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in coastal waters off Shari, eastern Hokkaido, Japan,
in relation to sea temperature**

by

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**Early marine growth of chum salmon (*Oncorhynchus keta*)
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Abstract

Early marine growth of thermal marked juvenile chum salmon was estimated using their otolith growth increments. Fish were collected from coastal waters off Shari, eastern Hokkaido, Japan, during May and June 2006. Of 974 fish examined, 315 were identified as one of the three marked groups released from the Shari Field Station of NSREC. Estimated daily growth rates for fish of each marked group showed increasing trends as the season progressed. The trend of the growth rates for each marked group was strongly associated with daily sea temperatures measured at 3 m depth in the study area (R square: 0.66-0.80), suggesting that variability in the early marine growth of juveniles is likely regulated by the ambient sea temperature. Within each marked group, large outmigrants tended to show higher daily growth rates than small ones at the beginning of the costal residency, but the difference in the growth rates became obscure as the time passed. Based on this finding, a hypothesized mechanism to regulate the timing of offshore migration was discussed.

Introduction

There are several studies indicating that early marine residence is a critical period for most species of Pacific salmon (*Oncorhynchus*, spp.) and that growth during this period often determines brood-year strengths of the species (Parker 1968; Ricker 1976; Bax 1983; Neilson and Geen, 1986; Holtby et al., 1990; Mortensen, et al., 2000; Moss, et al., 2005). Thus evaluating growths of juvenile salmon during their early marine life is thought to be one of the important approaches for understanding of the mechanism regulating the abundance of salmon stocks.

The main environmental factors affecting the marine growth of Pacific salmon are

reasonably assumed to be sea temperature, and abundance and availability of prey species (Weatherley and Gill, 1995). Recently, some researchers have tried to estimate the consumption demand and growth efficiency of juvenile salmon during the early marine life using bioenergetics models (e.g., Boldt and Haldorson, 2002; Orsi et al., 2004; Cross et al., 2005). These models seem to be very useful for giving insight about coastal carrying capacity for juveniles, but estimated values such as consumption demand by juveniles often exceeded the estimated biomass of key prey species (Cross et al., 2005). Such discrepancy between model output and actual estimates could stem from, at least in part, the difficulty of estimates of prey biomass in the ocean. Accordingly, further challenges to progress the methodology for assessing food conditions of juveniles and to accumulate actual feeding data would be still necessary for examining the effects of prey biomass on the growth and survival of juveniles in actual fields.

Ambient sea temperature probably affects the growth of juvenile salmon, not only through direct metabolic responses to temperature, but also through indirect effects on the productivity and species composition of prey organisms. Under the actual situations where the measurement of prey availability for juvenile salmon is technically difficult, estimating accurate growth responses of juveniles in relation to temperature regimes would be a simple and reliable approach to evaluate growth performance of juveniles during their coastal residency.

In the present study, daily marine growth rates were estimated by using otolith growth increments of juvenile chum salmon collected from coastal waters off Shari, eastern Hokkaido, Japan. The estimated daily growths were then regressed against daily sea temperatures so as to evaluate how sea temperatures affect the growth of juvenile salmon during their coastal residency. Furthermore, through a comparison of daily marine growths of juveniles in relation to their body size at sea entry, a hypothesized mechanism to regulate the timing of transition to offshore waters was discussed.

Materials and methods

Juvenile chum salmon were collected from four survey stations located in coastal waters off Shari, eastern Hokkaido, Japan, during 9 May and 5 July 2006 (Fig. 1). Each survey station was approximately 0.5, 1.0, 3.0, and 5.0 km from shore, respectively. At each survey station, a two-boat seine was used for collection of juveniles. The net was 13.3 m long × 1.3 m wide × 2.25 m deep, equipped with two wing nets each 11.5 m long,

and 5-mm cod-end mesh. The net was towed on the surface with average speed of two knots for 30 min. Collected fish were immediately put in a cooler on board, transported to the laboratory, and then frozen at -35°C for subsequent analyses.

During the study period, daily sea water temperatures were monitored using a logger placed at 3 m depth about 1 km off the coast of Shari (Fig. 1, $\text{N}43^{\circ} 55' 9''$, $\text{E}144^{\circ} 37' 7''$).

Near the survey areas, Shari River flows into the Okhotsk Sea. In 2006, about 29 millions chum fry were released from three salmon hatcheries located in the Shari River system. Among the salmon hatcheries, one is a field station of NASREC (Shari Field Station of NASREC), where about 12.5 million fry were produced in 2006 and all chum fry were otolith-thermal marked. The information on the release of otolith-thermal marked chum fry is shown in Table 1. Three different otolith marks were conducted for 2005 brood-year fish in the Sari Field Station (Takahashi, et al., 2006). For simplicity, the three groups, RBr code; 1:1.2/2.2w-3.3, 1:1.2/2.2w,3.2-4.2, and 1:1.2/2.2w-3.4, are hereafter called as mark A, mark B, and mark C, respectively. Chum fry released from the other two hatcheries had no otolith-thermal marks.

In the laboratory, 80 fish per survey station was randomly chosen at the maximum, and thawed fish were measured for fork length to the nearest 0.1 mm and weighed to the nearest 0.001 g. Otoliths (sagittae) were removed under a binocular with fine forceps, rinsed with distilled water, and then dried at room temperature. The preparation of otolith samples was done with the method proposed by Saito et al. (2007). Otolith samples were firstly examined for the otolith-thermal marks under a microscope with magnifications from 100 to $400\times$. If an otolith-thermal mark was detected, the pattern of the marks (mark A, B, or C) was identified, and the otolith was then utilized for further analyses.

For the otoliths with thermal marks, counts of otolith growth increments and measurement of otolith radii were conducted with an otolith measurement system (ARP/W Version 4.18, Ratoc System Engineering Co., Tokyo Japan). An otolith check and/or change in otolith appearance were identified as a benchmark of the transition of juveniles from fresh to marine waters (Saito et al., 2007). A measurement axis was set perpendicular to the axis passing through the otolith rostrum and the otolith core in the mid-ventral region of the otolith. Along the measurement axis, the number of otolith growth increments was counted from the otolith check to the edge of the otolith, and the width of each increment was also measured.

The fork length at sea entry was individually back-calculated from the otolith distance from the core to the otolith check, and daily somatic growths of juveniles after sea entry were also estimated with the widths of otolith growth increments that were formed after the otolith check. To back-calculate past fork lengths and daily somatic growths, individual otolith radius-body length relationships were assumed to be expressed by exponential equations (Saito, et al, 2006), and all relationships were also assumed to radiate from a common point called as 'biological intercept' (Campana, 1990). In the present study, the average length and otolith radius at hatch (fish length 20.44 mm, otolith radius 141.13 μm) was used as the biological intercept. Under these assumptions, the otolith radius-length relationship running through the two points, i.e., the biological intercept and the point consisting of the fork length and otolith radius at capture, was individually estimated using the Solver algorithms in Microsoft Excel®. Using these individual relationships, the otolith radius at the otolith check and the widths of otolith growth increments were converted to somatic lengths.

To evaluate how sea temperatures affect the growth of juvenile chum salmon in coastal waters off Shari, mean daily growth rates for juveniles of each marked group were regressed against daily sea temperatures. Since both variables were autocorrelated data, the autoregression procedure in SPSS® (Version 15.0J) was utilized to correct for correlated error. To obtain the best model, models having one of the independent variables (daily sea temperature) at lag 0 to 5 were generated, and the model with the lowest Akaike's information criterion (AIC) was selected.

In each marked group, small outmigrants and larger ones were distinguished at the mode of the distribution of fork length at sea entry, and mean daily growth rates were graphically compared between them.

Results

A total of 974 juvenile chum salmon was examined for otolith-thermal marks, and 317 were recognized as marked fish (mark A, 26 fish; mark B, 198; mark C, 91; Alizarin complexone (ALC) mark, 2). As the result of the otolith examination, 315 juveniles (32.3%) were identified as the origin of the Shari Field Station of NASREC. The ALC-marked chum fry were not released into the Shari River system in 2006. These fish were, therefore, thought to originate from other river, probably from Abashiri River. In 2006, ALC-marked chum fry were released in five river systems in Hokkaido (Takahashi

et al., 2006), and among them Abashiri River is the closest to the study area.

Among 315 fish of Shari Field Station, 107 fish having mark B were recaptured 18 May 2006, one day after their release (Table 1), and 24 fish had crystalline otoliths. Thus we did not use the otoliths of these 131 fish for the otolith microstructure analysis. Furthermore, 18 otoliths were hard to observe the otolith growth increments due to errors of the sample preparation. Consequently, 166 fish were analyzed for their otolith growth increments.

Mean daily growth rates of juvenile salmon for each marked group are shown in Fig. 2. All of mean daily growth rates showed increasing trends as the season progressed. At the beginning of their coastal residency, mean daily growth rates ranged from 0.48 to 0.56 mm/day, and attained on average about 0.68-0.91 mm/day in late June. A remarkable reduction of daily growth rates was evident for mark A fish after 28 June. This was due to the way of the reconstruction of the growth rates; the growth rates after 28 June was back-calculated from the otolith taken from an individual collected in the final survey (5 July 2006). This individual may have probably grown slower as compared with the counterparts. Daily sea temperatures were also getting warmer steadily during the study period; mean daily sea temperature was 5.0 °C in mid-May, and was 10.9 °C in late June.

Daily growth rates for fish of each marked group were well estimated using daily sea temperatures (Fig. 3). However, best models were obtained when independent variable at lag 1 or 3 was used, indicating that the growth rate at a given date may be affected by the sea temperature of one or three days before. The R square of the models ranged from 0.66 to 0.80. This means that variability in the daily growth rates of juveniles was strongly influenced by ambient sea temperatures.

Estimated fork lengths at sea entry of fish demonstrated a unimodal distribution (Fig. 4a). The fork lengths at sea entry (mean \pm S.D.) were as follows: mark A, 56.5 \pm 4.2 mm; mark B, 57.6 \pm 5.2 mm; mark C, 52.5 \pm 6.3 mm, respectively. The mean fork lengths at sea entry were very similar to those at release (Table 1), except for mark A. Mean daily growth rates for small outmigrants and those for large outmigrants are separately shown in Fig 4b. In all marked groups, daily growth rates for large outmigrants tended to be higher than those for small outmigrants at the early time of their coastal residency. The growth rates, however, became gradually identical between them, or in some cases the growth rates for the latter seemed to even exceed those of the former as the season proceeded. The timing when the growth rates became identical between them was likely

to be different among the mark groups.

Discussion

The emphasized point of the present study is that the early marine growth of juvenile chum salmon was reconstructed with daily resolution by using their otoliths. Information on the daily growth rates enabled us to compare the growth with daily sea temperatures. The comparisons revealed that variability in the growth rates is strongly affected by the ambient sea temperatures during the coastal residency of juveniles. Sea temperature, and abundance and availability of prey species are the main environmental factors that affect the marine growth of Pacific salmon (Weatherley and Gill, 1995). However, it is unknown how food conditions, e.g., prey abundance, species composition and the quality of prey, affected the growth of juveniles in coastal waters off Shari, because the feeding intensity of individual fish was not assessed in this study. Thus we cannot actually refer to which environmental factors would be more influential for variability in the early marine growth of juvenile salmon in coastal waters off Shari.

Relative influences of several environmental factors on the early marine growth of Pacific salmon have been investigated through sensitivity analyses in bioenergetics modeling (Boldt and Haldorson, 2002; Orsi et al., 2004; Cross et al., 2005). According to these studies, temperature regimes had less influence on growth performance as compared with diet composition (Cross et al., 2005). Orsi et al. (2004) reported that different temperature regimes had little effect on prey consumption by juveniles. Although it is very dangerous to draw an idea from the results of the different model simulations, we may be able to interpret these findings as follows; fish have to eat prey species with high quality (high energy) to realize observed growth, under the conditions where consumption of prey does not relate to temperature. If a survey program is carried out over several years in the same study area, our approach based on otolith growth increments may be useful to validate these model output in the field; if prey composition more strongly influences the growth performance of juveniles, then the predictive power of our autoregression models would vary among years when prey composition shows year-to-year difference.

The second emphasized point of this study is that daily growth rates were different between small outmigrants and large ones in the same marked fish but the difference became obscure as the time after sea entry passed. In all of the marked groups, large

outmigrants tended to grow faster as compared with small ones at the beginning of their coastal residency. These observations probably support the previous findings that large outmigrants are advantageous over small ones on the subsequent marine growth (e.g. Saito et al., 2006). However, the effect of the size advantage may not have been maintained over the coastal residency in coastal waters off Shari in 2006. A possible reason for this is that large outmigrants growing into a certain body size migrated to offshore waters (i.e., they left from our study area). If we assume the reason is true, the timing when daily growth rates between small outmigrants and large ones became identical would be considered as the threshold timing for the start of offshore migration. Under this hypothesis, growth trajectories for large outmigrants and small ones were separately estimated using the mean growth rates showed in Fig. 4b (Fig. 5). For large outmigrants, they attained about 70-80 mm in fork length at the threshold timing. The fork lengths were almost identical to the body length at offshore migration that was reported in previous studies conducted in Japanese coastal waters (reviewed by Mayama and Ishida, 2003). Moreover, the fork lengths at the threshold timing, i.e., the threshold lengths, gradually decreased as the season progressed. This suggests that the timing and body size at offshore migration would be determined in relation to coastal environments, probably sea temperatures and prey conditions. On the other hand, small outmigrants did not reach the threshold sizes yet when the large outmigrant of their counterparts did so (Fig. 5). Thus the small outmigrants probably stayed in coastal waters longer, and grew into more large size before leaving from coastal waters off Shari.

Previous studies demonstrated that transition to offshore waters is associated with potential body size thresholds or some temporal factors (LeBrasseur and Parker, 1964; Healy, 1980; Mayama and Ishida, 2003), but the mechanism of the offshore migration has been still unclear (Duffy et al., 2005). For better understanding of the mechanism, bioenergetics approaches and growth estimates like this study would effective for future research.

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Table 1. Information on the release of thermal-marked chum fry produced in the Shari Field Station of NASREC in 2006. The data were obtained from Takahashi et al. (2006).

Mark*	Release site	Date of release	Mean FL at release (mm)	Mean BW at release (g)	No. of fry released (million)
A	Shari River	1 May 2006	64	2.22	1.777
B	Shari River	17 May 2006	59	1.63	4.213
C	Shari River	27 May 2006	54	1.34	6.547

*RBr code of each mark group is as follows: mark A = 1:1.2/2.2w-3.3; mark B = 1:1.2/2.2w,3.2-4.2; mark C = 1:1.2/2.2w-3.4.

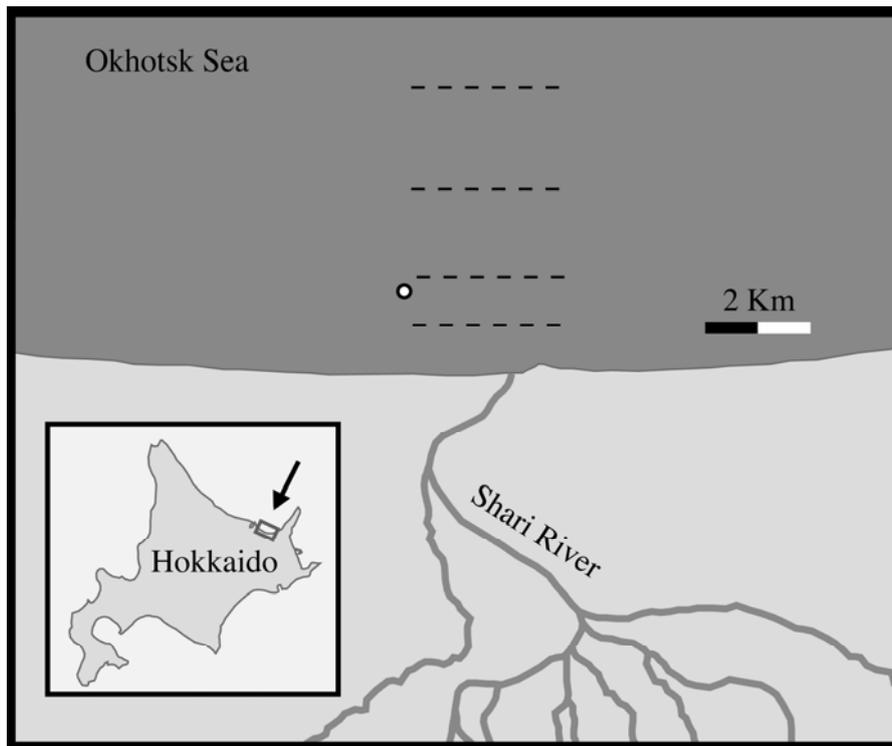


Fig.1. A Map showing survey stations in the coastal waters off Shari, eastern Hokkaido, Japan. Broken lines indicate the survey stations, along which a two-boat seine was operated for collection of juvenile chum salmon. Open circle represents the location of a logger for monitoring sea temperature at 3 m depth.

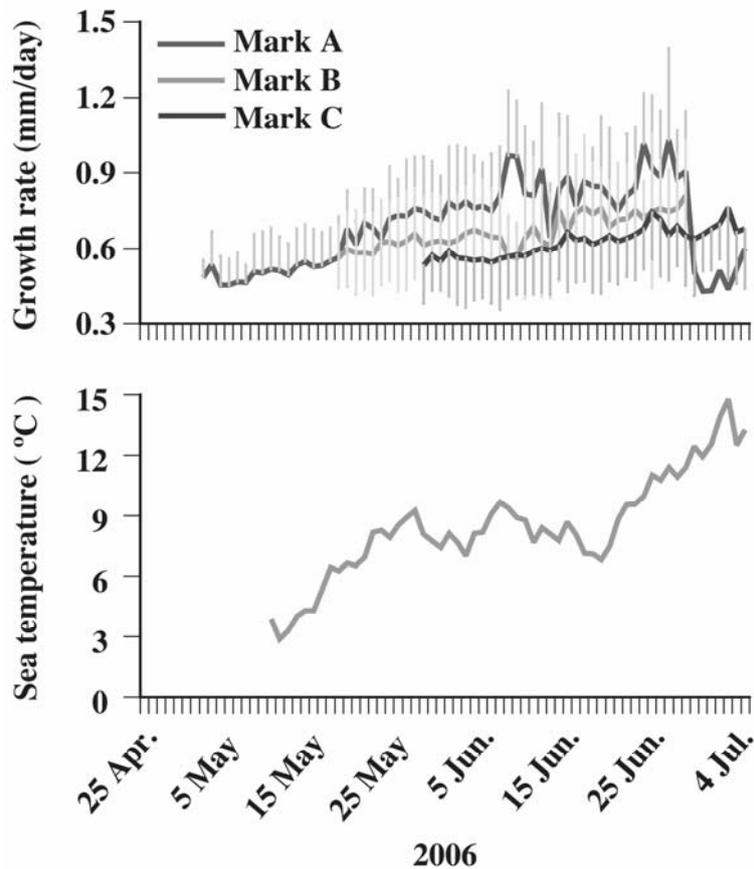


Fig. 2. Mean daily growth rates for juvenile chum salmon of each otolith-marked group during their coastal residency in coastal waters off Shari, eastern Hokkaido, Japan. Error bars represent standard deviations (Upper panel). Mean daily sea temperatures monitored at 3 m depth off the coast of Shari (Lower panel).

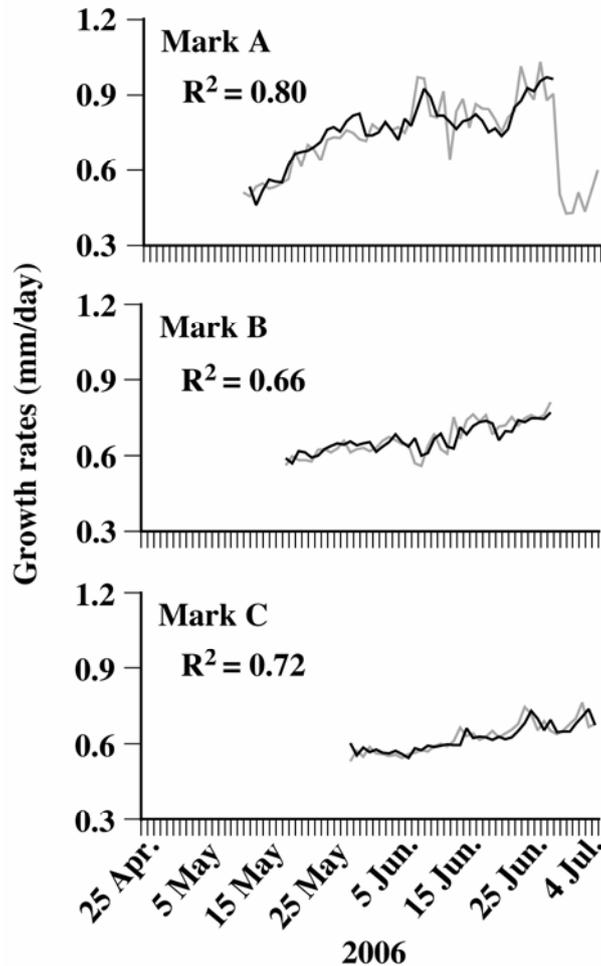


Fig.3. Mean daily growth rates for juvenile chum salmon of each otolith-thermal marked group (gray lines) and the predicted growth rates from sea temperatures in the study area (solid lines). ‘ R^2 ’ indicates R square values. The autoregression equations are as follows: Mark A, $G = 0.303 + 0.060 \cdot \text{Temp}(\text{lag } 1) + r(t)$, $r(t) = 0.354 \cdot r(t - 1) + u(t)$; Mark B, $G = 0.495 + 0.022 \cdot \text{Temp}(\text{lag } 3) + r(t)$, $r(t) = 0.737 \cdot r(t - 1) + u(t)$; Mark C, $G = 0.485 + 0.015 \cdot \text{Temp}(\text{lag } 3) + r(t)$, $r(t) = 0.800 \cdot r(t - 1) + u(t)$. ‘G’ and ‘Temp’ are growth rates and sea temperature, respectively. ‘t’ means numbers of time series and $r(t)$ errors of each model. $u(t)$ indicates white noise.

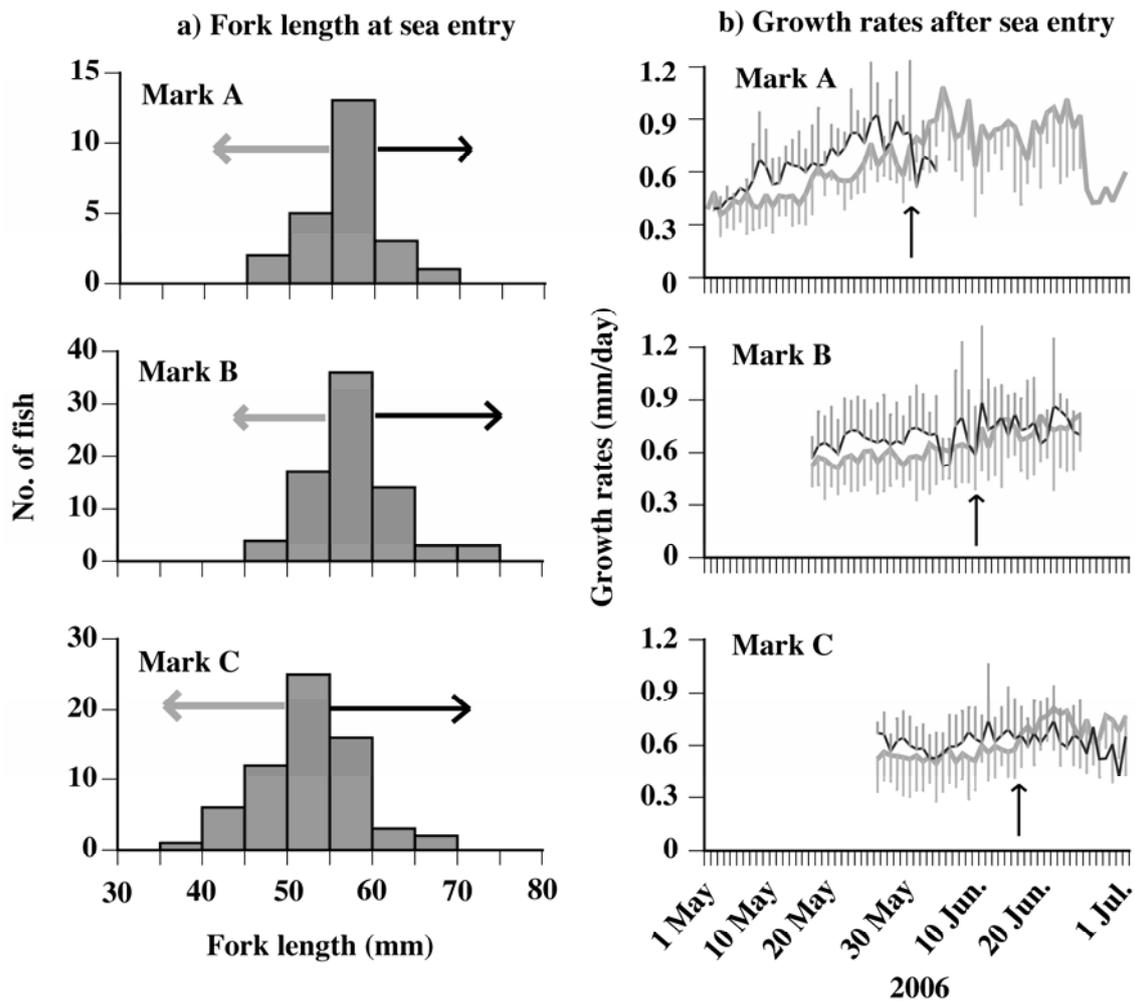


Fig. 4. (a) Estimated fork lengths at sea entry for juvenile chum salmon of each otolith-thermal marked group. Gray and solid arrows indicate small and large outmigrants, respectively, within each marked group. (b) Mean daily growth rates for small outmigrants (gray line) and large ones (solid line) within each marked group during their coastal residency in coastal waters off Shari. Error bars are standard deviations. Arrows indicate the timing when difference in the growth rates between small and large outmigrants became graphically obscure.

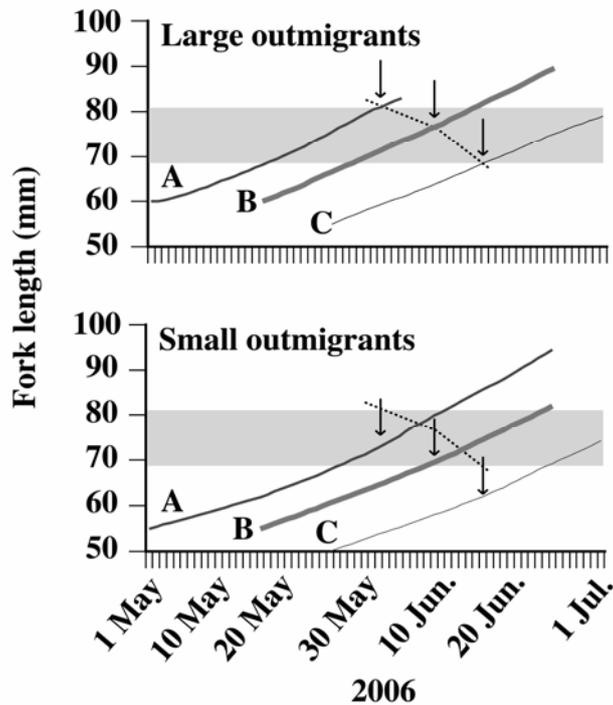


Fig. 5. Mean growth trajectories for large outmigrants and small ones. Distinction between large and small outmigrants was seen in Fig. 4a. The letter ‘A’, ‘B’, and ‘C’ in the panels indicate each otolith-thermal marked group (see, Table 1). For large outmigrants, fork lengths at sea entry for fish of mark A, B, and C are assumed as 60, 60, 55 mm, respectively. These fork lengths were the smallest within the large outmigrants of each group (Fig.4a). For small outmigrants, fork lengths at sea entry for mark A, B, and C fish are considered as 55, 55, and 50 mm, respectively. The fork lengths mentioned above were the largest within the small outmigrants of each group (Fig. 4a). Growth trajectories were constructed by accumulating mean daily growth rates showed in Fig. 4b. Arrows represent the timing when difference in the daily growth rates between large outmigrants and small ones was obscure (Fig. 4b). A broken line connects the fork lengths at this time. In the text, the broken line is hypothesized as the threshold size at offshore migration of juvenile chum salmon (see, Discussion). When large outmigrants started migrating to offshore waters (at the time indicated by the arrows), small outmigrants did not reach the broken line yet. Thus these small fish would probably stay longer in coastal waters.