ECOLOGY AND DISTRIBUTION OF THE NORTHERN SUBPOPULATION OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) OFF THE U.S. WEST COAST

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ABSTRACT

Northern anchovy (*Engraulis mordax*) are a dominant fish in the northern California Current and are important prey for many predators. However, little is known about how anchovy distribution and abundance are affected by oceanographic variability in the eastern Pacific Ocean. We examined the relationship between anchovy abundance and environmental variables at two spatial and temporal scales: mesoscale (surface temperature, salinity, density, chlorophyll *a*, distance from shore, and depth) and macroscale (Pacific Decadal Oscillation Index, Multivariate El Niño-Southern Oscillation Index, timing of the spring transition to upwelling conditions, and abundance of cold-water zooplankton). Anchovy densities increased significantly from 1999–2004, and decreased significantly from 2005–06 in conjunction with delayed coastal upwelling and decreases in the overall abundance of cold-water zooplankton. Sea surface temperatures and proximity to the shore explained most anchovy abundance and distribution variations. When lagged by one year, a northern copepod biomass anomaly strongly correlated to age-1 anchovy survival, suggesting that copepod abundance may determine year-class strength.

INTRODUCTION

Northern anchovy (*Engraulis mordax*; anchovy) often dominate pelagic nekton biomass in the California Current, along with a few other forage species, including Pacific sardine (*Sardinops sagax*) (Brodeur et al. 2005; Emmett et al. 2005). The northern subpopulation of northern anchovy ranges from Eureka, California, to the Queen Charlotte Islands, British Columbia, Canada (McHugh 1951), and supports a small bait fishery centered off the Columbia River. Live anchovy are captured in purse seines and sold to commercial and recreational fishermen targeting Pacific hake (*Merluccius productus*), coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon. The Department of Fisheries and Oceans Canada (DFO) closed the anchovy fishery off western Vancouver Island in 2002 because the small fishery could not pay for a stock assessment.

Previous investigations have revealed correlations between California Current climate changes and forage fish regime shifts (Baumgartner et al. 1992; Schwarzlose et al. 1999; Rodriguez-Sanchez et al. 2002; Chavez et al. 2003), yet no studies provide information about the distribution of the northern subpopulation of northern anchovy in relation to local and basin-wide changes in climate or the marine ecosystem. In this study, we explored spatial and temporal patterns of distribution of the northern subpopulation of northern anchovy in the California Current Large Marine Ecosystem (CCLME) from 1977–2006 using data from National Marine Fisheries Service (NMFS) time-series sampling efforts off Oregon and Washington. In particular, we tested the hypothesis that anchovy abundance is linked to cool ocean conditions by examining catch of the northern subpopulation of northern anchovy with reference to *in situ* physical oceanographic conditions in the eastern Pacific Ocean.

In addition to spatial and temporal patterns of distribution and abundance, biological parameters of interest to this study include anchovy size and age composition (from length and otolith analysis) over time and space. Our results provide ecological information about the northern subpopulation of northern anchovy relevant to ecosystem-based fishery management of the CCLME.

METHODS

Commercial Catch Information

Commercial catch data for northern anchovy from 1985–2006 in the Pacific Northwest were obtained from the Oregon Department of Fish and Wildlife (ODFW), the Washington Department of Fish and Wildlife (WDFW), and the Department of Fisheries and Oceans (DFO) Canada. These data represent time-series catch information from the purse seine fishery targeting anchovy as live bait, without a metric for effort.

Distribution and Abundance

Catch data from four separate fishery-independent studies conducted by NMFS through either the Northwest Fisheries Science Center (NWFSC) or the Alaska Fisheries Science Center (AFSC) from 1977–2006 were mapped geographically (tab. 1, fig. 1). All stations were not sampled equally in all years in a given study. With the exception of the Triennial Study, described more fully in Emmett and Brodeur (2000), all investigations targeted coastal pelagic species. We extracted data from recorded measurements of anchovy abundance and size (fork lengths [FL] in mm), as well as detailed oceanographic information relating to anchovy environment.

The first of the four studies, the AFSC West Coast Triennial bottom trawl study (Triennial Study), began in 1977 and was repeated every three summers (June–August) until 2004. Anchovy caught during these surveys were incidental by-catch, likely trapped in the bottom trawl gear in mid-water during deployment and retrieval of the nets. Anchovy were counted, measured, and weighed from each haul (data courtesy of M. Wilkins, NMFS, AFSC, Seattle, WA). We include only samples caught between 42° and 48°N latitude, that overlap spatially with our target surveys, although anchovy were captured as far south as 32°N latitude, off southern California.

The other three studies were conducted by the NWFSC. From 1998–2006, the NWFSC monitored pelagic fish resources off Oregon and Washington using surface trawls in: (1) the Bonneville Power Administration (BPA) Columbia River Plume Study (Plume Study), (2) the U.S. Global Ocean Ecosystem Dynamics (GLOBEC)–Northeast Pacific Study (GLOBEC Study), and (3) the Predator Study (fig. 1). The Plume Study consisted of daytime hydrographic surveys and fish sampling in the Columbia River plume and off the coasts of Oregon and Washington during June and September 1998–2006 (Brodeur et al. 2005), with additional cruises in May 1999–2006, November 2003, and August 2005. The GLOBEC Study consisted of four cruises conducted as part of a mesoscale and fine-scale sampling study within the U.S. GLOBEC Northeast Pacific Program (Batchelder et al. 2002; Reese and Brodeur 2006). Cruises occurred in nearshore (0–100 km) waters between Newport, Oregon, and Crescent City, California, during June and August 2000 and 2002. Stations were designated along transects that had been monitored for several years, and chosen for their proximity to features in the physical environment, such as fronts and eddies (Brodeur et al. 2004). The Predator Study consisted of a series of two-day sampling cruises occurring approximately every ten days associated with the Columbia River plume in 1998, and on two transects north and south of the Columbia River from April to August 1999–2006 (Emmett et al. 2001; Krutzikowsky and Emmett 2005; Emmett et al. 2006). While Plume and GLOBEC Study cruises sam-

TABLE 1
An inventory of all National Marine Fisheries Service (NMFS) cruises used for this paper. The duration of each cruise varied among studies; Predator Study cruises accounted for only two nights of sampling (12 stations total); Triennial Study cruises occurred from June–September and sampled ~600 stations per cruise. All stations depicted were not sampled equally in all years in a given study.

Year	Study	Dates	Area	Trawl Type	Physical data
1977–95	Triennial	June-September, every 3 years	West Coast	Bottom	N
1998	Triennial	June-September, every 3 years	West Coast	Bottom	N
	Plume	6/16-6/25, 9/20-9/29	OR, WA	Surface	Y
	Predator	4/16-8/12, ~ every 10 days	Columbia River	Surface	Y
1999	Plume	5/18-5/25, 6/16-6/24, 9/21-10/1	OR, WA	Surface	Y
	Predator	4/13-7/29, ~ every 10 days	Columbia River	Surface	Y
2000	Plume	5/22-5/24, 6/17-6/25, 9/19-9/24	OR, WA	Surface	Y
	Predator	4/29-7/24, ~ every 10 days	Columbia River	Surface	Y
	GLOBEC	5/29-6/11, 7/28-8/12	Southern OR	Surface	Y
2001	Triennial	June-September, every 3 years	West Coast	Bottom	N
	Plume	5/20-5/28, 6/24-7/2, 9/21-9/29	OR, WA	Surface	Y
	Predator	4/25-8/1, ~ every 10 days	Columbia River	Surface	Y
2002	Plume	5/21-5/29, 6/21-6/28, 9/20-10/3	OR, WA	Surface	Y
	Predator	4/23-8/3, ~ every 10 days	Columbia River	Surface	Y
	GLOBEC	6/1-6/18, 8/1-8/17	Southern OR	Surface	Y
2003	Plume	5/20-5/27, 6/23-7/3, 9/26-10/3, 11/13-11/18	OR, WA	Surface	Y
	Predator	4/23-7/30, ~ every 10 days	Columbia River	Surface	Y
2004	Triennial	June-September, every 3 years	West Coast	Bottom	N
	Plume	5/22-5/29, 6/22-6/29, 9/22-9/29	OR, WA	Surface	Y
	Predator	4/28-8/12, ~ every 10 days	Columbia River	Surface	Y
2005	Plume	5/29-5/31, 6/12-6/22, 8/21-8/27, 9/21-9/28	OR, WA	Surface	Y
	Predator	4/19-8/13, ~ every 10 days	Columbia River	Surface	Y
2006	Plume	5/24-5/30, 6/19-6/28, 9/20-9/28	OR, WA	Surface	Y
	Predator	5/11-8/30, ~ every 10 days	Columbia River	Surface	Y

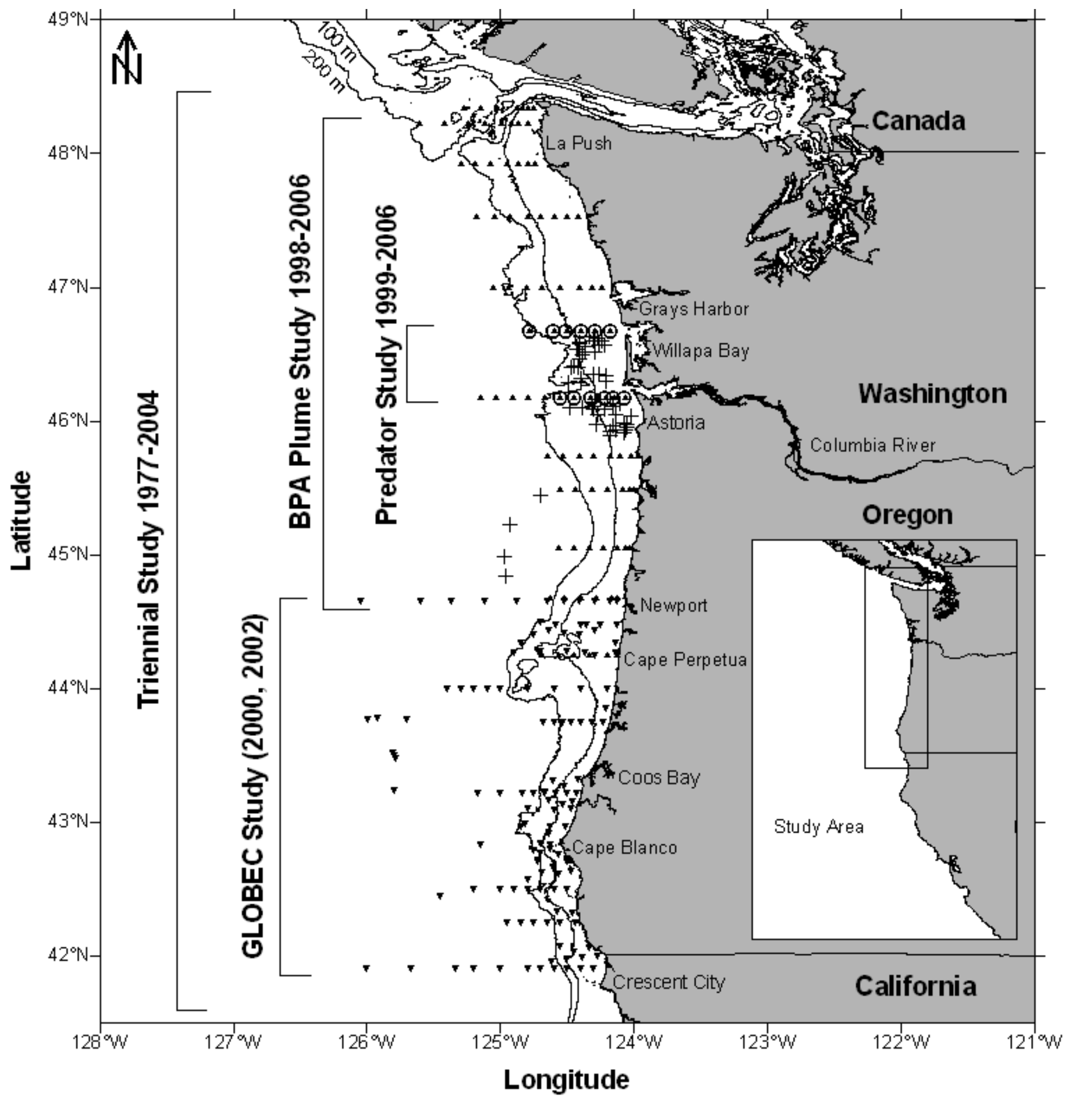

Figure 1. Map showing the four National Marine Fisheries Service (NMFS) pelagic sampling cruise locations (Triennial, Plume, GLOBEC, and Predator Study cruises). Triangles show Plume Study stations, inverted triangles represent GLOBEC Study stations, plus signs designate 1998 Predator Study stations, and open circles show 1999–2006 Predator Study stations. Also shown are the 100 and 200 m depth contours. Sampling efforts varied by year and cruise.

pled during the day or crepuscular periods, the Predator Study cruises sampled entirely at night.

All three of the pelagic fish surveys used a Nordic 264 rope trawl (NET Systems, Bainbridge Island, Washington) fished directly astern the vessel at the surface. The mouth of the trawl measured 12 m deep by 28 m wide (336 m^2), as determined during an early cruise using a third-wire Simrad FS3300 backwards-looking net sounder (Emmett et al. 2004). The trawl had variable mesh sizes (162.6 cm at the mouth to 8.9 cm at the cod end), with an additional 6.1 m long, 0.8 cm knotless liner sewn into the cod end. A pair of 3.0 m wide foam-filled doors spread the mouth apart, and the trawl was towed for 15–30 minutes with approximately 300 m of warp. To keep the net at the surface, two A-4 Polyform floats were tethered to each wing tip and two single floats were clipped on either side of the center of the headrope.

All anchovy captured in each trawl were counted and a random subsample (n = 30 or n = 50) measured for fork length (FL; mm). In the event of a very large catch, we counted and weighed a subsample of anchovy. In these hauls we used the measured weight of the remaining anchovy catch to calculate the total number from the determined number of anchovy/kg. We calculated anchovy density (number of fish/10^6 m^3) by dividing the number of anchovy in a haul by the volume of water the net fished, and by standardizing the density to number per 10^6 m^3. We calculated the volume of water by multiplying the trawling distance (m), identified by GPS, by the effective fishing mouth area (336 m^2).

Habitat Analysis

We collected environmental information immediately before fishing at each station during Predator, GLOBEC, and Plume Studies using a Sea-bird SBE 19 SeaCat conductivity-temperature-depth (CTD) profiler. Measurements of temperature (°C), salinity (psu), and density (σ-θ) were recorded at 1 m depth intervals from the surface to 100 m or 10 m from the bottom. Shifts in the basin-wide oceanographic conditions of the northern California Current ecosystem were assessed by the Pacific Decadal Oscillation (PDO) Index (Joint Institute for the Study of the Atmosphere and the Oceans, http://www.jisao.washington.edu/pdo/), the Multivariate El Niño Southern Oscillation (ENSO) Index (MEI; NOAA-CIRES Climate Diagnostics Center, http://www.cdc.noaa.gov/ENSO), and timing of the spring transition (Huyer et al. 1979; Logerwell et al. 2003) from winter coastal downwelling and poleward winds to spring or summer upwelling and equatorward winds. In addition, we collected chlorophyll *a* from water at 3 m depth on Whatman GF/C glass microfiber filters during Plume and GLOBEC Study cruises. We treated chlorophyll samples with acetone and measured them (µg/L; C) with a Turner Designs 10-AU Fluorometer.

Age Analysis

Anchovy ages were estimated from samples collected during the 2005 Predator Study between April and August. We randomly chose thirty individuals from each of ten hauls (n = 300), of which northern anchovy comprised more than 10% of the total catch. The fish were frozen whole on board the ship (–20°C) and returned to the lab for processing. We recorded FL (mm) and wet weight (to the nearest 0.01g), removed the saggital ototliths according to a protocol previously developed for anchovy otolith extraction (Messersmith 1969), and then cleaned and stored them in 95% ethanol. The otoliths from five fish were unreadable.

We photographed each otolith under a Leica MZ7.5 high-performance stereomicroscope equipped with digital imaging software at 50× magnification. For aging, one reader determined otolith annuli from surface reads, and the median from three reads taken on three separate days was recorded for each fish. We calculated an index of average percent error (APE) (Beamish and Fournier 1981) for all reads and generated a length-frequency age-overlay histogram, which proved useful for detecting year classes.

Data Analysis

All statistical analyses were run using the S-Plus 6.2 software package (Insightful Corp. Seattle, WA). We used a Kruskal-Wallis test to evaluate statistical differences in sea surface temperature (SST) at 3 m, salinity (SSS), and anchovy density (number of fish/10^6 m^3) determined from each haul among years for the Predator Study, among cruises for the GLOBEC Study, and among years for Plume Study cruises in June and September because the values were not normally distributed. When significant differences were found, we used a Wilcoxon signed-rank test to detect differences among cruises/years, adopting a Bonferroni adjusted significance level to account for the number of comparisons being made.

We used simple linear regression to identify the relationship between anchovy densities and distance from shore for Predator Study catches after accounting for the effect of year with an extra-sum-of-squares F-test. We used multiple linear regression models to explore any relationship between observed anchovy densities and physical and biological oceanography during Plume Study cruises (1998–2006) in June and September, modeling *in situ* surface (3 m) SST, SSS, sea surface density (SSD), chlorophyll *a*, and station depth as independent predictor variables and anchovy density as the dependent response. Anchovy densities were $\ln(x+1)$ transformed before analysis because of the high proportion of hauls containing zero catch. We tested residuals for normality using the χ^2 goodness-of-fit statistic and compared models with an extra-sum-of-squares F-test.

We conducted correlation analyses between age-1 anchovy densities (that were measured from Predator Study catches April through June 1998–2006) and PDO and MEI values. We also conducted correlation analyses between age-1 anchovy densities and one-year lagged northern copepod biomass anomalies off Newport, Oregon, and one-year lagged timing of the spring transition. Advantages of lagged models are their predictive power and their ability to forecast fish densities one year into the future using current physical oceanographic data; these are highly desirable abilities in managing coastal pelagic species. The spring transition date was recorded as day of the year. Values for the northern copepod anomaly came from three "cold-water" copepod species, *Pseudocalanus mimus*, *Acartia longiremis,* and *Calanus marshallae*, identified and enumerated from biweekly sampling cruises off Newport, Oregon (Keister and Peterson 2003; Peterson and Schwing 2003). We considered a $p < 0.05$ to indicate a significant relationship for regression models and statistical correlation tests.

RESULTS

Trends in Abundance

Commercial landings and fishery-independent surveys showed strong evidence that anchovy abundance increased over the study period. Commercial catches of the northern subpopulation of northern anchovy in the Pacific Northwest increased from 68 mt in 2001 to 239

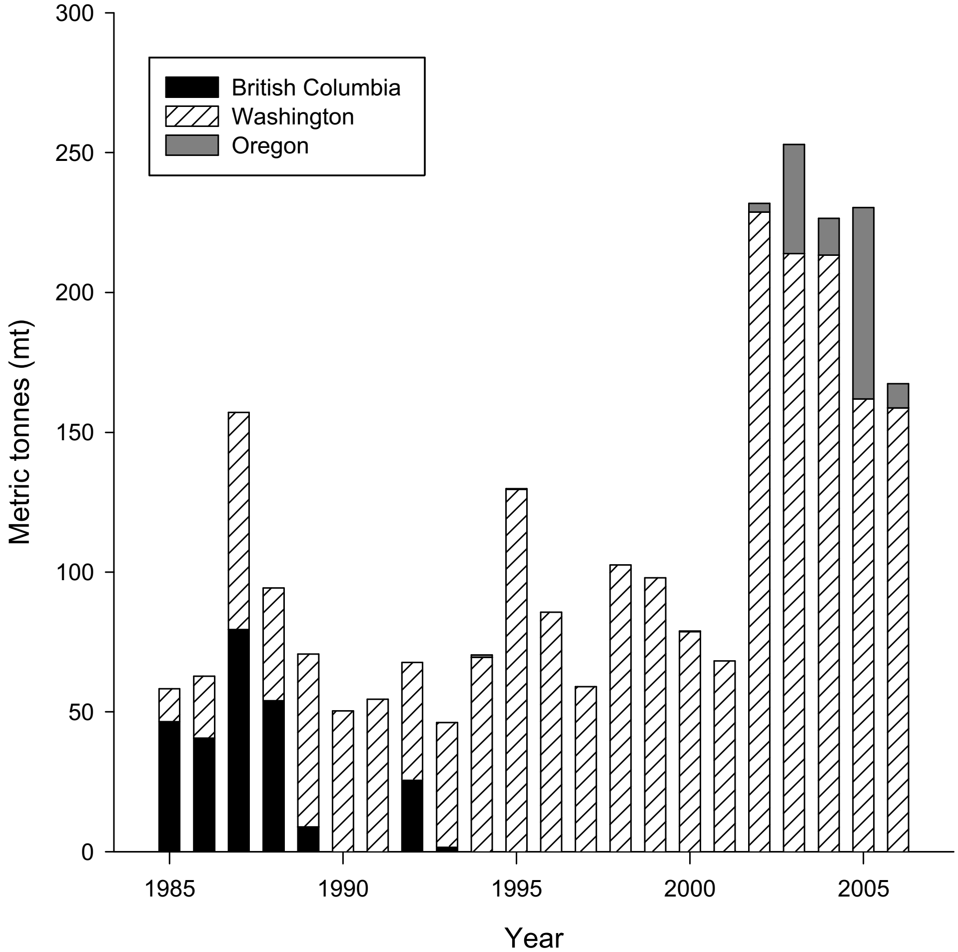

Figure 2. Annual commercial landings from 1985–2006 in mt of northern anchovy (*Engraulis mordax*) off Oregon, Washington, and British Columbia [data courtesy of B. Culver (WDFW), J. McCrae (ODFW), and T. Therriault (DFO)]. No metric for effort provided.

mt in 2002 (fig. 2). Anchovy landings were almost exclusively directed to a bait fishery centered off the Columbia River. Washington State recorded the highest catch numbers, with landings tripling between 2001 and 2002, but landings in Oregon also increased after 2001 (fig. 2). Anchovy have recently been observed to be relatively abundant in Puget Sound and north into the Juan de Fuca Strait, suggesting that interest in the fishery may increase with time (T. Therriault, DFO, pers. comm.).

Spatio-temporal Variance in Anchovy Abundance and Distribution

Fishery-independent sampling efforts show interannual variability in anchovy catch. Anchovy were landed as incidental bycatch in the Triennial Study beginning in 1977, although for the first two cruises, all catches occurred south of the Columbia River (fig. 3). Anchovy numbers increased during the ENSO event of 1983, and were encountered farther north than during any survey before or since. After 1986, northern anchovy were not encountered during Triennial Study surveys off the Pacific Northwest until 1998.

Anchovy distribution and abundance collected during the Plume Study had considerable inter-annual and seasonal variation. Anchovy landings during May (not shown) were patchy during all years except 2002, when we caught high densities of anchovy (53,118/10^6 m^3) off the mouth of the Columbia River. June Plume Study cruises sampled very few anchovy from 1998–2000 (fig. 4), with the exception of one huge haul (density = 12,127/10^6 m^3) recorded off the Columbia River in 2000. The catch leveled off from 2001–02, with densities measuring 0–55/10^6 m^3 (fig. 4). However, beginning in June 2003, a coast-wide expansion of anchovy was observed. Anchovy were caught at 17 of 60 stations with densities >3,000/10^6 m^3 at four of those stations located off Cape Meares and the Columbia River (fig. 4). From June 2004 through 2005, anchovy were observed at 56 out of 91 stations from 44.5° to 48°N latitude, with the

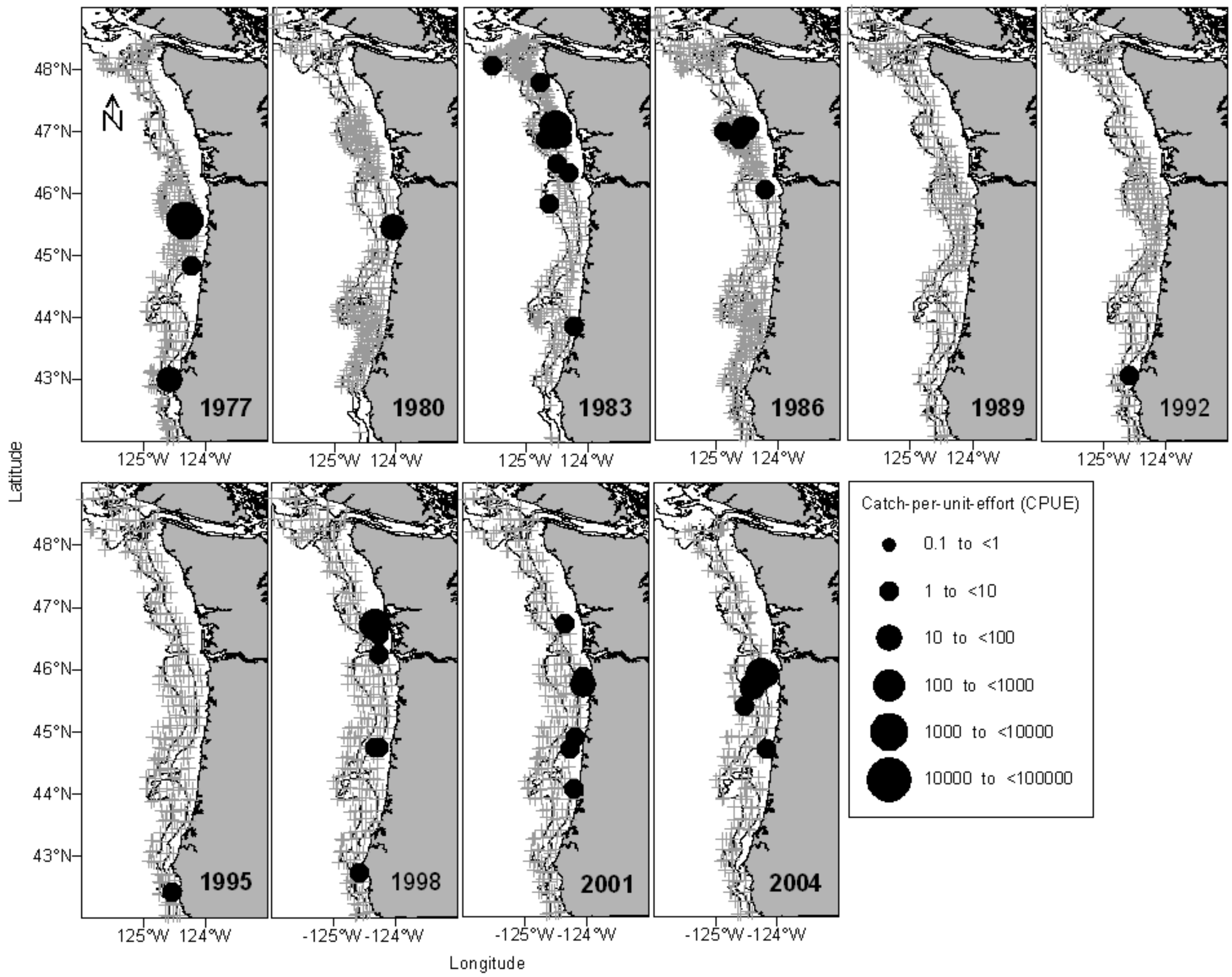

Figure 3. Catches of northern anchovy (*Engraulis mordax*) displayed as catch-per-unit effort (CPUE) from National Marine Fisheries Service (NMFS) Triennial Study cruises. All cruises occurred in June-September every three years from 1977–2004. Anchovy landed were incidental bycatch captured in the nets during deployment or retrieval of ground-fishing gear (bottom trawls). Stations fished where no anchovy were caught are denoted by a + symbol. Also shown are 100 and 200 m depth contours.

highest catches (22,913/10^6 m^3) found off the mouth of the Columbia River. In June 2006, anchovy numbers decreased (fig. 4), which coincided with increased southerly catches. For the first time during the Plume Study, the largest anchovy catches (106 and 180/10^6 m^3) occurred beyond the shelf break in deep water (>200 m), more than 50 km from the coast (fig. 4).

Distribution of anchovy during September Plume Study cruises did not always correspond well with Plume Study catch data during June of the same year. In September 1998, we caught higher densities of anchovy (0–61/10^6 m^3) than during the preceding June (0–35/10^6 m^3) (fig 5). However, in September 2000, anchovy were caught at record low densities (0–1/10^6 m^3). During September 2001, anchovy were mainly aggregated nearshore south of the Columbia River. We recorded small catches (1–15/10^6 m^3) south of the Columbia River in September 2002, at 18 of 65 stations along three transects (Cape Meares, Cascade Head, and Newport, Oregon). Higher densities of anchovy were caught (1–7,345/10^6 m^3) in September 2003, at 10 of 39 stations, with most occurring off Willapa Bay, Washington (fig. 5). In September 2004, we recorded anchovy at 33 of 47 stations along all eight transects sampled (1–21,400/10^6 m^3), indicating that the recruitment pulse observed in June 2004 persisted throughout the summer (fig. 5). Large anchovy densities were also recorded at 25 of 42 stations in September 2005 (1–12,809/10^6 m^3), although none occurred north of Grays Harbor, Washington. In September 2006, anchovy catch decreased, with densities ranging from 1–254/10^6 m^3 at 25 of the 55 stations fished (fig. 5).

GLOBEC Study distribution and abundance of anchovy off southern Oregon was patchy during all cruises

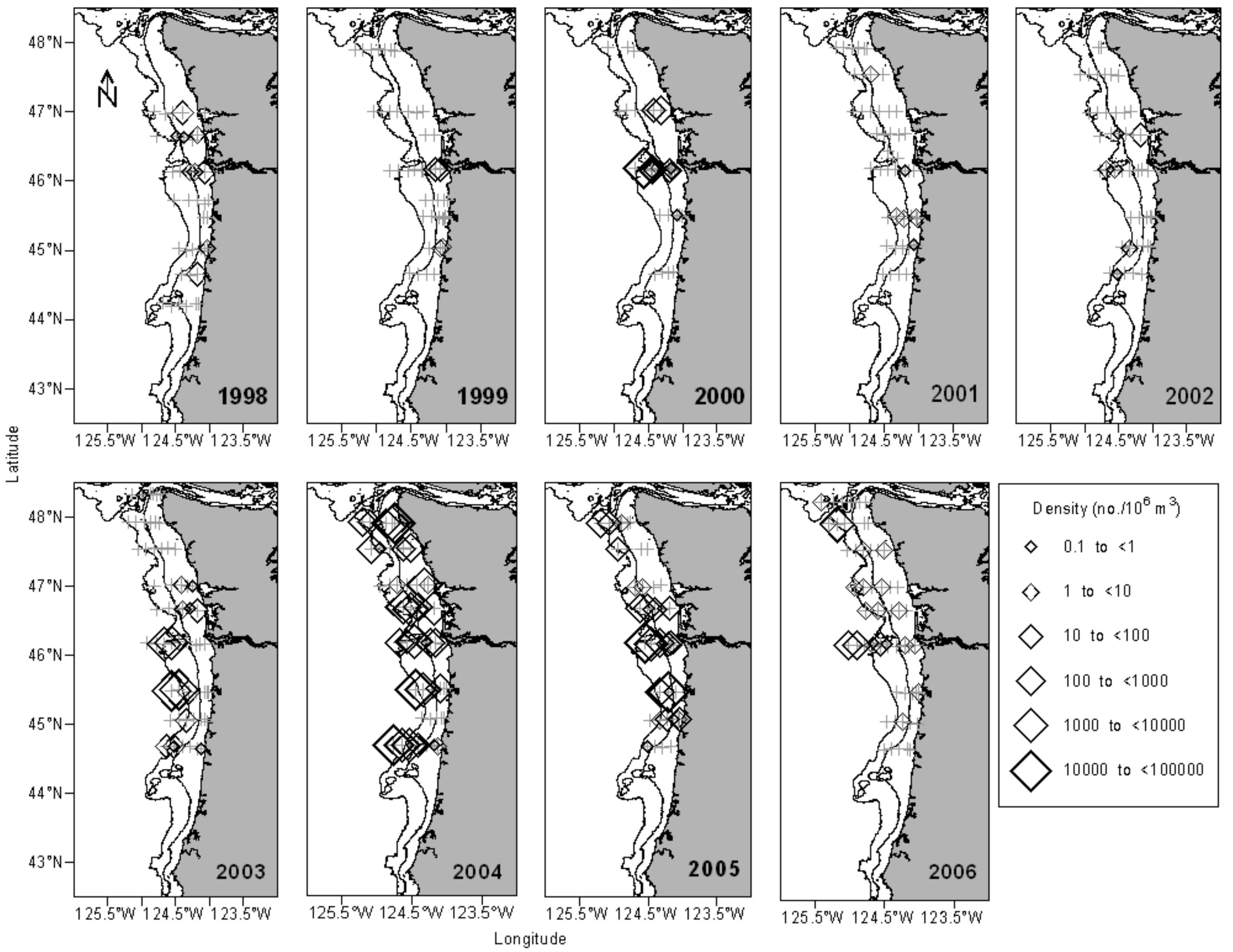

Figure 4. Distribution of northern anchovy (*Engraulis mordax*) density during Plume Study cruises (1998–2006) off Oregon and Washington in June standardized across hauls to number/10^6 m^3. The + signs show locations of surface trawls. Also shown are 100 and 200 m depth contours.

(fig. 6). No anchovy were captured in June 2000, but anchovy were caught at eight of 104 stations in June 2002 at densities orders of magnitude lower (0–15/10^6 m^3) than those in Plume Study catches at the mouth of the Columbia River during the same month (0–12,127/10^6 m^3) (fig. 4). In the GLOBEC Study, anchovy densities averaged 1/10^6 m^3 at 15 of 77 stations during August 2000, and ranged from 1–30/10^6 m^3 at 14 of 95 stations in August 2002 (fig. 6). We conducted an additional Plume Study cruise in August 2005 with transects sampled north of Newport, Oregon, to Grays Harbor, Washington. Large catches of anchovy were recorded, with densities (not shown) ranging from 0–4,546/10^6 m^3.

Predator Study anchovy densities from around the mouth of the Columbia River showed very large monthly and annual variability through spring and summer 1999–2006 (fig. 7). Large catches of anchovy were recorded in April 2003 (8,519/10^6 m^3). However, monthly averages from 1999–2006 were generally highest in May (2,458/10^6 m^3). Lowest anchovy densities were recorded in April and June 1999 and August 2001.

Anchovy densities were highest close to shore (fig. 8) during all Predator Study cruises, even after accounting for the effect of year (extra-sum-of-squares *F*-test, $F_{9,873} = 40.9$, $p < 0.001$). With the exception of 2003, highest anchovy catches were 0–10 km offshore, although anchovy were caught out to 60 km offshore every year (fig. 8). During 2001 and 2002, mean nearshore (<10 km) anchovy densities were three times greater than any offshore station (>10 km); in 2005 they were twice as large as any offshore station (>10 km).

Correlation of Abundance with Abiotic Factors

Northern anchovy distributions are likely strongly affected by abiotic factors such as sea surface temperature (3 m SST) and salinity (3 m SSS). Anchovy density var-

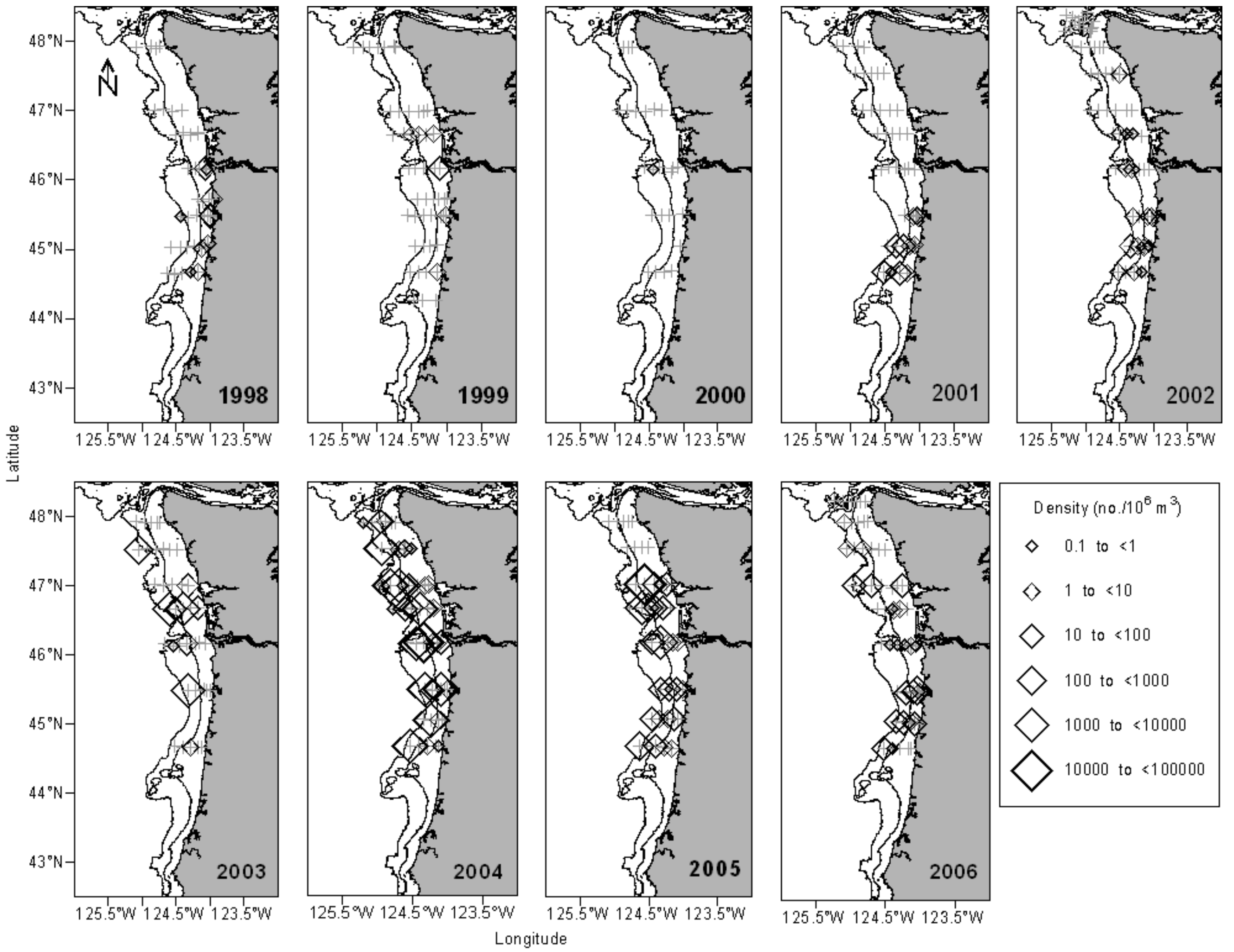

Figure 5. Distribution of northern anchovy (*Engraulis mordax*) density during Plume Study cruises (1998–2006) off Oregon and Washington in September standardized across hauls to number/10^6 m^3. The + signs show locations of surface trawls. Also shown are 100 and 200 m depth contours.

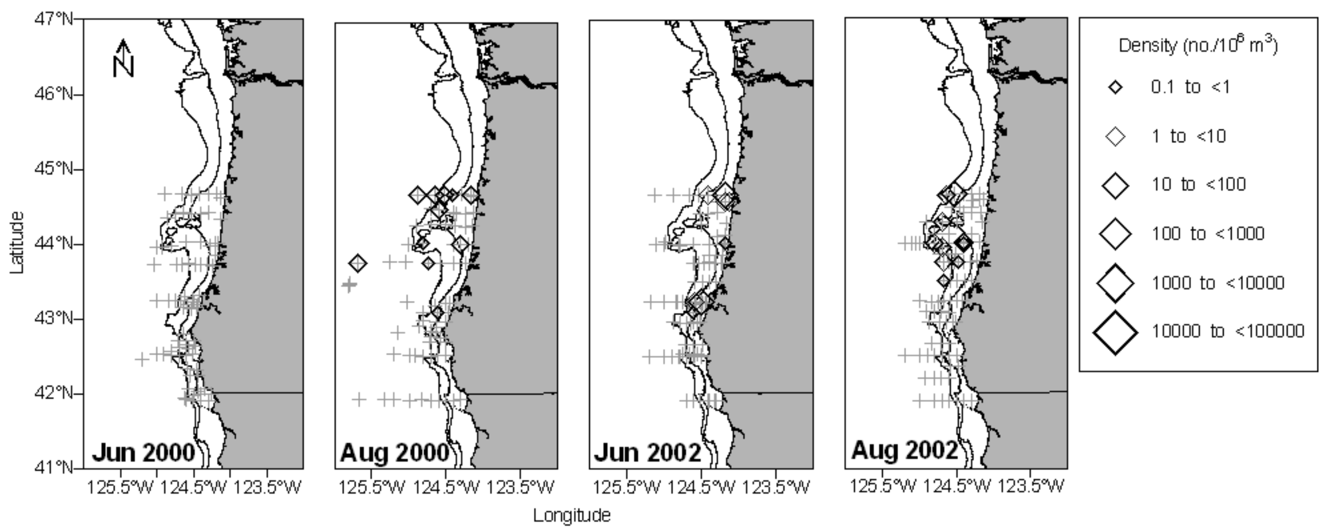

Figure 6. Northern anchovy (*Engraulis mordax*) density (standardized across hauls to number/10^6 m^3) for the 2000 and 2002 GLOBEC Study cruises off southern Oregon and northern California. The + signs show locations of surface trawls. Also shown are the 100 and 200 m depth contours.

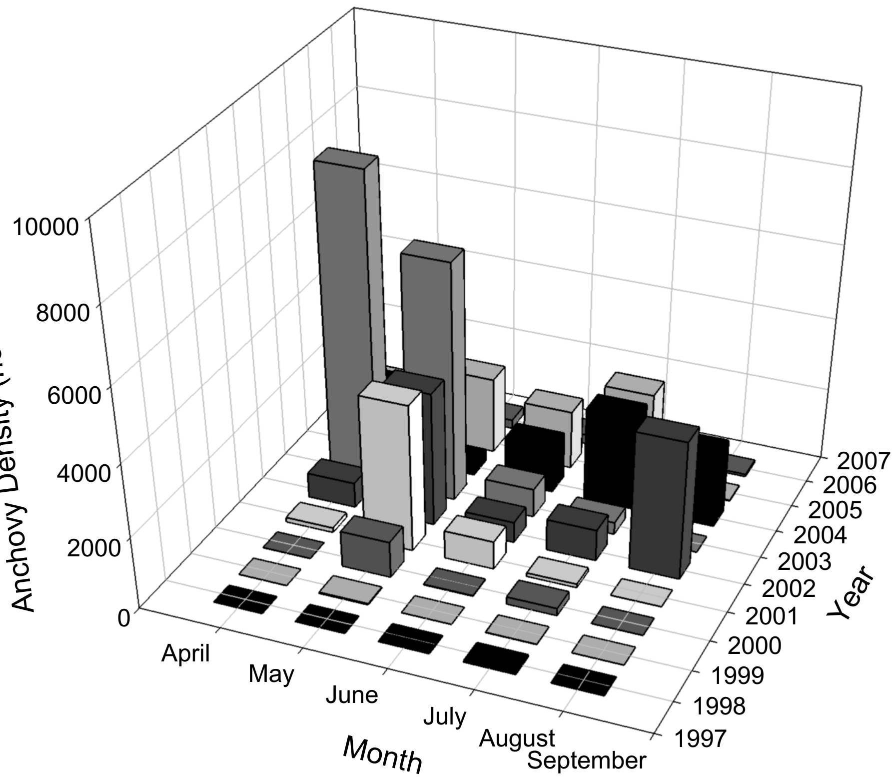

Figure 7. Average monthly densities (standardized across hauls to number/10^6 m^3) of northern anchovy (*Engraulis mordax*) captured from 1998–2006 during Predator Study cruises. Sampling occurred from April through September at stations associated with the Columbia River plume in 1998, and along two transects north and south of the Columbia River (1999–2006).

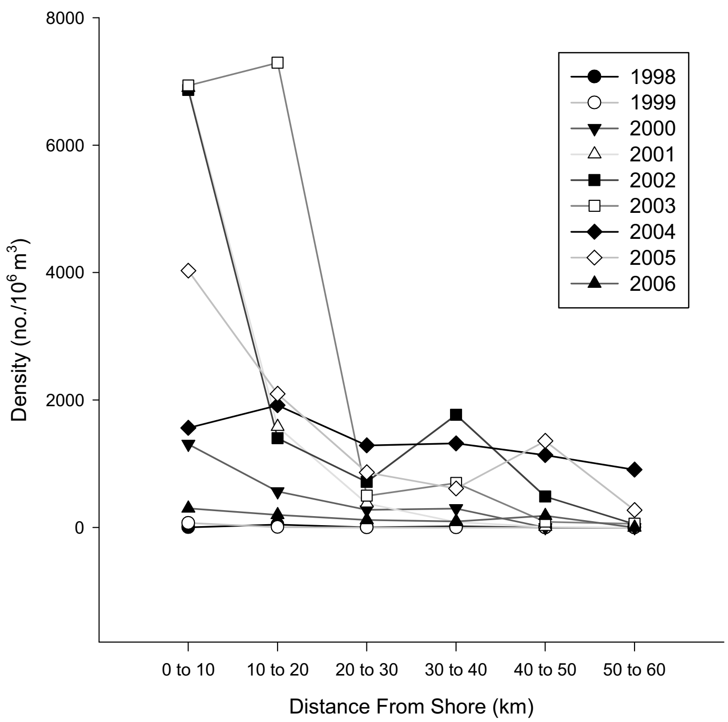

Figure 8. Average annual density (standardized to number/10^6 m^3) of northern anchovy (*Engraulis mordax*) at 0–60 km from shore, 1998–2006. Predator Study cruises that sampled from April through September at stations associated with the Columbia River plume in 1998, and along two transects north and south of the Columbia River (1999–2006).

TABLE 2
Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS Predator Study cruises (1998–2006) in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians (p < 0.001, Kruskal-Wallis rank sum test and p < 0.006, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	46	14.3^{a}	1.2	28.9^{ab}	3.5	23.8^{e}	115.0
1999	109	11.8^{d}	1.2	29.1^{b}	2.8	11.9^{e}	102.0
2000	96	12.7^{c}	1.3	29.3^{a}	3.0	458.0^{bd}	2293.0
2001	106	12.5^{c}	1.2	30.8^{a}	1.9	1668.0^{b}	12069.0
2002	110	12.8^{c}	2.2	29.4^{b}	2.8	1831.0^{ad}	9861.0
2003	113	13.0^{c}	1.6	29.7^{b}	2.2	3327.0^{ac}	12646.0
2004	105	14.1^{b}	1.5	29.4^{b}	2.6	1458.0^{bc}	3310.0
2005	118	13.9^{b}	1.6	29.2^{b}	2.7	1591.0^{b}	3501.0
2006	80	12.8^{c}	1.5	31.0^{a}	1.7	157.0^{d}	385.0

TABLE 3
Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS GLOBEC Study cruises (2000, 2002) in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians (p < 0.001, Kruskal-Wallis rank sum test and p < 0.006, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
June 2000	91	12.0^{a}	1.3	32.0^{d}	0.6	0.0^{b}	0.0
Aug 2000	77	12.2^{a}	2.4	33.0^{b}	0.5	0.6^{a}	1.6
June 2002	104	11.1^{b}	1.6	32.3^{c}	0.9	0.3^{ab}	1.8
Aug 2002	95	10.3^{c}	1.3	33.3^{a}	0.5	0.8^{a}	3.3

TABLE 4
Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS Plume Study cruises (1998–2006) in June in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians (p < 0.001, Kruskal-Wallis rank sum test and p < 0.006, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	39	12.4^{ef}	1.4	31.4^{ac}	1.6	2.6^{def}	7.9
1999	47	13.9^{b}	1.0	28.1^{f}	3.1	1.1^{f}	5.4
2000	48	12.4^{ef}	1.2	29.7^{ef}	2.3	265.0^{bcd}	1749.0
2001	49	13.2^{ce}	1.1	31.7^{a}	1.0	0.3^{ef}	1.2
2002	46	14.0^{b}	1.5	30.3^{cde}	2.4	1.3^{cf}	8.0
2003	60	12.3^{df}	1.7	31.7^{ab}	0.9	608.0^{def}	2652.0
2004	50	14.4^{ab}	1.9	30.8^{cd}	1.9	1603.0^{a}	3582.0
2005	41	14.9^{a}	1.0	30.1^{de}	1.4	952.0^{ab}	3899.0
2006	59	13.1^{bcd}	2.1	31.2^{bcd}	1.6	57.8^{de}	399.0

ied considerably among years during the Predator Study (tab. 2), among cruises during the GLOBEC Study (tab. 3), and among years during June and September Plume Study cruises (tabs. 4–5). SST differed significantly among years and cruises for all studies (Kruskal-Wallis; $p < 0.001$); among Predator and Plume Studies, SST was highest in 1998, 2004, and 2005 and lowest in 1999 (Wilcoxon, $p < 0.006$), with the exception of the June Plume Study (tab. 4) and the September 2005 Plume Study (tab. 5), when SST fell by an average of 3°C following delayed coastal upwelling (Schwing et al. 2006). Low SST values were recorded during Predator and September Plume Study cruises in 1999, and corresponded to La Niña conditions (tabs. 2, 4–5) (Brodeur et al. 2005).

TABLE 5

Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS Plume Study cruises (1998–2006) in September in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians ($p < 0.001$, Kruskal-Wallis rank sum test and $p < 0.006$, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	46	13.2^{bd}	1.2	31.8^{cd}	0.9	3.9^{bc}	11.4
1999	49	11.7^{f}	1.4	32.3^{ac}	0.6	1.7^{c}	8.9
2000	24	13.6^{abc}	2.1	30.6^{ef}	2.3	0.0^{bc}	0.2
2001	46	12.6^{bcd}	1.1	32.0^{acde}	0.9	4.6^{bc}	14.7
2002	65	12.1^{bd}	1.6	32.4^{ab}	0.3	0.9^{c}	2.4
2003	39	13.0^{bd}	1.5	31.7^{cde}	1.1	403.0^{abc}	1463.0
2004	47	14.5^{a}	1.4	31.0^{f}	1.7	1278.0^{a}	3705.0
2005	42	11.9^{cef}	1.6	32.4^{a}	0.8	472.0^{a}	2096.0
2006	55	12.6^{de}	1.1	31.7^{bef}	1.4	10.9^{b}	35.8

TABLE 6

Regression coefficients, standard errors, and *p*-values (statistically significant main effects in bold) from the multiple regression models applied to ln(χ+1) northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) during Plume Study cruises (1998–2006) in June and September.

Variable	Plume	June	$n = 265$	Plume	September	$n = 413$
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	–6.068	3.361	0.072	–0.284	7.379	0.969
Depth	0.000	0.001	0.919	0.000	0.001	0.823
Temperature	0.392	0.309	0.205	–0.417	0.728	0.567
Salinity	0.208	1.227	0.865	–3.081	2.960	0.299
Density	–0.201	1.575	0.898	–3.823	3.819	0.317
Chl-	0.034	0.023	0.138	0.034	0.021	0.113

Variable	Plume	June	$n = 265$	Plume	September	$n = 413$
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–6.489**	**2.269**	**0.004**	**–7.062**	**3.472**	**0.043**
Depth	0.000	0.001	0.918	0.000	0.001	0.828
Temperature	**0.442**	**0.078**	**<0.001**	**0.336**	**0.082**	**<0.001**
Density	0.066	0.067	0.324	0.150	0.112	0.180
Chl-	0.034	0.023	0.140	0.033	0.021	0.128

Variable	Plume	June	$n = 265$	Plume	September	$n = 413$
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–4.434**	**0.899**	**<0.001**	**–2.503**	**0.731**	**<0.001**
Depth	0.000	0.001	0.751	0.001	0.001	0.680
Temperature	**0.400**	**0.035**	**<0.001**	**0.259**	**0.059**	**<0.001**
Chl-	0.033	0.023	0.149	0.030	0.021	0.154

Variable	Plume	June	$n = 265$	Plume	September	$n = 413$
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–4.463**	**0.894**	**<0.001**	**–2.531**	**0.727**	**<0.001**
Temperature	**0.405**	**0.064**	**<0.001**	**0.266**	**0.057**	**<0.001**
Chl-	0.032	0.022	0.160	0.028	0.021	0.172

Variable	Plume	June	$n = 265$	Plume	September	$n = 413$
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–3.871**	**0.792**	**<0.001**	**–2.443**	**0.725**	**<0.001**
Temperature	**0.369**	**0.059**	**<0.001**	**0.269**	**0.057**	**<0.001**

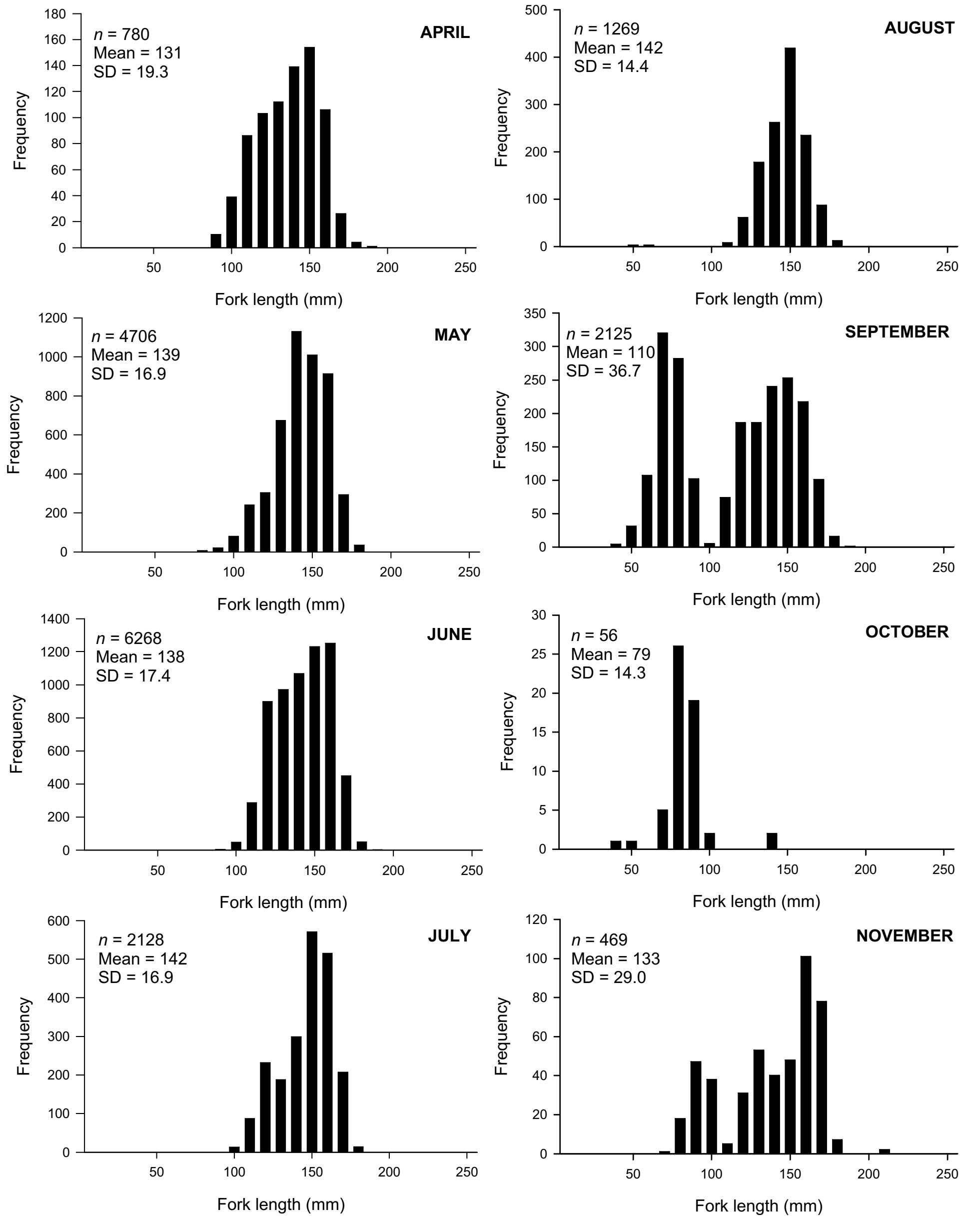

Figure 9. Monthly length-frequency histograms showing pooled northern anchovy (*Engraulis mordax*) fork lengths (mm) measured from 1998–2006 during National Marine Fisheries Service Predator and Plume Study cruises. For each month, we recorded the total number (n) of measurements, mean, and one standard deviation surrounding the mean (SD). Note the appearance of a second cohort from August through November, indicating recruitment of summer-spawned juveniles.

SSS was significantly different among all years and cruises for Predator, GLOBEC, and Plume Studies (Kruskal-Wallis, $p < 0.001$) however, seasonal variations were also detected. SSS values were highest in September during all Plume Study cruises (tab. 5). Differences in SSS were probably related to Columbia River flows and upwelling intensity. For example, mean SSS values were greatest during all GLOBEC Study cruises (tab. 3), which occurred at the southern end of the Columbia River plume front in a region of stronger coastal upwelling. We observed higher SSS values (Wilcoxon, $p < 0.006$) in Predator and Plume Studies in 2001 and 2006 compared to all other years (tabs. 2, 4–5).

Anchovy densities (number/10^6 m^3) varied significantly among all years/cruises for Predator, GLOBEC, and Plume Studies (Kruskal-Wallis, $p < 0.001$). We recorded zero to small catch densities in 1998 and 1999 during Predator and Plume Studies (tabs. 2, 4–5). From 2002–04, anchovy densities increased significantly (Wilcoxon, $p < 0.006$), although the year of peak abundance depended on the study. Predator Study anchovy densities peaked in 2003; Plume Study anchovy densities

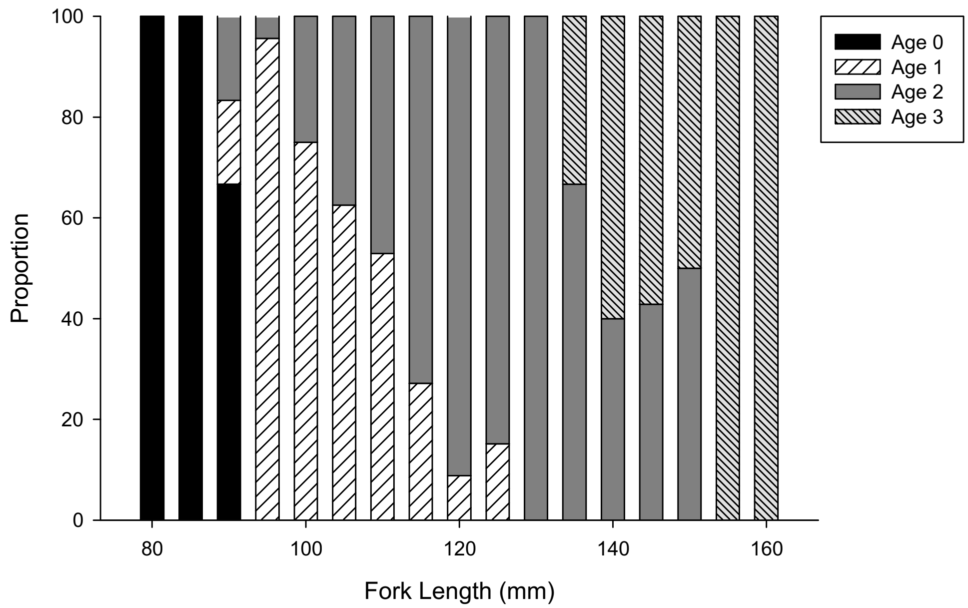

Figure 10. A length-frequency age-overlay histogram developed by aging 295 pairs of northern anchovy (*Engraulis mordax*) saggital otoliths, sampled from fish collected during April-August 2005 Predator Study cruises. Age was determined as the median of three reads performed on different days.

in June and September peaked in 2004. Following 2004, anchovy catch densities significantly decreased (Wilcoxon, $p < 0.006$) throughout Predator and Plume Study cruises (tabs. 2, 4–5), a trend that continued through 2006.

When modeled independently, SST was the single most consistent environmental parameter explaining anchovy abundance during Plume Study cruises (ANOVA, $p < 0.001$) in June and September. The relationship between catch and SST was positive for all cruises (tab. 6). SST alone explained anchovy density during June (extra-sum-of-squares *F*-test, $F_{1,437} = 39.46$, $p < 0.001$) and September (extra-sum-of-squares *F*-test, $F_{1,411} = 22.57$, $p < 0.001$). Most anchovy were caught when the 3 m depth temperature was >12°C. All other variables were insignificant predictors of anchovy density across all Plume Study cruises (tab. 6).

Length and Age Frequencies

Length measurements of anchovy caught during the summertime 1998 and 2001 Triennial Studies ranged from 90–180 mm FL, and during the April-November Plume, GLOBEC, and Predator Studies lengths ranged from 30–265 mm FL, representing several age classes. We developed monthly histograms of size frequency for the Predator and Plume Study cruises because fork length information was logged more habitually (fig. 9). Analysis of length frequencies indicated that three size classes of anchovies were caught, with small fish noticeable in April (70–110 mm FL), and September (30–40 mm FL) through November (70–100 mm FL). While the large size classes (140–180 mm FL) were present each year, the smaller classes were not. The smaller anchovies seen in April appear to be sub-yearlings spawned the previous summer. The smallest anchovies seen in September through November (fig. 9) were young-of-the-year (YOY) spawned off Oregon and Washington during summer months.

Age analysis of 295 anchovies captured from April through September during the nighttime Predator Study indicates that anchovy ranged from 0–3 years in age. We determined an average percent error of 0.06%, indicating extremely high reading precision, and created a length-frequency-by-age histogram (fig. 10).

A negative linear relationship was observed between timing of the spring transition and age-1 anchovy survival, and positive relationships between PDO, MEI, and age-1 survival (fig. 11), although none of the relationships were significant (GLM, $p > 0.05$). However, anomalies of northern copepod biomass showed a significant positive relationship to age-1 anchovy survival (fig. 11), accounting for 62% of the variation associated with the data (GLM, $p = 0.01$).

DISCUSSION

The large inter-annual variability in anchovy densities (number/10^6 m^3) off Oregon and Washington appears to be driven by SST and strong year-class strength due to environmental conditions affecting YOY. From 1998 to 2006, anchovy abundance in the CCLME showed very high temporal variability by year. Anchovy densities corresponded with fluctuations in the localized physical conditions off Oregon and Washington, namely

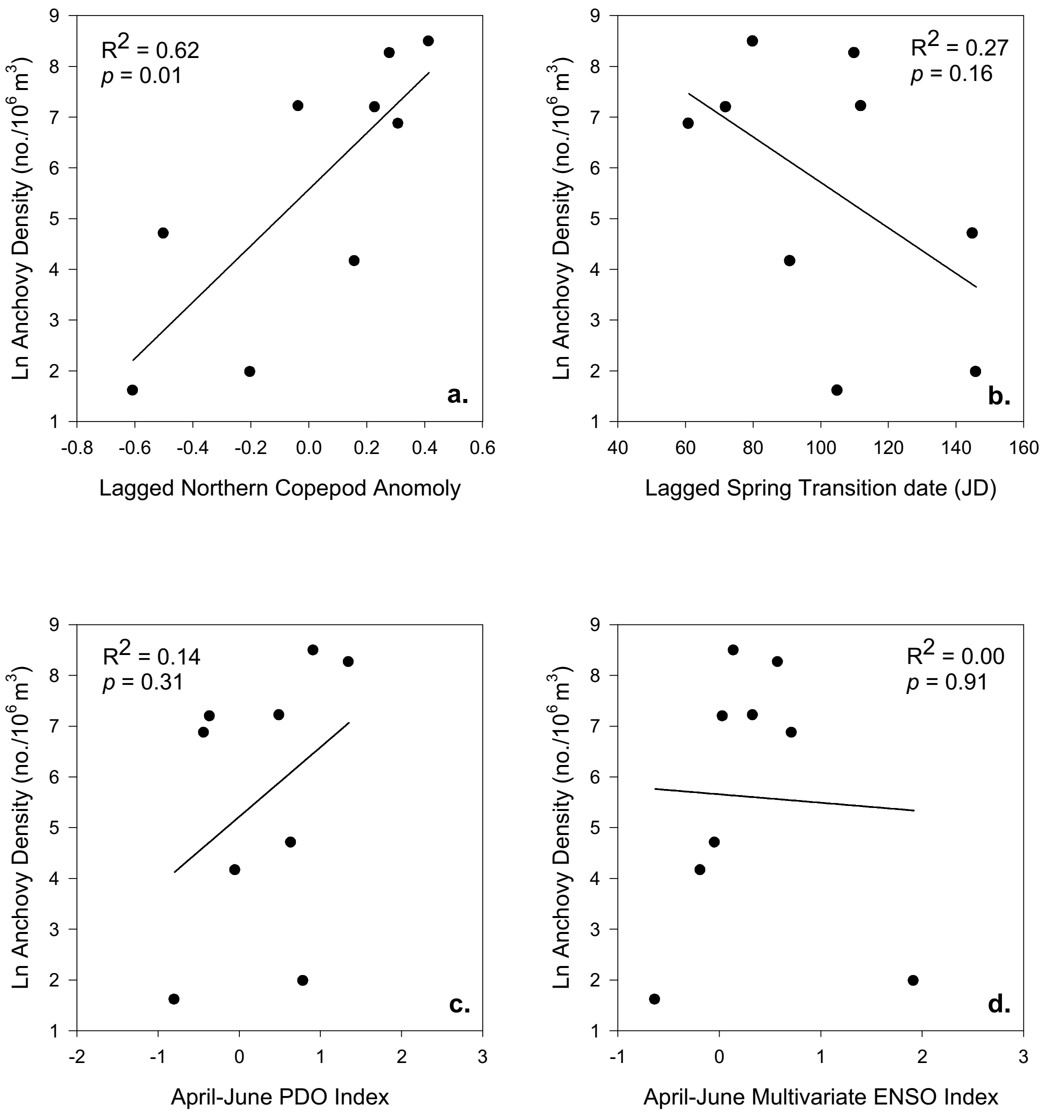

Figure 11. Correlation between log-transformed age-1 northern anchovy (*Engraulis mordax*) density (standardized to number/10^6 m^3) captured during Predator Study cruises in April-June (1998–2006) and (a) value of the one-year lagged northern copepod anomaly, (b) day of the year of the spring transition, (c) mean value of the April-June Pacific Decadal Oscillation (PDO) Index, and (d) mean value of the April-June Multivariate El Niño Southern Oscillation Index (MEI). *R*-squared values and corresponding *p*-values presented at a significance level <0.05.

SST. Warm SSTs were recorded in 1998, 2004, and 2005, and cool SSTs were recorded in 1999–2003 and in 2006. Low anchovy densities were recorded in 1998–2001 and 2005–06. High anchovy densities were recorded in 2002–04.

A shift in northeastern Pacific environmental conditions began in 1999 (Peterson and Schwing 2003), and is reflected in large-scale forcing indices of the North Pacific Ocean, including the PDO and MEI. From 1991 to 1998, PDO and MEI values were primarily positive. However, beginning in late-1998, they became negative, turning positive again in the middle of 2002 and staying positive through 2006. During the 1990s, a very warm period of the PDO was punctuated by ENSO events, and no forage fishes were captured in high abundances off Oregon and Washington (Emmett and Brodeur 2000) until Pacific sardine numbers increased dramatically in the Pacific Northwest accompanying the 1992–93 ENSO (Emmett et al. 2005). Warm ocean conditions persisted through 1997 and 1998, but from 1999 to 2002 the ocean was cold. Northern anchovy eggs and larvae were the most abundant of 34 taxa collected during plankton sampling that occurred approximately every two weeks off the mouth of the Columbia River during spring and summer 1999–2004 (Parnel et al. 2008). In fact, anchovy were frequently captured near the mouth of the Columbia River, within the plume area, indicating some tolerance for fresh water.

Spawning studies of the northern subpopulation of northern anchovy (Richardson 1981; Emmett et al. 1997) indicate that prior to 1997, the spawning peak occurred in July. Recent evidence suggests that spawning can begin as early as May when anchovy congregate near the mouth of the Columbia River (Parnel et al. 2008). Determining the age of YOY anchovy captured during the September Plume Study by counting daily increments will contribute to our understanding of the relationship between hatch date and cohort strength (Takahashi and Watanabe 2004). It is possible that older anchovy females have the capacity to spawn earlier than younger fish, taking advantage of earlier spring transition dates. Studies have successfully linked variations in Pacific salmon marine survival with variations in the spring transition date with a lag of one year (Ryding and Skalski 1999; Logerwell et al. 2003).

Our multiple regression models for Plume Study cruises in June and September show a positive significant linear relationship between SST and anchovy density. However, our scope of inference is limited by the small amount of variability associated with measured SST values over the study period, as well as the significant relationship between age-1 survival and the lagged northern copepod biomass anomaly. There is substantial evidence that anchovy prefer cooler (10°–14°C) rather than warmer SSTs (Lluch-Belda et al. 1992; Schwartzlose et al. 1999; McFarlane and Beamish 2001; Rodriguez-Sanchez et al. 2002; Chavez et al. 2003; Van der Lingen et al. 2006). It is possible that all nearshore habitats we sampled were within the SST tolerances of northern anchovy, thereby reducing our ability to distinguish among SSTs that significantly affect anchovy density. What is more likely is that in situ SST did not effectively predict anchovy density so much as provide insight into YOY survival, so that our catch numbers (number/10^6 m^3) were more a reflection of ocean conditions the year before. This is a common result of gear selectivity, whereby mesh size selects for age-1+ fish. The year class strength of many fish populations, including anchovy, is determined in the first year of life (Bradford and Cabana 1997). Because the northern anchovy is short-lived, its abundance depends on recruitment success from year to year. Peaks in abundance (2003, 2004) were more due to successful recruitment, coupled with cool SSTs, early spring transitions, high primary productivity, and abundant northern zooplankton leading up to 2004, than to in situ warm SSTs recorded in that year. The Predator Study peak in 2003 was attributed to high densities (8,519/10^6 m^3) of subyearling anchovy caught during April, suggesting high over-wintering survival of recruits. This could be related to an intrusion of cold, low oxygen, subarctic water in 2002 (Wheeler et al. 2003).

Northern anchovy are part of a guild of planktivorous coastal pelagic species, whose prey includes phytoplankton and zooplankton (Miller and Brodeur 2007). Northern zooplankton species, namely cold-water boreal copepods, exhibit conservative life-history strategies allowing them to accumulate higher concentrations of poly-unsaturated fatty acids compared to southern, warm-water copepods (Davis and Olla 1992). Poly-unsaturated fatty acids include essential fatty acids that can only be obtained through diet, and greatly influence larval growth rate and survival (Watanabe 1993; Budge et al. 2006). The relationship between age-1 northern anchovy and the lagged northern copepod biomass anomaly must be recognized as an important measurable biological indicator of ocean productivity. The abundance of cold-water copepods may, in fact, be determining anchovy year-class strength. However, it should also be considered that the differences in the copepod community may be due to advection, and that unfavorable advective currents may also carry anchovy from favorable recruitment. Further monitoring will provide the data needed to safely and effectively manage coastal pelagic species in the northeastern Pacific Ocean.

Conclusions

Anchovy continues to be a dominant pelagic forage fish in the CCLME, and is increasingly caught by commercial fishermen whose primary interest is in its value as bait. The coexistence of northern anchovy and Pacific sardine in the CCLME over the past decade (Emmett et al. 2005) appears contradictory to theories about regime shifts for these two species and suggests that plankton is abundant and available enough to support multiple plankton-feeding pelagic schooling fishes. However, there may be intrinsic properties associated with the available plankton community that may lead to differences in energetic availability, which could, in turn, affect growth and survival. Our data suggest that proximity to shore, SST, and timing of the spring transition are important predictors of anchovy density, and fluctuations in the physical oceanographic parameters may have contributed to the decline observed in anchovy density during 2005 and 2006. Under certain conditions, such as delayed coastal upwelling (Schwing et al. 2006), the zooplankton community is influenced by decreased productivity and bottom-up effects, which in turn influences anchovy recruitment. The high 2006 northern copepod index predicts a successful 2007 age-1 anchovy year-class. However, continued observations and studies will be necessary to confirm this.

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