Intra- and inter-population variations of early life history traits of Japanese anchovy *Engraulis japonicus*

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Japanese anchovy *Engraulis japonicus* is a key fish species in the northwest Pacific Ocean . However, anchovy stocks are collapsing dramatically along with severe habitat degradations and climate changes . To provide information on conserving and restoring anchovy resources, the intra-population variations in early growth of anchovy in Yangtze River Estuary (YRE) and inter-population variations in population from other regions were studied to assess the adaptation of anchovy under different environments. In YRE, anchovy hatching on different dates showed remarkable intra- population differences in early growth trajectories . When compared with populations from Northeast Japan and Northeast Taiwan, anchovy in YRE showed the medium onset of hatching but slowest growth rates. Growth rate of anchovy in YRE (0.30 mm/d) were clearly lower than population from Japan (0.64 mm/d) and Taiwan (0.60 mm/d). The depressed growth of anchovy will decrease the length of anchovy by the end of the first year, consequently resulting in the weaker strength of recruitment in YRE. Our research thus shed important lights on estimating anchovy recruitment dynamics by taking variations in hatching date and growth into account.

Intra- and inter-population variations of early life history traits of Japanese anchovy *Engraulis japonicus*

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Running title: Early life history of Japanese anchovy

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Abstract: Japanese anchovy *Engraulis japonicus* is a key fish species across the northwest Pacific Ocean. Concomitant with severe habitat degradation and climate changes, stocks of Japanese anchovyin the Yangtze River Estuary (YRE) are collapsing. In this study, we described inter-population variations in early growth for anchovy from YRE and compared growth rates of anchovy from this region with those from northeastern Japan and northeastern Taiwan. YRE anchovy that hatch within a season on different dates (early, middle and late seasonal hatching) have different early growth trajectories. When compared with populations from northeastern Japan(0.64 mm/d) and northeast Taiwan (0.60 mm/d), YRE anchovy showed the slowest growth rate (0.30 mm/d). Such reduced growth will decrease first-year fish length, resulting in reduced recruitment into YRE stocks. Our research indicates that hatching date should be taken into account when estimating anchovy recruitment dynamics.

Key words: Japanese anchovy; growth; hatch date; the Yangtze River Estuary

Introduction

Japanese anchovy (*Engraulis japonicus*Temminck & Schlegel, 1846) is an important commercial fish species widely distributed throughout the northwest Pacific Ocean(Iseki & Kiyomoto 1997; Takasuka & Aoki 2006). With an annual commercial catch reaching 1.9 billion kg in 1998(Fisheries and Aquaculture Department, FAO, Rome, Italy; available: http://www.fao.org/home/en/), Japanese anchovyis a major species contributing to world fishery resources - one that plays a key ecological role in connecting different trophic levels, for not only is it a plankton feeder, but it is also the main prey for piscivorous fishes(Iseki & Kiyomoto 1997; Zhao *et al.* 2003). In recent years, however, anchovy stocks have collapsed in recent years as a consequence of overfishing, habitat degradation and climate changes (Jiang & Zhuang 2005; Takasuka *et al.* 2007). Therefore, how anchovy respond to different environmental pressures is needed to developeffective strategies for restoring the fishery resource value of this species.

For pelagic fish, the early life history stage isa crucial window characterized by high mortality and variable growth(Takasuka *et al.* 2003;Starrs *et al.* 2016). Even slight environmental changes experienced during this stage can cause large fluctuations in population recruitment. The survival rate of fish during the early life stage is closely related to somatic growth(Campana 1990; Searcy & Sponaugle 2000). Within a population, fish hatching on different dates might experience different environmental conditions, resulting in inter-cohort differences ingrowth trajectories and survival rates(Quinn *et al.* 2002; Bacheler *et al.* 2012). Growth rate has also been used as a bio-indicator to compare habitat quality across different environments. Fish from poorer-quality environments have lower growth rates as a consequence redirecting increased energy towards tolerating pollution, rather than directing energy towards growth(Amara *et al.* 2007; Amara *et al.* 2009). Understanding intra-and inter-population variations in early growth can provide important insights into understanding the mechanisms of anchovy population dynamics.

The Yangtze River Estuary (YRE) is an important spawning, feeding and nursery ground for Japanese anchovy (Zhang *et al.* 2015). Sediments carried in the outflow of the Yangtze River contribute towards high productivity, supporting abundant anchovy resources(Zhou *et al.* 2008; Yu & Xian 2009; Zhang *et al.* 2009). However, areas around the YRE are also among the most developed regions of China(Zhou *et al.* 2008; Zhang *et al.* 2009). Intensive urbanization and industrial activities have resulted in severe degradation of the aquatic ecosystem, with about 5×10^6 tons of sewage discharged into the region daily (Dai & Gu 1990). Understanding early growth of anchovy in the YRE could provide valuable information to conserve fishery resources in degraded environments.

Otoliths are widely used to reveal chronological patterns in growth of early life stages of fish (Ding *et al.* 2015; Starrs *et al.* 2016). As growth increments within them are deposited on a daily scale, otoliths can be used to back-calculate days and rates of growth. Accordingly, studying variations in patterns of otolith deposition of Japanese anchovy could reveal key information on the early life history of this species(Starrs *et al.* 2016). We use information obtained from anchovy otoliths to achieve two overarching aims: 1) to relate patterns in early growth of fish hatching within a season on different dates to environmental variations throughout the hatching season; and 2), to compare growth rates ofYRE anchovy with those of populations elsewhere to determine if geographical patterns in growth exist. To our knowledge, this is the first research focusing on the early life history of anchovy in the YRE. Ourresults could improve the understanding of anchovy growth and recruitment in a highly exploited ecosystem.

1. Materials and methods

2.1 Field Sampling

Larval Japanese anchovy were collected in May 2012 during the "Spring investigation of fishery resources and ecology in Yangtze River Estuary" survey. Larvae were sampled at 40 stations set from the mouth of the Yangtze River to its offshore waters (Figure 1). At each station, anchovy were sampled using a 3 m horizontal plankton net (0.8 m diameter with 0.5 mm mesh size) towed at two knots for 10 minutes at the surface. Anchovy were collected from only two southwestern stations: 29 (1129 individuals) and 30 (1342 individuals). Larvae were immediately preserved in 90% ethanol and taken backto the laboratory.All specimens were collected in accordance with wild animal conservation law issued by the People's Republic of China for the purposes of conducting research on Japanese anchovy.

2.2 Environmental data collection

Daily sea surface temperatures (SST) for stations 29 and 30 from 26 February to 3 May 2012 (anchovy growth season in this study; see Results) were obtained from NOAA SST High Resolution Dataset (*http://www.esrl.noaa.gov/psd/*). SST data were generated from an Advanced Very High Resolution Radiometer (AVHRR), providing time series SST data at very high resolution (1.09 km).

2.3 Otolith microstructure analysis

A subset of 200 individuals were randomly selected for otolith microstructure analysis from the total larval catch from each station. Standard length (SL) of each larva was measured to the nearest mm, before both right and left sagittal otoliths were extracted under a dissecting microscope. Either the right or left otolith was mounted on a slide using melting thermoplastic glue and polished with lapping film until increments could be clearly interpreted. Each unbroken otolith section was photographed at 400× magnification using a digital camera fixed to a light microscope (BH2, Olympus Optical Co. Ltd., Tokyo, Japan). Numbers and widths of otolith increments were counted and measured along the maximum otolith radius (OR) from the nucleus to the edgefollowed detailed procedures described in Liu *et al.* (2015).

2.4 Data analysis

As the first otolith increment in anchovy is deposited on the fourth day after hatching, the age of each anchovy in days (D) was determined as three plus the increment number observed in otolith section (Figure 2) (Tsuji and Aoyama 1984). Hatch dates were back-calculated by subtracting age from the catch date (May 3 for both stations). The biological intercept method was used to back-calculate somatic growth rates (Campana 1990), with SL of anchovy at hatching (5.6 mm) used as the biological intercept (Tsuji and Aoyama 1984). Student *t* tests were used to compare frequency distributions of SL and age between stations. Linear regression was used to fit relationships between SL and OR and between SL and age. Analysis of covariance (ANCOVA) was used to compare inter-population variation in SL-OR and SL-age relationships.

Larval anchovy from each station were further divided into three nearly equal-sized groups (according to hatch dates) for the comparison in early growth trajectory. Anchovy hatching from February 26 to March 16 were categorized “early group”, from March 17 to March 26 as “middle group”, and from March 27 to April 6 as “late group”. A repeated measures analysis of variance (RM-ANOVA) was used to compare inter-group growth trajectories within a population. Given the minimum age of anchovy was 24, the level of RM-ANOVA was set at 24 to include all samples; the within-subject factor was growth rate, and the between-subject factor was group.

2.5 Inter-population comparison

Early life traits of anchovy in YRE were compared with published data for populations from other regions (for which both onset of hatching season and early growth rates were available). Data of populations with earliest hatchingdates were selected as representative if more than one study was reported for a region. Consequently, data from populations in northeastern Taiwan and northeastern Japan were used for intra-population comparisons. The median growth rate of a population was used because mean growth rate data were not available.

2. Results

3.1 Environmental conditions

SST in YRE increased during the growth season, from 6.2 to 16.6°C (station 29) and 6.7 to 16.0°C (station 30) (Figure 3). As the SST on 3 May was almost twice that of 26 February. Three groups (early, middle, late) experienced different thermal environments, with the "early group" experiencing the lowest SST and the "late group" the highest.

3.2 Standard length (SL), hatch date and growth of YRE anchovy

Range in SL at station 29 (14.0–30.1 cm) was slightly greater than station 30 (11.1–32.0 cm) (Table 1). Back-calculated hatch dates ranged from February 26 to April 6 at station 29, and from February 28 to April 5 at station 30 (Figure 4; Table 1). Relationships between anchovy SL, OR and D were significant at each station ($P<0.01$) (Figure 5; Figure 6), but no significant inter-population differences (ANCOVA; $P>0.05$); SL-OR and SL-D relationships were described by common regression equations for two populations: SL = 0.096 OR + 7.60 ($R^2 = 0.79$, $P < 0.01$) and SL= 0.386D + 4.87 ($R^2 = 0.55$, $P < 0.01$).

Anchovy growth rates ranged 0.20 to 0.46 mm/d for two populations (Table 1). There were significant differences in growth trajectories among three groups for two stations (RM-ANOVA; station 29, $P<0.05$, station 30, $P<0.01$) (Figure 7), with the "middle group" showing highest growth rates and the "early group" the lowest. Growth trajectories of three groups were similar before day 25, but inter-group variability increased considerably afterwards.

3.3 Between-population comparison of anchovy hatching onset and growth rates

Ranges of SL for YRE anchovy largely overlapped with those from northeastern Taiwan and northeastern Japan (Table 2), suggesting that three populations were of similar ontogenic stage.The onset of hatching season generally decreased at 15 d for every five degrees latitude, with the population from northeastern Taiwan having the earliest date and that from northeastern Japan the latest. However, there was no consistent trend between growth rates and latitude. The median growth rate from the YRE population (0.33 mm d^{-1}) was about half that of northeastern Taiwan (0.64 mm d^{-1}) and northeastern Japan (0.60 mm d^{-1}) anchovy.

4. Discussion

By back-calculating hatch dates and early growth trajectories of anchovy from YRE, we describedintra- and inter-population variations in growth patterns of anchovy at various temporal and spatial scales. Given the significant impacts of growth on survival, any factor affecting early growth might cause pronounced fluctuations in population dynamics. Our research demonstrates the need to take variations in hatching date and growth into account when estimating recruitment dynamics of fishery resources.

Anchovy hatching on different dates differed in early growth trajectory suggeststheexistence of relationship between hatching date and fish growth, which might be contributed to increased SST during the growth period. Water temperature is widely regarded as a primary factor regulating fish growth rate. Not only does temperature affect individual metabolic rate, but it also indirectly affects food availability, collectively contributing to variable growth rates (Takasuka *et al.* 2007; Bacha & Amara 2012). The highest growth rates occurred in “middle group” fish, which were also represented by the greatest number of larvae, suggests a possible coupling between growth and offspring production(Heino and Kaitala 1999; Zera and Harshman 2001).

Growth rates ofanchovy from YRE were lower than those from Japan and Taiwan. This result is unusual as the highly productive waters of the YRE were expected to promote fish growth (Zhou *et al.* 2008). We believe two factors might be responsible: 1) fish living in polluted waters grow slowly, redirecting energy for growth toward tolerance of polluted, degraded conditions (Amara *et al.* 2007; Amara *et al.* 2009); and 2) natural variation in life-history traits of fish from different areas account for observed differences in growth(Conover & Present 1990; Sexton et al. 2002).. Conover & Present (1990) reported that populations of Atlantic silverside from different latitudes have distinct growth rates as the adaptation to the living environment. Overall, reduced anchovy growth in the YRE will result in decreased fish length at the end of the first growing season, depressing first-year over-winter survival rates and causing weaker recruitment(Amara *et al.* 2007; Amara *et al.* 2009).

Later hatching dates for populations at higher latitudes fit a pattern of “counter-gradient variation”, revealing adaption of anchovy throughout the northwest Pacific Ocean (Conover & Present 1990; Carmona *et al.* 2011). Water temperature and photoperiod are recognized as the two main factors affecting the onset of spawning season for teleost fish(Lappalainen & Tarkan 2007; Benejam *et al.* 2009). Higher water temperature and longer day length at lower latitudes promote fish growth, accelerating maturation and advancing reproduction(Tarkan 2006; Benejam *et al.* 2009). Our results provide valuable new information for estimating hatching onsets of anchovy, which can be effectively integrated into the management of anchovy resources.

Estuaries provide important nursery grounds for freshwater, estuarine and marine fishes (Amara *et al.* 2009). However, increased environmental pollution and anthropogenic activities are threateningthe functional integrity and life-supporting capacity of estuaries (Gilliers *et al.* 2006; Bacheler *et al.* 2009). Not only do we report intra-population variation in early growth of anchovy hatching on different dates, but for anchovy from this region to have significantly lower growth rates compared with populations from other regions. Future habitat modification, such as through dam construction or as a consequence of climate change, might further change the estuarine environment and imperil fishery resources. We suggest greater conservation of YRE nursery grounds to promote sustainable development of fishery resources.

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Figure captions:

Figure 1 Survey stations (solid circles) in the Yangtze River Estuary, East China Sea.

Figure 2 Otolith section of a 55-d-old anchovy from the Yangtze River Estuary: nucleus (N) and maximum otolith radius indicated by arrows. Increment numbers and widths counted and measured along the maximum otolith radius.

Figure 3 Trend in sea surface temperature (SST) during growth seasons of anchovy at stations 29 and 30.

Figure 4 Frequency distributions of standard length (a) and hatch dates (b) of anchovy from stations 29 and 30.

Figure 5 Relationship between standard length (SL) and otolith radius (OR) of anchovy from stations 29 (SL = 0.097OR+ 6.77 (R^2 = 0.80, $P < 0.01$)), and 30 (SL= 0.089OR + 9.33 (R^2 = 0.82, $P < 0.01$)).

Figure 6 Relationship between standard length (SL) and age (days, D) of anchovy from stations 29 [SL= 0.37D + 4.6 (R^2 = 0.54, $P < 0.01$)) and 30 [SL= 0.37D + 6.4 (R^2=0.59, $P < 0.01$)).

Figure 7 Growth trajectories back-calculated from otolith microstructure of anchovy in three groups from stations 29 and 30, respectively (excluding days where anchovy numbers were less than five).

Table 1. Range of standard lengths, hatching dates andmean growth ratesof anchovy in the stations 29 and 30 in the Yangtze River Estuary. Population in each station was divided into three nearly equal-sized groups according to hatch dates. Please refer Materials and methods for more information.

Station	Group	N	Standard length (mm)		Hatching date	Mean growth rate (mm d^{-1})	
			Mean	Range		Mean	Range
29	Early	51	21.1	17.1 - 32.0	2/26-3/16	0.33	0.25 - 0.46
29	Middle	96	17.8	13.0 - 24.2	3/17-3/26	0.31	0.20 - 0.43
29	Late	41	14.4	11.1 - 17.2	3/27-4/6	0.3	0.21 - 0.40
30	Early	55	21.2	17.1 - 30.1	2/28-3/16	0.32	0.23 - 0.42
30	Middle	94	17.9	14.9 - 25.4	3/17-3/26	0.31	0.22 - 0.46
30	Late	27	14.5	14.0 - 18.7	3/30-4/5	0.29	0.20 - 0.41

Table 2. Comparisons of standard lengths, hatching onsets and mean growth rates of three main anchovy populations distributed overthe northwesternPacific Ocean.

Region	Latitude	Standard length (mm)		Hatching onset	Mean growth rate (mm		
		Minimum	Maximum		Minimum	Median	Max
Northeastern Taiwan	24 - 25°N	17.2	31.3	2/12	0.37	0.64	0
The Yangtze River Estuary	30 - 31°N	11.1	32	2/26	0.2	0.33	0
Northern Japan	35 - 40°N	20.0	35.0	3/3	0.49	0.6	0

Table 1 (on next page)

Range of standard lengths (mm), hatching dates and mean growth rates (mm d^{-1}) of anchovy in the stations 29 and 30 in the Yangtze River Estuary.

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29	Late	41	14.4	11.1 - 17.2	3/27-4/6	0.3	0.21 - 0.40
30	Early	55	21.2	17.1 - 30.1	2/28-3/16	0.32	0.23 - 0.42
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Table 2(on next page)

Comparisons of standard lengths (mm), hatching onsets and mean growth rates (mm d^{-1}) of three main anchovy populations distributed over the northwestern Pacific Ocean.

Region	Latitude	Standard length (mm)		Hatching onset	Mean growth rate (mm d^{-1})			Source
		Minimum	Maximum		Minimum	Median	Maximum	
Northeastern Taiwan	24 - 25°N	17.2	31.3	2/12	0.37	0.64	0.91	Chiu and Chen (2001)
The Yangtze River Estuary	30 - 31°N	11.1	32	2/26	0.2	0.33	0.46	Present study
Northern Japan	35 - 40°N	20.0	35.0	3/3	0.49	0.6	0.71	Takahashi et al. (2001)

Figure 1

Location of 40 survey stations in the Yangtze River Estuary, East China Sea. Each station was indicated by the solid circle.

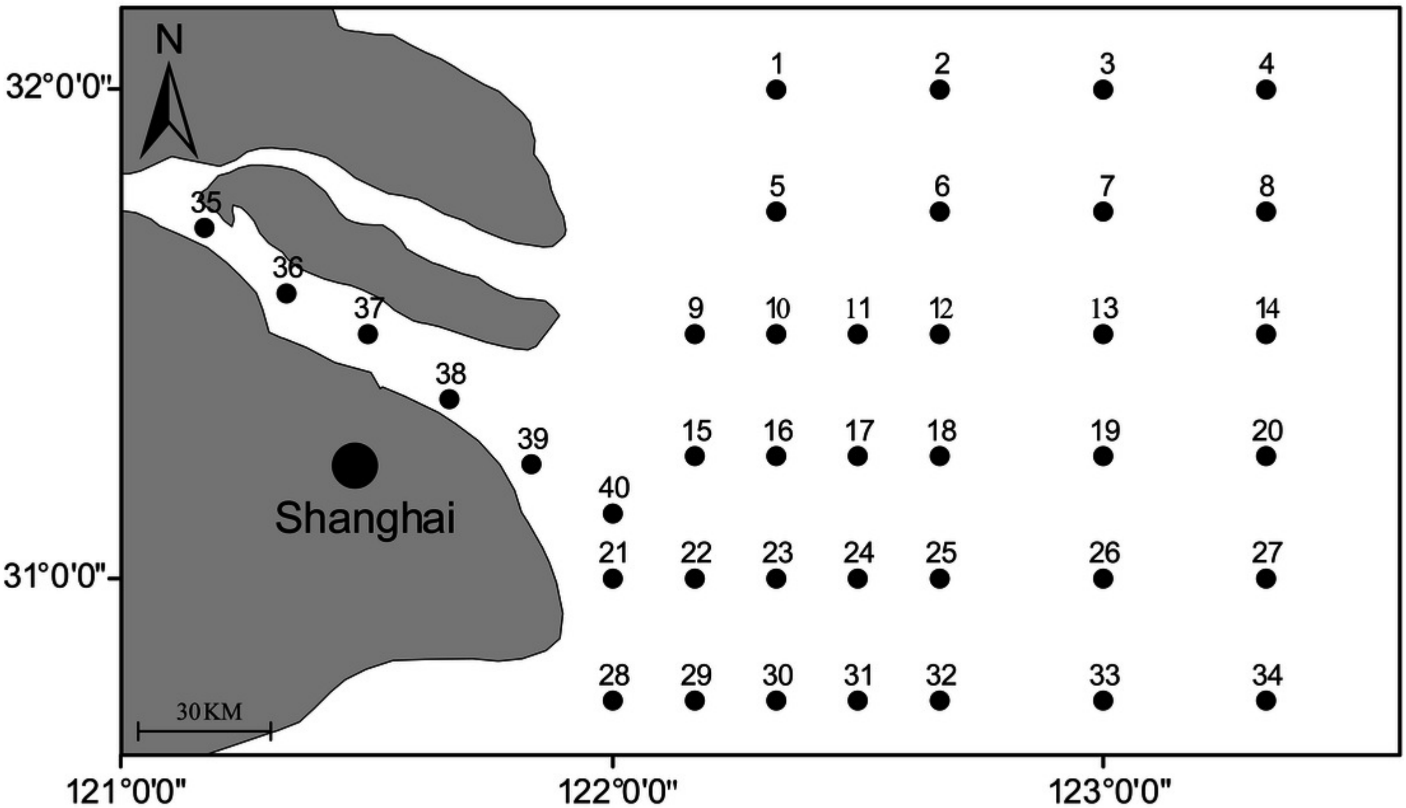


Figure 2

An otolith section of a 55-d-old anchovy in the Yangtze River Estuary.

The nucleus (N) and the maximum otolith radius are indicated by arrows. Increment numbers and widths were counted and measured along the maximum otolith radius.

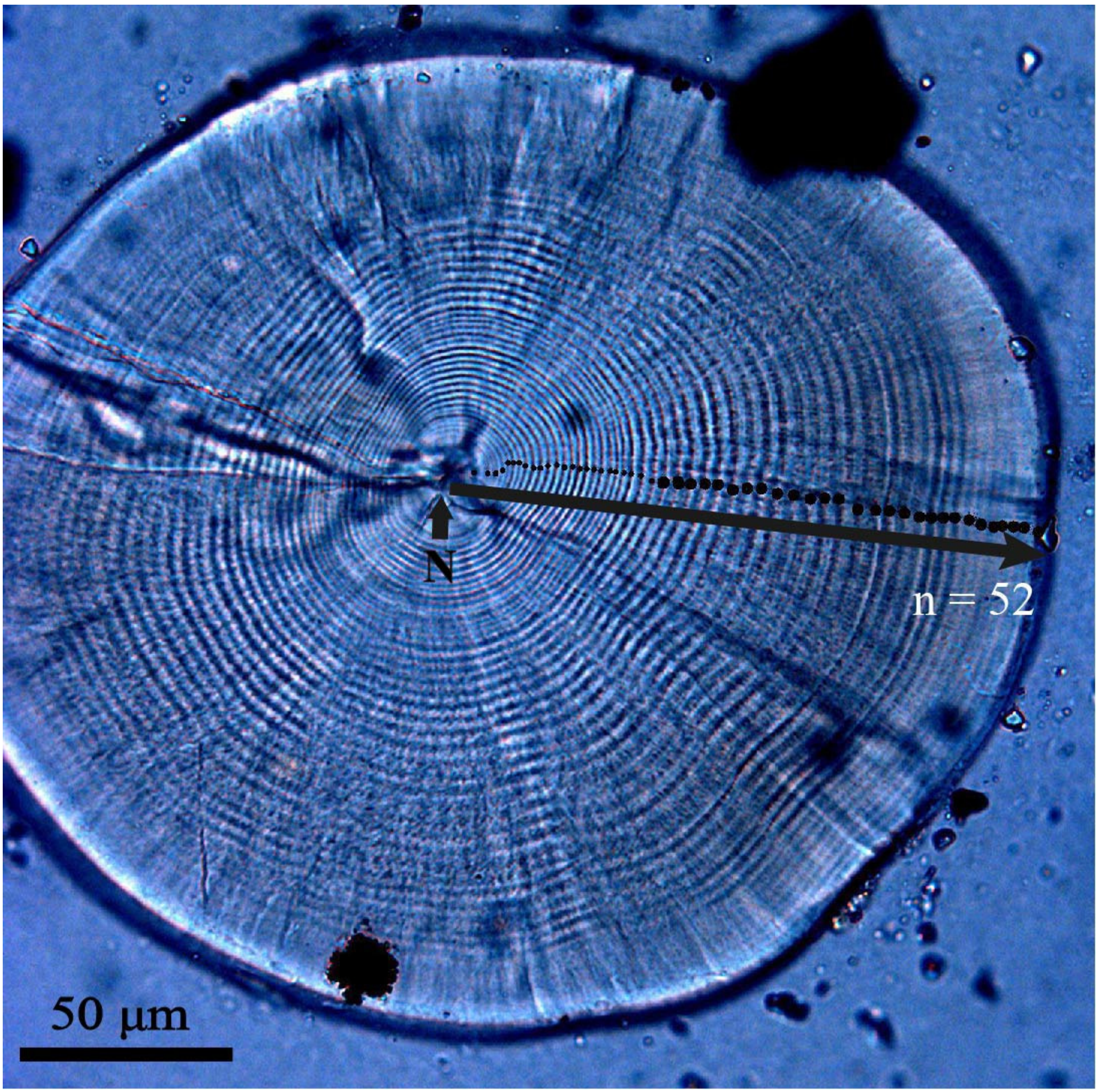


Figure 3

The increased trend of sea surface temperature (SST) during growth seasons of anchovy in the station 29 and 30. rs and widths.

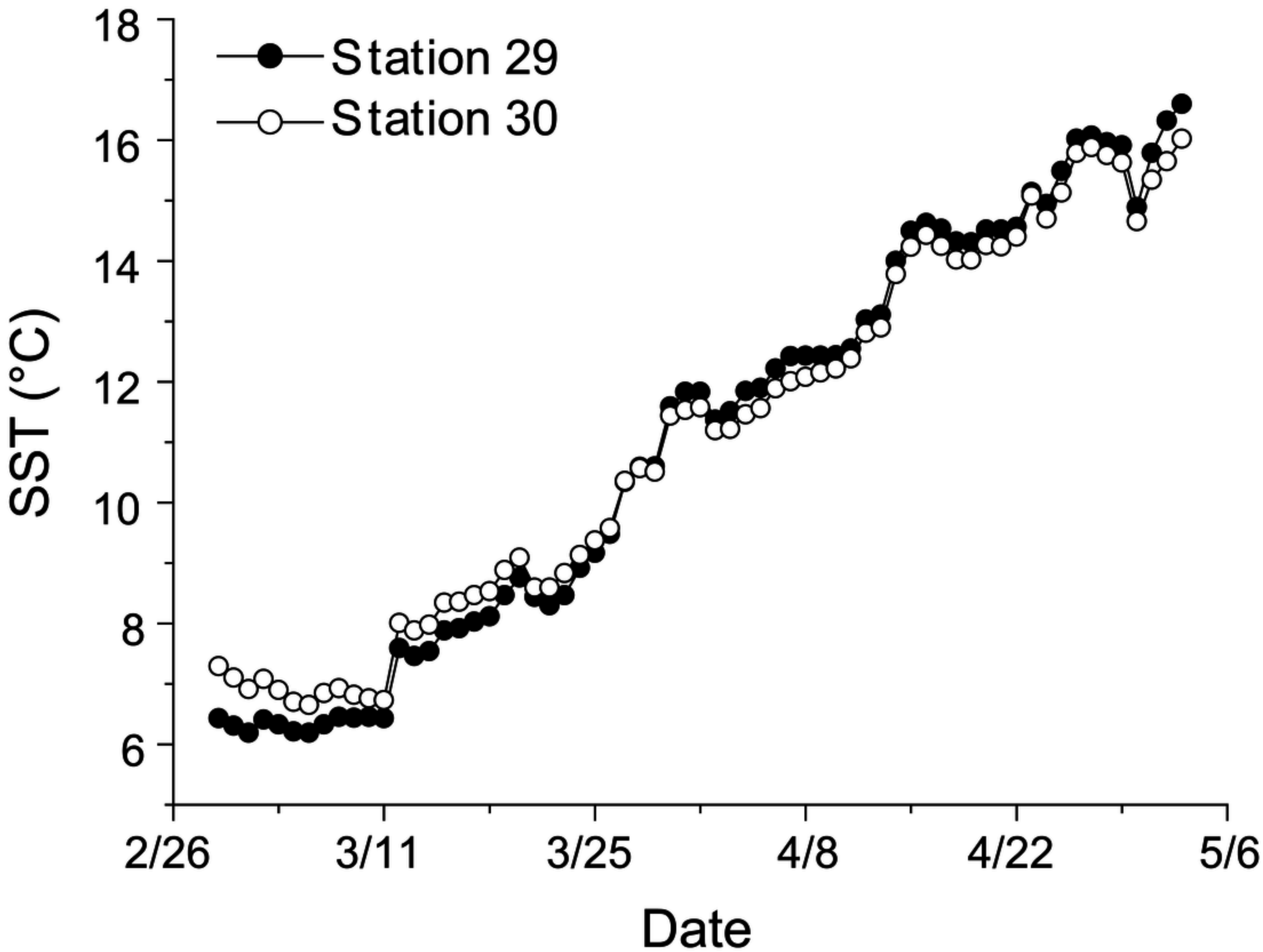


Figure 4

Frequency distributions of standard lengths and hatch dates of anchovy in stations 29 and 30. (a) standard length; (b) hatch date.

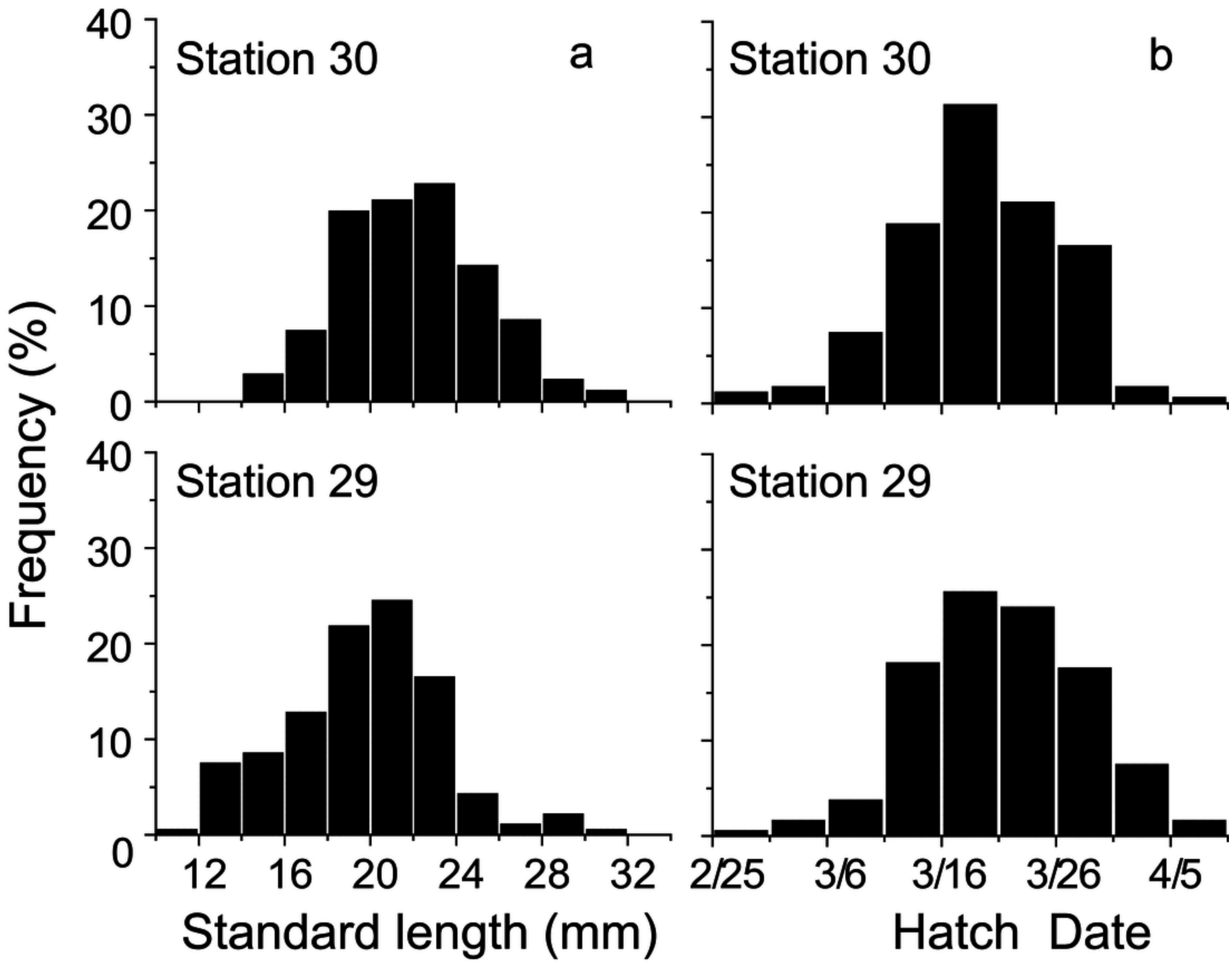


Figure 5

Relationships between standard length (SL) and otolith radius (OR) of anchovy in station 29, SL = 0.097OR+ 6.77 (R^2 = 0.80, P < 0.01) and station 30, SL= 0.089OR + 9.33 (R^2 = 0.82, P < 0.01).

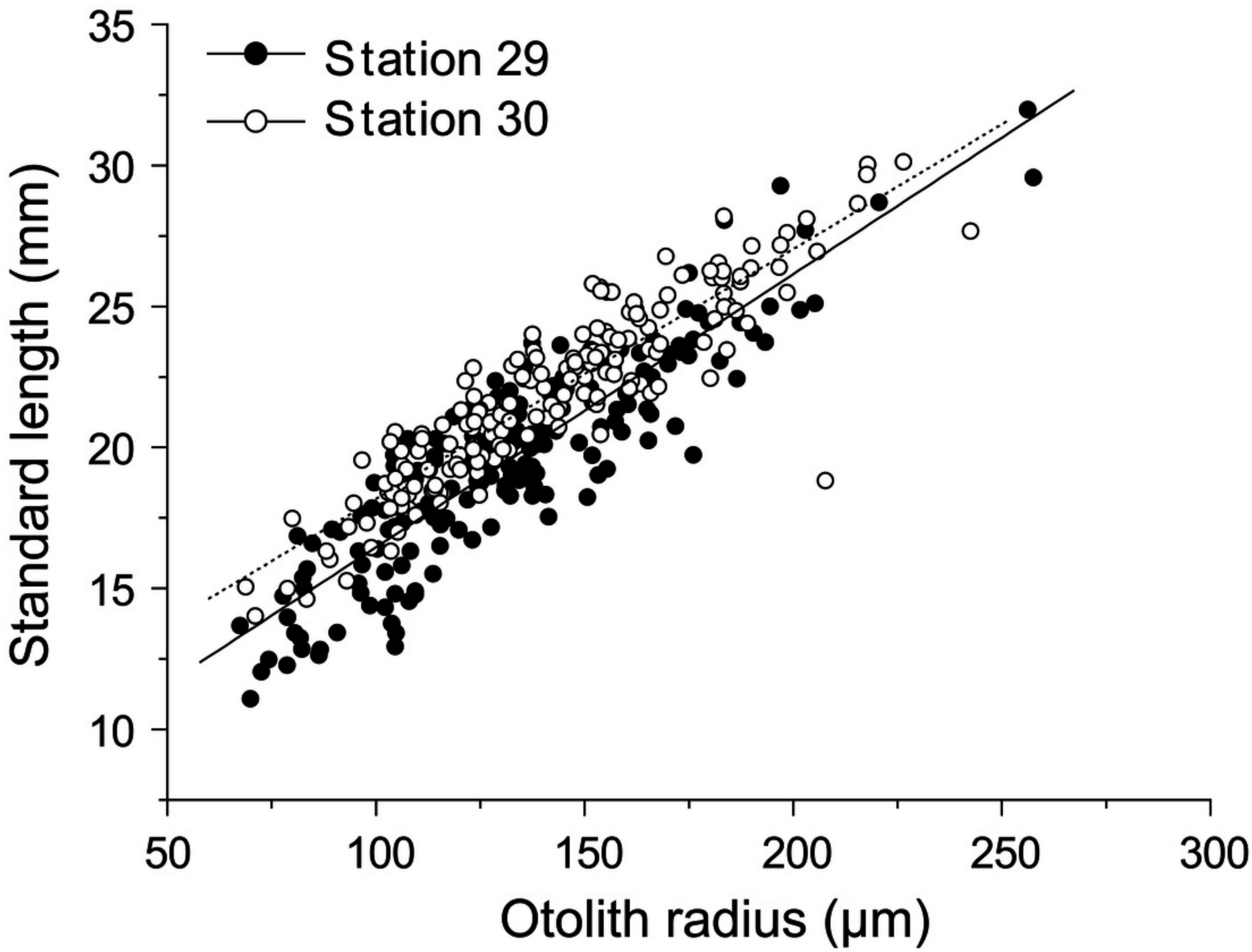


Figure 6

Relationships between standard length (SL) and age (in days, D) of anchovy in station 29, SL= 0.37D + 4.6 (R^2 = 0.54, P < 0.01) and station 30, SL= 0.37D + 6.4 (R^2=0.59, P < 0.01).

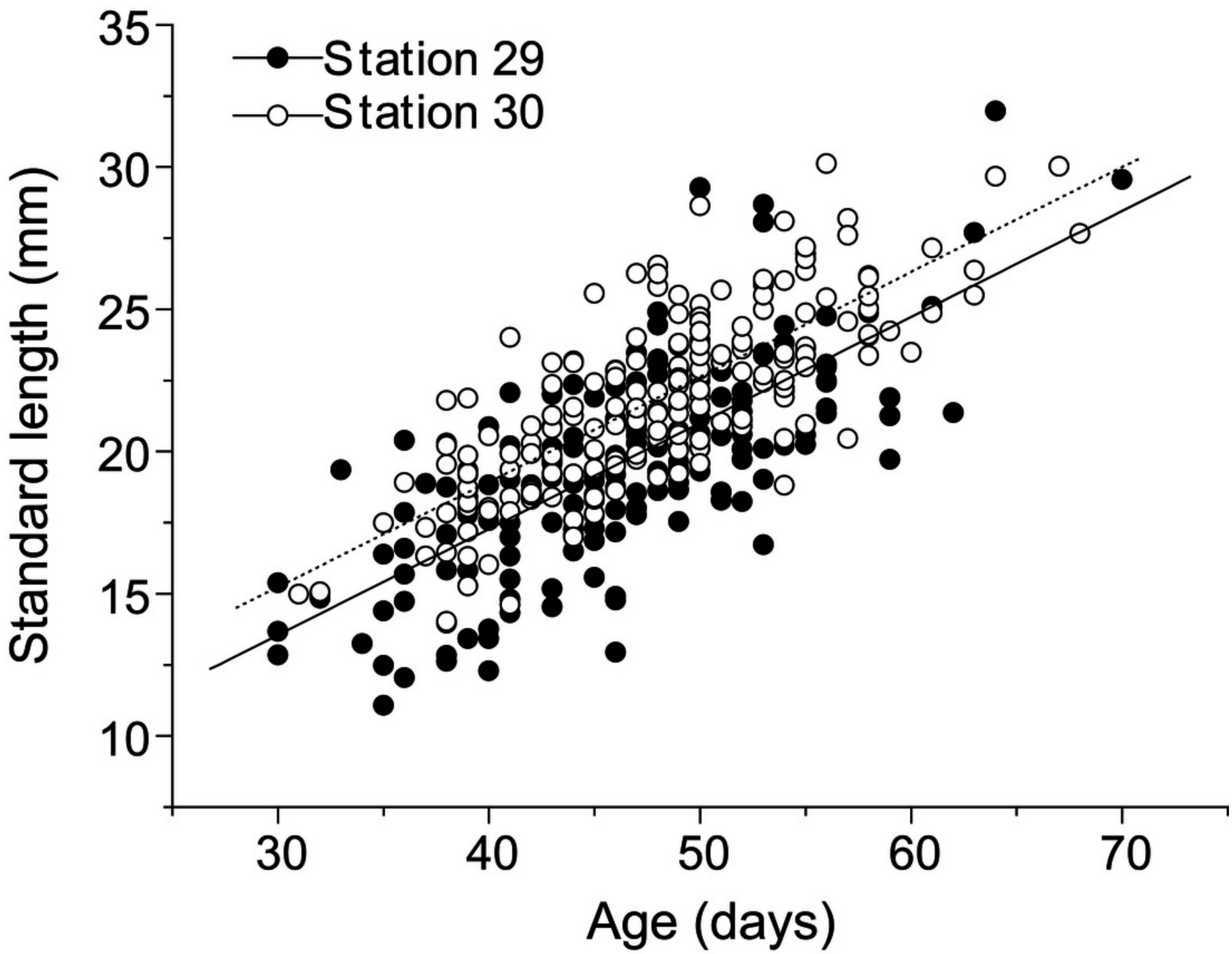
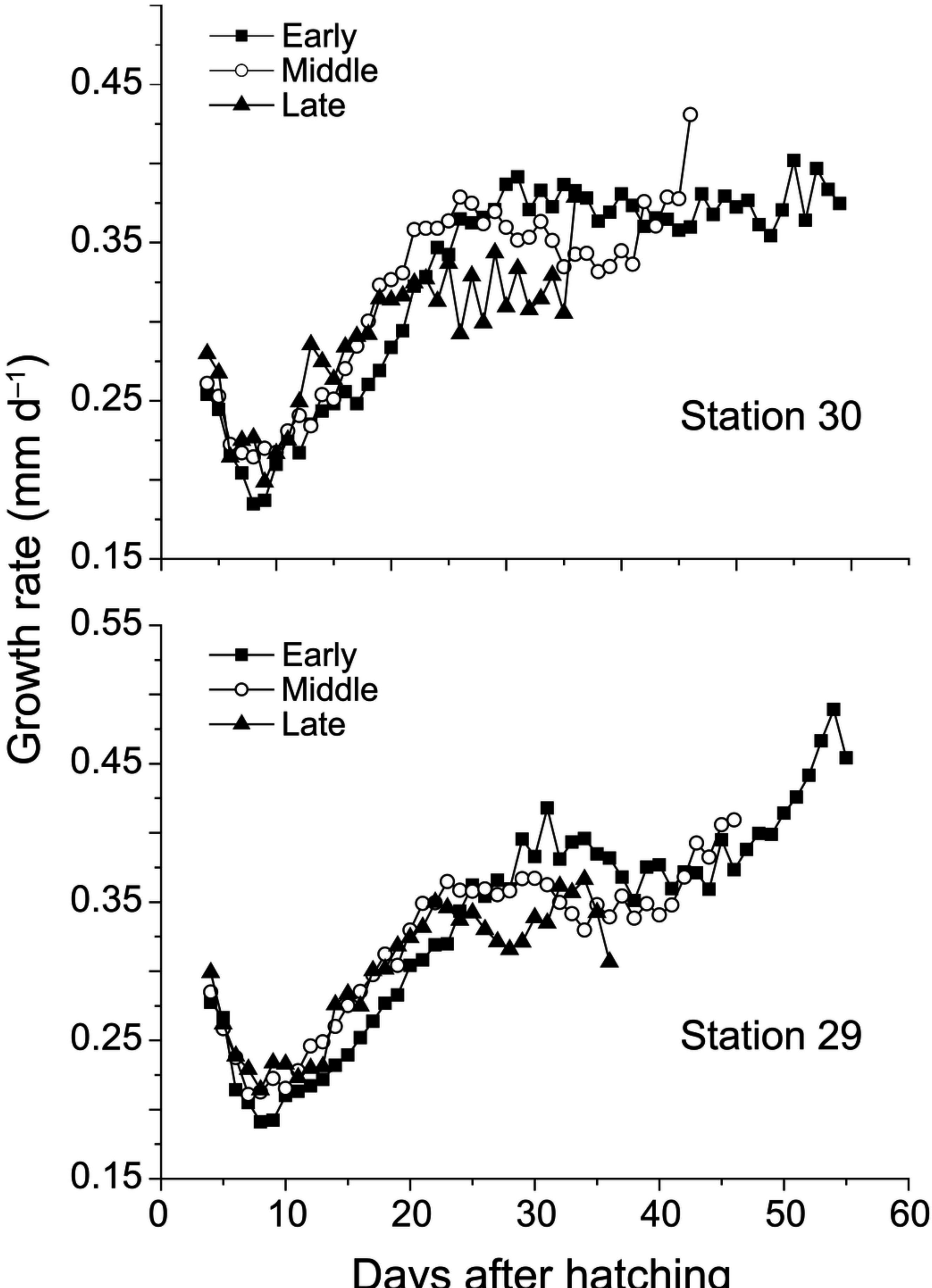


Figure 7

Growth trajectories back-calculated from otolith microstructure of anchovy of three groups in stations 29 and 30 respectively.

Days where anchovy numbers were less than five were excluded for reducing the bias among individuals.


Early
Middle
Late
Station 30
Early
Middle
Late
Station 29
Growth rate (mm d^{-1})
Days after hatching
0.45
0.35
0.25
0.15
0.55
0.45
0.35
0.25
0.15
0
10
20
30
40
50
60