

Larval and juvenile growth of chub mackerel *Scomber japonicus* in relation to recruitment in the western North Pacific

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Received: 3 June 2014 / Accepted: 11 March 2015 / Published online: 11 April 2015
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Abstract To detect indices of recruitment intensity of the Pacific stock of chub mackerel *Scomber japonicus*, the relationship between the growth rate during early life and recruitment variability and the effects of temperature on annual change of the growth rate were examined. Growth-trajectories in larval and juvenile stages were back-calculated by otolith microstructure analysis using juveniles collected in the Kuroshio–Oyashio transition region of the western North Pacific in May and June from 2002 to 2011. A total of 532 otoliths were analysed. Hatch dates were distributed from mid-March to mid-May and most chub mackerel hatched in April. Mean daily growth rates \pm standard deviation (SD) of the April cohort in larval and juvenile stages ranged between 1.03 ± 0.10 (2006) and 1.52 ± 0.23 mm day⁻¹ (2009). The mean daily growth rate and larval stage duration were significantly related to recruitment which had been estimated by virtual population analysis. The results indicated the growth rate of the April cohort was an important index of year-class strength. There was a significant correlation between sea surface temperature experienced by each fish and the mean daily growth rate during the larval period. Higher water temperature led to faster growth and shorter larval stage duration of the April cohort of the Pacific stock of chub mackerel.

Keywords Chub mackerel · Growth · Larval stage duration · Otolith · Recruitment · Temperature

Introduction

Early life survival is a determinant of recruitment dynamics of marine fish [1]. Field studies have suggested that variability in growth rate during early life is a cause of fluctuation in year-class abundance, and growth rate is a predictor of recruitment strength [1, 2]. In particular, scombrid fishes such as Japanese Spanish mackerel *Scomberomorus niphonius* and Atlantic mackerel *Scomber scombrus* are generally considered to have a survival strategy of rapid growth rates during the larval period and that faster growth is critical for survival and recruitment success [3, 4]. However, although chub mackerel *S. japonicus* is one of the most important fisheries resources in the western North Pacific, there are few studies about the relationship among early growth, survival and recruitment success based on field studies.

The Pacific stock of chub mackerel has been managed by the total allowable catch (TAC) system since 1997. The total catch of the Pacific stock showed a higher trend in the 1970s and peaked at 1474×10^3 metric tons in 1978 and then declined to 23×10^3 t in 1991 (Fig. 1) [5]. The total biomass and recruitment (the stock in number of individuals at age 0) have been estimated using virtual population analysis (VPA) [5]. The total biomass of the Pacific stock was highest in 1978 (4742×10^3 t), and then dramatically decreased and was lowest in 2001 (151×10^3 t; Fig. 1). Recruitment showed a trend similar to that of total biomass; it fluctuated between 175 (1998) and 14,206 million age-0 fish (1971; Fig. 1). The total biomass has shown a tendency to increase in recent years; however, catch and recruitment remain at low levels. Spawning mainly occurs from April

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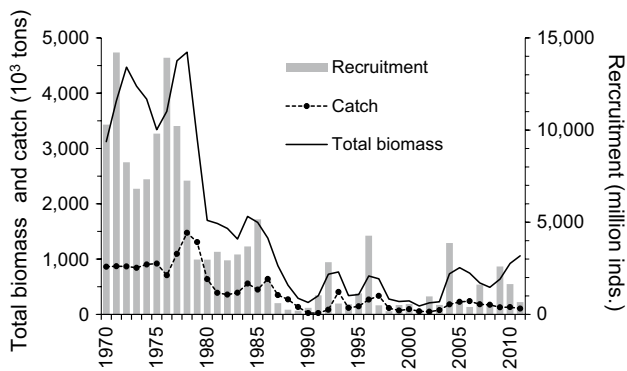


Fig. 1 Total biomass, total catch and recruitment (the stock in number of individuals at age 0) of the Pacific stock of chub mackerel *Scomber japonicus* (Kawabata et al. [5]). Solid line, dotted line and bars indicated the total biomass, total catch and recruitment, respectively

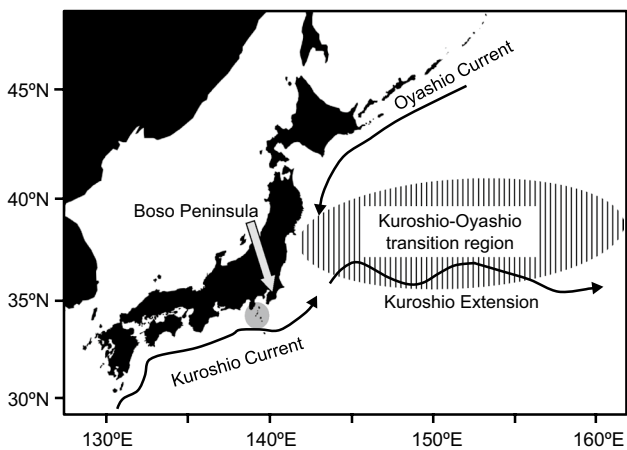


Fig. 2 Map showing oceanographic features of the western North Pacific. The shaded area shows the main spawning grounds around the Izu Islands. The vertical lines area indicates the sampling area of chub mackerel *Scomber japonicus*

to June [6] in the coastal waters around the Izu Islands of central Japan (Fig. 2) [7–11]. Eggs and larvae are transported by the Kuroshio Current and Kuroshio Extension [6, 8]. The larvae and juveniles are widely distributed in the Kuroshio–Oyashio transition region (Fig. 2), and then fish about six months old recruit to the fishery [7, 12]. Although there were recruitment successes in the 1990s, the Pacific stock of chub mackerel has not recovered because they were heavily fished before the age of maturity [13]. Population dynamics of chub mackerel in larval and juvenile stages is thought to be critical for recruitment variability, and conservation of age-0 fishes is indispensable for stock management [6, 14]. However, there is limited ecological information on the growth of wild chub mackerel in larval and juvenile stages [7, 15] compared to the maturity and spawning of adult fish in the North Pacific [10–12, 14, 16].

The aims of this study were to detect indices of recruitment intensity of the Pacific stock of chub mackerel and accumulate ecological information of chub mackerel during its early life stages. The relationship between the mean daily growth rates in early life stages and recruitment data was analyzed among ten year-classes of chub mackerel. We estimated mean daily growth rates during larval and juvenile stages and larval stage duration by otolith microstructure analysis. The effect of water temperature on the growth rate during the larval stage was analyzed.

Materials and methods

Fish Sampling

Juveniles of chub mackerel were collected in the Kuroshio–Oyashio transition region of the western North Pacific from 2002 to 2011 (Fig. 2; Table 1). Fish collections were conducted at 40–57 stations between May and June for each

Table 1 Sampling period, number of hauls, location, number of individuals and mean catch per unit effort (CPUE, number of individuals collected per 30 min) of juvenile chub mackerel *Scomber japonicus* in the western North Pacific

Year	Sampling period	Number of hauls	Location		Number of individuals collected	Mean CPUE
			Latitude	Longitude		
2002	10–28 May	46	35°59–39°09E	143°28–159°04N	197	4
2003	11–28 May	47	34°55–38°28E	143°05–159°50N	1659	35
2004	12–30 May	50	35°04–39°55E	142°57–164°00N	5337	107
2005	13–29 May	47	35°00–39°22E	143°58–162°00N	98,893	1978
2006	11–28 May	42	34°58–39°17E	143°58–163°01N	411	10
2007	12–28 May	43	35°01–39°08E	143°04–162°02N	15,871	369
2008	10–27 May	40	35°04–39°00E	142°59–159°56N	4407	110
2009	7–27 May	49	35°08–39°18E	142°59–160°04N	924	19
2010	26 May–20 June	57	35°47–39°41E	143°16–160°29N	16,590	291
2011	25 May–16 June	40	36°19–39°49E	143°32–159°31N	310	8

year (Table 1). A surface and mid water trawl net (10 mm codend mesh) was towed once at each station (30–60 min duration at 3.5–4.0 knots in 0–20 m depth). Collected samples were frozen on board. The fish were then identified, and juveniles of chub mackerel were measured to the nearest 0.1 mm in fork length (FL) and randomly selected juveniles were used for otolith analysis in the laboratory. A recent study of larval morphology of chub mackerel and spotted mackerel *S. australasicus* found that identification of the larvae of these two species (<9 mm in body length) requires genetic analysis [17]. However, collected chub mackerel were >16 mm FL juveniles in the present study, therefore all fish were identified based on morphological characters according to Nakabo [18].

Otolith analysis

Sagittal otoliths were used for growth analysis of chub mackerel. Daily periodicity of otolith increment formation of chub mackerel was validated using reared fish [19]. Otolith preparation was conducted using the same method as Takahashi et al. [19]. Sagittae of 22–129 specimens for each year were extracted and dried (Fig. 3). The microstructural increments were observed along the longest axes in the sagittal plane, which was previously identified as the optimal plane of the sagittal otolith until 90 days of age [19]. The otoliths were embedded in clear fingernail enamel on a glass slide with the distal side up. Each otolith was polished with waterproof sandpaper (#600–2000)

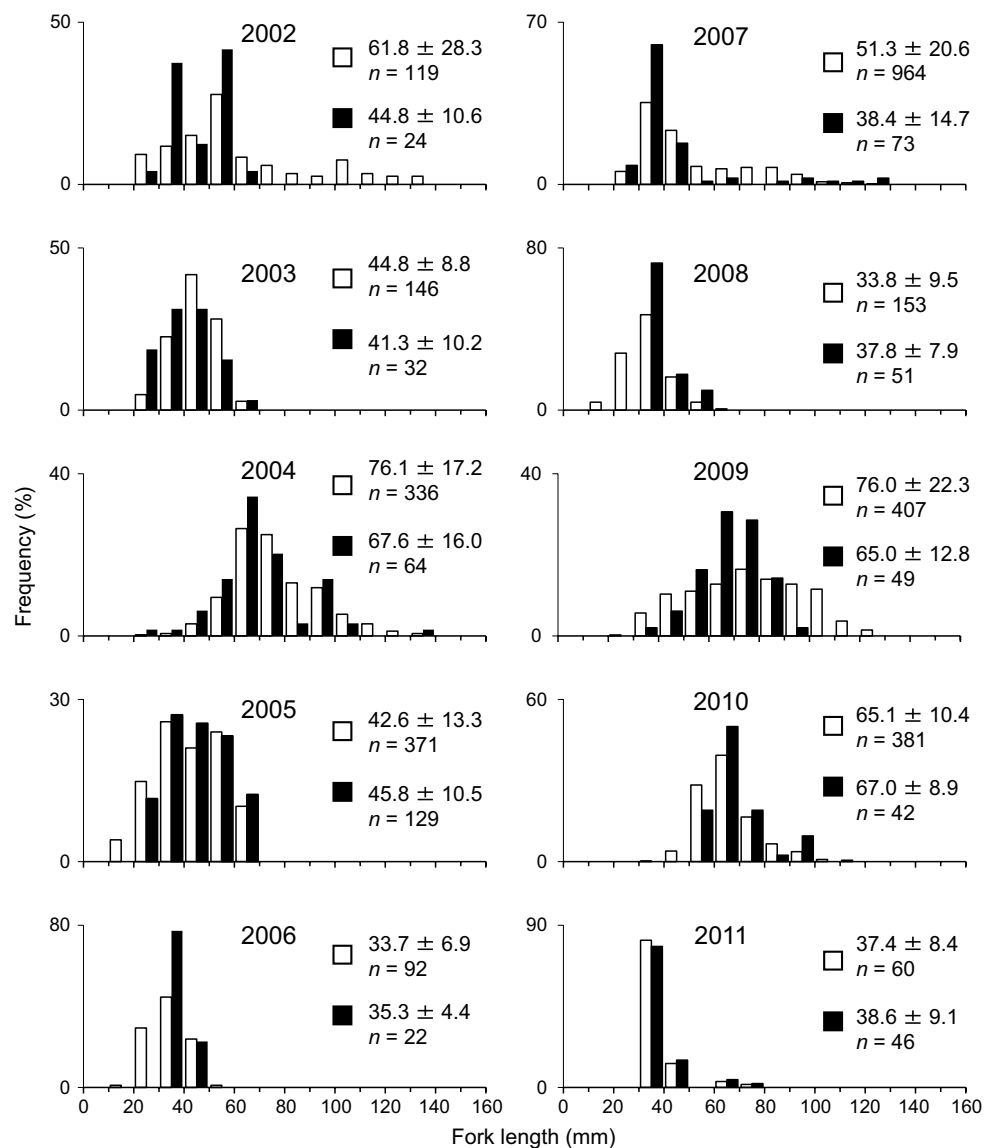


Fig. 3 Fork length (FL) distributions of juvenile chub mackerel *Scomber japonicus* collected in the Kuroshio–Oyashio transition region from 2002 to 2011. *Open bars* indicate collected juveniles

from 10 May to 8 June and *closed bars* indicate samples used for growth analysis. The mean FL ± standard deviation and sample size are indicated for each year

and an alumina polishing suspension (Baikalex 3.0CR, Baikowski Japan Co. Ltd., Chiba, Japan) until the nucleus was clearly visible. A measurement transect was set from the nucleus to the outermost margin (postrostrum direction). The number and width of otolith increments were measured using an otolith measurement system (Ratoc System Engineering, Tokyo, Japan), comprising a transmitting light or reflected UV light microscope (Olympus BX51) at 200–400 magnification.

Growth and temperature analyses

Juveniles collected during a 30-day window (from 10 May to 8 June) in each year were used for the growth analysis to minimize interannual variation in sampling dates. The age of juvenile chub mackerel was estimated by adding two to the increment counts, as the first increment appeared to start forming at three days age [19]. FL and daily growth rate at each age of juvenile chub mackerel were back-calculated by the biological intercept method [20]. Plots of FL against otolith radius could be expressed by an allometric formula (see “Results”) [21]. Allometric parameters a and b were calculated for each fish by solving the equations:

$$FL_3 = a OR_3^b \quad \text{and} \quad FL_{\text{catch}} = a OR_{\text{catch}}^b$$

where FL_3 and FL_{catch} are the mean FL at three days and at catch, respectively, and OR_3 and OR_{catch} are the otolith radii at the first increment deposition and at catch on the analyzed transect, respectively. Hunter and Kimbrell [22] reported that the mean standard length (SL) of chub mackerel at three days age was 3.5 mm. The mean FL was thought to be almost the same as the mean SL at three days age; therefore, FL_3 as 3.5 mm was fixed. The mean back-calculated FLs at age were estimated from the three days age to catch age. The occurrence of accessory primordia was shown in the microstructure of the sagittal otolith, and the otolith grows rapidly from the accessory primordia, giving the otoliths a fan-like morphology in the secondary growth layers [19, 23]. In addition, a previous study reported that accessory primordia started to form on the sagittae of juvenile chub mackerel at about a 35 mm FL [24]. Therefore, the mean daily growth rate from the first increment deposition to the 35 mm FL within each year was estimated to raise the reliability of otolith microstructure analysis in this study. The relationship between mean daily growth rate in larval and juvenile stages and recruitment data was examined. Chub mackerel larvae metamorphose into juveniles at about a 12 mm FL [8, 24]. The larval stage duration and mean daily growth rate were estimated by calculating the number of days and daily growth rate from the date of hatch to a 12 mm FL. Watanabe [8] reported that larval chub mackerel distributions were dense in the waters off the Boso Peninsula in

April and May (34–36°N and 140–142°E) and recent larval surveys also confirmed that post-hatch larvae of *Scomber* spp. were mainly collected in these waters in April (35–36°N and 141–142°E; Takahashi et al., unpubl data, 2012). Therefore, we considered that environmental variations in the waters off Boso Peninsula affected larval growth of chub mackerel in the present study. In order to detect any temperature effect on larval growth, daily sea surface temperature (SST) in the waters off Boso Peninsula (35–36°N and 141–142°E) from April to May was estimated from NOAA optimum interpolation 1/4 degree daily sea surface temperatures (AMSER + AVHRR) [25]. The mean daily SST experienced by chub mackerel from the first increment deposition to a 12 mm FL within each year was calculated.

Statistical analyses

Welch’s analysis of variance (ANOVA) with a Games-Howell post hoc test was used to test interannual differences in growth rate of chub mackerel in larval and juvenile stages. Recruitment per spawning stock biomass (RPS) data for chub mackerel in the western North Pacific were estimated by VPA from 2002 to 2011 by Kawabata et al. [5]. The relationships between mean daily growth rates and recruitment and RPS were expressed by linear and exponential regressions and the best model was selected by Akaike information criterion (AIC). Relationships between CPUE and the mean daily growth rate, the mean number of days from hatching to the 12 mm FL and recruitment and the mean daily SST experienced and the mean daily growth rate during larval stage were analyzed by Pearson’s correlation coefficient. Statistical analyses were conducted using the R 3.0.2 (The R Foundation for Statistical Computing).

Results

Relationship between otolith radius and FL

The FL of juveniles collected from 10 May to 8 June ranged between 16.9 (2008) and 137.6 mm (2002; Fig. 3). A total of 532 otoliths were analyzed from 2002 to 2011 (Fig. 4). The relationships between otolith radius (OR) and FL were expressed by allometric regressions (Table 2).

Fork length and hatch date distribution

The mean FL \pm SD of chub mackerel collected from 10 May to 8 June ranged between 33.7 ± 6.9 (2006) and 76.1 ± 17.2 mm (2004; Fig. 3). The mean FL \pm SD of chub mackerel used for otolith analysis ranged between 35.3 ± 4.4 (2006) and 67.6 ± 16.0 mm (2004; Fig. 3). The mean age of chub mackerel was estimated between

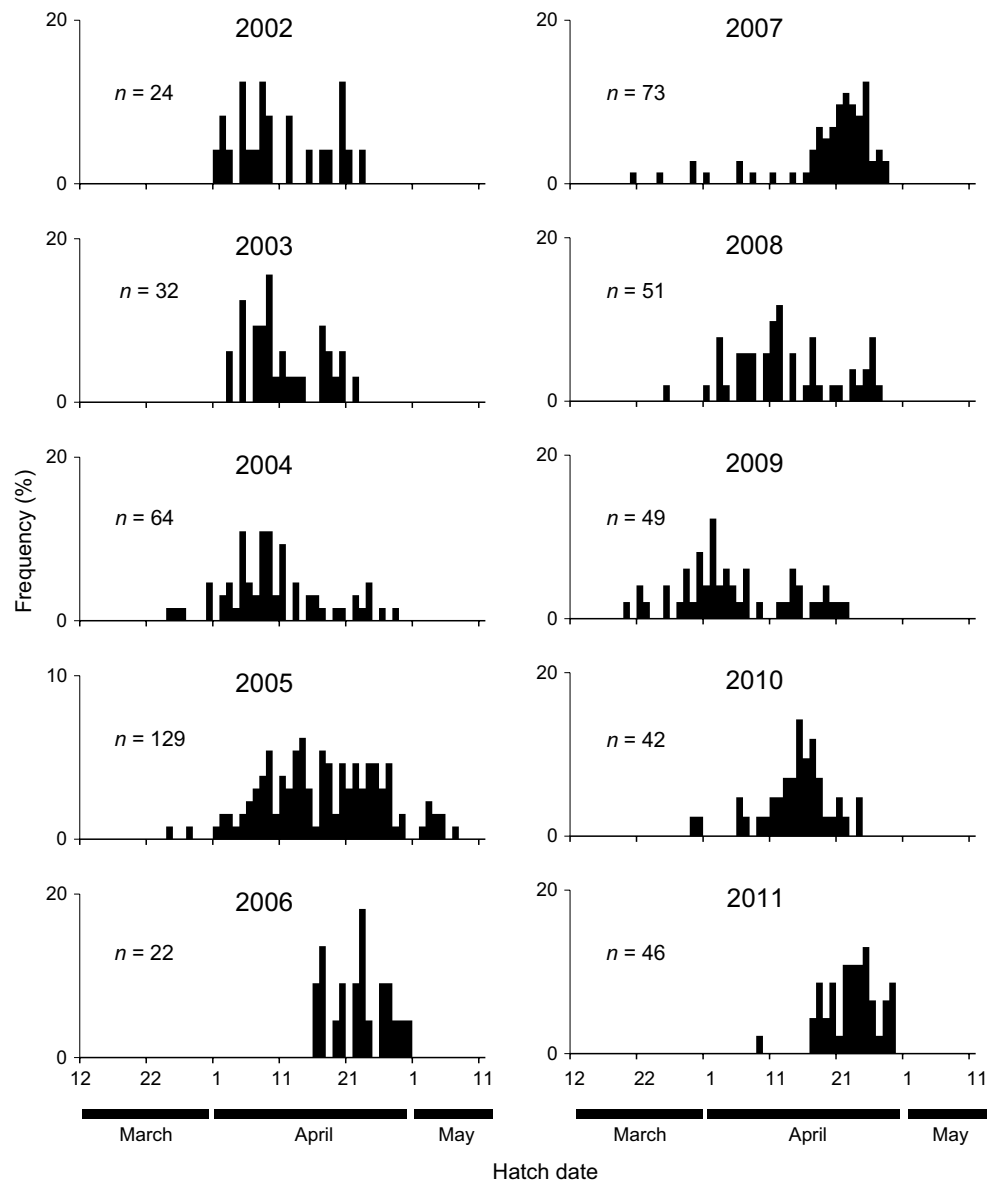


Fig. 4 Hatch date distributions of juvenile chub mackerel *Scomber japonicus* collected in the Kuroshio–Oyashio transition region from 2002 to 2011. n denotes sample size

33.1 ± 10.0 (2006) and 46.1 ± 4.9 days (2009) and hatch date was estimated from 20 March to 7 May and mainly in April (Fig. 4). Therefore, interannual variation in mean daily growth rate and relationships between growth rate and recruitment and RPS were examined by comparing early growth of chub mackerel hatched in April between the years 2002 and 2011.

Growth, recruitment and RPS analyses

The mean back-calculated FL of April cohorts for ages of 6–10, 11–15, 16–20, 21–25 and 26–30 days was estimated from 2002 to 2011 (Table 3). Mean daily growth rates

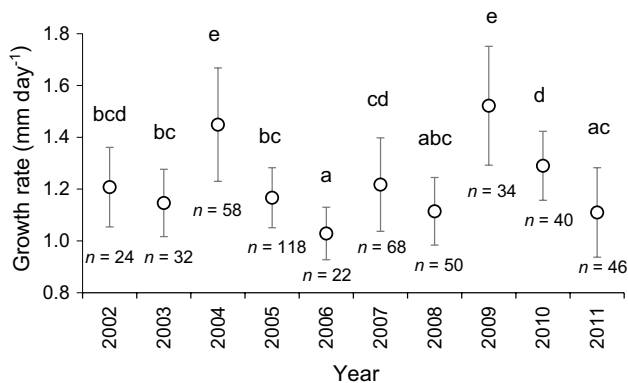
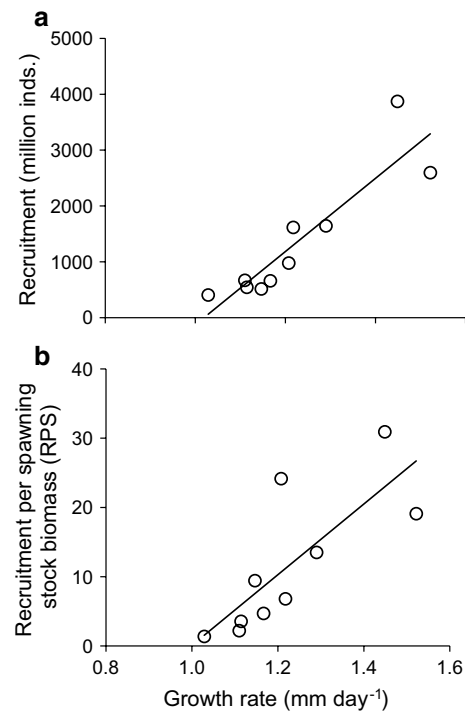
of April cohorts in larval and juvenile stages fluctuated between 1.03 ± 0.10 (2006) and 1.52 ± 0.23 mm day⁻¹ (2009; Fig. 5). There were significant differences in the mean daily growth rate of chub mackerel in larval and juvenile stages among the year-classes (Welch's ANOVA, $F = 28.6$, $p < 0.001$) and growth rates of the 2004 and 2009 cohorts were significantly higher than other cohorts, as per the Games-Howell post hoc test (Fig. 5). The mean daily growth rates were significantly related to recruitment and RPS (Fig. 6) and the relationships were expressed by linear (recruitment: $R = 6550 G - 6678$, RPS: $RPS = 51.0 G - 51.0$) and exponential regressions (recruitment: $R = 14.8 e^{3.58 G}$, RPS: $RPS = 0.38 e^{1.14 G}$).

Table 2 Relationships between otolith radius (OR, μm) and fork length (FL, mm) of chub mackerel *Scomber japonicus* from 2002 to 2011, expressed as allometric regressions

Year	<i>n</i>	Equation	r^2	<i>p</i>
2002	24	FL = 0.26 OR ^{0.85}	0.97	<0.001
2003	32	FL = 0.39 OR ^{0.79}	0.93	<0.001
2004	64	FL = 0.10 OR ^{1.01}	0.91	<0.001
2005	129	FL = 0.23 OR ^{0.88}	0.95	<0.001
2006	22	FL = 0.35 OR ^{0.79}	0.89	<0.001
2007	73	FL = 0.10 OR ^{1.01}	0.91	<0.001
2008	51	FL = 0.37 OR ^{0.79}	0.89	<0.001
2009	49	FL = 0.16 OR ^{0.94}	0.85	<0.001
2010	42	FL = 0.16 OR ^{0.94}	0.87	<0.001
2011	46	FL = 0.33 OR ^{0.82}	0.88	<0.001

Table 3 Mean back-calculated fork length (FL) \pm standard deviation (SD) of chub mackerel *Scomber japonicus* for ages of 6–10, 11–15, 16–20, 21–25 and 26–30 days from 2002 to 2011

Year	Ages				
	6–10	11–15	16–20	21–25	26–30
2002	7.0 \pm 0.5	11.5 \pm 1.1	18.1 \pm 2.1	25.5 \pm 3.1	33.2 \pm 4.3
2003	6.6 \pm 0.3	10.3 \pm 0.7	16.0 \pm 1.6	23.2 \pm 2.9	31.3 \pm 3.8
2004	7.3 \pm 0.6	12.8 \pm 1.5	20.9 \pm 3.0	30.7 \pm 6.0	41.3 \pm 7.8
2005	6.8 \pm 0.5	10.8 \pm 1.1	16.6 \pm 2.1	23.7 \pm 3.0	31.4 \pm 3.9
2006	6.4 \pm 0.4	9.6 \pm 1.2	14.3 \pm 2.0	20.7 \pm 3.0	27.5 \pm 3.1
2007	7.5 \pm 0.8	12.2 \pm 2.1	19.3 \pm 3.4	26.9 \pm 4.1	33.3 \pm 5.1
2008	6.2 \pm 0.5	9.8 \pm 1.3	16.0 \pm 2.3	23.5 \pm 2.9	30.7 \pm 3.5
2009	7.3 \pm 0.6	12.6 \pm 1.9	21.5 \pm 4.0	32.9 \pm 6.8	44.4 \pm 9.0
2010	7.3 \pm 0.5	11.3 \pm 1.5	17.8 \pm 3.6	27.1 \pm 5.8	37.9 \pm 7.7
2011	6.7 \pm 0.6	10.5 \pm 1.6	16.5 \pm 3.1	24.0 \pm 4.7	31.4 \pm 5.5

**Fig. 5** Mean daily growth rates \pm standard deviations of chub mackerel *Scomber japonicus* in larval and juvenile stages hatched in April from 2002 to 2011. Different letters above bars indicate significant differences among years (Welch's ANOVA with Games-Howell post hoc test: $p < 0.05$). *n* denotes sample size**Fig. 6** Relationship between **a** recruitment (*R*) and **b** recruitment per spawning stock biomass (RPS) and mean daily growth rate (*G*) of chub mackerel *Scomber japonicus* in larval and juvenile stages hatched in April from 2002 to 2011. Equation of the linear regression are **a** $R = 6550 G - 6678$, $n = 10$; **b** $RPS = 51.0 G - 51.0$, $n = 10$

Linear regressions were selected by an Akaike information criterion (AIC) score in both relationships (linear versus exponential regression for recruitment: AIC = 157 versus 160 and for RPS: AIC = 70 versus 72; Fig. 6). There were no significant correlations between the mean CPUE and the mean daily growth rate (Pearson's correlation coefficient, $r = -0.10$, $p = 0.77$, $n = 10$). The mean number of days from hatching to a 12 mm FL varied between 12.1 (2004) and 15.5 days (2006) and was inversely correlated with recruitment ($r = -0.86$, $p < 0.001$, $n = 10$; Fig. 7). The mean SST experienced by each fish in the larval stage ranged between 17.8 (2003, 2008 and 2011) and 19.0 °C (2010), and the mean daily growth rate for the larval stage varied between 0.60 (2006) and 0.86 mm day⁻¹ (2007). A positive correlation was found between the mean SST experienced and the mean daily growth rate of chub mackerel in the larval stage ($r = 0.63$, $p < 0.05$, $n = 10$; Fig. 8).

Discussion

Larval and juvenile growth of chub mackerel of the April cohort was one of the important indices for recruitment for the Pacific stock of chub mackerel, since there were

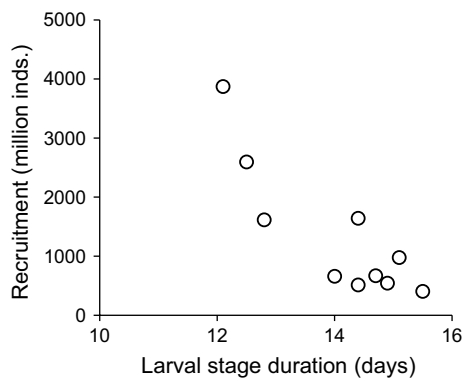


Fig. 7 Relationship between recruitment and larval stage duration of chub mackerel *Scomber japonicus* hatched in April from 2002 to 2011

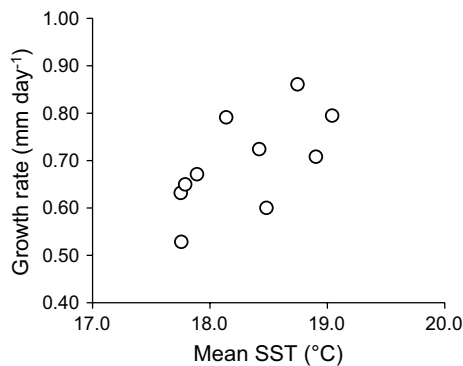


Fig. 8 Relationship between mean daily growth rate of chub mackerel *Scomber japonicus* and mean daily temperature experienced by each fish during larval stage hatched in April from 2002 to 2011

significant relationships between the mean daily growth rates and recruitment and RPS. However, there were some effects of bias due to re-sampling of specimens for otolith analysis from the samples collected in 2002, 2006, 2008 and 2009 (Fig. 3), and recruitment probably consisted of other cohorts such as March, May and June. Therefore, comparative studies of hatch date distribution between juveniles and recruitment are needed in the future.

Previous studies confirmed that higher growth rates during early life stages are related to higher recruitment for many fish species [26–28]. In general, fast-growing individuals in the early life stages confer survival advantages such as developing a larger body size [29] and shorter vulnerable stages [1, 30]. In the present study, a significant correlation was found between the mean number of days from hatching to a 12 mm FL and recruitment of the Pacific stock of chub mackerel. A laboratory experiment demonstrated that the larval duration was shorter with increased growth rate and water temperature [22]. In addition, Masuda et al. [31] reported that there was a remarkable improvement in burst

and cruise swimming speed of reared chub mackerel with an SL larger than 10 mm. Piscivorous fishes such as tunas, *Thunnus orientalis* and *T. alalunga*, the swordfish *Xiphias gladius*, Pacific pomfret *Brama japonica*, spiny dogfish *Squalus acanthias* and salmon shark *Lamna ditropis*, are thought to be major predators of mackerel at the Kuroshio–Oyashio transition region [15, 32]. A slight decrease in the larval stage duration due to faster growth possibly greatly increases larval survival because the larval mortality coefficient of scombrid fish (Atlantic mackerel: 0.35–0.69) was estimated to be extremely high [2].

Water temperature and food availability are important determinants of early fish growth variability and recruitment success for the genus *Scomber* [33–36]. There was a significant correlation between the mean SST experienced (17.8–19.1 °C) by chub mackerel and the mean daily growth rate (0.60–0.86 mm day⁻¹) during the larval stage in the present study. Hunter and Kimbrell [22] and Mendiola et al. [37], using water temperatures between 17 and 22 °C and 16 and 25 °C, respectively, showed that an increase in temperature accelerated growth of reared larval and juvenile chub mackerel. Scombridae, which show fast-growing characteristics, require a high metabolism and abundant prey organisms [3, 22, 37, 38]. It has been reported, per stomach content analyses, that the dominant prey organisms of larval and juvenile chub mackerel are copepods, appendicularians, mysids and fish larvae such as Japanese anchovy *Engraulis japonicus* [15, 39–42]. The effects of food availability and water temperature on growth variation of chub mackerel during the process of transportation from the spawning area to the nursery area require further verification in the future (Kuroshio–Oyashio transition region).

Previous studies examining the relationship between size at catch of post-recruitment individuals and recruitment variability suggested density-dependent growth of juvenile chub mackerel [14, 43]. However, in the present study, there was a positive correlation between the early growth of chub mackerel and recruitment (Fig. 6) and no significant correlation between CPUE and the early growth. These previous studies included data from the 1970s when there was a 4–20 fold greater total biomass of chub mackerel compared to 2002–2011, and, therefore, potentially affecting the data by density-dependent growth.

Hatch date distribution of strong recruitment year classes such as 2004 and 2009 shows a relatively higher proportion of hatching in March compared to other year classes. This result implies that an earlier spawning period and/or higher larval and juvenile survival of the earlier hatched individuals leads to strong year classes. Watanabe [6] suggested that during 2002 and 2007, the egg production peak of mackerels (*S. japonicus* and *S. australasicus* combined) did not change dramatically, although the peak

shifted from March–May in the 1970s (strong recruitment period; Fig. 1) to April–June in the 2000s. However, the larval mortality rate of early hatched individuals needs to be compared between strong and weak recruitment years to be able to confirm this point.

In conclusion, the present study found that larval and juvenile growth rate is an important index for recruitment prediction for the Pacific stock of chub mackerel. Higher temperature led to faster growth of larvae and juveniles and shorter larval stage duration. Robert et al. [4] compared the larval growth and recruited juvenile growth in four year classes of Atlantic mackerel in the southern Gulf of St. Lawrence and revealed that the interaction between early growth and selection for fast growth appears to be an important regulator of recruitment. Analyzing the relationship between intensity of size- and growth-selective survival in early life stages and recruitment variability could provide further understanding of the recruitment mechanism of chub mackerel. Fluctuation of the Pacific stock of chub mackerel has shown a tendency to increase from the lowest period (1990) in recent years (Fig. 1). Examining whether stock level and density-dependence influence the relationship between larval and juvenile growth rates and the subsequent recruitment variability are important topics for future studies.

Acknowledgments We thank K. Mori and H. Nishida of the Fisheries Agency, S. Honda and H. Kubota of the Fisheries Research Agency of Japan (FRA), T. Kaga of the Hokkaido National Fisheries Research Institute, FRA, and members of the National Research Institute of Fisheries Science, FRA, for their help with fish sampling and otolith analyses. We are grateful to the captain, officers and crews of the training vessel *Hokuho-Maru* and the research vessel *Soyo-Maru* for helping with collection and measurement. We thank Japan Scientific Texts for English proofreading. Three anonymous reviewers provided valuable comments on the manuscript. This research was financially supported by the Fisheries Agency and FRA of Japan.

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