yatsu and Kidokoro, 2002). Around Japan, the effects of population density and sea water temperature on fish growth have been shown for the Pacific stock of chub mackerel (*Scomber japonicus*) (Iizuka, 1974), Japanese Spanish mackerel (*Scomberomorus niphonius*) (Kishida, 1990), the Pacific and Tsushima Current stocks of Japanese sardine (*Sardinops melanostictus*) (Hiyama et al., 1995; Wada et al., 1995), and Japanese common squid (*Todarodes pacificus*) (Kidokoro, 2001).

The Pacific stock of chub mackerel is one of the most important commercially exploited fish populations in Japan and has been managed by the total allowable catch (TAC) system in Japan since 1997. Chub mackerel seasonally migrate along the Pacific coast of Japan from Kyushu to Hokkaido. They spawn in the coastal waters around Izu Islands and off southwestern Japan between February and June (Fig. 1, Watanabe, 1970; Usami, 1973; Murayama et al., 1995; Watanabe et al., 1999). Adult fish (after spawning) and their offspring migrate eastward along the Pacific

coast with the Kuroshio Current. Juvenile mackerel of about 6 months old usually recruit to the purse-seine and set-net fisheries off the coast of north-eastern Japan at the end of summer (Fig. 1, Odate, 1961; Kawasaki, 1966; Watanabe, 1970; Iizuka, 1974). The total catch of the Pacific stock of chub mackerel increased during the 1960s and 1970s, peaked at 1.5 million metric tons in 1978, and then declined to 2.3 thousand tons in 1990 (Fig. 2). The estimated total biomass increased in the 1970s from 2.8 million tons in 1970 to 5.9 million tons in 1977, and the consecutive occurrences of large year classes exceeded 7 billion age-0 (6-month-old) fish in the early and mid 1970s. In 1990, the biomass was reduced to a minimum of 0.2 million tons in 1990 (Table 1, Fig. 2; Yatsu et al.¹). Relatively large year classes occurred in 1992 (2.8 billion fish) and 1996 (4.5 billion fish), and the total biomass increased in the mid 1990s, but it remained at about 10% of the level attained in the mid 1970s (Yatsu et al.¹).

On the basis of year-class strength and variations in fork length (FL) at ages 0–2 for the 11 year classes present from 1963 to 1973, Iizuka (1974) suggested an effect of density-dependent growth on young chub mackerels. In

¹ Yatsu, A., C. Watanabe, and H. Nishida. 2001. Stock assessment of the Pacific stock of chub mackerel in fiscal 2000 year. In Stock assessment report, p. 64–87. [In Japanese. Available from Fisheries Research Agency, 2-12-4 Fukuura, Kanazawa, Yokohama 236-8648, Japan.]

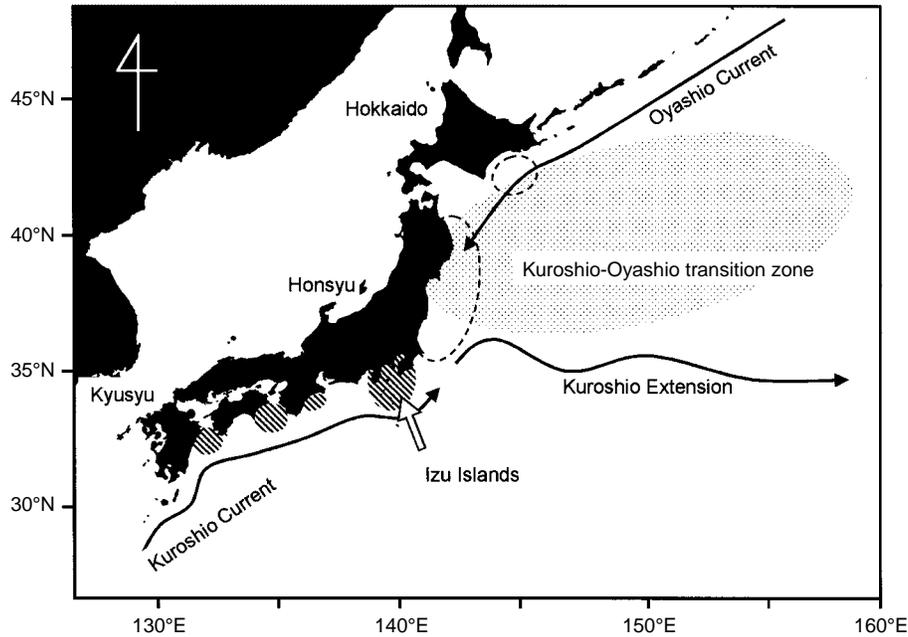


Figure 1

Distribution of the Pacific stock of chub mackerel (*Scomber japonicus*) and major oceanographic features around Japan. The hatched areas show spawning grounds. The dotted areas show feeding grounds. Major purse-seine fishing grounds are surrounded by dashed lines. The fishing grounds around the eastern coast of Hokkaido failed in 1977 with the decline in biomass (Hirai, 1991).

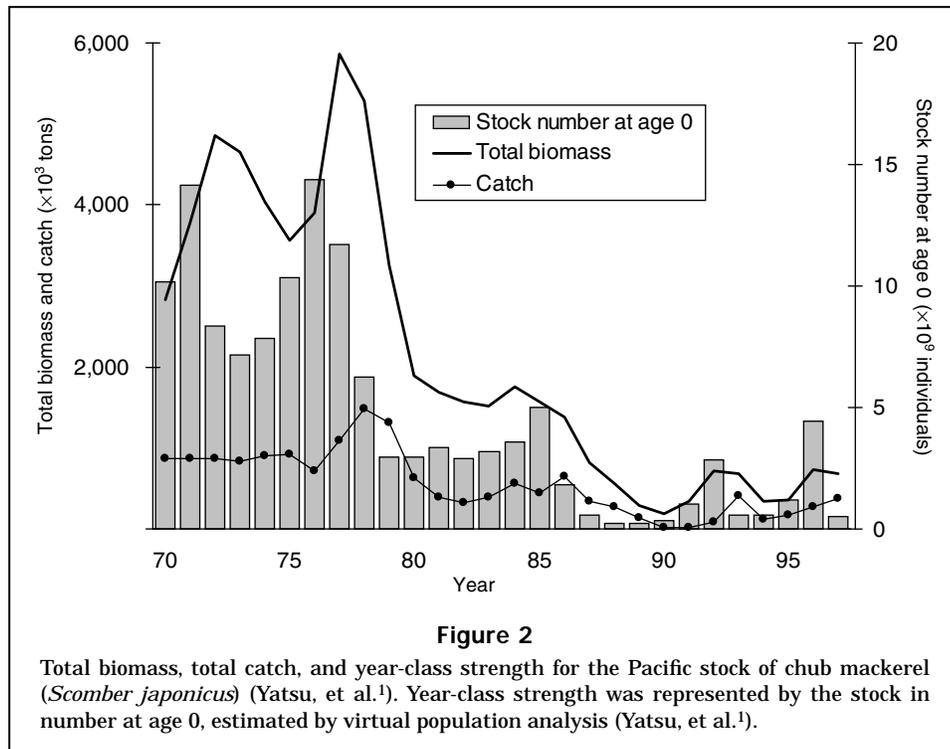


Figure 2

Total biomass, total catch, and year-class strength for the Pacific stock of chub mackerel (*Scomber japonicus*) (Yatsu, et al.¹). Year-class strength was represented by the stock in number at age 0, estimated by virtual population analysis (Yatsu, et al.¹).

this study we describe the variation in FL at age of the Pacific stock of chub mackerel in the Kuroshio–Oyashio area, using data from 1970 to 1997 when the stock biomass

fluctuated between 0.2 and 5.9 million metric tons. We use these data to evaluate the effects of population density and sea surface temperature on FL at age.

Materials and methods

Biological data

Biological data have been compiled since 1964 for purse-seine, set-net, dip-net catches, and other catches by national fisheries research institutes and local government fisheries experimental stations in Japan. Fork length (FL) was measured for one thousand to 100 thousand fish per year and body weight (BW) and gonad weight were measured for 10–100% of these fish. The monthly FL compositions and the relationships of FL to BW were established for each year with this data set. Year-specific age-length keys from 1970 to 1994 were adopted from the reports of cooperative research on Pacific mackerel by local government agencies in Chiba, Kanagawa, Shizuoka, and Tokyo.² Between 1995 and 1997, age-length keys were developed by national fisheries research institutes and local government fisheries experimental stations.

For calculating the mean FL for ages 0, 1, 2, 3, 4, 5, and 6 years and older, we used data from the purse-seine fishery of northeastern Japan during September–December for 28 years, from 1970 to 1997. The catch of this fishery in these four months constituted 26–80% (the 28-year mean is about 63%) of the total annual catch of the Pacific stock of chub mackerel. Catch in number at FL class i (cm) of each month were calculated by

$$n_{a,i} = C_a \frac{d_{a,i}}{\sum_{k=1}^{50} d_{a,k} W_{a,k}}, \quad (1)$$

where $n_{a,i}$ = catch in number at FL class i (cm) $\{= 1, \dots, k, \dots, 50\}$ of month a $\{= \text{Sep., Oct., Nov., Dec.}\}$;
 $d_{a,i}$ = frequency at FL class i of month a ;
 $w_{a,i}$ = a mean weight of each FL class derived from the FL-BW relationship; and
 C_a = a total catch of month a .

We then summed $n_{a,i}$ of 4 months to derive the annual catch in number at FL class i :

$$n_i = \sum_{a=\text{Sep.}}^{\text{Dec.}} n_{a,i} \quad (2)$$

where n_i = the annual catch in number at FL class i .

Using the age-length key, we converted n_i to catch at FL class i at age j :

$$n_{i,j} = n_i \times r_{i,j}, \quad (3)$$

where $n_{i,j}$ = the annual catch in number at FL class i at age j ; and

$$r_{i,j} = \frac{\text{proportion of age } j \text{ at FL class } i}{(r_{i,0} + r_{i,1} + \dots + r_{i,k} = 1)}.$$

From $n_{i,j}$ we calculated the mean and variance of FL at age j :

$$I_j = \frac{\sum_{i=1}^k n_{i,j} I_{i,j}}{\sum_{i=1}^k n_{i,j}} \quad (4)$$

and

$$\text{Var}(I_j) = \frac{\sum_{i=1}^k n_{i,j} (I_{i,j} - I_j)^2}{\left(\sum_{i=1}^k n_{i,j}\right) - 1} \quad (5)$$

where I_j = mean FL at age j ; and

$I_{i,j}$ = mean FL at FL class i at age j .

Sea surface temperature

Time-series data for sea surface temperature (SST, temperatures averaged over 10 days for 1° latitude \times 1° longitude blocks over the northwestern North Pacific between 0–53°N and 110–180°E since 1950) were provided by the Oceanographical Division of the Japan Meteorological Agency. The SST data for each block was averaged for periods of three months (i.e. January–March, April–June, July–September, and October–December). The relationship between the SST of each block and FL at age 0 were examined from 1970 to 1997.

Autocorrelation

For correlation analysis, effective sample sizes (n^*) were calculated for all time series data to take autocorrelation into account. n^* was computed by the formula (Pyper and Peterman, 1998):

$$\frac{1}{n^*} = \frac{1}{n} + \frac{2}{n} \sum_{j=1}^{n/5} r_{XX}(j) r_{YY}(j), \quad (6)$$

where $r_{XX}(j)$ and $r_{YY}(j)$ are the autocorrelations of X and Y at lag j , defined here with the additional weighting factor proposed by Pyper and Peterman (1998):

$$r_{XX}(j) = \frac{n}{n-j} \frac{\sum_{t=1}^{n-j} (X_t - \bar{X})(X_{t+j} - \bar{X})}{\sum_{t=1}^n (X_t - \bar{X})^2} \quad (7)$$

Growth model

We used the modified von Bertalanffy growth model to incorporate the effects of population density and sea sur-

² Age-length keys. In Kanto Kinkai no Masaba ni tuite, Appendix 1, vol. 30, 30 p. [In Japanese. Available from Kanagawa Prefectural Fisheries Research Institute, Jyogashima, Misaki, Miura, Kanagawa 238-0237, Japan.]

face temperature according to Millar and Myers,³ who investigated three formulations of the modified von Bertalanffy equations: 1) a reversible effect on the growth constant k ; 2) a reversible effect on the asymptotic length L_∞ ; and 3) an irreversible effect on L_∞ or k . We tested two of the models, 1 and 2, to investigate the effect of population density and SST. We did not test model 3 because we did not consider that the environmental effects on growth were permanent. Mean length at age i of year-class y was estimated with the following formulas:

Model 1: reversible environmental effect on k

$$\hat{L}_{i,y} = L_\infty(1 - e^{-k_0,y t_0}) \quad (8)$$

$$\hat{L}_{i,y} = \hat{L}_{i-1,y} + (L_\infty - \hat{L}_{i-1,y})(1 - e^{-k_{i,y}}) \quad (9)$$

$$k_{i,y} = k + \beta_1 T_{i+y} + \beta_2 D_{i,y}. \quad (10)$$

Model 2: reversible environmental effect on L_∞

$$\hat{L}_{0,y} = L_{\infty,0,y}(1 - e^{-k t_0}) \quad (11)$$

$$\hat{L}_{i,y} = \hat{L}_{i-1,y} + (L_{\infty,i,y} - \hat{L}_{i-1,y})(1 - e^{-k}) \quad (12)$$

$$L_{\infty,i,y} = L_\infty + \beta_1 T_{i+y} + \beta_2 D_{i,y}, \quad (13)$$

where t_0 = the age at length 0 (year);
 L_∞ = the asymptotic length; and
 k = the growth coefficient;
 $L_{\infty,i,y}$ = L_∞ at age i of year-class y ;
 $k_{i,y}$ = k at age i of year-class y ;
 T_{i+y} = the sea surface temperature in year $i+y$; and
 $D_{i,y}$ = a population density presented by the number of stock at age i of year-class y .

These variables were z-score standardized. The model parameters α_1 and β_2 were estimated to represent the effects of T_{i+y} and $D_{i,y}$ on k or L_∞ .

The parameters were estimated by maximizing the likelihood function which is represented by

$$L(i, y) = \hat{L}_{i,y} + \varepsilon_i \quad (14)$$

$$\varepsilon_i \sim N(0, \sigma_i^2), \quad (15)$$

and

$$L(L_\infty, k, t_0, \beta_1, \beta_2, \sigma_i^2) = \prod_y \prod_i \left[2\pi\sigma_i^2 \right]^{-\frac{1}{2}} \exp \left[-\frac{\{L(i,y) - \hat{L}_{i,y}\}^2}{2\sigma_i^2} \right]. \quad (16)$$

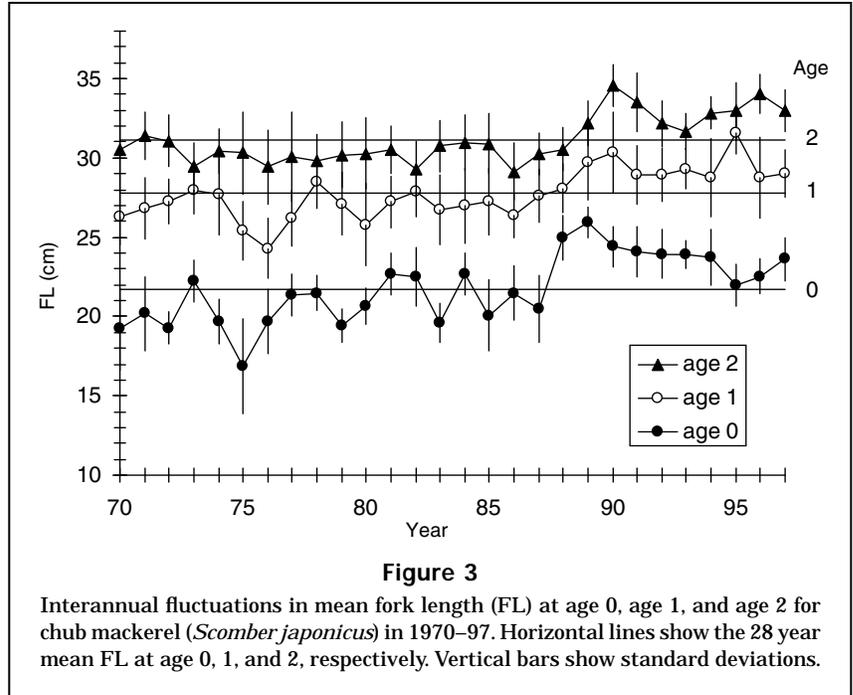


Figure 3
 Interannual fluctuations in mean fork length (FL) at age 0, age 1, and age 2 for chub mackerel (*Scomber japonicus*) in 1970–97. Horizontal lines show the 28 year mean FL at age 0, 1, and 2, respectively. Vertical bars show standard deviations.

We ran the models with all possible combinations of explanatory variables (T , D , T , and D), and compared AIC with that obtained with the base parameters (L_∞ , t_0 , k).

Results

Fork length at age

Mean FL at age 0 varied substantially over the time series examined. For example, it ranged from 16.9 (Sd ± 3.0) cm in 1975 to 25.9 (Sd ± 1.0) cm in 1989. The mean FL for the 28 years period was 21.7 (± 2.1) cm (coefficient of variation: CV=9.8%, Table 1, Fig. 3). The FL-at-age-0 values were smaller than the 28-year mean FL for the 1970s, varied around the mean in the early and mid 1980s, reached a maximum in 1989, and were at about 22–24 cm in the 1990s (Fig. 3).

Mean FL at age 1 was similarly variable; it ranged from 24.3 (± 1.9) cm in 1976 to 31.6 (± 1.4) cm in 1995. The 28-year mean FL was 27.7 (± 1.6) cm (CV=5.6%, Table 1). The trend in interannual variability was similar to that in age 0, i.e. it was smaller in the 1970s and larger in the 1990s (Fig. 3). In age-2 fish the 28-year minimum FL of 29.1 (± 1.8) cm was observed in 1986 and the maximum of 34.5 (± 1.3) cm was observed in 1990 (the 28-year mean FL=31.1 (± 1.5) cm, CV=4.7%, Table 1, Fig. 3).

In fish age 3 and older, mean FL varied year-to-year in a manner similar to that found in the younger ages (Table 1). Annual mean FLs for 3-, 4-, and 5-year-olds were 33.7 (± 1.3) cm (3.8%), 36.2 (CI ± 1.4) cm (CV=4.0%), and 38.5 (CI ± 1.5) cm (CV=3.8%), respectively (Table 1). The mean FLs for ages 0–5 of each year were significantly different among different years (one-way ANOVA, $P < 0.01$).

³ Millar, R. B., and R. A. Myers. 1990. Modeling environmentally induced change in growth for Atlantic Canada cod stock. ICES CM 1990/G:24.

Table 1

Total biomass, year class strength (stock number at age 0; Yatsu, et al.¹), SST, and mean fork length (FL) of *Scomber japonicus* from 1970 to 1997. Blanks show the lack of data.

Year	Total Biomass (10 ³ t)	Stock number at age 0 (10 ⁶ individuals)	SST (°C) ¹	Mean FL (SD) cm					
				0	1	2	3	4	5
1970	2833	10,199	11.5	19.2 (2.6)	26.3 (1.8)	30.5 (2.4)	34.2 (1.7)	37.7 (1.6)	40.5 (1.4)
1971	3781	14,138	10.9	20.2 (2.3)	26.8 (1.9)	31.4 (1.5)	34.3 (1.6)	37.7 (1.6)	40.4 (1.3)
1972	4860	8342	13.2	19.3 (1.0)	27.2 (1.4)	31.1 (1.6)	34.3 (1.5)	37.3 (1.7)	40.0 (1.5)
1973	4650	7154	11.1	22.2 (1.4)	27.9 (1.5)	29.4 (1.6)	31.2 (1.8)	33.1 (2.0)	36.1 (1.9)
1974	4048	7854	10.5	19.7 (1.4)	27.7 (2.5)	30.4 (1.4)	31.9 (1.7)	33.9 (1.8)	37.6 (1.7)
1975	3558	10,353	12.3	16.9 (3.0)	25.4 (1.8)	30.3 (2.6)	32.7 (1.6)	33.8 (1.6)	35.5 (1.7)
1976	3896	14,402	11.5	19.7 (2.0)	24.3 (1.9)	29.4 (2.4)	33.7 (1.9)	35.3 (1.8)	38.1 (1.8)
1977	5868	11,701	10.9	21.4 (1.3)	26.2 (1.8)	30.1 (2.8)	33.5 (2.2)	35.7 (1.7)	37.4 (1.4)
1978	5285	6249	10.0	21.5 (1.1)	28.5 (1.7)	29.8 (1.6)	32.1 (2.3)	34.5 (2.1)	36.1 (1.9)
1979	3250	2931	12.3	19.5 (1.1)	27.1 (2.0)	30.2 (2.0)	33.0 (1.7)	35.2 (1.6)	37.2 (1.3)
1980	1898	2952	11.3	20.7 (1.1)	25.8 (2.6)	30.3 (2.2)	32.4 (1.8)	33.9 (1.8)	35.6 (1.6)
1981	1683	3374	9.4	22.7 (1.3)	27.2 (1.7)	30.5 (1.5)	33.1 (2.1)	36.5 (1.8)	38.0 (1.5)
1982	1567	2883	10.8	22.5 (1.8)	27.9 (1.6)	29.3 (1.8)	33.6 (2.2)	36.6 (1.6)	38.3 (1.4)
1983	1516	3175	11.5	19.6 (1.2)	26.7 (2.2)	30.8 (1.6)	33.6 (1.5)	35.5 (2.0)	37.8 (1.2)
1984	1759	3605	9.3	22.7 (1.3)	27.0 (2.4)	31.0 (1.8)	34.8 (1.9)	36.6 (1.8)	38.2 (2.0)
1985	1565	4998	11.4	20.1 (2.2)	27.3 (2.1)	30.9 (1.9)	33.3 (1.9)	37.4 (1.7)	39.0 (1.8)
1986	1373	1833	9.7	21.5 (1.7)	26.4 (1.4)	29.1 (1.8)	32.5 (2.4)	35.9 (2.1)	38.9 (1.9)
1987	812	583	10.9	20.5 (2.1)	27.6 (1.7)	30.2 (1.3)	32.8 (1.6)	36.4 (2.3)	39.2 (0.8)
1988	555	236	11.4	24.9 (1.4)	28.1 (1.5)	30.5 (1.4)	32.8 (1.7)	36.8 (1.6)	40.1 (1.2)
1989	289	219	9.8	25.9 (1.0)	29.7 (2.3)	32.2 (1.4)	34.6 (1.5)	35.7 (1.5)	39.2 (1.5)
1990	185	356	11.7	24.4 (1.3)	30.3 (2.6)	34.5 (1.3)	35.8 (1.5)	38.2 (1.1)	39.7 (0.8)
1991	338	1017	12.2	24.1 (1.6)	28.9 (1.8)	33.5 (1.9)	35.5 (1.2)	36.7 (1.9)	39.0 (1.8)
1992	724	2839	9.7	24.0 (1.6)	29.0 (1.7)	32.1 (1.4)	34.1 (1.5)	37.5 (1.6)	40.5 (1.6)
1993	685	589	10.7	23.9 (0.9)	29.3 (1.3)	31.7 (1.1)	33.2 (0.5)		
1994	343	547	11.3	23.7 (1.7)	28.8 (2.5)	32.8 (1.0)	34.6 (0.8)	35.9 (0.7)	39.1 (1.0)
1995	351	1183	11.3	22.0 (1.3)	31.6 (1.4)	32.9 (1.8)	35.5 (1.8)	38.0 (1.3)	39.2 (0.8)
1996	726	4452	9.9	22.5 (1.1)	28.7 (2.5)	34.1 (1.2)	36.1 (1.1)	37.8 (0.9)	39.7 (0.7)
1997	682	529	9.9	23.6 (1.4)	29.0 (1.5)	33.0 (1.3)	35.4 (1.7)	37.6 (0.7)	38.6 (0.5)
28-year mean of FLs at ages				21.7 (2.1)	27.7 (1.6)	31.1 (1.5)	33.7 (1.3)	36.2 (1.4)	38.5 (1.5)

¹ SST during April–June in the waters bounded by 38–40°N and 141–143°E.

Mean growth increments I of each year class from age 0 (6 months old) to ages 1–5 (I_{0-p}) showed significantly negative correlations (Table 2). Correlations between the two variables tended to increase with age: -0.69 for I_{0-1} , -0.71 for I_{0-2} , -0.80 for I_{0-3} , and -0.77 for I_{0-4} .

The relative FL at age 0 for any given year class was maintained throughout the life span. A correlation between the mean FL at age 0 and age 1 within each year class (1970 to 1996 year class) was positive and statistically significant ($P < 0.05$, Fig. 4). Similarly, the positive correlations between the mean FL at age 0 and age 3 (1970 to 1994 year class, $P < 0.01$, Fig. 4), and age 0 and age 4 (1970 to 1993 year class, $P < 0.05$, Fig. 4) were significant ($P < 0.05$, Fig. 4).

Correlation between FL and population density

Population densities represented by stock in number at age 0 and total biomass were negatively correlated to FL at age. Negative correlations between the logarithm of abundance of age 0 ($\ln N_0$) and FL at ages were relatively high in age 0 to 3 (-0.69 to -0.83 , Table 3) and low in age 4 and 5 (-0.63 and -0.64 , Table 3). Correlations were statistically significant for ages 0, 2, and 3 (Table 3). Negative correlations between the logarithm of total biomass and FL at ages were relatively high at ages 0 to 2 (-0.73 to -0.75) and moderate for age 3 to 5 (-0.50 to -0.52 , Table 4). However, the relationships were not statistically significant for all ages (Table 4).

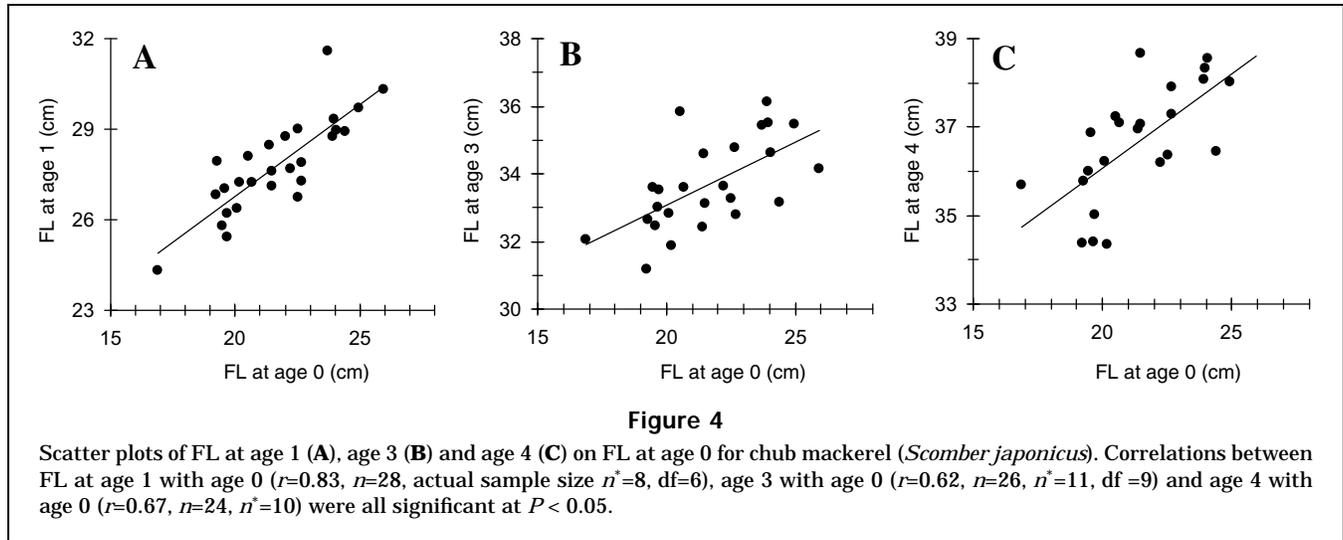


Table 2

Correlation of FL at age 0 and growth increment after age 0. n = actual sample size. n^* and degree of freedom (df) show the effective n and df when the data were corrected for autocorrelation (Pyper and Peterman, 1998). Significance level: **, $P < 0.01$.

Growth increment	r	r^2	n	n^*	df
Ages 0–1	-0.69**	0.48	27	21	19
Ages 0–2	-0.71**	0.51	26	25	23
Ages 0–3	-0.80**	0.64	25	23	21
Ages 0–4	-0.77**	0.59	23	24	22
Ages 0–5	-0.78**	0.61	22	22	20

Table 3

Correlation between the natural logarithm of the abundance of age 0 and mean FL for each age. n = actual sample number. n^* and degree of freedom (df) show the significant n and df when autocorrelation was considered (Pyper and Peterman, 1998). Significance levels: *, $P < 0.05$.

Age	r	r^2	n	n^*	df
0	-0.75*	0.57	28	8	6
1	-0.69	0.48	27	7	5
2	-0.83*	0.69	26	6	4
3	-0.71*	0.51	25	9	7
4	-0.63	0.40	23	8	6
5	-0.64	0.40	22	6	4

Correlation between FL and SST

Growth in the first six months of life was correlated with SST. We detected significant negative correlation between FL-at-age 0 and SST between April and June in the waters bounded by 38–40°N and 141–143°E ($r=-0.45$, $r^2=0.20$, $n=28$, $n^*=27$, $df=25$, $P < 0.05$, Fig. 5). The SST between July and September of this area was also negatively correlated with FL at age 0 although the correlation coefficient was not significant at 5% level.

Growth analysis

Model 1 that incorporated SST (T) and population density (D) gave a minimum Akaike's information criterion (AIC) of 457.68 (Table 5) and the model was expressed by

$$\hat{L}_{i,y} = 43.98 \left\{ 1 - \exp(-2.585) \exp\left(-\sum_{j=0}^5 k_{i,y}\right) \right\} \quad (17)$$

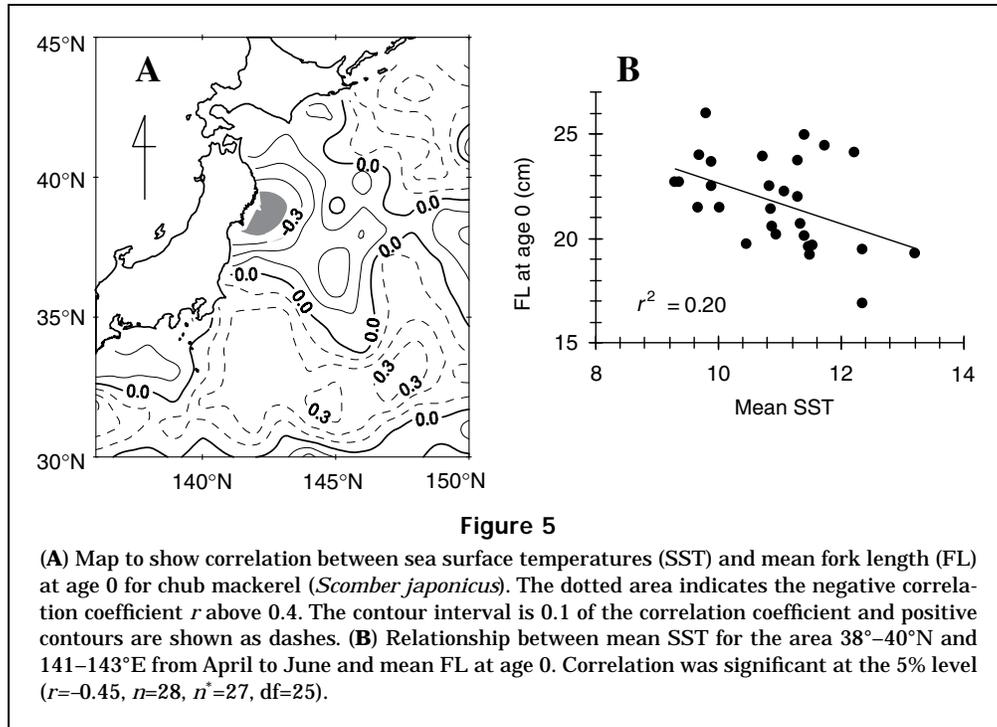
$$k_{i,y} = 0.271 - 0.008T_{i,y} - 0.21D_{i,y} \quad (18)$$

Table 4

Correlation between natural logarithm of total biomass and mean FL for each age. n = actual sample size. n^* and degree of freedom (df) show the effective n and df when the data were corrected for autocorrelation (Pyper and Peterman, 1998). No correlations were significant ($P > 0.05$).

Age	r	r^2	n	n^*	df
0	-0.74	0.38	27	6	4
1	-0.73	0.32	27	6	4
2	-0.75	0.36	27	5	3
3	-0.52	0.26	27	11	9
4	-0.51	0.26	26	9	7
5	-0.50	0.22	26	7	5

This model estimated the FL at ages 0–5 well (Fig. 6). The AIC of model 1 incorporating T and D was smaller than the AIC of model 2; therefore the environmental factors had an affect on k rather than L_{∞} .



To investigate the effect of T and D , we calculated the total effect on k for year-class y according to Sinclair et al. (2002):

$$\frac{\sum_{i=0}^5 \beta_1 T_{i,y}}{6} \text{ for } T, \text{ and } \frac{\sum_{i=0}^5 \beta_2 D_{i,y}}{6} \text{ for } D.$$

Discussion

Estimated population abundance of age-0 fish and total biomass may explain density-dependent growth. FL at age 0, 2, and 3 of the Pacific stock of chub mackerel were negatively correlated with the number of age-0 recruits. Correlations between biomass and FL at ages 0–5 were low and not significant. Therefore, year-class strength is indicated to have a greater negative influence on the growth of the Pacific stock of chub mackerel than total biomass, as reported for the Atlantic mackerel (*Scomber scombrus*) (Agnalt, 1989; Overholtz, 1989; Neja, 1995) and Atlantic herring (*Clupea harengus*) (Toresen, 1990).

Density-dependent growth in fish populations seems to be a common phenomenon for pelagic fishes found in the temperate waters of Japan. The FL at age 0 of the 1963–69 year classes ranged from 16 to 20 cm, and were smaller than those of the 1970s, possibly indicating density-dependent growth (Iizuka, 1974). According to Honma et al. (1987), the stock abundance of the Pacific stock of chub mackerel from 1963 to 1969 was larger than it was in the 1970s. Wada et al. (1995) and Hiyama et al. (1995) found negative relationships between total biomass and body length in the Pa-

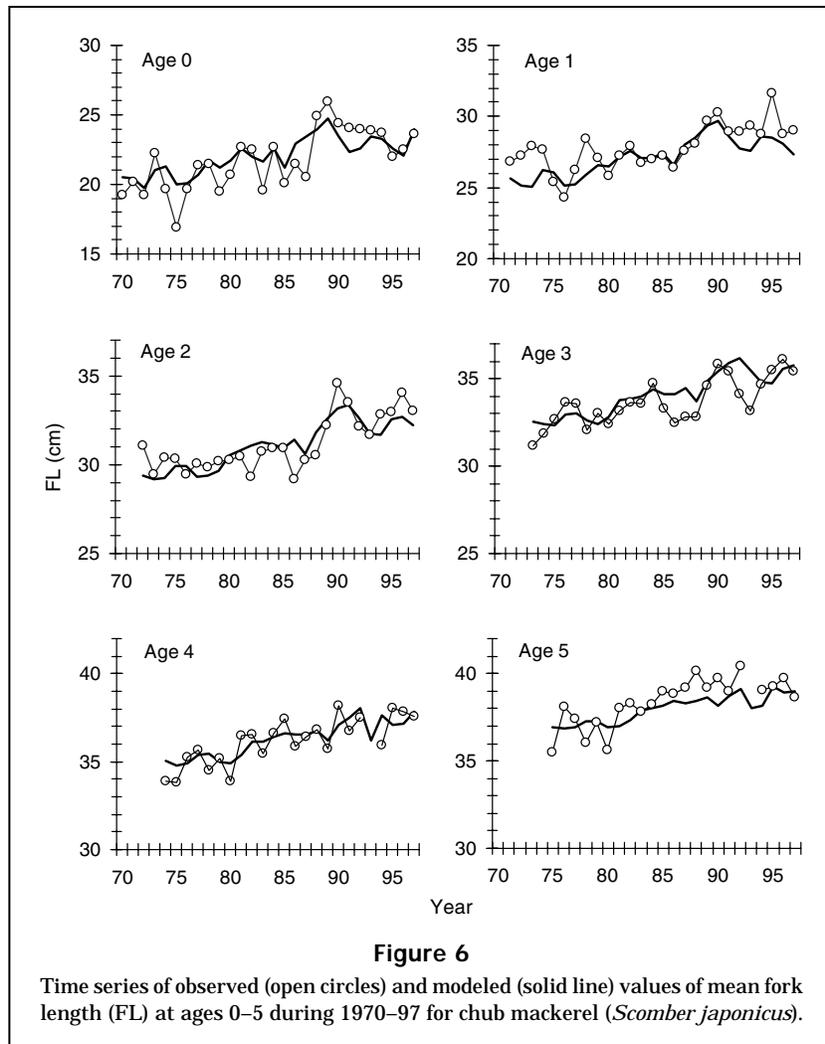
Table 5

Summary of statistics from the estimation of growth for chub mackerel (*Scomber japonicus*). AIC = Akaike's information criterion.

Model	Variables	No. of unknown parameters	Log likelihood	AIC
1	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5$	9	-280.20	578.40
	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5, \beta_1$	10	-270.10	560.20
	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5, \beta_2$	10	-222.38	464.77
	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5, \beta_1, \beta_2$	11	-217.84	457.68
2	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5$	9	-280.20	578.40
	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5, \beta_1$	10	-268.63	557.25
	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5, \beta_2$	10	-224.01	468.02
	$L_{\infty}, k, t_0, \sigma_1 \dots \sigma_5, \beta_1, \beta_2$	11	-220.81	463.62

cific and Tsushima Current stock of the Japanese sardine (*Sardinops melanostictus*). Kishida (1990) demonstrated a density-dependent relationship between the growth and total stock density (CPUE) of Japanese Spanish mackerel (*Scomberomorus niphonius*).

Our results do not agree with the positive effect of sea water temperature on somatic growth that has been shown for several species, including Japanese common squid (Kidokoro, 2001), Atlantic herring (Moore and Winters, 1981; Toresen, 1990), and Atlantic cod (*Gadus morhua*) (Brander, 1995; Dutil et al., 1999; Rätz et al. 1999; Otterson et al., 2002).



There was a positive correlation between FL at age 0 and $1^{\circ} \times 1^{\circ}$ block SST in the waters of $32\text{--}34^{\circ}\text{N}$ and $144\text{--}149^{\circ}\text{E}$, located south of the Kuroshio Extension flowing eastward at the latitude of $35\text{--}37^{\circ}\text{N}$ from April to June (Figs. 1 and 5A). But the correlation coefficient was not significant, and this area was not considered to be inhabited by juvenile mackerel (Watanabe, 1970). Thus, we considered that the SST in the waters of $32\text{--}34^{\circ}\text{N}$ and $144\text{--}149^{\circ}\text{E}$ was not a significant factor on the variation of FL at age 0.

The low SST in the waters bounded by $38\text{--}40^{\circ}\text{N}$ and $141\text{--}143^{\circ}\text{E}$ is indicative of a large inflow of Oyashio Current waters (Hirai and Yasuda, 1988), which is a cold water current and has high productivity (Odate, 1994), into the Kuroshio–Oyashio transition zone, where is one of the main feeding grounds of mackerels (Odate, 1961; Watanabe, 1970; Watanabe and Nishida, 2002; Fig. 1). Thus, we hypothesized that the large inflow of Oyashio current waters into the Kuroshio–Oyashio transition zone improved the feeding condition and accelerated the growth of juvenile mackerel. Jobling (1988) suggested a parabolic relationship between water temperature and fish growth. The range of SST in this area, which was negatively cor-

related with FL at age 0 of mackerel, was $9\text{--}13^{\circ}\text{C}$ (Table 1). This temperature range is near the lowest nonstressful temperatures for mackerel ($10\text{--}12^{\circ}\text{C}$, Schaefer, 1986). Thus, we do not consider that the negative relationship between growth and SST was the result of suppressed growth by the high ambient temperature.

In mackerel, maximum egg production appears to have shifted to later in spring during the 1990s, as compared to the late 1970s and 1980s, resulting in a shorter period of growth and thus smaller fish (Fig. 8, Mori et al.⁴; Kikuchi and Konishi⁵; Ishida and Kikuchi⁶; Zenitani et al.⁷; Kubota et al.⁸). In the early 1970s, the main spawning period was

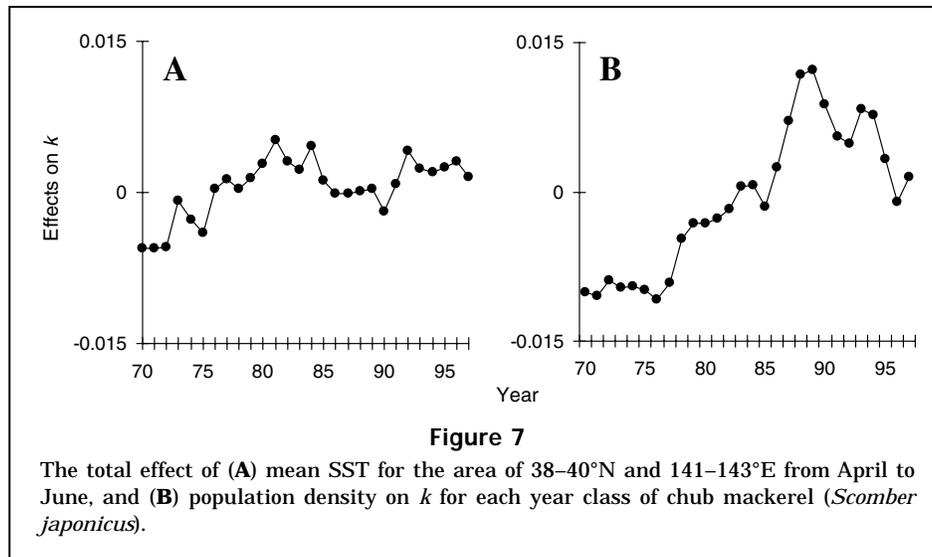
⁴ Mori, K., K. Kuroda, and Y. Konishi. 1988. Monthly egg production of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses. Datum Collect. Tokai Reg. Fish. Res. Lab. 12:1–321. [In Japanese. Available from National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa, Yokohama 236-8648, Japan.]

⁵ See next page.

⁶ See next page.

⁷ See next page.

⁸ See next page.



also in April (Kuroda⁹). Delayed spawning in the 1990s should have resulted in a reduction in the mean FL at ages during September–December in the 1990s compared to the 1970s and 1980s; however the present study showed the opposite result (Table 1). We hypothesize that the effect of the shift of spawning period on the FL at ages may have been overwhelmed by the effect of population density (Fig. 7).

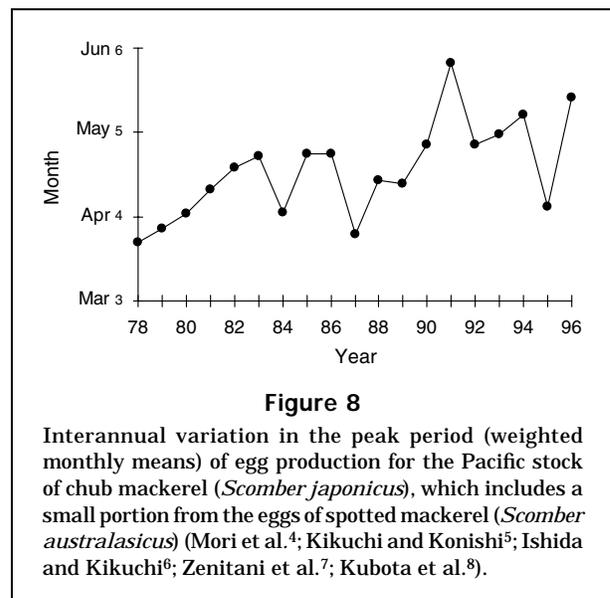
⁵ Kikuchi, H., and Y. Konishi. 1990. Monthly egg production of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1987 through December, 1988, 72 p. National Research Institute of Fisheries Science, Tokyo. [In Japanese. Available from National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa, Yokohama 236-8648, Japan.]

⁶ Ishida, M. and H. Kikuchi. 1992. Monthly egg production of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1989 through December, 1990, 86 p. National Research Institute of Fisheries Science, Tokyo. [In Japanese. Available from National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa, Yokohama 236-8648, Japan.]

⁷ Zenitani, H., M. Ishida, Y. Konishi, T. Goto, Y. Watanabe, and R. Kimura. 1995. Distributions of eggs and larvae of Japanese sardine, Japanese anchovy, mackerels, round herring, jack mackerel and Japanese common squid in the waters around Japan, 1991 through 1993. Resources Management Research Report Series A-2, 368 p. National Research Institute, Japan Fisheries Agency, Tokyo. [In Japanese. Available from National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa, Yokohama, 236-8648 Japan.]

⁸ Kubota, H., Y. Oozeki, M. Ishida, Y. Konishi, T. Goto, H. Zenitani, and R. Kimura. 1999. Distributions of eggs and larvae of Japanese sardine, Japanese anchovy, mackerels, round herring, jack mackerel and Japanese common squid in the waters around Japan, 1994 through 1996, 352 p. Resources Management Research Report Series A-2., National Research Institute, Japan Fisheries Agency, Tokyo. [In Japanese. Available from National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa, Yokohama 236-8648, Japan.]

⁹ Kuroda, K. 2002. Personal commun. 1-1-3-406, Kasumi, Narashino, Chiba 275-0022, Japan.



The estimated FL at age from our growth model, with the use of AIC, fitted well to the observed FL at age (Fig. 6). Mean growth increments I of each year class from age 0 (6 months old) to ages 1–5 (I_{0-5}) were significant and negatively correlated with FL at age 0 (Table 2), indicating that the growth rate of mackerel had changed from year to year for a given year class. This negative correlation indicated that the effects of population density and SST was temporal, and influenced k rather than L_{∞} . The negative correlation between FL at age 0 and growth increments also suggested that the FL at age of mackerel approximated the asymptotic length. Thus, mackerel growth was best fitted to the modified von Bertalanffy growth model with the temporal environmental effect on k (Table 5).

The effect of population density on growth of mackerel was higher than the effect of SST (Fig. 7, Table 6). Our result agreed with the results for Japanese sardine (Wada et al., 1995) and Atlantic cod (Sinclair et al., 2002). Particularly, the effect of population density was significant in the late 1980s, which resulted in a remarkable increase in FL at age 0 (Figs. 3 and 7).

The relative size at age 0 was carried over to older ages (Fig. 4), indicating that the cohorts that were small at age 0 could not compensate for this early small size. Iizuka (1974) reported that the trend of growth established at age 0 for chub mackerel was maintained until age 2 for the 1963–73 year classes. Toresen (1990) demonstrated from length data that a trend in rate of growth for a given year class of Norwegian herring was determined at the immature stage and was consistent after maturation. Total length of Hokkaido-Sakhalin herrings (*Clupea pallasii*) at age 5 and older was positively correlated with the length at age 4 (Watanabe et al., 2002). Because fish first mature at age 4, this implied that the trend in total length of each year class was determined by the age at maturity. From these results we hypothesize that the variability in size at age in the Pacific stock of chub mackerel is largely attributable to growth before maturity, especially during the first 6 months after hatching.

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Literature cited

- Agnalt, A. -L.
1989. Long-term changes in growth and age at maturity of mackerel, *Scomber scombrus* L., from the North Sea. *J. Fish Biol.* 35 (suppl. A):305–311.
- Brander, K. M.
1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES J. Mar. Sci.* 52:1–10.
- Dutil, J. -D., M. Castonguay, D. Gilbert, and D. Gascon.
1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 56: 1818–1831.
- Haddon, M.
2001. Modelling and quantitative methods in fisheries, 406 p. Chapman&Hall/CRC, New York, NY.
- Hirai, M.
1991. Fisheries oceanographic study on purse-seine fishing-grounds for chub mackerel in the Sanriku coastal waters. *Bull. Tohoku Natl. Fish. Res. Inst.* 53:59–147. [In Japanese.]
- Hirai, M., and I. Yasuda.
1988. Interannual variability of the temperature field at 100 m depth near the east coast of Japan. *Bull. Otsuchi Ocean Res. Center, Univ. Tokyo.* 14:184–186.
- Hiyama, Y., H. Nishida, and T. Goto.
1995. Interannual fluctuations in recruitment and growth of the sardine, *Sardinops melanostictus*, in the Sea of Japan and adjacent waters. *Res. Popul. Ecol.* 37(2):177–183.
- Honma, M., Y. Sato, and S. Usami.
1987. Estimation of the population size of the Pacific mackerel by the cohort analysis. *Bull. Tokai Reg. Fish. Res. Lab.* 121:1–11. [In Japanese.]
- Iizuka, K.
1974. The ecology of young mackerel in the north-eastern sea of Japan IV. Estimation of the population size of the 0-age group and the tendencies of growth patterns on 0, I, and II age groups. *Bull. Tohoku Reg. Fish. Res. Lab.* 34: 1–16. [In Japanese.]
- Jobling, M.
1988. A review of the physiological and nutritional energetics of Cod, *Gadus morpha* L., with particular reference to growth under farmed conditions. *Aquaculture*, 70:1–19.
- Kawasaki, T.
1966. Structure of the Pacific population of the mackerel. *Bull. Tokai Reg. Fish. Res. Lab.* 47:1–34. [In Japanese.]
- Kidokoro, H.
2001. Fluctuations in body size and abundance of Japanese common squid (*Todarodes pacificus*) in the Sea of Japan. *GLOBEC report* 15:42.
- Kishida, T.
1990. Relationship between growth and population density of Japanese Spanish mackerel in the central and western waters of the Seto Inland Sea. *Bull. Nansei Natl. Fish. Res. Inst.* 23:35–41. [In Japanese.]
- Mace, P. M., and M. O. Sissenwine.
1993. How much spawning per recruit is enough? *Can. Spec. Publ. Fish. Aquat. Sci.* 120:101–118
- Moore, J. A., and G. H. Winters.
1981. Growth patterns in a Newfoundland Atlantic herring (*Clupea harengus harengus*) stock. *Can. J. Fish. Aquat. Sci.* 39:454–461.
- Moyle, P. B., and J. J. Cech Jr.
2002. *Fishes: An introduction to ichthyology*, 4th ed., 612 p. Prentice Hall, Englewood Cliffs, NJ.
- Murayama, T., I. Mitani, and I. Aoki.
1995. Estimation of the spawning period of the Pacific mackerel *Scomber japonicus* based on the changes in gonad index and the ovarian histology. *Bull. Jpn. Soc. Fish. Oceanogr.* 59:11–17. [In Japanese.]
- Neja, Z.
1995. The stock size and changes in the growth rate of the northwest Atlantic mackerel (*Scomber scombrus* L.) in 1971–1983. *Acta Ichthyologica et Piscatoria* 25:113–121.
- Odate, K.
1994. Zooplankton biomass and its long-term variation in the western north Pacific ocean, Tohoku sea area, Japan. *Bull. Tohoku Natl. Fish. Res. Inst.* 56, 115–173. [In Japanese.]
- Odate, S.
1961. Study on the larvae of the fishes in the north-eastern sea area along the Pacific coast of Japan. Part 1. Mackerel, *Pneumatophorus japonicus* (Houttuyn). *Bull. Tohoku Reg. Fish. Res. Lab.* 19:98–108. [In Japanese.]
- Otterson, G., K. Helle, and B. Bogstad.
2002. Do abiotic mechanisms determine interannual vari-

- ability in length-at-age of juvenile Arcto-Norwegian cod? *Can. J. Fish. Aquat. Sci.* 59:57–65.
- Overholtz, W. J.
1989. Density-dependent growth in the northwest Atlantic stock of Atlantic mackerel (*Scomber scombrus*). *J. Northw. Atl. Fish. Sci.* 9:115–121.
- Pauly, D.
1987. Application of information on age and growth of fish to fishery management. *In* Age and growth of fish (R. C. Summerfelt and G. E. Hall, eds.) p.495–506. Iowa State Univ Press, Ames, IA.
- Pyper, B. J., and R. M. Peterman.
1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* 55:2127–2140.
- Rätz, H. -J., M. Stein, and J. Lloret.
1999. Variation in growth and recruitment of Atlantic cod (*Gadus morhua*) off Greenland during the second half of the twentieth century. *J. Northw. Atl. Fish. Sci.* 25:161–170.
- Schaefer, K. M.
1986. Lethal temperature and the effect of temperature change on volitional swimming speeds of chub mackerel, *Scomber japonicus*. *Copeia* 1986:37–44.
- Sinclair, A. F., D. P. Swain, and J. M. Hanson.
2002. Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Can. J. Fish. Aquat. Sci.* 59:372:382.
- Toresen, R.
1990. Long-term changes in growth of Norwegian spring-spawning herring. *J. Cons. Int. Explor. Mer* 47:48–56.
- Usami, S.
1973. Ecological studies of life pattern of the Japanese mackerel, *Scomber japonicus* Houttuyn: on the adult of the Pacific subpopulation. *Bull. Tokai Reg. Fish. Res. Lab.* 76: 71–178. [In Japanese.]
- Wada, T., Y. Matsubara, Y. Matsumiya, and N. Koizumi.
1995. Influence of environment on stock fluctuations of Japanese sardine, *Sardinops melanostictus*. *Can. Spec. Publ. Fish. Aquat. Sci.* 121:387–394.
- Watanabe, C., and H. Nishida.
2002. Development of assessment techniques for pelagic fish stocks: applications of daily egg production method and pelagic trawl in the northwestern Pacific ocean. *Fisheries Science.* 68:97–100.
- Watanabe, C., T. Hanai, K. Meguro, R. Ogino, Y. Kubota, and R. Kimura.
1999. Spawning biomass estimates of chub mackerel *Scomber japonicus* of Pacific subpopulation off central Japan by a daily egg production method. *Nippon Suisan Gakkaishi* 65(4):695–702. [In Japanese.]
- Watanabe, T.
1970. Morphology and ecology of early stages of life in Japanese common mackerel, *Scomber japonicus* Houttuyn, with special reference to fluctuation of population. *Bull. Tokai Reg. Fish. Res. Lab.* 62:1–283. [In Japanese.]
- Watanabe, Y., Y. Hiyama, C. Watanabe, and S. Takayanagi.
2002. Inter-decadal fluctuations in length-at-age of Hokkaido-Sakhalin herring and Japanese sardine in the Sea of Japan. *PICES Scientific Report* 20:63–67.
- Yatsu, A., and H. Kidokoro.
2002. Coherent low frequency variability in biomass and in body size of Japanese common squid, *Tadorodes padificus*, during 1964–2002, 89 p. Abstracts of PICES 11th annual meeting.