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Growth and Survival of Pacific Sardine (*Sardinops sagax*) in the California Current Region

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Abstract

We hypothesized that faster growth during the larval and juvenile stages results in higher survival in Pacific sardine (*Sardinops sagax*) in the California Current region. Growth rate estimated from the width of otolith daily increments was compared among larval, juvenile and pre-recruit *S. sagax* spawned in 2004 and 2006. Larvae, juveniles and pre-recruits were collected in spring, autumn and the spring of the subsequent year, respectively. Hatch-date distribution of the pre-recruits ranged from April to August with peaks in late spring and summer, corresponding to the seasons of spawning and larval production in the Southern California Bight. The pre-recruits, from eggs hatched in the late spring, were assumed to originate from the larvae and juveniles from eggs hatched in April to June. Fish collected as pre-recruits grew faster than those collected as juveniles during the 3–5 months after hatching. Growth-selective survival for the late spring-hatched cohorts took place during July–November for the early juveniles. These results are consistent with the hypothesis that early juveniles with faster growth rate during summer and autumn had a higher probability of survival to the adult stock in the California Current region.

Key words: California Current, growth, increment width, otolith, Pacific sardine, recruitment, Southern California Bight, survival.

Introduction

The annual catch of Pacific sardine (*Sardinops sagax*) in the Pacific coastal waters off Mexico, the United States of America (USA) and Canada increased from 10 000 metric ton (t) in the early 1980s to over 600 000 t in the early 2000 (FAO, 2007), which is equivalent to the maximum catch in the 1930s–1940s (McFarlane *et al.*, 2002). Fishing grounds for *S. sagax* expanded northward from the Pacific coastal waters off Baja California and southern California in the 1980s to the waters off Oregon, Washington and Canada in the 1990s with an increase in the population (McFarlane and Beamish, 2001; Rodríguez-Sánchez *et al.*, 2002; Smith, 2005). Spawning was reported off Oregon and Washington beginning in the 1990s (Emmett *et al.*, 2005).

Survival rate and recruitment to the adult stock have been considered to be a positive function of the rates of growth and development during the early life stages in marine fishes (Houde, 1987; Andersen, 1988; Leggett and Deblois, 1991). Based on stage-specific numerical models for *S. sagax*, mortality of eggs and growth rate during larval stage were important determinants for population growth since late 1980s (Smith *et al.*, 1992; Butler *et al.*, 1993; Lo *et al.*, 1995).

Mechanisms relating recruitment to growth rate for *S. sagax*, however, are still unclear. For Japanese sardine (*Sardinops melanostictus*), interannual variations in growth rate during the early juvenile stage explained variation in recruitment in the western North Pacific (Takahashi *et al.*, 2008). Understanding of growth and survival processes during the early life stages off California would reveal mechanisms of population dynamics and be valuable for the management of the *S. sagax* fishery in the California Current region.

Otolith increment analysis enables examination of growth-selective survival during the early life stages of marine fishes. Methot (MS 1981, 1983) estimated the hatch date of juvenile northern anchovy (*Engraulis mordax*) based on the number of otolith increments. He compared the hatch date distribution to the larval production for the same year class and found that larvae spawned in the second half (April–May) of the entire spawning season (January–May) had faster growth rate and a higher probability of surviving to the juvenile

stage. Width of otolith increments for Japanese anchovy (*Engraulis japonicus*) was positively correlated with the daily growth rate in rearing experiments (Takahashi and Watanabe, 2004). Comparison of the widths between larvae and adult survivors showed that metamorphosing larvae with faster growth rates had a higher probability of survival to the adult stage than those with slower growth rates (Takahashi and Watanabe, 2004). Comparing growth patterns, manifest in the width of otolith increments, for *S. sagax* among different life stages could reveal processes for selective survival during the early life stages.

We hypothesized that larvae and juveniles with faster growth rates comprise a larger portion of the survivors collected as juveniles and pre-recruits for *S. sagax* in the California Current region. Developmental stages of *S. sagax* in this study were defined by standard length (SL) (Smith *et al.*, 1992; Butler *et al.*, 1993; Moser, 1996); fish with SL of 3.5–15 mm and 15–35 mm were defined as in the early larval and late larval stages, respectively. Fish with SL of 35–110 mm were defined as in the juvenile stage. Fish with SL from 110–160 mm were defined as pre-recruits based on the fact that *S. sagax* can grow as large as 160 mm approximately 1 year after hatching (Butler *et al.*, 1993, 1996) and 50% of females are mature at *ca* 160 mm SL (Macewicz *et al.*, 1996). We collected early larval, late larval, juvenile and pre-recruit *S. sagax* off California, and compared hatch-date distributions and growth patterns during early life, by analysis of otolith increments, among the four different stages.

Materials and Methods

Fish sampling

Early and late larvae, juveniles, and pre-recruits were collected in the spring and autumn and in the spring of the subsequent year for fish spawned in 2004 and 2006 (Table 1). Early larval *S. sagax* were collected using the Bongo nets off California in 2004, sorted from the plankton catch, and preserved in 95% ethanol. Standard procedures for the CalCOFI Bongo net tow have been described by Kramer *et al.* (MS 1972) and Smith and Richardson (1977). Late larval *S. sagax* were collected using mid-water trawls off California in 2006. Juvenile *S. sagax* were collected using a beach seine at the La Jolla Shores beach in 2004 and obtained from the fishery off La Jolla in 2006. Pre-recruit *S. sagax* were collected using mid-water trawls off California in 2005 and 2007. The late larvae, juvenile and pre-recruits were immediately frozen at -25°C. Early larvae were photographed with a digital camera and a dissecting microscope at 10–20× magnification, and the SL measured to the nearest 0.1 mm on a video monitor using measurement software (Scion Image, Scion Corporation). Standard lengths of the late larvae, juveniles and pre-recruits were measured using a digital caliper.

Otolith processing and measuring

Sagittal otoliths were dissected out, cleaned under a dissecting microscope at 10–50× magnification, and mounted, with the sulcus of the otolith facing down, on a glass slide using mounting media (EUKITT, O. Kindler, Germany). Since the otoliths of sardine thicken after metamorphosis, the otoliths of juveniles and pre-recruits were ground using sandpaper (grit #2000) and polished using lapping film (grit #8000) to allow enough light to be transmitted to clearly see the nucleus and increments.

A random sample of up to 20 otoliths at each sampling station was used for the growth analysis of the early and late larvae, and the pre-recruits. Since the juveniles were collected only off La Jolla in November, a total 50 otoliths was used for growth analysis of the juveniles in each year. Otolith radius (OR) was measured from the nucleus to the margin and increment width (IW) was measured along a transect to the post rostrum portion of the otolith. Otolith measurement was conducted using an otolith measurement system (Ratoc System Engineering Co., Ltd.) consisting of a light microscope with 100–1000× magnification, CCD camera, video monitor, and image analyzer controlled by a personal computer. Measurement error generally increases in otoliths of older fish, especially pre-recruits, because the increments in the marginal area, formed in the winter, are narrow and thus difficult to resolve. Otoliths of juveniles and pre-recruits were measured separately twice by the same reader, and individuals with differences in estimated age of more than 15 days were excluded from the growth analysis.

Growth analysis

Daily formation of otolith growth increments has been validated for the larval and juvenile stages of *S. sagax* in rearing experiments (Butler, MS 1987). The first increment is deposited at the completion of yolk absorption and first feeding. The development rate of early larvae of *S. sagax* varies with water temperature (Lasker, 1964). The lower jaw became functional *ca* 156 hours after hatching at 14oC, which was the average temperature for positive collections of *S. sagax* eggs off California during 1994–2004 (Lo *et al.*, 2005). Hence, daily age was calculated by adding seven to the total number of daily increments, and hatch date was estimated by subtracting the age from the collection date for each individual fish.

Standard length at age n days (d) after hatching was calculated using the biological intercept method (Campana, 1990; Campana and Jones, 1992). The relationship between OR and SL changed from non-linear during the larval stage to linear after the juvenile stage for *S. sagax* (Butler, MS 1987). The non-linear equation, was used for early and late larvae, $L_n = aR_n^b$ and the linear equation, $L_n = aR_n + b$ was used for juveniles and pre-recruits ($n = 7, 8,..., c-1, c$) where L_n is SL at age n, R_n represents OR at age n, and c is daily age at capture. Coefficients a and b were estimated from OR and SL at first increment deposition and the date of fish collection. Since Lasker (1964) reported that SL at first feeding (7 d) ranged from 5.5–6.0 mm, we assumed SL at first increment deposition was 5.5 mm. Since the juvenile stage begins at *ca* 80 d (see Results), there might be error in the back-calculated SL during the larval stage (<80 d) for the

juveniles and pre-recruits. We excluded back-calculated SLs for age <80 d for fish collected as juveniles and pre-recruits. In order to reconstruct growth rate history during the larval stage of fish collected as juveniles and pre-recruits, we used IW at age as a proxy of somatic growth rate, because IW is linearly correlated with daily somatic growth rate during the larval stage for *E. japonicus* (Takahashi and Watanabe, 2004). Pre-recruits were assigned to two cohorts, those hatched in spring and those hatched in summer, based on the frequency distribution of hatch dates (see Results). Since hatch dates of the early larvae, late larvae, and juveniles were in the spring, we compared growth patterns between cohorts spawned in the spring.

Results

Distribution

Early larvae were found in higher concentration north of Pt. Conception than south of Pt. Conception, including the Southern California Bight in 2004 (Fig. 1). Late larvae were found only in the Southern California Bight in 2006. Pre-recruits were distributed in the waters north of Pt. Conception and in the Southern California Bight in 2005 and 2007. The number of pre-recruits collected per trawl haul in 2005 was 5–10 times larger than that in 2007.

Hatch dates

The modal frequency of hatch date of the early larvae collected from late March to late April 2004 in the CalCOFI region was in early April 2004 (Fig. 2). The modal frequency of hatch date of the juveniles collected on 8 November 2004 off La Jolla was early to mid-May 2004. The range of hatch dates of pre-recruits collected from late March to late April 2005 between San Diego and San Francisco was from mid-April to the end of August, with peaks in May and July 2004.

The frequency distribution of hatch date of the late larvae collected from early May to mid-June in 2006 showed two peaks, in early spring, from late March to early April, and in late spring, from late April to early May 2006 (Fig. 2). The modal frequency of hatch date of the juveniles collected on 3 November 2006 off La Jolla was early May 2006. The range of hatch dates of pre-recruits collected from mid-April to mid-June 2007, between San Diego and San Francisco, was late April to late August, with peaks in May and June 2006.

Otolith Increment Width at age

Mean IW of pre-recruits hatched in late spring (late April to mid-June) 2004 increased from 3.0 ± 0.8 (S.D.) μm at 20 d to 8.2 ± 1.6 μm at 80 d, and then decreased to 3.9 ±1.0 μm at 150 d (Fig. 3). Although no significant differences in mean IW were found between juveniles and pre-recruits at 20 d (*t*-test, $P = 0.471$) and at 80 d (*t*-test, $P = 0.711$), mean IW at 150 d for pre-recruits was significantly larger than that of juveniles (*t*-test, $P <0.001$). Since hatch dates for the early larvae were out of the ranges for the juveniles and pre-recruits, we excluded the early larvae from the comparative analysis for growth-selective survival.

Mean IW of pre-recruits hatched in the late spring (late April to mid-May) 2006 increased from 3.0 ± 0.3 μm at 20 d to 7.5 ± 2.3 μm at 80 d, and then decreased to 4.0 ± 1.1 μm at 150 d. Mean IW at 20 d was not significantly different among the three developmental stages (ANOVA, $P = 0.663$). Although no significant difference in the mean was found between pre-recruit and juveniles at 80 d (*t*-test, $P = 0.121$), mean IW at 150 d of pre-recruits was significantly larger than that of juveniles (*t*-test, $P <0.001$).

Back-calculated Standard Length

Mean back-calculated SL of pre-recruits hatched in the late spring 2004 increased from 45.5 ± 7.7 mm at 80 d to 94.1 ± 8.6 mm at 150 d (Fig. 4). Mean SL of juveniles was 36.4 ± 4.1 mm at 80 d and 67.7 ± 3.4 mm at 150 d and significantly smaller than that of pre-recruits at both 80 d (*t*-test, $P <0.001$) and 150 d (*t*-test, $P <0.001$). Mean back-calculated SL of pre-recruits hatched in late spring 2006 increased from 48.2 ± 6.9 mm at 80 d to 94.4 ± 6.6 mm at 150 d. Mean SL of juveniles was not significantly different from that of pre-recruits at 80 d (*t*-test, $P = 0.949$) but was significantly smaller than that of pre-recruits at 150 d (*t*-test, $P <0.001$). Mean back-calculated SL of late larvae hatched in late spring was 22.2 ± 1.9 mm at 40 d.

Discussion

Source populations

Hatch dates of pre-recruits from mid-April to late August with peaks in spring and summer (Fig. 2) were comparable to the times of egg and larval production in the Southern California Bight. The main spawning season of *S. sagax* ranged from February to September with a peak in May and June during 1951–1989 (Hernandez-Vazquez, 1994). Larval production occurred from February to August with peaks in April and August during 1983–1998 (Logerwell and Smith, 2001). This suggests that pre-recruits hatched in late spring were survivors of the larvae and juveniles collected in this study. Since no survey was conducted after May for the early larvae and after June for the late larvae, we could not observe early and late larvae hatched after that date.

Our results are consistent with sardine spawning and larval development having occurred primarily off central California, north of Pt.

Conception, in 2004, and off the Southern California Bight in 2006. Abundance of early larvae collected in April 2004 was higher in the waters north of Pt. Conception than in the Southern California Bight (Fig. 1). Most *S. sagax* eggs collected with Continuous Underwater Fish Egg Sampler (CUFES, Checkley *et al.*, 1997; Lo *et al.*, 2001) in April 2004 were north of Pt. Conception (Lo *et al.*, 2005). Late larvae were collected in the Southern California Bight but not in the waters north of Point Conception in 2006, as were eggs and early larvae in April 2006 (David Griffiths, Southwest Fisheries Science Center, La Jolla, California, USA, unpublished data). We acknowledge that our results are based on limited sampling and thus that spawning and larvae may have occurred at other times and places.

Otolith and somatic growth

Mean IW of juveniles and pre-recruits hatched during late spring in 2004 and 2006 showed that IW increased with age up to 70–90 d, sharply decreased thereafter to *ca* 150 d, and then decreased gradually after *ca* 200 d; no obvious peak of mean IW was found for the early and late larvae (Fig. 3). Mean back-calculated SL at 80 d ranged from 36–49 mm for juveniles and pre-recruit (Fig. 4). Moser (1996) showed that allometry of the length from the tip of the snout to the anus and the body depth relative to SL change dramatically in the SL range of 25–40 mm, which he defined as the period of transformation from the larval to the juvenile stages, *i.e.*, metamorphosis. This suggests that age at maximum IW of juvenile and pre-recruit *S. sagax* is indicative of the completion of metamorphosis and the initiation of the juvenile stage. Takahashi and Watanabe (2004) pointed out that the age at maximum IW for adult *E. japonicus* corresponds to the end of metamorphosis.

Growth-selective survival

The limited times and places our samples were collected preclude a rigorous test of the hypothesis that faster-growing early larvae had higher survival rate than those that grew slowly. However, the following results are consistent with this hypothesis.

The modal frequency of hatch date for early larvae appeared in the second half of the period of hatch dates in 2004 (Fig. 2). No survey was conducted to collect early larvae after mid-April. Hatch date distribution for the late larvae showed two peaks in the early and late spring in 2006 (Fig. 2). The late larvae hatched in late spring had faster growth and developmental rates than did those hatched in the early spring and late larvae hatched in the late spring had a higher probability of successful metamorphosis and survival to the juvenile stage than those hatched in the early spring (Takahashi, unpublished data). These results demonstrate that fish spawned after the early spring grew faster and had a higher probability of survival to the juvenile and pre-recruit stages than fish spawned earlier.

Mesoscale eddies in offshore waters contribute to faster growth and higher survival rates for *S. sagax* larvae 2–3 weeks after hatching (Logerwell and Smith, 2001; Logerwell *et al.*, 2001). A recent study showed that annual surplus production for *S. sagax* was positively correlated with nutrient and chlorophyll concentrations and, in turn, with open ocean upwelling forced by wind-stress curl from May to July (Rykaczewsky and Checkley, 2008). Thus, environmental conditions from spring to summer in the offshore waters could affect the population dynamics for *S. sagax* through growth-selective survival during the early larval stage.

Mean IW and back-calculated SL at 150 d were significantly larger for pre-recruits than for juveniles (Figs. 3 and 4). This indicates that larger juveniles with a faster growth rate had a higher probability of survival to the pre-recruit stage than smaller juveniles with a slower growth rate. Butler (1989) showed that variability in IW at age of juvenile *E. mordax* was larger in the early juvenile stage than in the larval stage during 1980–1984 in the California Current region. During the El Niño event of 1983, reduced zooplankton biomass caused growth rate to decline during the early juvenile stage but not during the larval stage compared to other years. Based on the hatch-date distribution of the pre-recruits spawned in the early spring in this study, the juvenile stage at three to five months after hatching corresponded to period of July–November. This is consistent with the hypothesis that food availability during summer and autumn controls sardine population dynamics through the mechanism of growth-selective survival in the early juvenile stage.

Acknowledgements

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