

Responses in growth rate of larval northern anchovy (*Engraulis mordax*) to anomalous upwelling in the northern California Current

MOTOMITSU TAKAHASHI,^{1*}† DAVID M. CHECKLEY JR.,¹ MARISA N.C. LITZ,² RICHARD D. BRODEUR³ AND WILLIAM T. PETERSON³

¹Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Dr., La Jolla, CA 92039-0218, USA

²Cooperative Institute for Marine Resources Studies, Oregon State University, Hatfield Marine Science Center, 2030 Marine Science Dr., Newport, OR 97365, USA

³NOAA Fisheries, Northwest Fisheries Science Center, Hatfield Marine Science Center, 2030 Marine Science Dr., Newport, OR 97365, USA

ABSTRACT

We examined variability in growth rate during the larval stage of northern anchovy (*Engraulis mordax*) in response to physical and biological environmental factors in 2005 and 2006. The onset of spring upwelling was anomalously delayed by 2–3 months until mid-July in 2005; in contrast, spring upwelling in 2006 began as a normal year in the northern California Current. Larval and early juvenile *E. mordax* were collected in August, September, and October off the coast of Oregon and Washington. Hatch dates ranged from May to September, with peaks in June and August in 2005 and a peak in July in 2006, based on the number of otolith daily increments. Back-calculated body length-at-age in the June 2005 hatch cohort was significantly smaller than in the August 2005 cohort, which had comparable growth to the July 2006 cohort. Standardized otolith daily increment widths as a proxy for seasonal variability in somatic growth rates in 2005 were negative until late July and then changed to positive with intensification of upwelling. The standardized increment width was a positive function

of biomass of chlorophyll *a* concentration, and neritic cold-water and oceanic subarctic copepod species sampled biweekly off Newport, Oregon. Our results suggest that delayed upwelling in 2005 resulted in low food availability and, consequently, reduced *E. mordax* larval growth rate in early summer, but once upwelling began in July, high food availability enhanced larval growth rate to that typical of a normal upwelling year (e.g., 2006) in the northern California Current.

Key words: California Current, delayed upwelling, growth rate, increment width, northern anchovy, otolith

INTRODUCTION

Subtle changes in vital rate during early life stages of marine fishes cause large variations in survival rate and hence abundance of recruitment to the adult stage (Houde, 1987). In the California Current ecosystems, survival during the early life stages of northern anchovy (*Engraulis mordax*) has been related to the frequency of winter storms through successful first feeding (Lasker, 1975; Peterman and Bradford, 1987). For Pacific sardine (*Sardinops sagax*), recruitment variability was linked with intensity of offshore upwelling driven by wind-stress curl through primary production and food availability (Ryckaczewski and Checkley, 2008). The production of small pelagic fishes depends on upwelling of nutrients from deep waters to the surface layers in the California Current ecosystems (Checkley and Barth, 2009).

Changes in wind direction from southerly to northerly in spring, called the spring transition, generally occur in March or April and initiate coastal upwelling in the northern California Current region (Bograd *et al.*, 2009; Checkley and Barth, 2009). The spring transition in 2005 was delayed until late May (Kosro *et al.*, 2006) and strong persistent upwelling-favorable winds did not occur until mid-July (Hickey *et al.*, 2006; Kudela *et al.*, 2006). Once upwelling began in July, it was stronger than the 1967–2004 climatological mean (Schwing *et al.*, 2006). The anomalous

*Correspondence. e-mail: takahamt@fra.affrc.go.jp

†Seikai National Fisheries Research Institute, Fisheries Research Agency, 1551-8 Taira-machi, Nagasaki, Nagasaki 851-2213, Japan.

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upwelling in 2005 altered the biological production of marine ecosystems in the northern California Current (Barth *et al.*, 2007). Blooms of phytoplankton (as indicated by chlorophyll *a*) were rarely found from April to June off Oregon and Washington, but were common after upwelling intensification in July, based on satellite observations and *in situ* water sampling (Hickey *et al.*, 2006; Thomas and Brickley, 2006).

In contrast, spring upwelling in 2006 began in early May off Oregon and Washington and was strong from June through September (Goericke *et al.*, 2007). Copepod biomass off Oregon in 2006 was double that observed in 2005 (Goericke *et al.*, 2007). Growth rates of euphausiids (i.e., *Euphausia pacifica*) in early summer 2006 were significantly faster than those in early summer 2005 (Shaw *et al.*, 2009). Nutritional condition, as shown by total lipid content of adult *E. mordax* collected in 2006, was significantly higher than that measured in specimens collected in early summer 2005 off Oregon and Washington (Litz *et al.*, 2010). Fishery landings of *E. mordax* off Oregon and Washington decreased from 250 metric tons (mt) in 2003 to 9 mt in 2006, and then increased to 850 mt in 2009 (Pacific Fishery Management Council, 2011; Fig. 1). The age structure of anchovy off Oregon and Washington in 2005 consisted of 0–3-yr-olds, based on aging of sagittal otoliths (Litz *et al.*, 2008). Fishery landings of *E. mordax* in 2007 were more than 10-fold larger than those in 2006, suggesting that successful recruitment of the 2006 year class contributed more to increased landings (and population size) than the 2005 year class.

Population growth for *E. mordax* is driven in large part by mortality during the egg stage and vital rates during the larval stage, based on stage-specific numerical models (Smith *et al.*, 1992; Butler *et al.*, 1993; Lo *et al.*, 1995). In Japanese anchovy (*Engraulis*

japonicus), otolith growth analysis demonstrated that larvae and juveniles with faster growth rates had higher probabilities of successful survival up to the adult stage than those with slower growth rates (Takahashi and Watanabe, 2004a). Hence, a comparison of the interannual and interseasonal variability in growth rate during early life-stages of *E. mordax* in response to the two contrasting years of productivity may provide insights into our understanding of the mechanisms that regulate their population dynamics in the northern California Current ecosystem.

In this study, we examined seasonal variability in growth rate during the larval stage of *E. mordax* in response to physical and biological factors in 2005 using otolith daily increment analysis, and compared these results with the more normal upwelling year of 2006. We hypothesized that interseasonal and interannual variations in temperature and food availability caused by contrasting upwelling conditions resulted in differential growth rate during the early life stages of *E. mordax* in 2005 and 2006 in the northern California Current ecosystem.

MATERIALS AND METHODS

Larval and early juvenile *E. mordax* were collected from a total of 113 stations using surface and subsurface trawl nets off Oregon and Washington in August, September, and October in 2005 and from 101 stations using a surface net in August and September 2006 (Fig. 2, Table 1). The surface and subsurface trawl nets had a mouth opening of 12 m deep \times 28 m wide and a gradation of mesh sizes from 162.6 to 8.9 cm in the net body with a 0.3/0.8-cm mesh liner in the cod end. Although two different mesh sizes were used in the two different cruises in August 2005, the mean standard length (SL) of *E. mordax* larvae collected was comparable between the cruises (Table 1) and so it is assumed that effects of size-selective net retention due to different mesh size would be negligible among the cruises. The nets were towed for 15–30 min at a vessel speed of 5.4–7.2 km h⁻¹ in the upper 40 m of the water column. Larval and early juvenile *E. mordax* were sorted from the trawl catch, enumerated, then frozen immediately at -10°C or preserved at sea in 95% ethanol. The concentration of fish is presented as the number of individual fish per 10⁶ m³, a volume derived by multiplying the area of the mouth opening by the distance over which the net was towed.

In the laboratory, a SL of up to 50 larval and juvenile individuals from each trawl was measured to the nearest 0.1 mm using a digital caliper. Sagittal otoliths were removed with the aid of a dissecting

Figure 1. Annual catches of *Engraulis mordax* off Oregon and Washington reported by the Pacific Fishery Management Council (PFMC 2011).

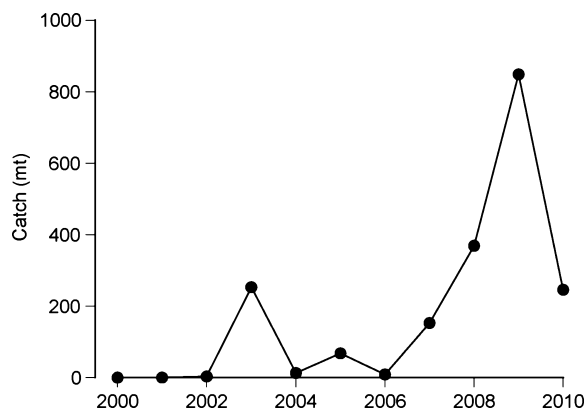
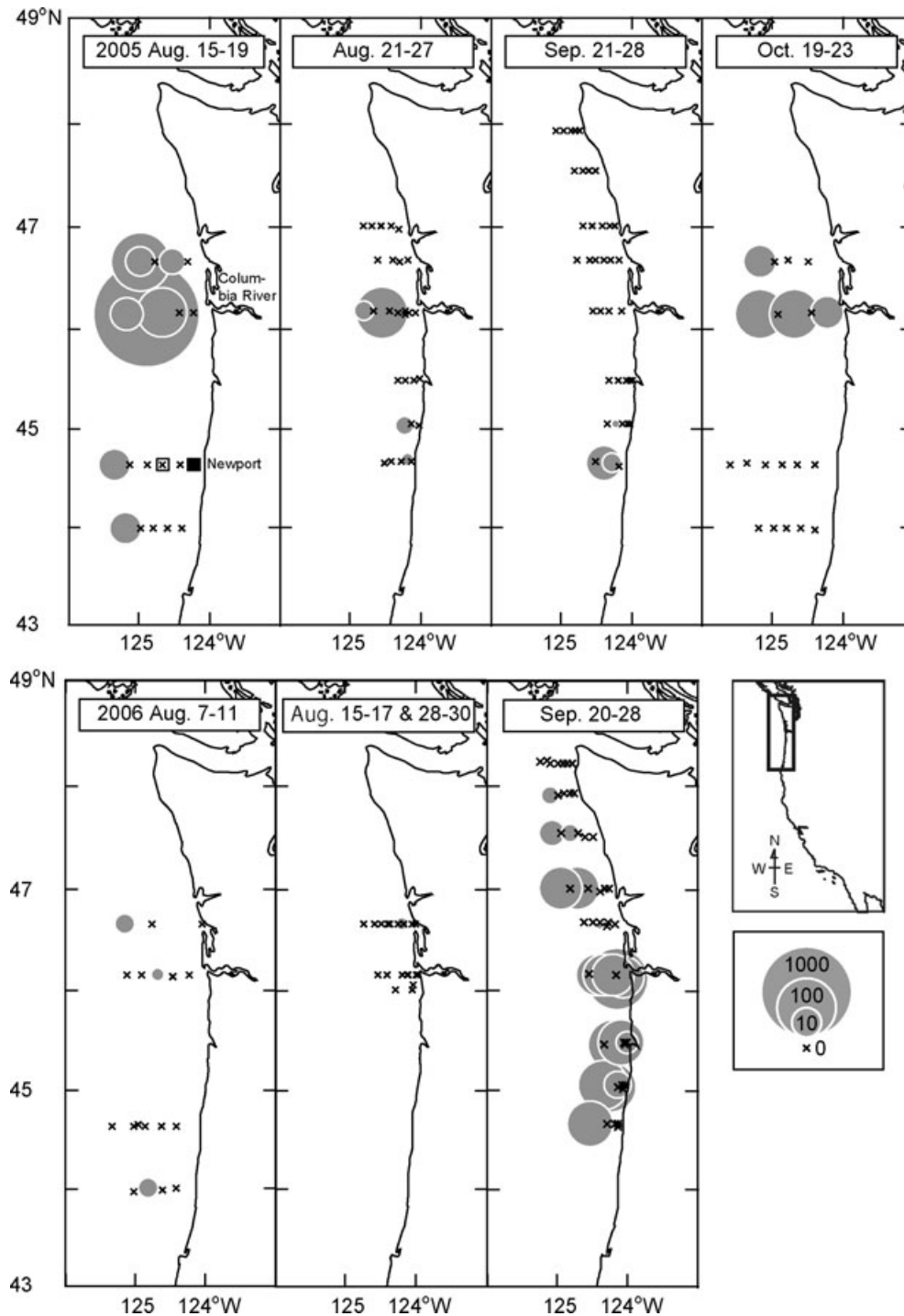


Figure 2. Abundances of larval and early juvenile *Engraulis mordax* off Oregon and Washington in 2005 and 2006. Diameters of shaded circles indicate numbers of larvae and early juveniles per 10^6 m^3 water filtered with the relative sizes indicated in the bottom right. Crosses indicate zero catch. Open and solid squares in the upper left panel represent locations of the NOAA buoy 46050 and the Newport Hydrographic line station, NH-5, respectively.



microscope at 10–50 \times magnification and mounted on a glass slide with mounting media (EUKITT; O. Kindler, Freiburg, Germany) or enamel resin.

Larval otoliths thicken after metamorphosis at ~ 35 mm SL, therefore juvenile otoliths were ground using 1500–2000-grit sandpaper and polished using

Table 1. Mean standard length (SL) and age of larval and early juvenile *Engraulis mordax* collected in August, September, and October 2005 and September 2006.

Year	Date	N	SL (mm)			Age (d)		
			Mean \pm SD	Min.	Max.	Mean \pm SD	Min.	Max.
2005	15–19 Aug	48	36.4 \pm 2.5	31.0	41.3	67.1 \pm 6.2	55	79
	21–27 Aug	59	36.5 \pm 3.3	30.2	44.7	76.4 \pm 9.0	64	101
	21–28 Sep	4	50.7 \pm 9.3	44.6	66.8	101.8 \pm 8.8	93	102
	19–23 Oct	64	34.1 \pm 3.6	25.9	44.8	62.9 \pm 7.8	49	93
2006	20–28 Sep	203	39.3 \pm 6.5	29.0	60.0	71.1 \pm 11.2	46	101

N, number of fish analyzed in each time period.

8000-grit lapping film or 0.05- μ m alumina powder until otolith growth increments around the nuclei were visible. The total number of otolith growth increments and widths between the increments were measured in the post-rostrum portion of the otolith using a measurement system consisting of a light microscope at 40–1000 \times magnification equipped with charge coupled device (CCD) cameras and examined using imaging software for 2005 (JISEKI Software; Ratoc System Engineering Ltd., Tokyo, Japan) and 2006 (IMAGE-PRO DISCOVERY Software, Media Cybernetics, Inc., Bethesda, MD, USA).

Daily otolith growth increments of *E. mordax* have been validated up to 100 days after hatching under experimental conditions and the period from hatching to the first deposition of a daily growth increment on the otolith has been shown to vary with water temperature (Brothers *et al.*, 1976; Zweifel and Lasker, 1976; Methot and Kramer, 1979). Since *E. mordax* eggs are known to occur in sea surface temperatures (SSTs) ranging from 13 to 16°C off Oregon and Washington (Richardson, 1981), the first otolith increment was assumed to have been deposited 5 days after hatching (see Materials and Methods in Methot and Kramer, 1979). We therefore calculated daily ages by adding 5 days to the final increment count and subtracting this value from the capture date to determine hatch dates. Since mean SL of larval and early juvenile *E. mordax* were comparable among collection months except for only four individuals in September 2005 (see Results), we assumed that effects of size- or growth-selective mortality on analysis for the growth–environmental relationships would be negligible in this study.

As the period from hatching to collection of larval and early juvenile *E. mordax* ranged from May to October (see Results), physical and biological environmental variables were assessed off Oregon and Washington for the same time period in 2005 and 2006. Daily upwelling intensity at 45°N was obtained from the National Oceanic and Atmospheric

Administration (NOAA) Pacific Fisheries Environmental Laboratory website (<http://www.pfeg.noaa.gov>) and averaged as a 3-day running mean. Daily SST was obtained from the NOAA buoy 46050 (<http://www.ndbc.noaa.gov>), located 36 km off Newport, Oregon (44.6°N, 124.5°W; Fig. 2). Chlorophyll *a* concentration was assessed using water samples taken biweekly at station NH-5 (44.65°N, 124.17°W) along the Newport Hydrographic line off the Oregon coast (Fig. 2). The 100-mL water samples were filtered through GF/F filters and chlorophyll was extracted from the filters using 90% acetone and stored for 24 h in the dark at 4°C. The fluorescence from the chlorophyll samples was then read on a Turner Designs 10-AU fluorometer (Turner Designs, Sunnyvale, CA, USA), and chlorophyll concentrations were calculated from the fluorescent readings following standard equations (Strickland and Parsons, 1972).

Species-specific copepod biomass was measured as units of carbon (mgC m⁻³) using the zooplankton net samples collected biweekly at the NH-5 station (Fig. 2). A zooplankton net with 0.2-mm mesh aperture attached to a 50-cm diameter ring was towed vertically from several meters above the bottom to the surface. The water volume sampled was measured using a TSK flowmeter attached to the center of the plankton net. The zooplankton catch was preserved in a 5% seawater/formalin solution. Copepod species were assigned into four assemblages (cold-water neritic, warm-water neritic, subarctic oceanic, and subtropical oceanic; see Table 2) and enumerated based on the procedures outlined in Hooff and Peterson (2006).

Otolith increment width of *E. japonicus* has been shown to be positively correlated with somatic growth rate during the larval and early juvenile stages in rearing experiments (Takahashi and Watanabe, 2004a). To examine differences in patterns in otolith and somatic growth among hatch cohorts, absolute increment width and back-calculated SL at age were

Table 2. Assemblages of copepod species grouped by water-types as indices of food availability for larval and early juvenile *Engraulis mordax* off Oregon and Washington.

Assemblage	Taxa
Cold neritic	<i>Acartia hudsonica</i>
	<i>Acartia longiremis</i>
	<i>Calanus marshallae</i>
	<i>Centropages abdominalis</i>
	<i>Epilabidocera amphitrites</i>
	<i>Pseudocalanus mimus</i>
	<i>Tortanus discaudatus</i>
Subarctic oceanic	<i>Metridia pacifica</i>
	<i>Microcalanus pusillus</i>
	<i>Neocalanus plumchrus</i>
	<i>Scolecithricella minor</i>
	<i>Acartia tonsa</i>
Warm neritic	<i>Corycaeus anglicus</i>
	<i>Ctenocalanus vanus</i>
	<i>Paracalanus parvus</i>
	<i>Acartia danae</i>
Warm oceanic	<i>Calanus pacificus</i>
	<i>Calocalanus pavo</i>
	<i>Calocalanus tenuis</i>
	<i>Candacia bipinnata</i>
	<i>Clausocalanus arcuicornis</i>
	<i>C. furcatus</i>
	<i>C. lividus</i>
	<i>C. mastigophorus</i>
	<i>C. parapergens</i>
	<i>C. paululus</i>
	<i>C. pergens</i>
	<i>Eucalanus hyalinus</i>
	<i>Euchirella rostrata</i>
	<i>Mesocalanus tenuicornis</i>
	<i>Pleuromamma abdominalis</i>
	<i>Rhincalanus nasutus</i>
	<i>Sapphirina</i> sp.

compared among larvae and early juveniles hatched in June and August 2005 and July 2006. Previous work on *E. japonicus* and *E. mordax* (Butler, 1989; Takahashi *et al.*, 2001) demonstrated that an allometric relationship existed between SL and otolith radius; therefore SL at age was back-calculated based on an allometric relationship using the biological intercept method (Campana, 1990; Campana and Jones, 1992). Variation in back-calculated SL among monthly cohorts hatched in 2005 and 2006 were tested by one-way ANOVA followed by a Tukey–Kramer *post-hoc* test.

Mean absolute increment widths increase with age during the larval stage (Pepin *et al.*, 2001; Baumann *et al.*, 2003; see Results). To estimate seasonal patterns

in increment width as a proxy of somatic growth rate, increment widths need to be standardized at age. As most larvae and juveniles that we collected had a daily age >60 days, we used an age-detrended increment width up to 60 days (standardized increment width, SIW) for each individual fish to investigate seasonal variability in somatic growth rates based on the following equation:

$$\text{SIW} = (X - x) \cdot D^{-1}$$

where X is otolith increment width at a given age of an individual, x is the mean increment width of all individuals including 2005 and 2006 at a given age, and D is the standard deviation of increment width at a given age.

To examine seasonal changes in otolith growth patterns during May to October 2005 and 2006, SIW of each increment of an individual was plotted by calendar date when increments were deposited and averaged for those dates with more than 10 individuals. Dates with fewer than 10 individuals were deleted from the growth analysis. Mean SIW of *E. mordax* was then related to previously described abiotic and biotic environmental variables from May to October 2005 and 2006. Relationships among all abiotic and biotic variables including mean SIW were tested using a linear regression analysis. Abiotic and biotic environmental variables were standardized as an anomaly from the mean of the time series divided by the standard deviation of the mean to achieve homogeneity to relate to mean SIW. To determine the environmental variables contributing most to the mean SIW, interactions between the mean SIW and all environmental variables were tested using a partial least-squares analysis with variable importance for projection statistics (Wells *et al.*, 2008).

RESULTS

Larval and early juvenile E. mordax distribution patterns

Larval and early juvenile *E. mordax* generally occurred at densities of <100 fish (10⁶ m³)⁻¹ off the mouth of the Columbia River in 2005 (Fig. 2). More than 95% of the total number of fish caught in 2005 and analyzed were collected around the mouth of Colombia River. Larvae and early juveniles in September 2006 occurred in high densities in the northern and southern transects in addition to the waters off the Columbia River mouth, but only a few larvae and early juveniles were collected in August 2006. Most larvae and early juveniles were collected off the Columbia River mouth in 2005, so only the larvae and early juveniles collected off the Columbia River mouth in September

2006 were used for the interannual comparison of growth.

Engraulis mordax hatch date and environmental histories

Mean SL and age of larvae and early juveniles used for the growth analysis ranged from 34.1 to 39.3 mm and 62.9 to 76.4 days, except for four individuals collected in September 2005 (Table 1). More than 80% of total individuals were aged ≥ 60 days. Hatch dates of larvae and early juveniles collected in 2005 ranged from mid-May to early September with peaks in mid-June and late August (Fig. 3a). However, the hatch date distribution in 2006 ranged from mid-June to early August with a peak in late July.

Strong upwelling ($>100 \text{ m}^3 \text{ s}^{-1}$) corresponded to the onset of a sharp decline in SST (Fig. 3b,c). SST in 2005 began to drop sharply in mid-July, whereas in

2006, SST markedly decreased to $<10^\circ\text{C}$ in early May, late June and late July (Fig. 3c). Chlorophyll *a* concentration in 2005 increased sharply to $>10 \text{ mg m}^{-3}$ in early August, whereas that in 2006 appeared to be $>10 \text{ mg m}^{-3}$ from May through October (Fig. 3d). Chlorophyll *a* concentration positively correlated with upwelling intensity in 2005 (Table 3). Biomass of neritic cold-water copepod species in 2005 increased by nearly an order of magnitude after August, while the biomass in 2006 increased to $>10 \text{ mg m}^{-3}$ after late June (Fig. 3e). The biomass levels of neritic warm-water copepods and that of oceanic subarctic and subtropical oceanic copepods were $<5 \text{ mgC m}^{-3}$ throughout the survey period (Fig. 3e,f). Biomass of neritic cold-water copepods and oceanic subtropical copepod species negatively correlated with SST in 2005 (Table 3). No

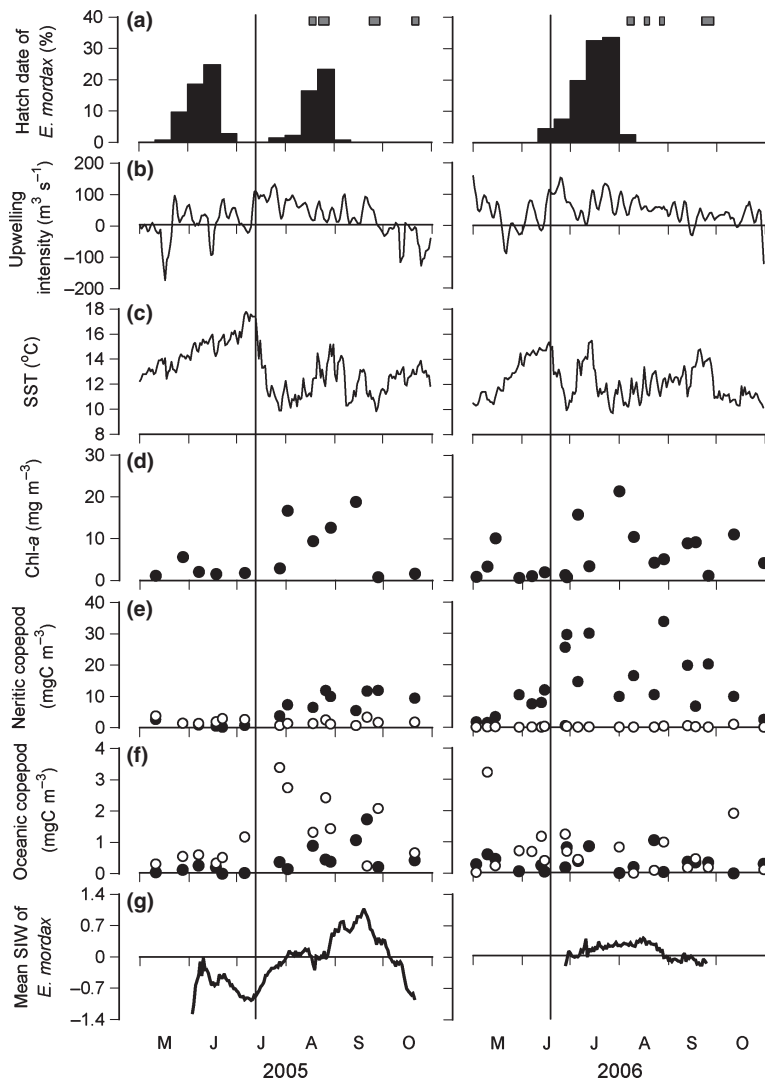


Figure 3. Seasonal variations in hatch dates of *Engraulis mordax* with collection date (shaded boxes) (a), upwelling intensity at 45°N (b), sea surface temperature (SST, c), chlorophyll *a* concentration (d), biomass of neritic cold (solid) and warm (open) water copepod species (e), biomass of oceanic subarctic (solid) and subtropical (open) copepod species (f), and mean standardized increment width (SIW) of *Engraulis mordax* (g) in 2005 and 2006. Vertical lines indicate the onset of the major upwelling in 2005 and 2006 (SST decline).

Table 3. Relationships among abiotic and biotic variables off Oregon and Washington in 2005 and 2006.

2005	UI	SST	Chl- <i>a</i>	CBnc	CBnw	CBarc	CBtrop
SST	NS						
Chl- <i>a</i>	+	NS					
CBnc	NS	–	NS				
CBnw	NS	NS	–	NS			
CBarc	NS	NS	+	+	NS		
CBtrop	NS	–	NS	NS	NS	NS	
SIW	NS	--	+	+	NS	+	NS
2006	UI	SST	Chl- <i>a</i>	CBnc	CBnw	CBarc	CBtrop
SST	NS						
Chl- <i>a</i>	NS	NS					
CBnc	NS	NS	NS				
CBnw	NS	NS	NS	NS			
CBarc	NS	NS	NS	NS	NS		
CBtrop	NS	NS	NS	NS	NS	NS	
SIW	++	--	NS	NS	–	NS	NS

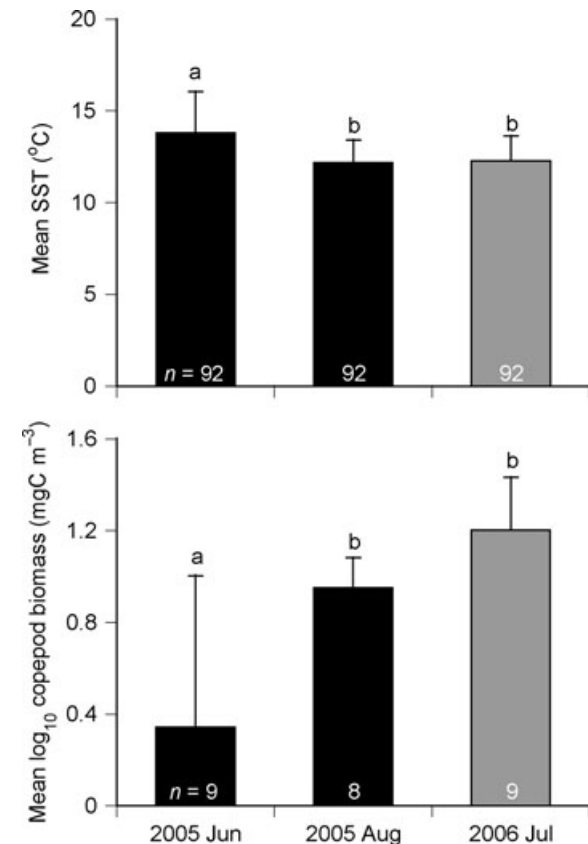
UI, Chl-*a*, CBnc, CBnw, CBarc, CBtrop indicate upwelling intensity, chlorophyll *a* concentration, copepod biomass of neritic cold- and warm-water species and that of oceanic subarctic and subtropical species, respectively. – or + and -- or ++ indicate significant negative or positive relationships with $P < 0.05$ and $P < 0.01$, respectively. NS denotes not significant.

significant correlations were found among environmental variables in 2006.

Mean SST and biomass of neritic cold-water copepod species during June–August, August–October 2005, and July–September 2006 were considered to reflect environmental conditions for the June, August 2005, and July 2006 hatch cohorts. Mean SST for the June 2005 hatch cohort was 13.8°C and was significantly higher than those for the August 2005 and July 2006 cohorts (Tukey–Kramer *post-hoc* test, $P < 0.05$; Fig. 4). The mean biomass of neritic cold-water copepod species for the June 2005 cohort was significantly smaller than those for the August 2005 and the July 2006 cohorts.

Growth patterns in relation to environment

Mean increment widths of the August 2005 and the July 2006 cohorts were larger than those of the June 2005 cohort up to approximately 40 days (Fig. 5a,b). Mean back-calculated SL at 20, 40, and 60 days of larvae and early juveniles hatched in June 2005 were significantly smaller than for those hatched in August 2005 and July 2006 (Fig. 5c,d, Table 4). No significant differences were found in SLs at 20 and 60 days between the August 2005 and July 2006 hatch cohorts (Table 4). Although the SL at 40 days of the July

Figure 4. Mean sea surface temperature (SST) and \log_{10} biomass of neritic cold-water copepod species during June–August, August–October 2005, and July–September 2006 as environmental variables for the June, August 2005, and July 2006 hatch cohorts of *Engraulis mordax*, respectively. Different letters above standard deviation error bars indicate significant differences ($P < 0.05$). The numbers of temperature observations and plankton samples are given inside each bar.

2006 hatch cohort was significantly smaller than the August 2005 cohort, the difference was negligible (0.9 mm) compared with the differences to the June 2005 cohort (4–5 mm).

Mean SIW at date with >10 individuals were available for 3 June–21 October in 2005 and for 28 June–25 September in 2006 (Fig. 3g). Mean SIW in 2005 was negative during May–late July, changed to positive on 2 August, attained a maximum in mid-September, and then became negative in early October again. Mean SIW in 2006 was consistently positive during early July to late August, and changed to negative on 1 September. Mean SIW in 2005 ranged from –1.3 to 1.1, a larger variability than that in 2006.

Mean SIW in 2005 was a positive function of chlorophyll *a* concentration, the biomass of neritic

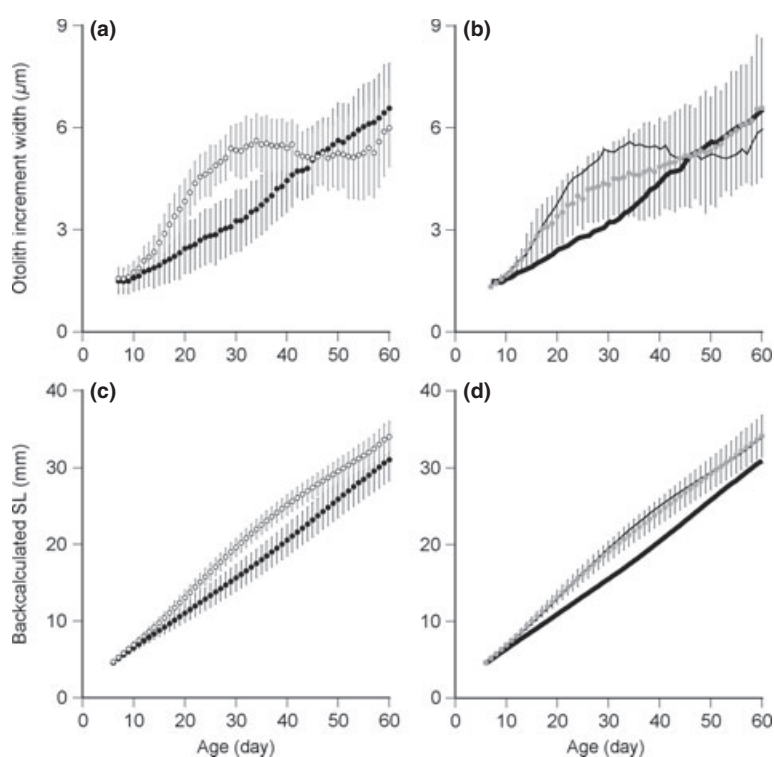


Figure 5. Mean otolith increment width and back-calculated standard length (SL) at age of larval and early juvenile *Engraulis mordax* hatched in June (solid circles) and August (open circles) 2005 (a,c) and hatched in July (gray circles) 2006 (b,d). Vertical bars indicate standard deviation. Thick and thin lines in (b) and (d) indicate mean increment width and backcalculated SL shown in (a) and (c), respectively.

Table 4. Back-calculated standard length (SL, mm) at 20, 40, and 60 days of larval and early juvenile *Engraulis mordax* hatched in June and August 2005, and those hatched in July 2006.

Hatch cohort			20 days		40 days		60 days	
Year	Month	N	Mean	SD	Mean	SD	Mean	SD
2005	June	89	11.0 ^b	1.2	20.5 ^c	2.1	31.0 ^b	2.8
2005	August	61	13.0 ^a	0.9	25.2 ^a	1.3	34.0 ^a	2.0
2006	July	172	13.2 ^a	0.8	24.3 ^b	1.7	34.2 ^a	2.7

Superscripts in different letters indicate significant differences ($P < 0.05$). N, number of fish analyzed in each time period.

cold-water and oceanic subarctic copepod species, but a negative function of SST (Fig. 6, Table 3). Mean SIW in 2006 was a positive function of upwelling intensity but a negative function of SST and the biomass of neritic warm-water copepod species. Coefficients in the partial least-squares analysis showed that seasonal variations in the mean SIW in both survey years were positively representative of upwelling intensity, chlorophyll *a* concentration, the biomass of neritic cold-water and oceanic subarctic copepod species, and negatively representative of SST, the biomass of neritic warm-water and oceanic subtropical copepod species (Table 5). Variable importance for projection (VIP) statistics showed that seasonal variability in the mean SIW in 2005 was mostly

representative using SST, chlorophyll *a* concentration, the biomass of neritic cold-water and oceanic subarctic copepod species.

DISCUSSION

Larval occurrence

The hatch date distribution of this study indicated that the strong upwelling that occurred in July 2005 had a significant effect on the survival of larval and early juvenile *E. mordax* off Oregon and Washington. Eggs and larvae of *E. mordax* have been collected mostly from April to July in ichthyoplankton surveys from 1997 to 2004 off the Columbia River mouth (Parnel *et al.*, 2008). In 2005, eggs and larvae of

Figure 6. Mean standardized increment width (SIW) of *Engraulis mordax* in relation to anomalies of environmental variables in 2005 (top) and 2006 (bottom). UI, Chl-*a*, CBnc, CBnw, CBarc, CBtrop indicate upwelling intensity, chlorophyll *a* concentration, copepod biomass of neritic cold- and warm-water species and that of oceanic subarctic and subtropical species, respectively. Only significant correlations ($P < 0.05$) were shown using linear regressions.

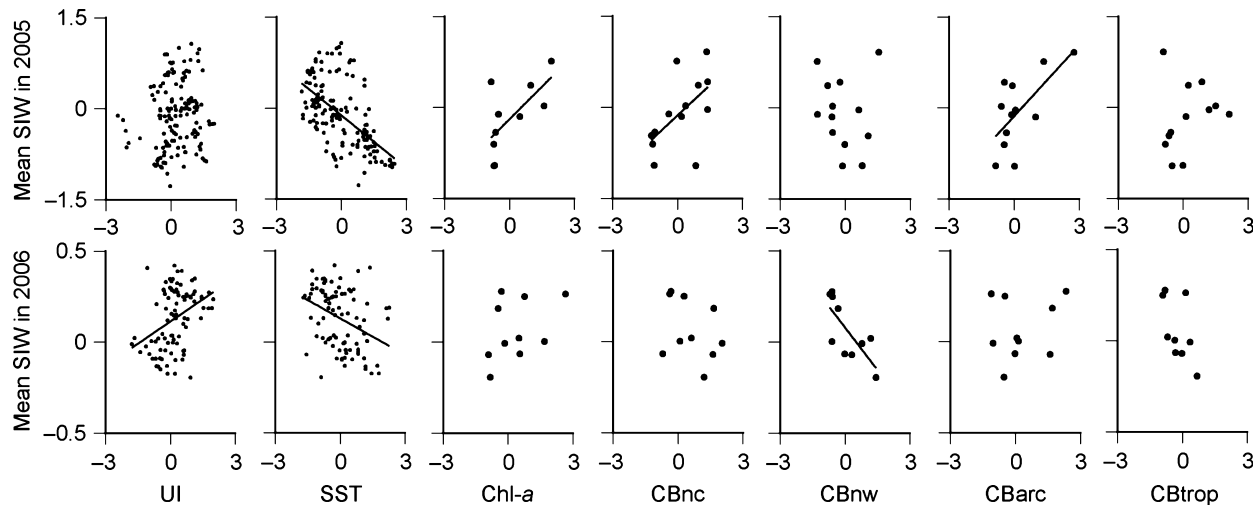


Table 5. The partial least-squares analysis for relationships between standardized increment width (SIW) during larval stage of *Engraulis mordax* and anomaly of environmental variables off Oregon and Washington in 2005 and 2006.

Variables	2005		2006	
	Coefficients	VIP statistics	Coefficients	VIP statistics
Upwelling intensity	0.19	0.35	0.06	0.96
SST	-0.18	1.15	-0.26	1.00
Chlorophyll <i>a</i> concentration	0.29	1.41	0.48	0.84
Neritic cold-water copepods	0.35	1.14	0.61	1.31
Neritic warm-water copepods	-0.34	0.90	-0.59	1.70
Oceanic subarctic copepods	0.17	1.14	0.01	0.66
Oceanic subtropical copepods	-0.21	0.72	-0.47	1.16

E. mordax were collected from late May to mid-July (Auth 2008, 2011), but hatch date estimated in this study showed no late larvae and early juveniles hatched in July 2005. This indicates that newly hatched larvae in mid-July 2005 may have experienced a severe decline in water temperature due to the strong upwelling and may have had a lower probability of survival up to the late larval and early juvenile stages. This also suggests that late larvae and early juveniles hatched in June 2005 were successful survivors even with the substantial decline in temperature in July. In August 2005, only a few eggs and larvae were found off Willapa Bay, just north of the Columbia River mouth, based on ichthyoplankton surveys (Auth, 2011). Late larvae and early juveniles hatched in August were

collected mainly in October in 2005, suggesting that larvae hatched in August had a higher survival rate than those hatched before July in 2005. Hatch date distribution in 2006 in this study was consistent with the production of eggs and larvae in 2006 (Auth 2011). Although late larval and early juvenile *E. mordax* in 2006 had hatch dates in late June and late July due to the dramatic declines in SST, favorable temperature conditions for *E. mordax* were present in the Columbia River plume during that period (W. T. Peterson, unpublished data). Larval *E. mordax* generally occurs in the plume water with SST ranging from 13 to 16°C during normal upwelling years, though larvae occurred outside of the plume in 2005 (Richardson, 1981; Brodeur *et al.*, 2006).

Seasonal changes in growth and environmental conditions in 2005

Increase in temperature accelerates growth rate during the early life stages of small pelagic fishes in the presence of sufficient food. The somatic growth rate of late larval *E. japonicus* was represented as a positive function of SST in waters with higher prey concentrations in the western North Pacific (Takahashi and Watanabe, 2005). Otolith increment widths of larval *E. japonicus* were larger in higher water temperature under given food concentrations in the rearing experiments (Takahashi and Watanabe, 2004a). Baumann *et al.* (2006) also demonstrated that relative otolith growth rate in Baltic sprat (*Sprattus sprattus*) changed in parallel with abrupt changes in temperature in the central Baltic Sea.

However, relative otolith growth rate (SIW) of larval *E. mordax* was inversely related to seasonal trends in daily SST off Oregon and Washington (Fig. 6, Tables 3). A negative relationship between mean SIW and SST could reflect more enhanced food availability with intensification of upwelling, as shown in the positive relationships between SST and the biomass of neritic cold-water copepod and oceanic subarctic copepod species (Table 3). Therefore, VIP statistics in the partial least-squares analysis showed that the biomass of neritic cold-water and oceanic subarctic copepod species was a positive function of the mean SIW (Table 5). Early larvae of *E. mordax* up to 10 mm SL feed mainly on nauplii of copepods (Arthur, 1976). Although the biomass of copepods measured in this study could not always show food availability during the early larval stage of *E. mordax*, production of nauplii might have been enhanced after the upwelling intensification in mid-July and hence improved food availability for the larval *E. mordax*. Egg production rate of adult female *Calanus marshallae* and *Calanus pacificus*, neritic cold-water and oceanic subtropical copepod species, respectively (see Table 2), in August after the upwelling intensification was significantly higher than that in June of 2005 (Shaw *et al.*, 2009).

Our results suggest that increase in food availability in terms of quality and quantity can compensate the negative growth effects due to decreased temperature in the field. Northern subarctic copepod species tend to accumulate higher amounts of polyunsaturated fats compared with more southern species due to their feeding histories (Davis and Olla, 1992). Although no information exists on feeding habits of larval and early juvenile *E. mordax* in the northern California Current region, late larvae of *E. mordax* and *E. japonicus* with

20–30 mm SL have a maximum esophagus diameter of ~900 μm , which is equivalent to the prosomal width of copepods of *C. marshallae* (Arthur, 1976; Uotani, 1985; Peterson, 1986). Fatty acid analysis of adult *E. mordax* indicated that the prey organisms present before the upwelling intensification were of significantly lower food quality than those present after upwelling was finally initiated in 2005 in the northern California Current (Litz *et al.*, 2010). Thus, our results suggest that delayed upwelling in 2005 may have resulted in lower food quality and quantity and, consequently, reduced larval growth rates of *E. mordax* until July. Once upwelling began in July, increased food availability may have enhanced larval growth rates even under suboptimal temperatures in the northern California Current ecosystem.

Interannual variations in larval growth and recruitment

Larval and early juvenile *E. mordax* hatched in August 2005 after the upwelling intensification showed similar growth patterns as those hatched in July 2006 under near-normal upwelling conditions (Fig. 5). The growth rates for both hatch cohorts were comparable to those found in rearing experiments (Hunter, 1976) and in a field study in the southern California Bight (Methot and Kramer, 1979) over a temperature range of 13–16°C. Mean SST and biomass of neritic cold-water copepod species showed that the July 2006 hatch cohort experienced similar ambient temperature and food availability to the August 2005 cohort (Fig. 4). Growth rates of *E. mordax* hatched in June 2005 before upwelling intensification were slower than those hatched in July 2006. Thus, larvae and early juveniles in 2005 experienced greater seasonal variations in growth patterns than did those in 2006, resulting in larger ranges in SIW in 2005 than in 2006. Slower growth rates of juvenile *E. mordax* under lower food availability with higher temperature have been reported during the strong El Niño in 1983 in the southern California Bight, compared with the previous years from 1980 to 1982 under normal upwelling conditions (Butler, 1989). Further study on the food composition of larvae and early juveniles could reveal the importance of lipid-rich cold-water copepod species for growth and survival during early life-stages of *E. mordax* in the northern California Current.

Possible factors for successful recruitment of *E. mordax*, such as lower SST, early spring transition, higher primary production and higher biomass of cold-water copepod species, have been proposed in the northern California Current (Litz *et al.*, 2008). Our results demonstrate that these factors may have led to an increased growth rate during the larval stage of

E. mordax due to high food availability off Oregon and Washington. Faster growth results in faster development of organs and a shorter duration of the vulnerable larval life-stage in *E. japonicus* off Japan (Takahashi and Watanabe, 2004b). Faster-growing larvae and early juveniles of *E. japonicus* had a higher probability of escaping from predatory fish species and consequently a higher survival rate to the adult stage compared with slower-growing individuals (Takahashi and Watanabe, 2004a; Takasuka *et al.*, 2007). As shown in changes in fishery landings (Fig. 1), our results suggest that the reduced growth rate during the larval stage of *E. mordax* due to low food availability with delayed spring upwelling may have contributed to the recruitment failure of the 2005 year class compared with the 2006 year class in the northern California Current ecosystem.

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