AN ABSTRACT OF THE THESIS OF

Marisa N. C. Litz for the degree of Master of Science in Fisheries Science presented on March 21, 2008.
Title: Ecology of the Northern Subpopulation of Northern Anchovy (*Engraulis mordax*) in the California Current Large Marine Ecosystem

Abstract approved:

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Selina S. Heppell

Northern anchovy (*Engraulis mordax*) are a dominant forage fish in the California Current large marine ecosystem (CCLME). However, little is known about northern anchovy abundance, distribution, age structure, or population fluctuations relative to ocean conditions in the eastern boundary upwelling system off the U.S. West Coast. This thesis includes three primary studies of northern anchovy in the CCLME off Oregon and Washington using data collected during four National Marine Fisheries Service (NMFS) surveys (1977-2006): inter- and intra-annual variation in anchovy distribution and its relationship to oceanography, growth rates of larval and juvenile anchovy that indicate the timing of major spawning events and changes in mortality rates, and analysis of whole lipids and fatty acid profiles to determine food sources in years of contrasting oceanographic conditions. First, I quantified the relationship between northern anchovy abundance with environmental variables at two spatial and temporal scales: 1) mesoscale, including sea surface temperature (SST), salinity (SSS), density (SSD), chlorophyll *a*, distance from shore, and depth; and 2) macroscale, including Pacific Decadal Oscillation Index, Multivariate El Niño Southern Oscillation Index, timing of the Spring Transition, and abundance of cold-water

zooplankton. Anchovy densities increased significantly from 1999-2004, and decreased significantly from 2005-2006. SST and proximity to shore were the most consistent parameters explaining anchovy distribution. Year-class strength was highly correlated with, and presumably driven by, the abundance of cold-water copepods. Second, I characterized recruitment for northern anchovy by conducting microstructure analysis of saggital otoliths from late larval and juvenile life history phases collected in September 2006. I identified a protracted spawning period for northern anchovy ranging from June-August 2006. Juveniles that were spawned and hatched early in the summer 2006 had higher growth rates, but smaller back-calculated sizes-at-age during the larval phase, when compared to congeners spawned later that summer. Finally, I determined total lipid content and fatty acid signatures of northern anchovy and three other forage fish species during two contrasting periods of oceanographic conditions (summers of 2005 and 2006): Pacific sardine (*Sardinops sagax*), Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*). Forage fish lipid levels were lowest in 2005 and increased in 2006. Fatty acid biomarkers in 2005 indicated that the food web was based mainly on dinoflagellates, corroborating observations of delayed coastal upwelling and low primary productivity in the CCLME. In 2006, fatty acids reflected higher levels of diatom feeding and zooplankton carnivory. The results of these studies confirm that in the CCLME, northern anchovy are sensitive to even small environmental perturbations, which is important because this work provides metrics for evaluating climate-mediated, bottom-up ecological processes affecting anchovy survival.

Ecology of the Northern Subpopulation of Northern Anchovy (*Engraulis mordax*) in the California Current Large Marine Ecosystem

by
Marisa N. C. Litz

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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CONTRIBUTION OF AUTHORS

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TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

Ecology of the Northern Subpopulation of Northern Anchovy (*Engraulis mordax*) in the California Current Large Marine Ecosystem

Chapter 1 - General Introduction

The northern anchovy, (*Engraulis mordax* Girard 1854) is a small, schooling fish widely distributed along the west coast of North America from Cape San Lucas, Baja California, Mexico to the Queen Charlotte Islands, British Columbia, Canada (Hart 1973; Hubbs 1925; Miller 1955; Miller and Lea 1972). Anchovy belong to the Family Engraulidae, and three subpopulations are recognized (McHugh 1951), based on otolith weight and standard length differences (Spratt 1972), blood serum and muscle extract proteins (Diaz-Jaimes et al. 1999; Vrooman and Paloma 1975; Vrooman et al. 1981) and genetics (LaCompte et al. 2004). The northern subpopulation occurs in waters off British Columbia to northern California. The central, and most abundant, subpopulation is found off San Francisco to Magdelena Bay, Mexico. The southern subpopulation is associated with warmer water off central and southern Baja California, Mexico. This thesis investigates spatial and temporal patterns of abundance and processes of recruitment of the northern subpopulation of northern anchovy with respect to the variable environment of the California Current off Washington and Oregon.

As one of the dominant species of the Northeast Pacific, the northern anchovy plays a key role in marine ecology of the California Current large marine ecosystem (CCLME). Anchovy are one of a group of coastal pelagic species managed by the Pacific Fishery Management Council (PFMC) in U.S. waters and the Department of Fisheries and Oceans (DFO) in Canada. Anchovy are important forage for marine predators including piscivorous fish (Brodeur et al. 1987; Brodeur and Pearcy 1992;

Livingston and Alton 1982; Tanasichuk et al. 1991), seabirds (Roby et al. 2002), and pinnipeds (Riemer and Brown 1997). Anchovy are one of very few small, plankton-feeding, schooling pelagic fish that link lower and upper trophic levels, transferring energy from primary and secondary production to higher consumers. Their populations may vary drastically in size under intensive exploitation. Top-down control on zooplankton and bottom-up control on top predators is an important intermediary process in the overall energetic budget of marine ecosystems, referred to as "wasp-waist" dynamics (Bakun 2006; Cury et al. 2000).

I have studied the ecology of the northern subpopulation of northern anchovy off Oregon and Washington for this thesis. Little is known about the status of this subpopulation, despite a commercial anchovy fishery that has existed along the west coast of North America for several decades. The anchovy fishery emerged with the collapse of Pacific sardines (*Sardinops sagax*) off central California in the 1940s (Huppert et al. 1980), and anchovy research and fishing effort have been limited to the southern California Bight ever since. By contrast, the northern subpopulation in the Pacific Northwest (PNW) has traditionally supported only a small purse seining bait fishery, focused off Oregon and Washington (USA), at the mouth of the Columbia River, in Grays Harbor and Willapa Bay. The Canadian-based northern anchovy bait fishery closed indefinitely in 2002, when it became apparent that costs for an anchovy stock assessment exceeded projected profits (T. Therriault DFO, *personal communication*). Scientific investigations into the northern subpopulation have produced two stock assessments, the first in 1975-76 (Richardson 1981) and the

second in 1994-95 (Emmett et al. 1997). Both examined northern anchovy populations associated with the Columbia River plume using the egg production method (Stauffer and Parker 1980).

Critical habitat for the northern subpopulation of northern anchovy includes the upper 10-20 m of the water column in marine and estuarine waters across the continental shelf and slope off the U.S. west coast, collectively termed the Coastal Upwelling Domain (Ware and McFarlane 1989). This region is characterized by the broad, southward meandering California Current, which extends from the northern tip of Vancouver Island to the southern tip of Baja, along the eastern margin of the North Pacific Gyre and travels at a mean current speed of ~10 cm/s (Hickey and Banas 2003). Extensive upwelling of colder sub-surface waters occurs along the shelf during spring and summer months, caused by prevailing northwesterly winds acting through Ekman transport (Huyer 1983). The upwelling supports a highly productive nearshore ecosystem, including coastal pelagic species. During winter months, water over the shelf moves northward as the Davidson Current in response to southwesterly winds and Ekman transport, a coastal countercurrent to the California Current (Hickey 1979; Hickey 1998). Freshwater intrusion by the Columbia River is highly seasonal, and influences water mass stratification in the PNW (Brodeur et al. 2005; Hickey and Banas 2003).

The North Pacific experiences dramatic shifts in climate/circulation on a frequency of years to decades, known as Pacific Decadal Oscillation (PDO), caused by eastward-westward jumps in the position and intensity of the Aleutian Low

atmospheric pressure system in winter (Mantua and Hare 1997; Mantua and Hare 2002). The PDO has been described as a persistent El Niño Southern Oscillation (ENSO) pattern of climate variability, marked by variations in Pacific basin sea surface temperature (SST), sea level pressure (SLP), as well as land surface temperature, precipitation and stream flow (Mantua and Hare 1997). Typically, anchovy numbers decrease during persistent ENSO conditions, when surface water temperatures tend to be warmer, upwelling is dampened and the PDO index is positive (Baumgartner et al. 1992; Chavez et al. 2003). During these periods, anomalous warm water ichthyofauna are often encountered along the PNW Coast (Pearcy 2002). However, the mechanism(s) leading to anchovy decline have yet to be established.

Anchovy (*Engraulis* spp.) feed upon both marine primary producers (phytoplankton) and secondary producers (zooplankton) (Brodeur et al. 1987; Emmett et al. 1991; Miller and Brodeur 2007), and are most abundant worldwide in strong upwelling regions, including the California, Humboldt, Japanese, Canary and Bengeula Current Systems. Regardless of the system, anchovy abundance seems to fluctuate inter-annually, out of phase with sardine (*Sardinops sagax* and *Sardina pilchardus*) with regular frequency (Baumgartner et al. 1992; Chavez et al. 2003; Lluch-Belda et al. 1992; Mantua and Hare 1997; Mantua and Hare 2002; Schwartzlose et al. 1999). Anchovy scales deposited in the anaerobic sediments of both the Santa Barbara basin (Baumgartner et al. 1992) and Lo Démas (Sandweiss et al. 2004), a former fishing village on the coast of Peru, show evidence of regime shifts between anchovy and sardine populations dating back 1500 years. Forage fish like anchovy are

particularly sensitive to basin-wide physical disturbances affecting primary and secondary production levels because they are short-lived and their population size can change year-to-year depending on annual recruitment success (Rodriguez-Sanchez et al. 2002). As such, anchovy abundance can be used as an ecological indicator of basin-wide disruptions related to ENSO, upwelling or the PDO (McFarlane and Beamish 2001; McFarlane et al. 2002).

Compared to the central and southern stocks, the northernmost stock of northern anchovy is the smallest and least exploited of the three subpopulations. During the early 1970s, anchovy were observed spawning actively in the summer off the Columbia River (Laroche and Richardson 1980; Richardson 1981). Following an apparent regime shift in 1976 (Emmett and Brodeur 2000; Hare and Mantua 2000; McFarlane and Beamish 2001; McFarlane et al. 2002), anchovy numbers decreased dramatically in the PNW, due in part to a warming event associated with 1983's ENSO (Brodeur et al. 1985; Brodeur et al. 1987; Fiedler et al. 1986). Northern anchovy numbers declined while sardine population numbers increased, resulting in a basin-wide change in the overall biomass make-up of pelagic fishes in the eastern Pacific (Emmett and Brodeur 2000; Rodriguez-Sanchez et al. 2002). In 1999, the upwelling season was long and intense, southward transport was high and zooplankton biomass doubled, leading researchers to suspect another large-scale ecosystem regime shift had occurred (Peterson and Schwing 2003) A resurgence of forage fish in the PNW followed, and between 1999-2004, the incidence of both anchovy and sardine caught in purse seine and trawl nets increased. Since 2004, forage fish captured in

fisheries independent pelagic sampling studies have declined, corresponding with positive PDO values, delayed timing of the Spring Transition (Schwing et al. 2006), and an expansion of the Oregon coast hypoxic "dead zone" (Grantham et al. 2004; Chan et al. 2008).

Northern anchovy play a critical role in the marine ecosystem of the CCLME. In 2000, the PFMC (2000) recommended more research to understand the dynamics of forage fish such as anchovy, by way of more frequent monitoring and improved stock assessments. Factors influencing population dynamics include ocean temperature, which affects distribution, growth and spawning; ocean productivity, which affects the feeding environment of larval, juvenile and adult fish; and ocean circulation, which affects transport of eggs and larvae. Fish harvest plans must consider ecosystem needs and climate effects (Pikitch et al. 2004), as defined by the Magnuson-Stevens Fishery Conservation and Management Act (amended 2007) to better understand the processes of recruitment for northern anchovy.

This thesis examines ecology of the northern subpopulation of northern anchovy, focusing on the relationships between environmental parameters and inter-annual variability in abundance, distribution and recruitment success. Chapter 2 considers spatial and temporal patterns of anchovy abundance in relation to regional and basin-wide scales of the physical oceanographic environment. Data used for this analysis comes from National Marine Fisheries Service (NMFS) sampling efforts by NOAA Fisheries occurring between 1977-2006. Chapter 3 re-examines what is currently accepted as anchovy spawning timing by examining age distribution and

growth rates of late-larval and juvenile phases of northern anchovy spawned and hatched during summer 2006, using otolith microstructure analysis. Chapter 4 examines differences in total whole lipids and fatty acid signatures of northern anchovy and three other common species of forage fish, Pacific sardine (*Sardinops sagax*), Pacific herring, (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*), encountered off Oregon and Washington during two contrasting years of oceanographic conditions (summers of 2005 and 2006). These results provide new and invaluable information to researchers interested in population dynamics of anchovy and other small pelagic species, particularly with reference to the physical environment of the CCLME. Information on the seasonal and inter-annual variability of anchovy abundance presented will be useful to seabird and marine mammal researchers interested in forage patch dynamics. The early life-history growth models will be of interest to biologists interested in recruitment dynamics. Trophic ecologists will value the information presented on lipids and fatty acids, results of which are likely to contribute to ongoing discussions about bottom-up processes controlling trophic food web structure, and related mechanisms driving biological regime shifts.

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Chapter 2 - Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the U.S. West Coast

ABSTRACT

Northern anchovy are a dominant fish in the California Current large marine ecosystem (CCLME) and prey for many piscivorous predators. However, little is known about how anchovy distribution and abundance is affected by oceanographic variability in the Eastern Pacific. We examined the relationship between anchovy abundance with 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 2005-2006, 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, the northern copepod biomass anomaly was highly correlated to age-1 anchovy survival, suggesting that they may determine year-class strength.

INTRODUCTION

Northern anchovy (*Engraulis mordax*) 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). Previous investigations have revealed correlations between California Current climate changes and forage fish regime shifts (Baumgartner et al. 1992; Schwartzlose et al. 1999; Rodriguez-Sanchez et al. 2002; Chavez et al. 2003), yet no studies provide information about anchovy distribution in relation to local and basin-wide changes in climate or the marine ecosystem. We explore 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.

The northern subpopulation of northern anchovy range from Eureka, California to the Queen Charlotte Islands, British Columbia, Canada (McHugh 1951) and support a small bait fishery centered off the Columbia River. 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. These results provide valuable ecological information about the northern subpopulation of northern anchovy that is relevant to ecosystem-based fishery management (EBFM) 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.

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 (Table 2.1, Fig. 2.1). 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.

NMFS West Coast Triennial bottom trawl studies (**Triennial Study**) began in summer 1977, and were repeated every three summers (June-August) up to 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 48º N latitude, to overlap spatially with our target surveys, although anchovy were distributed as far south as 32º N latitude, off southern California.

Since 1998, pelagic fish resources off Oregon and Washington have been monitored using surface trawls by the NWFSC 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. 2.1). The **Plume Study** consisted of daytime hydrographic and fish sampling of the Columbia River plume and 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 US 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, 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 approximately every ten days on two transects north and south of the Columbia River from April to August 1998-2006 (Emmett et al. 2001; Krutzikowsky and Emmett 2005; Emmett et al. 2006). While

Plume and **GLOBEC Study** cruises sampled 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, WA) 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 measured (mm) for either fork length (FL; > 80 mm) or standard length (SL; ≤ 80 mm). In the event of a very large catch, we measured, counted and weighed a subsample of anchovy. Using the mass of the remaining anchovy catch, the total number caught was calculated from the known 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 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 at each station before beginning the trawls during **Predator**, **GLOBEC** and **Plume Studies** using a Sea-bird SBE 19 SeaCat conductivity, temperature and depth (CTD) profiler. Measurements of sea temperature (ºC), 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 PDO index (Joint Institute for the Study of the Atmosphere and the Oceans, http://www.jisao.washington.edu/pdo/), the Multivariate ENSO (MEI) Index (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 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 (-20º C), and returned to the lab for processing. We recorded FL (mm) and wet weight (to the nearest 0.01g), removed

the saggital otoliths according to a protocol previously developed for anchovy otolith extraction (Messersmith 1969), and then cleaned and stored them in 95% ethanol.

We photographed each otolith under a Leica MZ7.5 high performance stereomicroscope equipped with digital imaging software at 50x magnification. For ageing, 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 (3 m) temperature (SST), 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, a Wilcoxon signed rank test was used 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, 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 extra-sum-of-squares *F*-tests.

We conducted correlation analyses between age-1 anchovy densities measured from **Predator Study** catches April through June (1998-2006) with PDO and MEI values and between age-1 anchovy densities and one-year lagged northern copepod biomass anomalies (Peterson and Schwing 2003) off Newport, Oregon and one-year lagged timing of the Spring Transition. The Spring Transition (Huyer et al. 1979) occurs when coastal conditions change from those dominated by coastal downwelling and wind from the south to those dominated by coastal upwelling and wind from the north. One advantage of these models are their predictive power, and their ability to forecast fish densities one year into the future using current physical oceanographic data, highly desirable in the management of coastal pelagic species. Spring Transition date was recorded in 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 (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 of increasing anchovy abundance over the study period. Commercial catches of the northern subpopulation of northern anchovy in the PNW increased from 68 metric tonnes (mt) in 2001 to 239 mt in 2002. Anchovy landings were almost exclusively for 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 have also increased after 2001 (Fig. 2.2). 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. Anchovy have been recently 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, *personal communication*).

Spatio-temporal variance in anchovy abundance and distribution

Interannual variability has been a common trend in logged anchovy catch with fishery-independent sampling efforts. 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. 2.3). Anchovy numbers increased during the ENSO event of 1983, and were seen farther north than encountered during any survey before or since. After 1986, northern anchovy were not encountered during **Triennial Study** surveys off the PNW until 1998.

Distribution and abundance of anchovy collected during the **Plume Study** showed 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 ($53{,}118/10^6m^3$) off the mouth of the Columbia River. June **Plume Study** cruises sampled very few anchovy from 1998-2000 (Fig. 2.4), with the exception of one huge haul (density = $12{,}127/10^6m^3$) recorded off the Columbia River in 2000. The catch leveled off from 2001-2002, with densities measuring $0\text{-}55/10^6m^3$ (Fig. 2.4). However, beginning in June 2003, a coast-wide expansion of anchovy was observed. Anchovy were caught at 17 of 60 stations, with densities measuring $>3{,}000/10^6m^3$ at 4 of those stations, located off Cape Meares and the Columbia River (Fig. 2.4). From June 2004 through 2005, anchovy were observed at 56 out of 91

stations from 44.5° N to 48° N latitude, with the highest catches (22,913/10^6m^3) found off the mouth of the Columbia River. In June 2006, anchovy numbers decreased (Fig. 2.4), which coincided with what appeared to be increased southerly catches. For the first time during the **Plume Study**, the largest anchovy catches (106 and 180/10^6m^3) occurred beyond the shelf break in deep water (>200 m), more than 50 km from the coast (Fig. 2.4).

Distribution of anchovy during September **Plume Study** cruises did not always correspond well with catch data recorded during June **Plume Study** cruises in the same year. In September 1998 we caught more anchovy (61/10^6m^3) than during the preceding June (Fig 2.5). However, from 1999-2000, anchovy were caught at record low densities (1/10^6m^3). During September 2001, anchovy were mainly aggregated nearshore south of the Columbia River. We recorded small catches (1-15/10^6m^3) south of the Columbia River in September 2002, at 18 of 65 stations along three transects (Cape Meares, Cascade Head and Newport). Higher densities of anchovy were caught (1-7,345/10^6m^3) in September 2003, at 10 of 39 stations, with most occurring off Willapa Bay (Fig. 2.5). In September 2004, we recorded anchovy at 33 of 47 stations along all eight transects sampled (1-21,400/10^6m^3), indicating that the recruitment pulse observed in June 2004 persisted throughout the summer (Fig. 2.5). Large anchovy densities were also recorded at 25 of 42 stations in September 2005 (1-12,809/10^6m^3), although none occurred north of Grays Harbor. In September 2006, anchovy catch decreased, with densities ranging from 1-254/10^6m^3 at 25 of the 55 stations fished (Fig. 2.5).

GLOBEC Study distribution and abundance of anchovy off southern Oregon was patchy during all cruises (Fig. 2.6). No anchovy were captured in June 2000, but anchovy were caught at 8 of 104 stations in June 2002 at densities orders of magnitude lower (0-15/$10^6 m^3$) than **Plume Study** catches at the mouth of the Columbia River during the same month (0-12,127/$10^6 m^3$) (Fig. 2.4). Anchovy densities during the August 2000 **GLOBEC Study** averaged 1/$10^6 m^3$ at 15 of 77 stations and ranged from 1-30/$10^6 m^3$ at 14 of 95 stations in August 2002 (Fig. 2.6). We conducted an additional **Plume Study** cruise in August 2005 with transects sampled north of Newport, OR to Grays Harbor, WA. Large catches of anchovy were recorded, with densities (not shown) ranging from 0-4,546/$10^6 m^3$.

Predator Study anchovy densities around the mouth of the Columbia River showed very large monthly and annual variability through spring and summer 1999-2006 (Fig. 2.7). 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. 2.8) 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. 2.8). During 2001 and 2002 mean nearshore (<10 km) anchovy densities were three

times greater than any offshore station (>10 km), and twice as large as any offshore station (>10 km) in 2005.

Correlation of abundance with abiotic factors

Anchovy distributions are likely strongly affected by abiotic factors such as sea surface temperature (3-m SST) and salinity (3-m SSS). Anchovy density varied considerably among years during the **Predator Study** (Table 2.2), among cruises during the **GLOBEC** Study (Table 2.3), and among years during June and September **Plume Study** cruises (Tables 2.4-2.5). SST differed significantly among years/cruises for all studies (Kruskal-Wallis; $p<0.001$), and among **Predator** and **Plume Studies**, SST was highest in 1998, 2004 and 2005 and lowest in 1999 (Wilcoxon, $p<0.006$), except for September 2005 (Table 2.5), 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 **Plume Study** cruises in 1999, and corresponded to La Niña conditions that year (Tables 2.2, 2.4-2.5) (Brodeur et al. 2005).

SSS was significantly different among all years/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 (Table 2.5). Differences in SSS were probably related to Columbia River flows, but also stronger upwelling along the coast. For example, mean SSS values were greatest during all **GLOBEC Study** cruises (Table 2.3), which occurred south of the Columbia River plume front. Between **Predator** and **Plume Studies**

(Tables 2.2, 2.4-2.5), we observed higher SSS values (Wilcoxon, $p<0.006$) in 2001 and 2006 compared to all other years.

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 all studies (Tables 2.2-2.5). From 2002-2004, anchovy densities increased significantly (Wilcoxon, $p<0.006$) for all studies, although the year of the peak abundance depended on the study. **Predator Study** anchovy densities peaked in 2003; **Plume Study** anchovy densities in June and September peaked in 2004. Following 2004, anchovy catch densities significantly decreased (Wilcoxon, $p<0.006$) throughout **Predator** and **Plume Study** cruises (Tables 2.2, 2.4-2.5), 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 (Table 2.6). 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 3-m depth temperature was >12°C. All other variables were insignificant predictors of anchovy density across all **Plume Study** cruises (Table 2.6).

Length and age frequencies

Length measurements of anchovy caught during the 1998 and 2001 **Triennial Studies** ranged from 90-180 mm FL, and during the **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 Studies**, because fork length information was logged more habitually (Fig. 2.9). Analysis of length frequencies indicated that three size classes of anchovies were caught, with small fish noticeable in April (70-110 mm FL), September [30-40 mm standard length (SL)] 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 and flushed out of the Columbia River estuary during spring run-off. The smallest anchovies seen in September through November (Fig. 2.9) were young-of-the-year (YOY) spawned off Oregon and Washington during summer months.

Age analysis of 295 anchovies captured from April-September during the nighttime **Predator Study** show 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. 2.10).

Using fork length as a proxy for age based on our earlier analysis, we determined the proportion of age-1 fish captured from 1998-2006 during **Predator Study** cruises and modeled their first year survival (age-1 density) against indices of basin-wide oceanography (Fig. 2.11), including one year lags for northern copepod

biomass anomalies and timing of the Spring Transition. We observed a negative linear relationship between timing of the Spring Transition and age-1 survival, and positive relationships between PDO, MEI and age-1 survival, 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. 2.11), 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 young-of-the-year (YOY). From 1998 to 2006, anchovy abundance in the Coastal Upwelling Domain of the CCLME showed very high temporal variability by year. Anchovy densities corresponded with fluctuations in the localized physical conditions off Oregon and Washington, namely SST. Warm SST were recorded in 1998, 2004 and 2005 and cool temperatures in 1999-2003, and in 2006. Low anchovy densities were recorded in 1998-2001, and 2005-2006. High anchovy densities were recorded in 2002-2004.

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, 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 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 abundance off Oregon and Washington (Emmett and Brodeur 2000) until sardine numbers increased dramatically in the Pacific Northwest accompanying the 1992-1993 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 approximately every two weeks off the mouth of the Columbia River during spring and summer 1999-2004 (Parnel et al. in press). In fact, anchovy were frequently captured near the mouth of the Columbia River, within the plume area, indicating some tolerance for freshwater.

Northern anchovy spawning surveys (Emmett et al. 1997; Richardson 1981) in the PNW identified July as the peak of anchovy spawning prior to 1997. Recent evidence (Parnel et al. in press) suggests that spawning can begin as early as May, with anchovy congregating near the mouth of the Columbia River. Determining the age of young-of-the-year (YOY) anchovy captured during the September **Plume Study** by counting daily increments (Takahashi and Watanabe 2004) will contribute to our understanding of the relationship between hatch date and cohort strength. It is possible that older anchovy females have the capacity to spawn earlier than younger fish, taking advantage of earlier Spring Transition dates, and therefore earlier chlorophyll-*a* production (Wheeler et al. 2003). Studies have been successful linking variations in Pacific salmon (*Onchorhynchus* spp.) marine survival with variations in

the Spring Transition date lagged by one year (Logerwell et al. 2003; Ryding and Skalski 1999).

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, SST (Chavez et al. 2003; Lluch-Belda et al. 1992; McFarlane and Beamish 2001; Rodriguez-Sanchez et al. 2002; Schwartzlose et al. 1999; 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 significant SSTs that 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). Being short-lived, northern anchovy abundance is dependent on recruitment success from year to year. Peaks in abundance (2003, 2004) were because of successful recruitment, coupled with cool SST, early Spring Transition, high primary productivity and abundant northern zooplankton leading up to 2004, rather than to *in*

situ warm SSTs recorded in that year. The **Predator Study** peak in 2003 was attributed to high densities ($8519/10^6 m^3$) of anchovy caught during April, suggesting high over-wintering survival of recruits related to an intrusion of cold, low oxygen, subarctic water in 2002 (Wheeler et al. 2003).

Anchovy are part of a guild of planktivorous coastal pelagic species, whose prey includes plankton and zooplankton (Miller and Brodeur 2007). Northern zooplankton species, namely cold water boreal copepods, exhibit conservative life history strategies allowing them to accumulate high concentrations of polyunsaturated fatty acids (PUFA) compared to southern, warm water copepods (Davis and Olla 1992). PUFA include essential fatty acids (EFAs) that can only be obtained through diet and greatly influence larval growth rate and survival (Budge et al. 2006; Watanabe 1993). 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 and endangered salmonid species in the Northeastern Pacific.

Conclusions

Anchovies continue to be a dominant pelagic forage fish in the CCLME, and are increasingly caught by commercial fishermen whose primary interest is in their value as bait. The coexistence of anchovy and sardines in the northern California Current 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 enough and available 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 affect growth and survival. Our data suggests that proximity to shore, SST and timing of the Spring Transition are important predictors of anchovy density and 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 impacted through decreased productivity and bottom-up effects, which 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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Table 2.1. An inventory of all National Marine Fisheries Service (NMFS) cruises used for this paper. The duration of each cruise varied among studies, with **Predator Study** cruises accounting for only 2 nights of sampling (12 stations total) versus **Triennial Study** cruises, which lasted months and sampled ~600 stations per cruise.

Year	Study	Dates	Area	Trawl Type	Physical data (Y/N)
1977-1995	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

Table 2.2. 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.

		Temperature	(°C)	Salinity	(psu)	Anchovy	(no./$10^6 m^3$)
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	46	14.3^{a}	1.17	28.9^{ab}	3.46	23.8^{e}	115
1999	109	11.8^{d}	1.71	29.1^{b}	2.84	11.9^{e}	102
2000	96	12.7^{c}	1.26	29.3^{a}	2.97	458^{bd}	2293
2001	106	12.5^{c}	1.17	30.8^{a}	1.89	1668^{b}	12069
2002	110	12.8^{c}	2.20	29.4^{b}	2.80	1831^{ad}	9861
2003	113	13.0^{c}	1.63	29.7^{b}	2.17	3327^{ac}	12646
2004	105	14.1^{b}	1.48	29.4^{b}	2.62	1458^{bc}	3310
2005	118	13.9^{b}	1.56	29.2^{b}	2.71	1591^{b}	3501
2006	80	12.8^{c}	1.45	31.0^{a}	1.67	157^{d}	385

[1]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)

[2]Significance levels for superscript values are: a > b > c > d > e

Table 2.3. 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.

		Temperature (°C)		Salinity (psu)		Anchovy (no./$10^6 m^3$)	
	n	Mean	±SD	Mean	±SD	Mean	±SD
June00	91	12.0[a]	1.30	32.0[d]	0.63	0.00[b]	0.00
Aug00	77	12.2[a]	2.38	33.0[b]	0.53	0.58[a]	1.58
June02	104	11.1[b]	1.56	32.3[c]	0.86	0.32[ab]	1.77
Aug02	95	10.3[c]	1.34	33.3[a]	0.47	0.75[a]	3.27

[1]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)

[2]Significance levels for superscript values are: a > b > c > d

Table 2.4. 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.

		Temperature	(°C)	Salinity	(psu)	Anchovy	(no./$10^6 m^3$)
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	39	12.4^{ef}	1.39	31.4^{ac}	1.57	2.58^{def}	7.89
1999	47	13.9^{b}	0.97	28.1^{f}	3.07	1.13^{f}	5.37
2000	48	12.4^{ef}	1.19	29.7^{ef}	2.29	265^{bcd}	1749
2001	49	13.2^{ce}	1.07	31.7^{a}	1.01	0.34^{ef}	1.20
2002	46	14.0^{b}	1.45	30.3^{cde}	2.39	1.33^{cf}	8.03
2003	60	12.3^{df}	1.69	31.7^{ab}	0.91	608^{def}	2652
2004	50	14.4^{ab}	1.91	30.8^{cd}	1.89	1603^{a}	3582
2005	41	14.9^{a}	1.02	30.1^{de}	1.41	952^{ab}	3899
2006	59	13.1^{bcd}	2.09	31.2^{bcd}	1.61	57.8^{de}	399

[1]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)

[2]Significance levels for superscript values are: a > b > c > d > e > f

Table 2.5. 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.

		Temperature	(°C)	Salinity	(psu)	Anchovy	(no./$10^6 m^3$)
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	46	13.2^{bd}	1.15	31.8^{cd}	0.94	3.91^{bc}	11.4
1999	49	11.7^{f}	1.37	32.3^{ac}	0.59	1.66^{c}	8.91
2000	24	13.6^{abc}	2.10	30.6^{ef}	2.34	0.04^{bc}	0.20
2001	46	12.6^{bcd}	1.08	32.0^{acde}	0.91	4.62^{bc}	14.7
2002	65	12.1^{bd}	1.62	32.4^{ab}	0.32	0.93^{c}	2.35
2003	39	13.0^{bd}	1.53	31.7^{cde}	1.07	403^{abc}	1463
2004	47	14.5^{a}	1.38	31.0^{f}	1.70	1278^{a}	3705
2005	42	11.9^{cef}	1.56	32.4^{a}	0.76	472^{a}	2096
2006	55	12.6^{de}	1.06	31.7^{bef}	1.37	10.9^{b}	35.8

[1]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 tests)

[2]Significance levels for superscript values are: a > b > c > d > e > f

Table 2.6. Regression coefficients, standard errors and p-values (statistically significant main effects in bold) from the multiple regression models applied to ln(*x*+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-α	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-α	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-α	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-α	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**

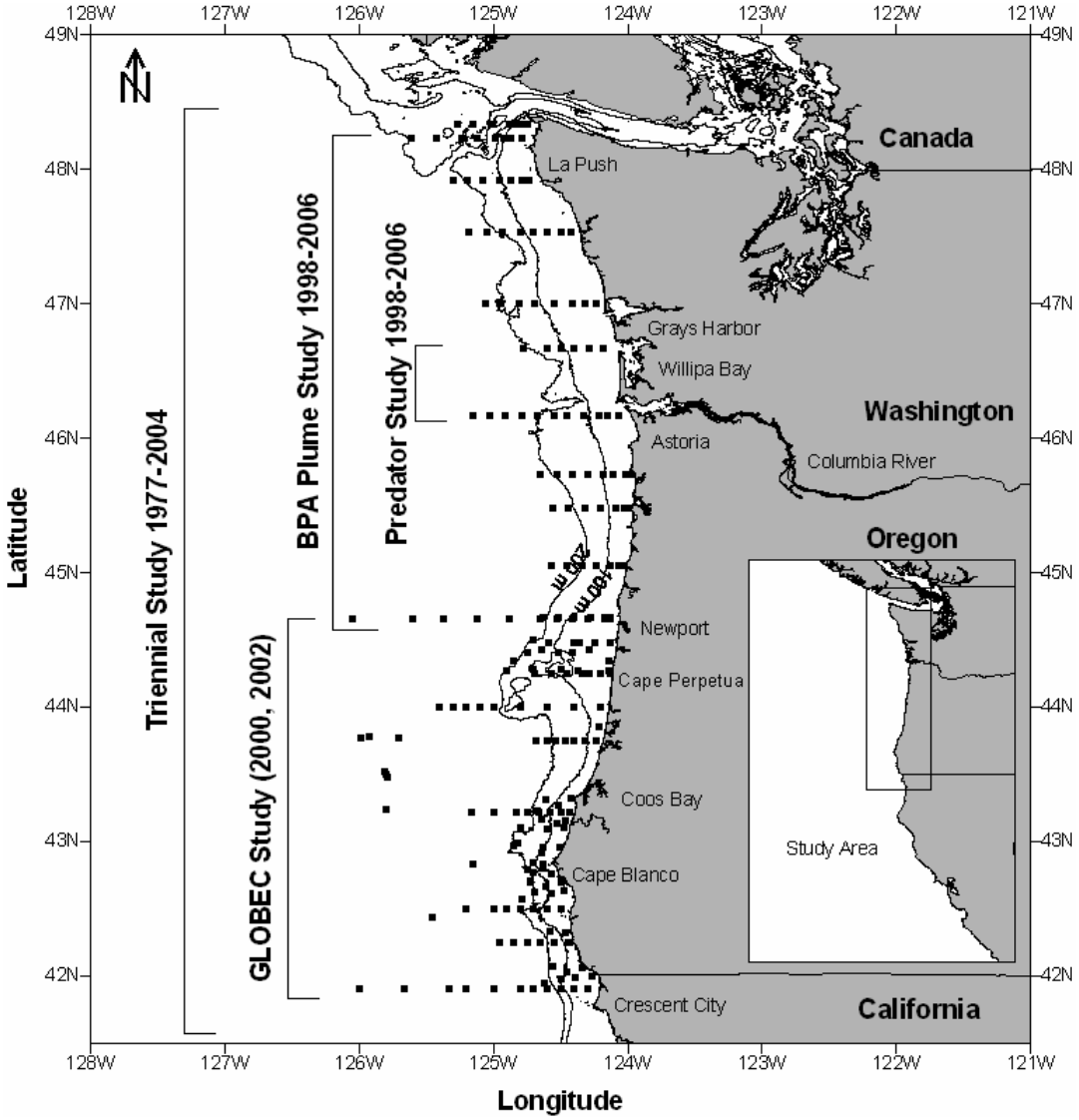

Figure 2.1. Map showing the four National Marine Fisheries Service (NMFS) pelagic sampling cruise locations (**Triennial**, **Plume**, **GLOBEC** and **Predator Study** cruises). Dots show the NMFS fishing stations where the same type of gear was deployed at the surface to trawl for fish. Also shown are the 100 and 200 m depth contours.

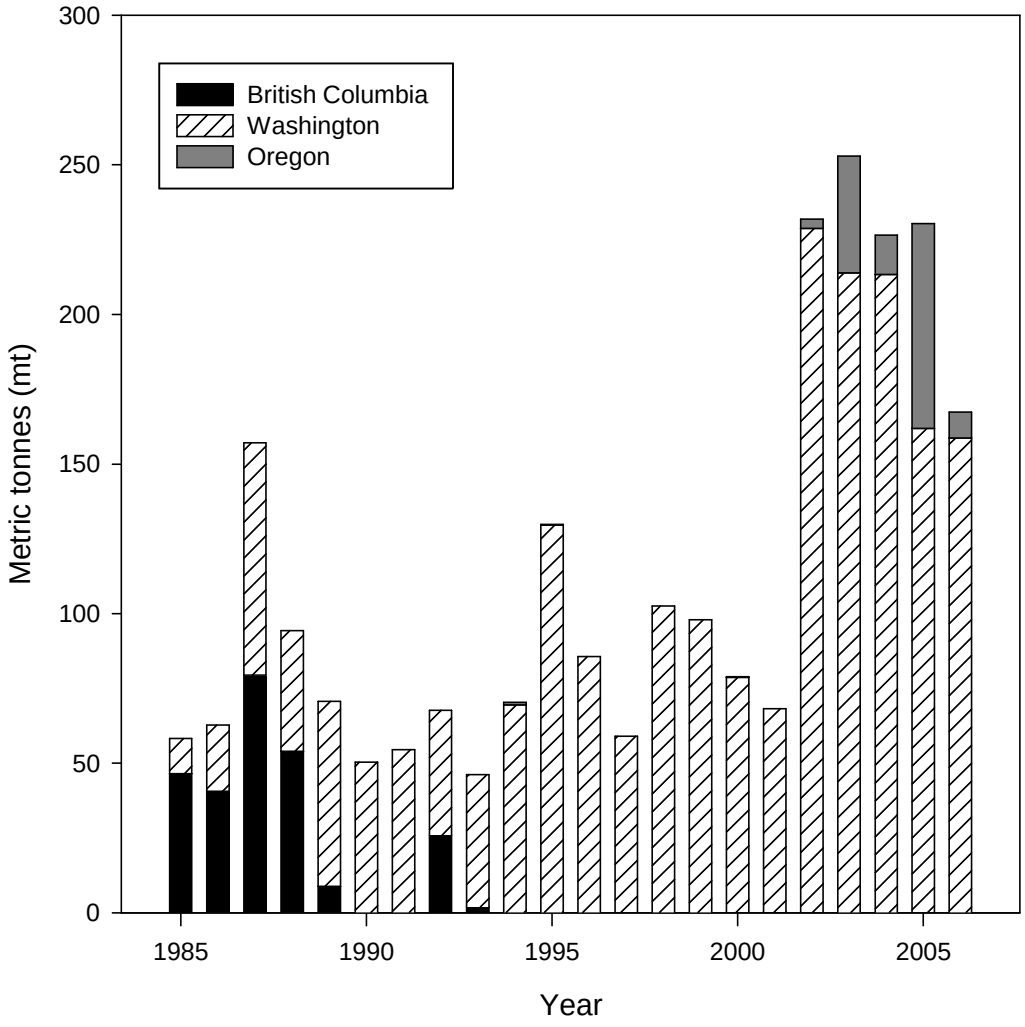

Figure 2.2. Annual commercial landings from 1985-2006 in metric tonnes (mt) of northern anchovy (*Engraulis mordax*) off Oregon, Washington, and British Columbia [data courtesy of B. Culver, (WDFW) J. McCrae (ODFW) and T. Therriault (DFO)].

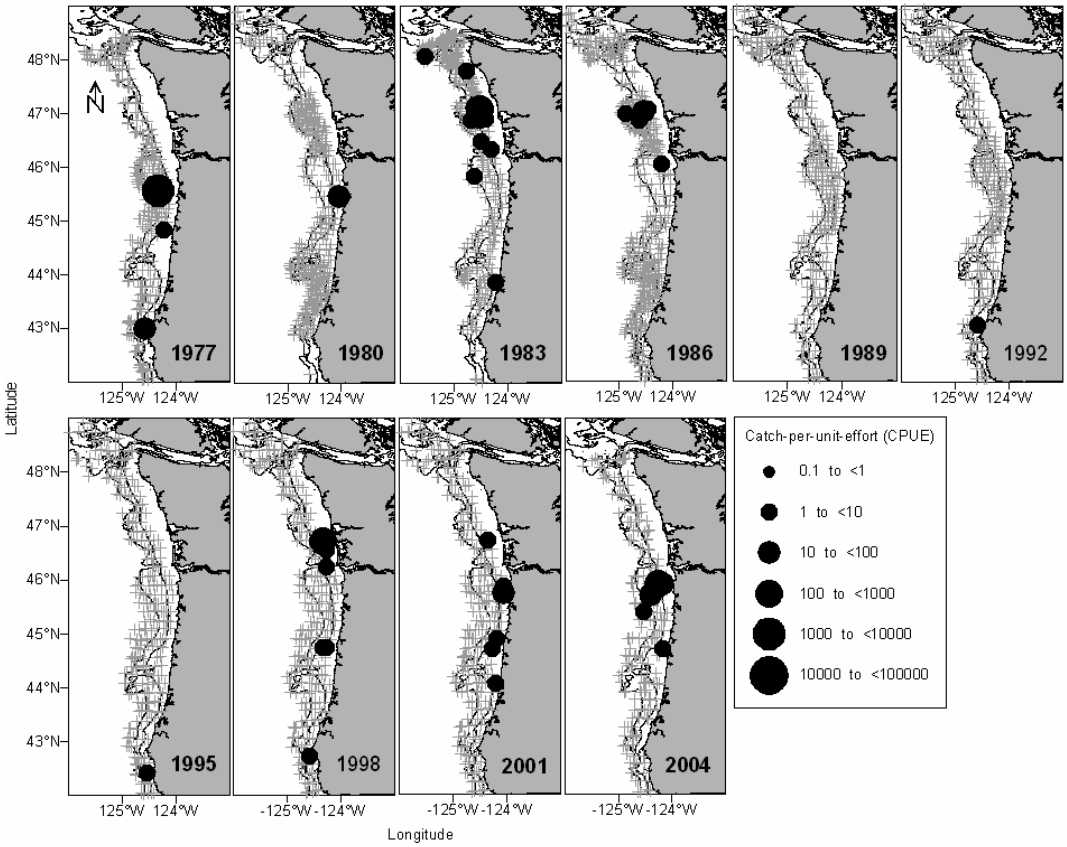

Figure 2.3. Catches of northern anchovy (*Engraulis mordax*), displayed as catch-per-unit effort (CPUE), from National Marine Fisheries Service (NMFS) **Triennial Study** cruises. All cruises occurred in June-September every three years from 1977-2004. Anchovy landed were incidental by-catch captured 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.

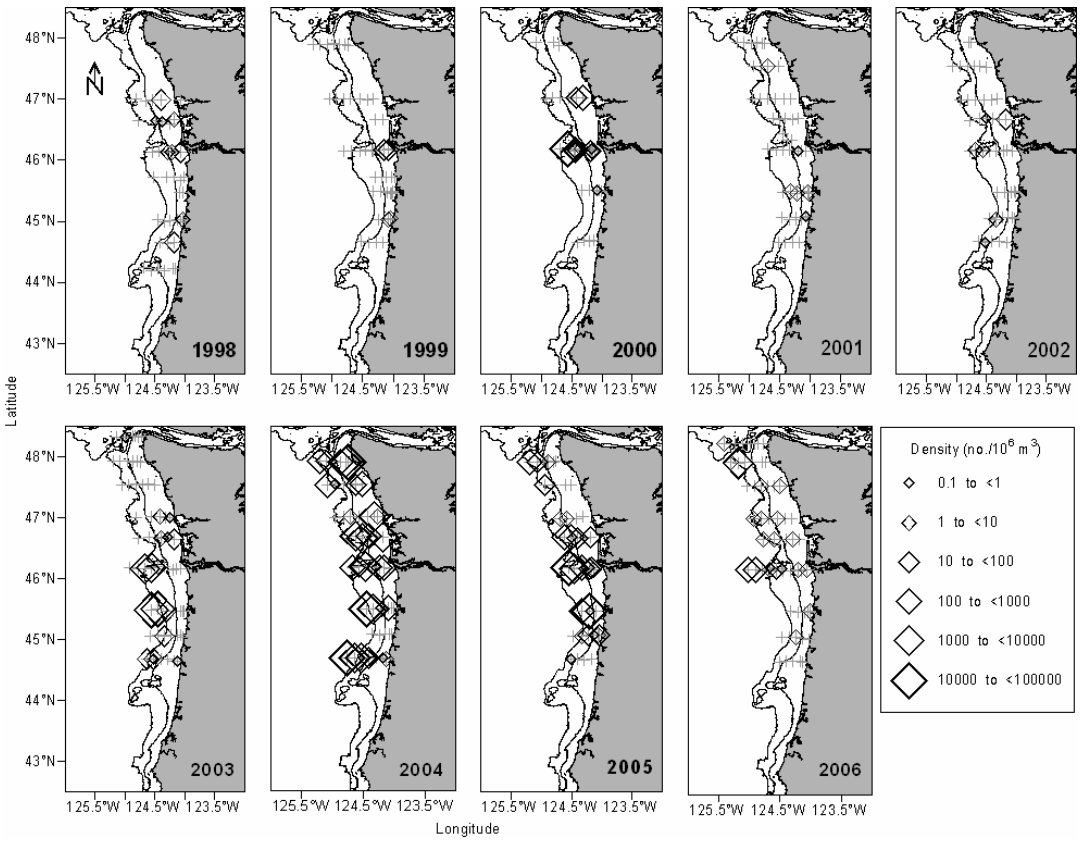

Figure 2.4. Distribution of northern anchovy (*Engraulis mordax*) density during **Plume Study** cruises (1998-2006) off Oregon and Washington in June standardized across hauls to number/10^6m^3. The + signs show locations of surface trawls. Also shown are 100 and 200 m depth contours.

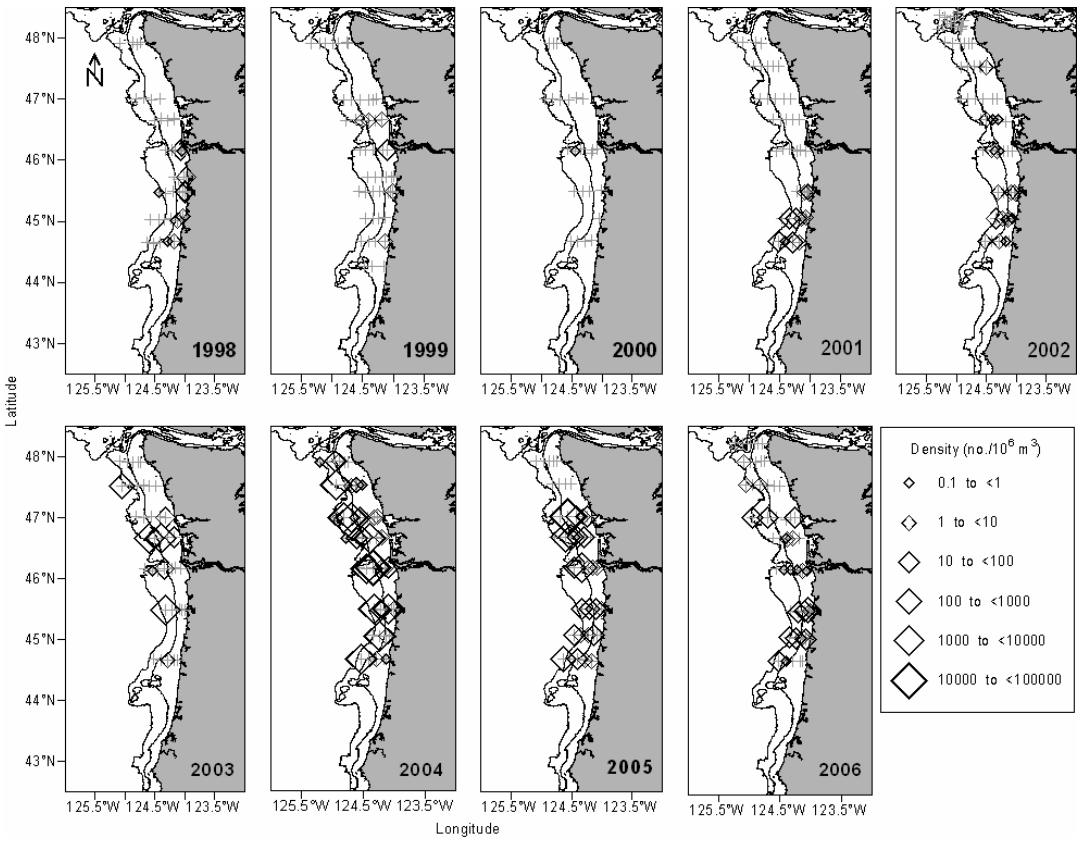

Figure 2.5. Distribution of northern anchovy (*Engraulis mordax*) density during **Plume Study** cruises (1998-2006) off Oregon and Washington in September standardized across hauls to number/$10^6 m^3$. The + signs show locations of surface trawls. Also shown are 100 and 200 m depth contours.

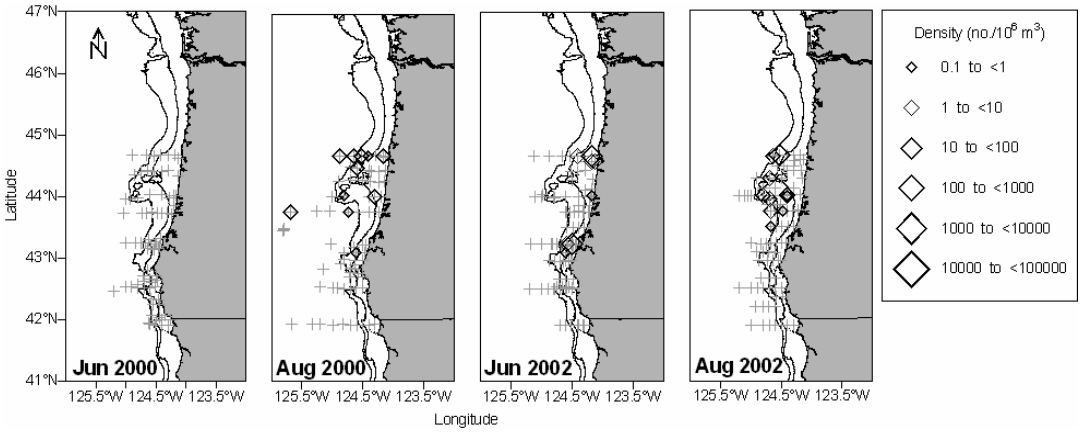

Figure 2.6. Northern anchovy (*Engraulis mordax*) density (standardized across hauls to number/10^6m^3) for the 2000 and 2002 **GLOBEC Study** cruises off southern Oregon and northern California. The + signs show locations of surface trawls. Also shown are the 100 and 200 m depth contours.

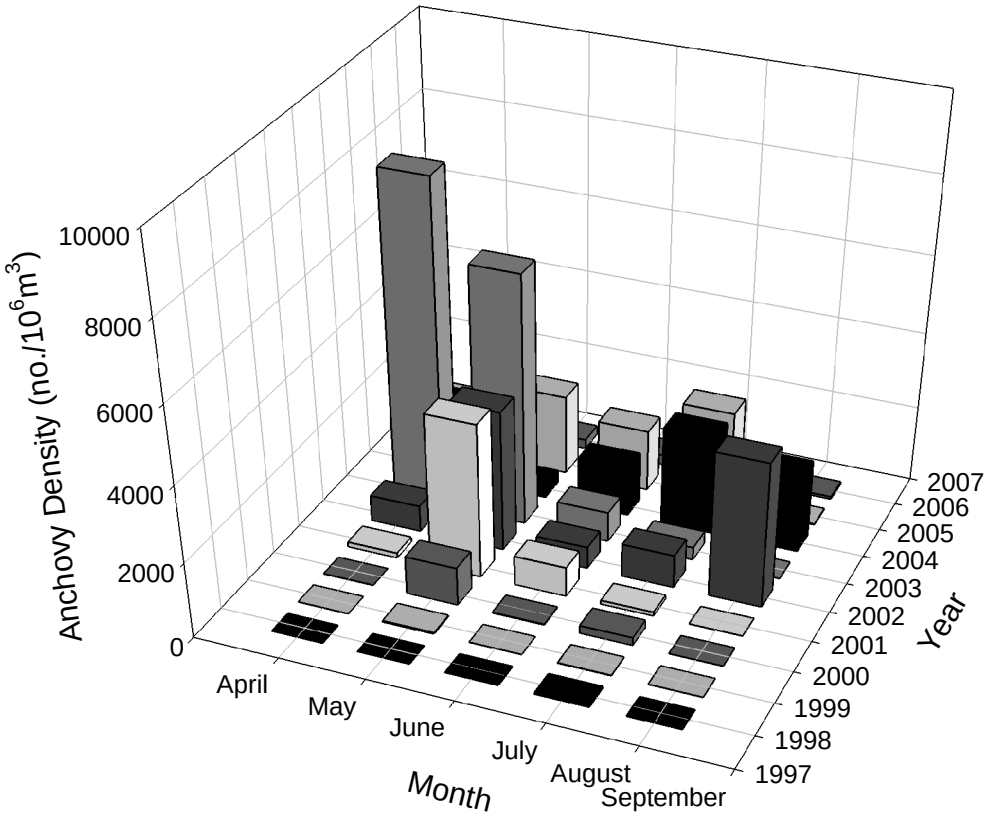

Figure 2.7. Average monthly densities (standardized across hauls to number/10^6m^3) of northern anchovy (*Engraulis mordax*) captured from 1998-2006 during **Predator Study** cruises that sampled from April through September along two transects north and south of the Columbia River.

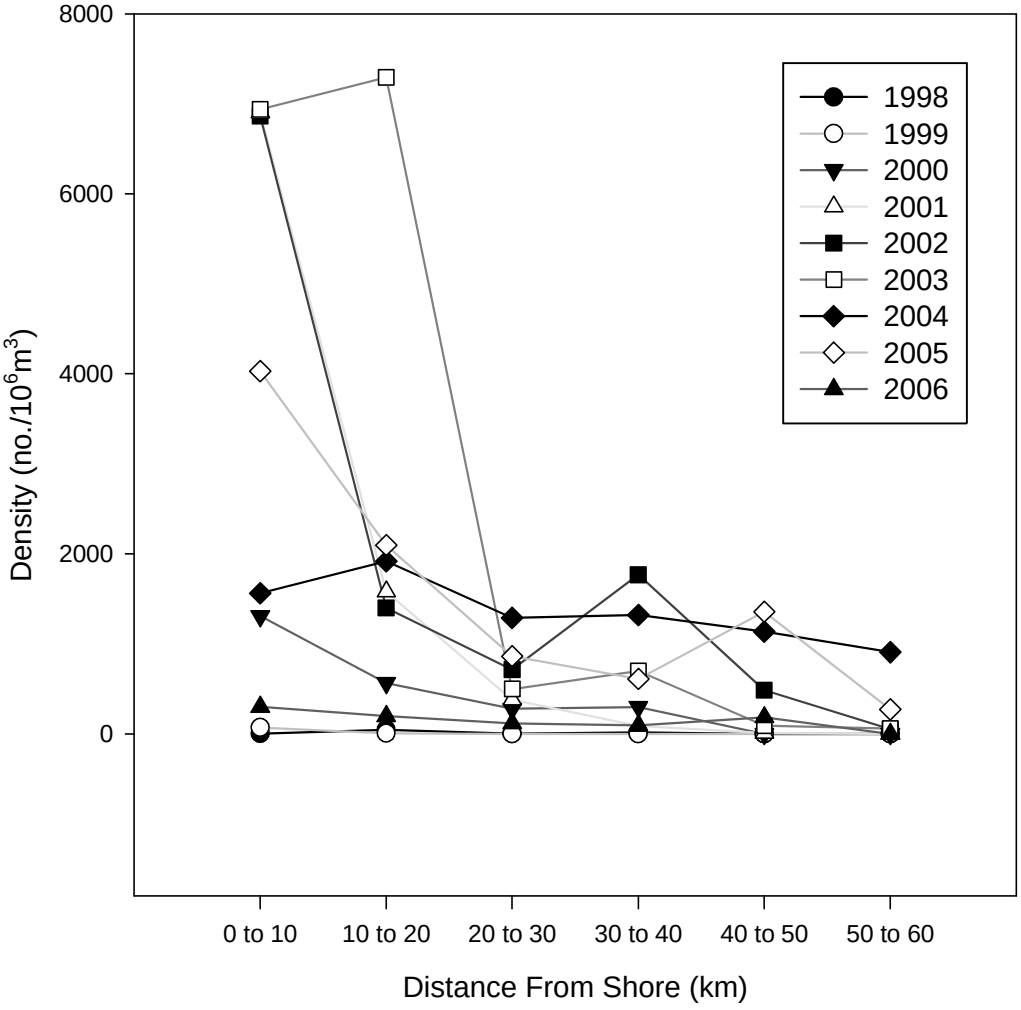

Figure 2.8. Average annual density (standardized to number/10^6m^3) of northern anchovy (*Engraulis mordax*) at 0-60 km from shore during 1998-2006 **Predator Study** cruises that sampled from April through September along two transects north and south of the Columbia River.

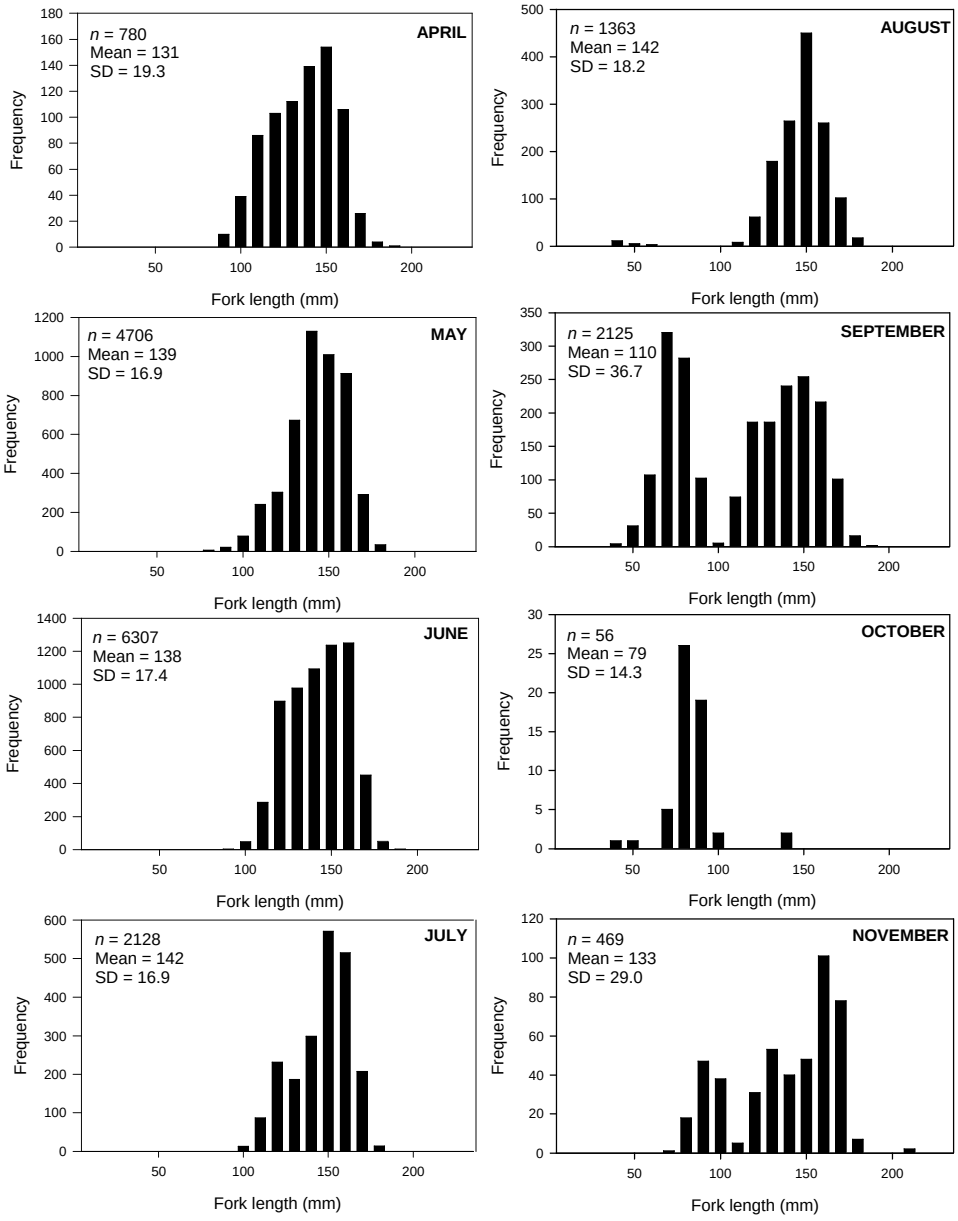

Figure 2.9. Monthly length-frequency histograms showing pooled northern anchovy (*Engraulis mordax*) fork lengths (mm) measured from 1998-2006 during National Marine Fisheries Service (NMFS) **Predator** and **Plume Study** cruises. For each month, we recorded the total number (*n*) of measurements, mean and one standard deviation surrounding the mean (SD). Note the appearance of a second cohort from August through November, indicating recruitment of spring-spawned juveniles.

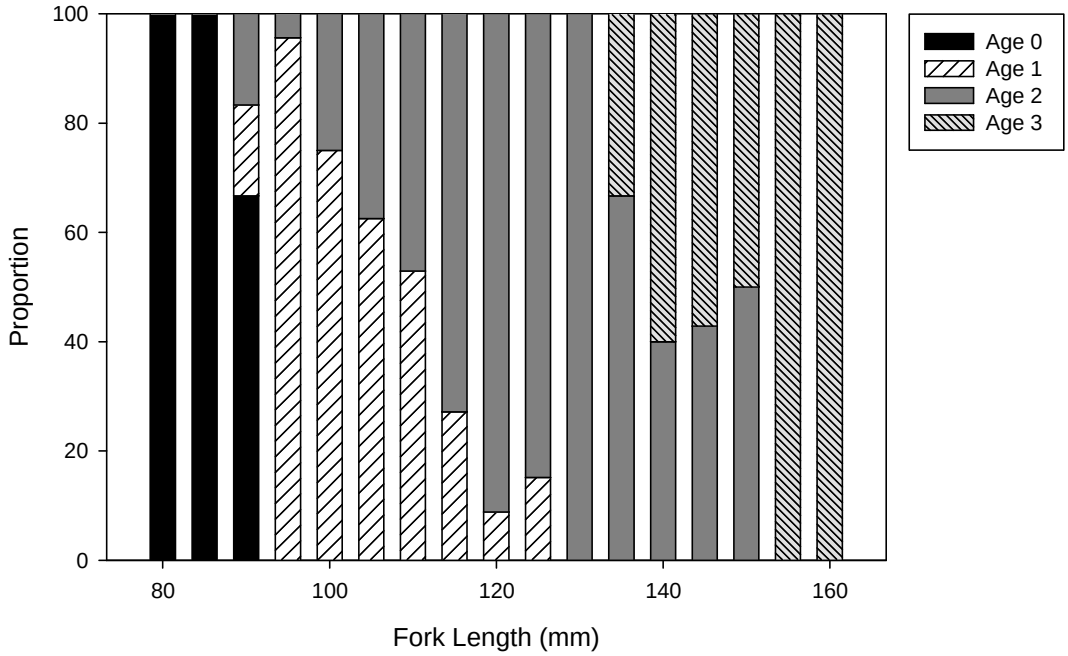

Figure 2.10. A length-frequency age-overlay histogram developed by ageing 295 pairs of northern anchovy (*Engraulis mordax*) saggital otoliths, sampled from fish collected during April-August 2005 **Predator Study** cruises. Age was determined as the median of three reads performed on different days.

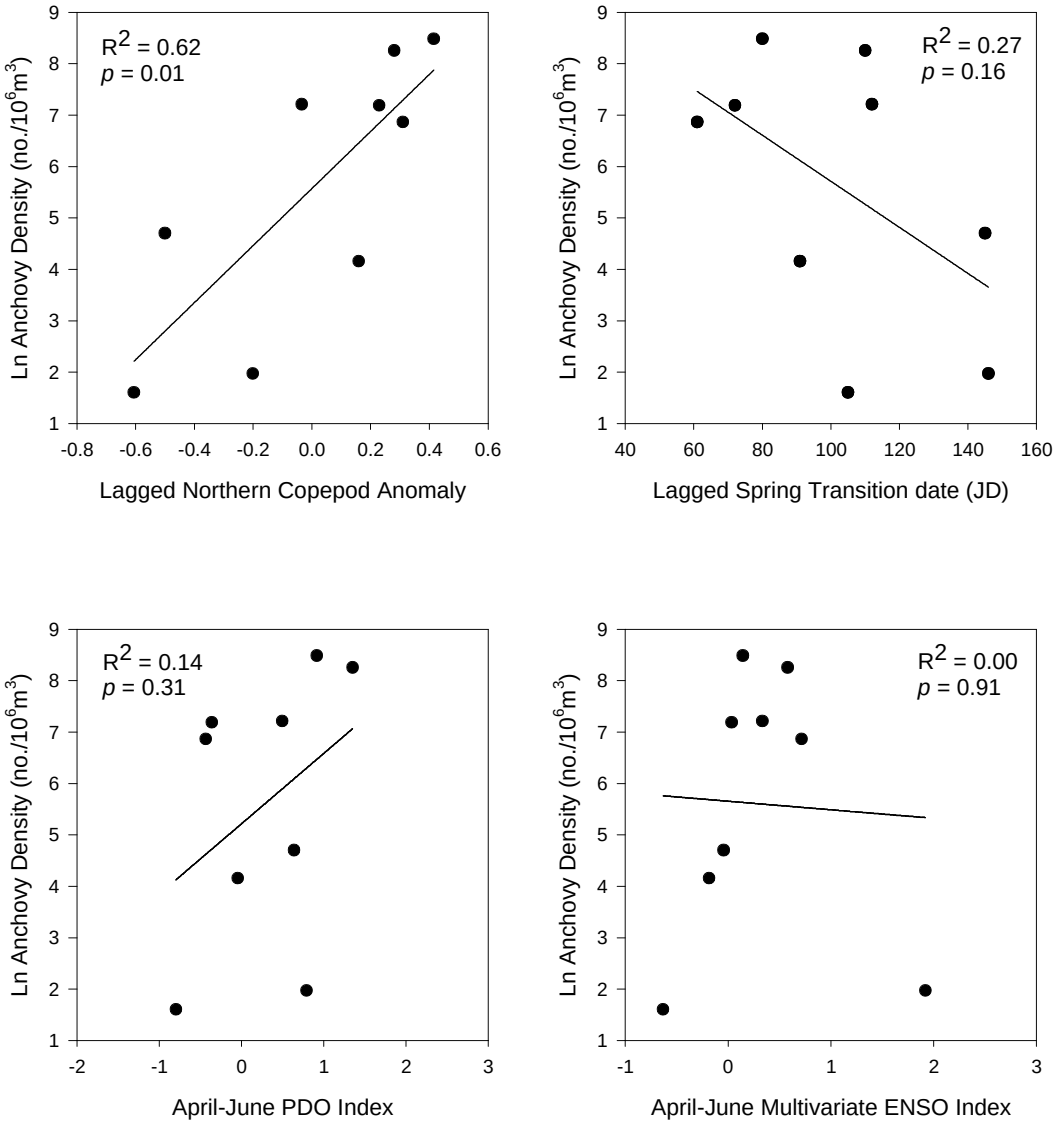

Figure 2.11. Correlations between log-transformed age-1 northern anchovy (*Engraulis mordax*) densities (standardized to number/10^6m^3) captured during **Predator Study** cruises in April-June (1998-2006) and one-year lagged northern copepod anomalies, timing of the Spring Transition (Julian date), mean April-June Pacific Decadal Oscillation (PDO) Index values, and mean April-June Multivariate El Niño Southern Oscillation Index (MEI) values. R-squared values and corresponding *p*-values presented (significance level < 0.05).

Chapter 3 – Spawning timing and growth rates of post-larval and juvenile northern anchovy (*Engraulis mordax*) in the California Current large marine ecosystem

ABSTRACT

This study compares characteristics of recruitment for northern anchovy (*Engraulis mordax*), from late larval and juvenile life history phases sampled in shelf waters off Oregon and Washington in September 2006. We assigned a total of 217 fish to one of three developmental stages based on the degree of guanine deposition on their surface, then removed saggital otoliths for microstructure analysis of daily increments to test the hypothesis that anchovy spawned earlier in the season have higher growth rates, leading to increased probability of survival. Characteristics include spawning timing, body length-otolith radius relationships, weight-length relationships, Gompertz growth curves, hatch dates, increment widths, and back-calculated daily records of size-at-age using the biological intercept method. Our results confirm protracted spawning in the northern subpopulation of northern anchovy from mid-June through early August 2006. Late-stage larvae (Gu-0) displayed compensatory growth in their first 50 days, obtaining significantly larger sizes-at-age than early juvenile (Gu-1) and juvenile (Gu-2) anchovy. But beginning at metamorphosis from the larval to juvenile phase at 60 days (or ~35mm standard length) older Gu-2 anchovy gained more weight and grew faster than younger fish. Gu-2 anchovy also had wider mean increment widths, and higher mean and recent growth rates (0.56 and 0.78 mm/day respectively) than either Gu-0 or Gu-1 congeners,

supporting our hypothesis that northern anchovy spawned earlier in the season have higher probability of recruitment to the fishery.

INTRODUCTION

Both biological and physical sources of mortality influence year-class strength in fish populations, but these factors may be mediated by larval characteristics. It has long been accepted that the survival of early northern anchovy (*Engraulis mordax*) larvae is not correlated with the number of subsequent 1-year old recruits (Peterman and Bradford 1987, Peterman et al. 1988). This is contrary to hypotheses set forth by Hjort (1914, 1926) and Lasker (1975; 1981) that year-class strength of anchovy is determined at an early stage, during the "critical period" following yolk-sac absorption, and negatively correlated with wind-driven turbulent mixing. However, survival probabilities during the larval and juvenile stages may be a function of growth rate (Anderson 1988), with faster growing individuals more likely to survive than slower growing individuals. Selective mortality is thought to occur because fast-growing fish require less time through phases when they are most vulnerable to predators (the stage-duration hypothesis; Houde 1987; Cushing 1990). This scenario has been demonstrated in many studies (Meekan and Fortier 1996; Meekan et al. 2006; Searcy and Sponaugle 2001; Wilson and Meekan 2002). Japanese anchovy (*Engraulis japonicus*) larvae with faster developmental and growth rates have a higher probability of recruitment to the adult stock than those with lower developmental and growth rates (Takahashi and Watanabe 2004a, b). In addition, Takasuka et al. (2003;

2004) showed that anchovy larvae with lower growth rates are more susceptible to predation than larvae with higher growth rates, even if they are the same size, based on comparisons of growth increments in the otoliths of larvae ingested by juvenile anchovy and skipjack tuna predators with those of larvae surviving in corresponding waters off Japan.

Very little information is available on environmental requirements for larval northern anchovy growth in the California Current large marine ecosystem (CCLME), although it is well established that patterns of primary productivity in the eastern-boundary upwelling system off Oregon and Washington are highly seasonal and initiated by the Spring Transition (Hickey and Banas 2003). We hypothesize that northern anchovy spawned earlier in the season exhibit faster growth rates than those spawned in later months, presumably leading to higher probability of survival. We used saggital otolith microstructure analysis to address this issue, targeting the northern subpopulation of northern anchovy that occurs in waters off Oregon and Washington.

Much discrepancy exists over the exact timing and location of anchovy spawning off Oregon and Washington, but ichthyoplankton surveys confirm that peak spawning occurs in coastal waters associated with the Columbia River plume sometime between April and August (Smith and Richardson 1977; Laroche and Richardson 1980; Richardson 1981; Brodeur et al. 1985; Emmett et al. 1997; Parnel et al., in press). The objective of this study is to determine hatch date and estimate larval growth of northern anchovy captured in nearshore waters of the northern CCLME.

The results will provide useful information on growth and survival processes during early life phases in northern anchovy and contribute to our understanding of spawning behavior associated with the Columbia River plume. Early larval growth has been modeled in northern anchovy off Oregon and Washington (Methot 1981), but we believe this is one of the first attempts to model growth in late-larval and juvenile life history phases of the northern subpopulation of northern anchovy, particularly using the biological intercept method (Campana 1990; Campana and Jones 1992). We expect that our study will reveal information pertaining to the processes of recruitment in northern anchovy, and aid in the management of this developing bait fishery off Oregon and Washington.

METHODS

We sampled for late larval and juvenile northern anchovy during the 2006 annual National Marine Fisheries Service (NMFS) Bonneville Power Administration (BPA) Plume Study cruise, September 20-28, 2006. Since its inception in 1998, BPA Plume Study cruises have occurred in June and September of every year as part of a larger pelagic fish sampling effort by the Northwest Fisheries Science Center targeting juvenile salmonids along the continental shelf off Oregon and Washington. We collected adult, late larvae and juvenile northern anchovy using a Nordic 264-rope trawl (NET Systems, Bainbridge Island, WA) fished behind the vessel at the surface. . Collection stations ranged from 2-60 km offshore and 44.5° to 48° N latitude (Fig. 3.1). The trawl measured 12 m by 28 m (336 m^2) and has variable mesh sizes from

162.6 to 8.9 cm, with an additional 6.1 m long, 0.8 cm knotless liner sewed into the cod end. Anchovy egg samples were collected using either 1-m or Bongo zooplankton sampling nets and preserved in 10% formalin. We used a flow meter to detemine the volume of water filtered through the nets. Anchovy eggs were identified, counted and standardized to density (number/m^3) back at the laboratory.

We preserved late larval (25-35 mm standard length, SL) and early juvenile (35-60 mm SL) anchovy in 95% ethanol and transported them back to the laboratory for processing. We measured SL to the nearest mm and recorded weight to the nearest 0.001 g. We assigned late larvae and early juveniles (< 60 mm SL) to one of three developmental stages, based on the amount of guanine deposition on the surface of the fish: Gu-0, none; Gu-1, guanine on the peritoneal surface, but not the trunk surface; and Gu-2, guanine on both the peritoneal and trunk surfaces. In Japanese anchovy, the degree of guanine deposition has been shown to be an effective criterion for determining the end of the metamorphosis from larval to juvenile stages (Takahashi and Watanabe 2004c).

We removed 217 pairs of saggital otoliths under a dissecting microscope at 10x-50x magnifications, using a scalpel and fine probes, then rinsed and mounted them on a glass slide, distal side up, using enamel resin. We ground otoliths by hand along the saggital plane using 1,500-grit wet/dry sandpaper to gain proximity to the core, and polished them using 0.05-μm alumina powder, until daily increments were visible along the entire diameter of the otolith (see Brothers et al. 1976).

We counted and measured daily increments to the nearest 0.01 μm using an otolith measurement system, consisting of a Leica DMLS light microscope at 40x-1000x magnification, equipped with digital camera (Leica DC 300 V2.0, Leica, Wetzlar, Germany), computer monitor and Image-Pro Discovery software (Media Cybernetics, Inc., Bethesda, MD). One reader measured daily increments and otolith radius (OR) from the nucleus to the posterior edge along the leading growth axis. The reader measured all otoliths three times on different dates to obtain an estimate of precision. Median age obtained from the three reads was used in all subsequent analyses. For this study, daily age was calculated by adding eight to the total number of daily increments, corresponding with complete yolk-sac absorption at 12.5°C (Methot and Kramer 1979).

To determine otolith-fish size relationships, we regressed OR and fish weight on SL for each developmental stage. We determined hatch dates by subtracting the age of the fish in days from its date of capture. We calculated overall mean growth rate (G) for each developing stage based on the degree of guanine deposition as:

$$G = (L_c - L_0)/d \qquad [1]$$

Where L_c = SL in mm of the fish at capture; L_0 = SL in mm of newly hatched larvae, set at 3.4 according to Lasker et al. (1970); and d = age in days. We then fit the Gompertz growth function (Zweifel and Lasker 1976; Methot and Kramer 1979) to SL data from each of three developmental stages of northern anchovy as follows:

$$\text{Ln}(L_d) = \text{Ln}(L_0) + A_0/\alpha\,(1 - e^{-\alpha d}) \qquad [2]$$

Where L_d = the back-calculated SL in mm at time d; and A_0, α = parameters to be estimated, using a nonlinear least-squares method. We also calculated SL in mm at age d for each cohort using the biological intercept algorithm (Campana 1990; Campana and Jones 1992):

$$L_d = L_c + [(O_d - O_c)(L_c - L_i)] / (O_c - O_i) \quad [3]$$

Where O_d = the radius of the otolith (μm) at age d; O_c = the radius of the otolith (μm) at capture; L_i = the length of the fish at the biological intercept, set at 4.2 mm, according to Methot and Kramer (1979); and O_i = the radius of the otolith (μm) at the biological intercept. The Gompertz model accurately models growth rates solely for the population sampled. Therefore, our use of the biological intercept algorithm to estimate growth back-calculation from otolith IW was chosen because of the reduced bias associated with using a biologically determined, rather than statistically estimated intercept (Campana 1990). The recent mean growth rate in the 5 days before capture (G_5) was calculated for each cohort as:

$$G_5 = (L_c - L_{c-5})/5 \quad [4]$$

Where L_{c-5} = the back-calculated L in mm at 5 days before the deposition of the last daily ring.

We compared mean growth rates (G and G_5) among fish of each stage of guanine deposition by means of a Student's *t*-test. We also compared back-calculated otolith increment width (IW) at 10, 20, 30 and 40 days, and back-calculated SL at 10-day increments from 10-70 days, for each of the three cohorts using Student's t-tests. For all t-tests, we adopted a Bonferroni adjusted level of significance (α=0.017),

accounting for the number of comparisons being made. All statistical analyses were run using S-Plus 6.2 (Insightful Corp., Seattle, WA) statistical software.

RESULTS

Abundance and distribution

In all, we captured adult, late larval (<35 mm) and juvenile (35-72 mm) anchovy in 45% of 58 stations fished during September 2006, and standardized catch to number/$10^6 m^3$ (Fig. 3.1). Late larvae and juvenile stages were widely distributed along the continental shelf from Queets River, Washington to Newport, Oregon. Late larval and juvenile anchovy were captured in 33% of all hauls (n= 19), and adults in only 16% of all hauls (n = 9).

Size, age and hatch date distribution

Sizes of late larval and juvenile fish ranged from 25-66 mm SL, and of 217 anchovy aged, we staged 98 fish late larvae, Gu-0 (29-41 mm SL), 50 fish staged early juvenile, Gu-1 (35-47 mm SL) and 69 fish staged juvenile, Gu-2 (38-60 mm SL). An average percent reading error of 2.55% was estimated using procedures outlined in Beamish and Fournier (1981), providing high reading precision. Ages ranged from 45-76 days old for Gu-0 fish, 55-88 days old for Gu-1 fish and 61-97 days old for Gu-2 fish. Hatch dates ranged from July 12-August 12 for stage Gu-0 fish, June 30-August 2 for Gu-1 fish and June 21-July 27 for Gu-2 fish (Fig. 3.2). All larval and juvenile fish were likely progeny of adults spawning off Oregon and Washington during

summer 2006. See Fig. 3.3 for a time series record of anchovy egg densities captured during June BPA cruises (1998-2006).

Otolith radius and fish weight regressed on fish length

The relationship between OR and SL (Fig. 3.4) for all developmental stages was an exponential growth function [Gu-0 OR= 38.34 * exp 0.05 SL (n= 98, R^2= 0.69, p<0.001); Gu-1 OR= 45.35 * exp 0.05 SL (n= 50, R^2= 0.46, p<0.001); Gu-2 OR= 56.31 * exp 0.05 SL (n= 69, R^2= 0.66, p<0.001)]. The relationship between fish weight (W) and SL (Fig. 3.5) was linear for late larval (Gu-1) fish, but an exponential growth function for juveniles [Gu-0 W= 0.02 SL – 0.49 (n= 98, R^2= 0.81, p< 0.001); Gu-1 W= 0.0039 * exp 0.11 SL (n= 50, R^2= 0.85, p<0.001); Gu-2 W= 0.03 * exp 0.07 SL (n= 69, R^2= 0.89, p<0.001)]. The relationship changed in the 35-40 mm SL range, corresponding with metamorphosis from larval to juvenile stage.

Growth rates

Mean daily growth rates (G) were 0.53 ± 0.04 (mean ± SD) mm/day in Gu-0 fish, 0.55 ± 0.05 mm/day in Gu-1 fish, and 0.56 ± 0.05 mm/day in Gu-2 fish. Growth rates in Gu-0 fish were significantly lower than in Gu-1 juveniles (Student's t-test, p=0.015) and in Gu-2 juveniles (Student's t-test, p<0.001), although there were no significant differences between mean daily growth rates in Gu-1 and Gu-2 juveniles (Student's t-test p=0.076). G corresponded well with values (0.43-0.55 mm/day) determined for juvenile northern anchovy off southern California (Methot 1983) and

values (0.45-0.52 mm/day) determined for northern anchovy larvae off Oregon and Washington (Methot 1981). Recent mean growth rates (G_5) were 0.67 ± 0.13 (mean ± SD) mm/day in Gu-0 fish, 0.74 ± 0.20 mm/day in Gu-1 fish, and 0.78 ± 0.21 mm/day in Gu-2 fish. Growth rates in Gu-0 fish were significantly lower than in Gu-1 (Student's *t*-test, p=0.004) and Gu-2 juveniles (Student's *t*-test, p<0.001), although there were no significant differences in G_5 between Gu-1 and Gu-2 juveniles (Student's *t*-test p=0.346).

Back-calculated standard length and growth

Back-calculated SL was assessed using both Gompertz (Fig. 3.6) and biological intercept (Fig. 3.7) methods. Mean increment width (IW) increased from 2.71 ± 0.82 (mean ± SD) μm at 10 days to 5.03 ± 1.82 μm at 40 days in post larval (Gu-0) fish. IW increased from 2.79 ± 0.67 μm at 10 days to 5.42 ± 1.34 μm at 40 days in early (Gu-1) juvenile fish, and from 3.18 ± 0.88 μm at 10 days to 6.23 ± 2.20 μm at 40 days in (Gu-2) juvenile fish (Fig. 3.8), indicating a rapid increase in growth rate for larvae in later stages of development. While there were no significant differences between IW in Gu-0 and Gu-1 fish, or IW in Gu-1 and Gu-2 fish at 10, 20 or 40 days (Student's *t*-test, p>0.017), we found that IW in Gu-2 fish was significantly larger (Student's *t*-test, p<0.017) than late larvae (Gu-0) at 10 and 40 days (Student's *t*-test, p<0.001), but not at 20 days (Student's *t*-test, p>0.017).

Mean back-calculated SL, using the biological intercept method, was not significantly different (Student's *t*-test, p>0.017) between juveniles (Gu-1) and both

late larvae (Gu-0), and (Gu-2) juveniles at 10 days (Table 3.1). However, SL at 10 days was significantly larger (Student's *t*-test, $p<0.001$) in Gu-0 late larval fish than in Gu-2 juveniles. Back-calculated SL was significantly different (Student's *t*-test, $p<0.017$) among all pairwise comparisons of developmental stages (Gu-0, Gu-1 and Gu-2) from 20 through 50 days (Table 3.1), with older juveniles (stage Gu-2) smaller than both Gu-1 and Gu-0 individuals. Beginning at 60 days, however, Gu-2 fish had the largest overall size-at-age (Table 3.1), although there were no significant differences between back-calculated SL of Gu-0, Gu-1, and Gu-2 fish (Student's *t*-test, $p>0.017$).

DISCUSSION

Results of this study show that older northern anchovy juveniles (stage Gu-2) from the 2006 year-class had faster mean and recent growth rates (G, G_5), wider mean increment widths (IW), and larger mean back-calculated standard lengths (SL) after the age of 60 days than younger northern anchovy late larvae (stage Gu-0) and early juveniles (stage Gu-1). These findings support our hypothesis that fish spawned earlier in the season grow faster, presumably leading to higher probability of survival, although the increase in growth rate may not be detected until after metamorphosis from larval to juvenile stages after approximately 60 days old. In fact, back-calculated SL in older fish (Gu-2) was significantly smaller than late larvae (Gu-0) from 10-50 days, evidence of compensatory growth in anchovy spawned later in the summer. Younger individuals must grow faster if they stand any chance of survival over the

winter, but high growth rates may also impose costs, including adverse effects on future development, growth, reproduction, and swimming performance (Ali et al. 2003).

Northern anchovy deposit daily growth increments that may be used to determine age in days of larval and juvenile fish with great accuracy, first described in Brothers et al. (1976). Daily growth increments appear on the otoliths only after complete absorption of the yolk sac, which can take varying amounts of time depending on ocean temperature. Under laboratory conditions, at 19° C the difference between hatch date and first increment deposition in *E. mordax* is 3 days, at 16° C, the lag is 5 days and at 12.5° C it is approximately 9 days (Methot and Kramer 1979). In the laboratory, median size (standard length; SL) at hatching is 3.4 mm (Lasker et al. 1970) and SL at first increment deposition is 4.2 mm, validated in laboratory rearing experiments (Methot and Kramer 1979). Larval growth to metamorphosis is complete at about 35 mm SL (Hunter 1976, Butler 1989), which is when we observed weight gain transitioning from a linear to an exponential growth function.

It is critical to know the timing and location of spawning in the northern subpopulation of northern anchovy to assess both size and distribution of the stock off Oregon and Washington. Unfortunately, efforts to define spawning centers and make spawning biomass estimates of the anchovy population north of California have been patchy at best. Ichthyoplankton surveys in 1975 and 1976 (Laroche and Richardson 1980; Richardson 1981) confirmed the hypothesis that the anchovy-spawning center is in July, approximately 80 km offshore beyond the continental slope associated with

the Columbia River plume. A repeated ichthyoplankton survey during July 1994 and 1995 by Emmett et al. (1997) detected a similar location for the spawning peak, but found anchovy to be less abundant compared to 1975 and 1976. Both surveys found anchovy off Oregon and Washington spawn when current flow to the south is at a maximum, water temperatures are at maximum levels for the year (>12° C), upwelling is at a maximum and daylight is at maximum duration. This is in direct contrast to the central subpopulation off California, which spawns from January through April when southward current flow, water temperatures, upwelling and day length are all at a minimum. More recent ichthyoplankton and larval fish collections (Miller and Shanks 2005; Auth and Brodeur 2006; Parnel et al. in press, Fig. 3.3) suggest that anchovy are spawning closer to shore with variability in peak spawning period from April through October. Brodeur et al. (1985) documented anchovy eggs in April during anomalous conditions associated with the 1983 El Niño, and Jones et al. (1990) recorded anchovy egg catches in the Columbia River estuary from April-September 1980. Anchovy eggs and larvae have also historically been reported in certain inlets of Vancouver, British Columbia, the Strait of Georgia, in Puget Sound, Washington, and in Yaquina and Coos Bays, Oregon (Richardson 1973; 1981; Miller and Shanks 2005). Clearly, spawning locations have not been well defined and data are somewhat contradictory.

Northern anchovy eggs reared in both field and laboratory settings indicate that incubation time is temperature-dependent (Zweifel and Lasker 1976; Methot and Kramer 1979; Lo 1985). Sea surface temperatures at 3-m (mean ± SD) during our

sampling period (September 20-28, 2006) were 12.6 ± 1.06°C, and 13.1 ± 2.09°C during the June Plume Study period (June 19-28, 2006), which coincided spatially with our sampling design in September 2006. Under these temperature conditions in the laboratory, egg incubation lasted 80-113 hours (Zweifel and Lasker 1976). Assuming a four-day lag between spawning date and hatch date, this study confirms a spawning event associated with the Columbia River plume on dates ranging from June 17 through August 8 for the 2006 year-class, and although this spawning period overlaps major spawning events documented by Richardson (1981) and Emmett et al. (1997), neither of the earlier studies sampled during any month but July.

2007 northern anchovy year-class

Seasonal variability in factors like sea surface temperature or food supply probably influences the timing of spawning in northern anchovy, and greatly affects the spatial distribution of spawners (Chapter 2). During our September 2007 Plume Study, we found a large number of pre-recruits. We staged all of the sub-adult fish as late juveniles (Gu-2), with the exception of three early juveniles (Gu-1). SL ranged from 37-72 mm and mean weight ± SD equaled 2.162 ± 0.765, over three times the weight recorded for stage Gu-2 in 2006, characteristics corroborating our findings that fish spawned early in the season have high survival rates.

Conclusions

It is possible that growth rate-dependent survival in northern anchovy varies inter-annually, and is related to environmental conditions impacting food availability, such as temperature and timing of the Spring Transition. Methot (1983) found that a difference in survival of the central subpopulation during April to May in 1978 compared to 1979 was nearly sufficient to account for the observed greater recruitment in 1978. Butler (1989) found that the size and body condition factor of juvenile anchovy was reduced during the 1983 El Niño compared to the 1980 year-class, and attributable to reduced growth rates (G) after 100 days. In the present study, we found that increased growth rate in the older (Gu-2) fish occurred after 60 days; in fact, back-calculated SL at 10-50 days old was significantly smaller in older juveniles (Gu-2) than in late larvae (Gu-0), possibly because the younger fish exhibited compensatory growth. During the late larval phase (10-35 mm SL), we found that weight gain was linear, until completion of metamorphosis from late larval to juvenile stage, when weight gain became an exponential growth function. Our results also indicate that the critical growth period for recruitment occurs after the larval phase (>35 mm SL). As fish grow, the ration needed to sustain growth increases, so it is conceivable that food can become limiting under unfavorable environmental conditions. Older juveniles may out-compete younger fish for resources post metamorphosis (>35 mm SL), when weight gain becomes an exponential growth function. Juvenile growth rates affect adult size, and in broadcast spawners like northern anchovy, batch fecundity is a function of body size. Therefore, the link

between environmental conditions, spawning timing and food availability may be influencing population size of northern anchovy in the northern CCLME, beginning as early as metamorphosis from larval to juvenile stages.

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Table 3.1. Mean ± one standard deviation surrounding the mean (SD) back-calculated standard lengths (SL in mm) at 10-70 days for late larvae (Gu-0), early juvenile (Gu-1) and juvenile (Gu-2) northern anchovy (*Engraulis mordax*), computed using the biological intercept algorithm (Campana 1990; Campana and Jones 1992). Values in each row that do not share a common superscript are significantly different from one another (Student's *t*-test, a > b > c).

	Stage		
Age (days)	Gu-0	Gu-1	Gu-2
10	4.56^{a} ± 0.11	4.52^{b} ± 0.10	4.49^{b} ± 0.09
20	9.04^{a} ± 0.99	8.60^{b} ± 1.00	8.05^{c} ± 0.92
30	14.65^{a} ± 1.60	13.89^{b} ± 1.80	12.54^{c} ± 1.76
40	20.76^{a} ± 2.19	19.71^{b} ± 2.64	17.72^{c} ± 2.69
50	27.37^{a} ± 2.73	26.05^{b} ± 3.67	23.71^{c} ± 3.63
60	32.42^{a} ± 2.29	32.60^{a} ± 4.04	31.34^{a} ± 4.66
70	38.74^{a} ± 2.28	37.27^{a} ± 3.47	39.17^{a} ± 5.07

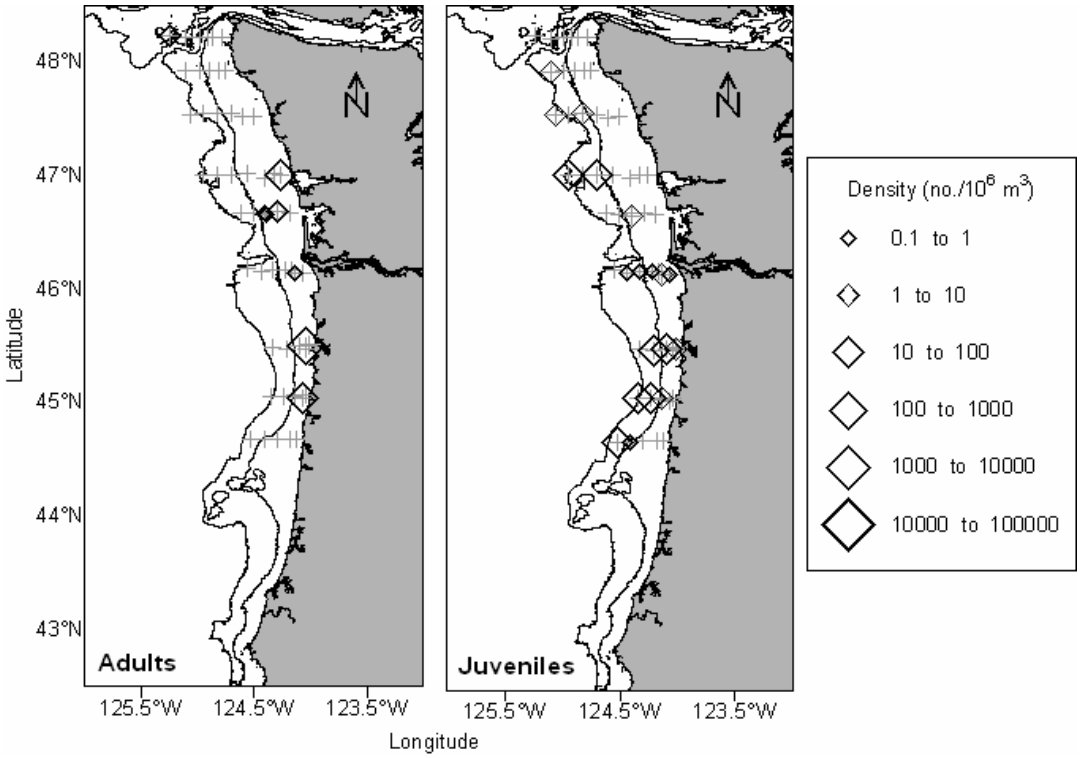

Figure 3.1. Density (standardized to number/10^6m^3) and distribution of adult (> 80 mm SL) and juvenile (≤ 80 mm SL) northern anchovy (*Engraulis mordax*) caught during September BPA Plume Study cruises off Oregon and Washington in 2006. The + symbol signifies stations fished where no anchovies were caught. Also shown are the 100 and 200m depth contours along the continental shelf.

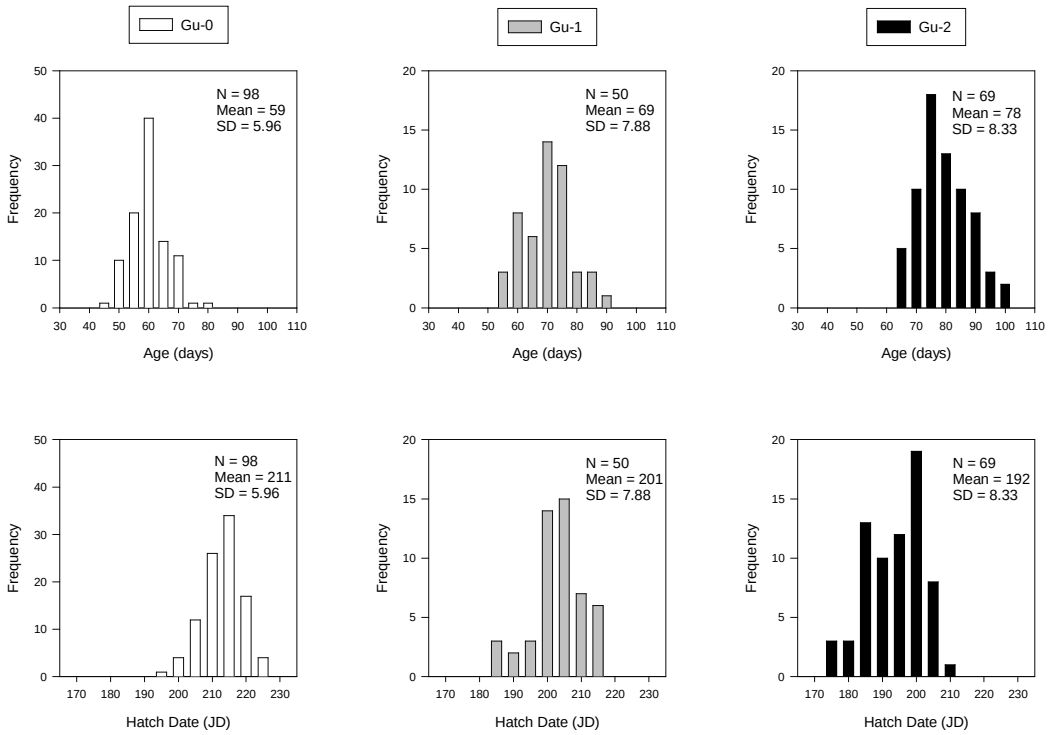

Figure 3.2. Age in days (top) and hatch date (bottom) of northern anchovy (*Engraulis mordax*) late larvae (Gu-0), early juveniles (Gu-1) and juveniles (Gu-2). Fish were assigned to one of three cohorts based on the level of guanine deposition on their surface (see Takahashi and Watanabe 2004c). Hatch date is reported as Julian day. For each developmental stage, we report the number of observations (*n*), mean and one standard deviation surrounding the mean (SD).

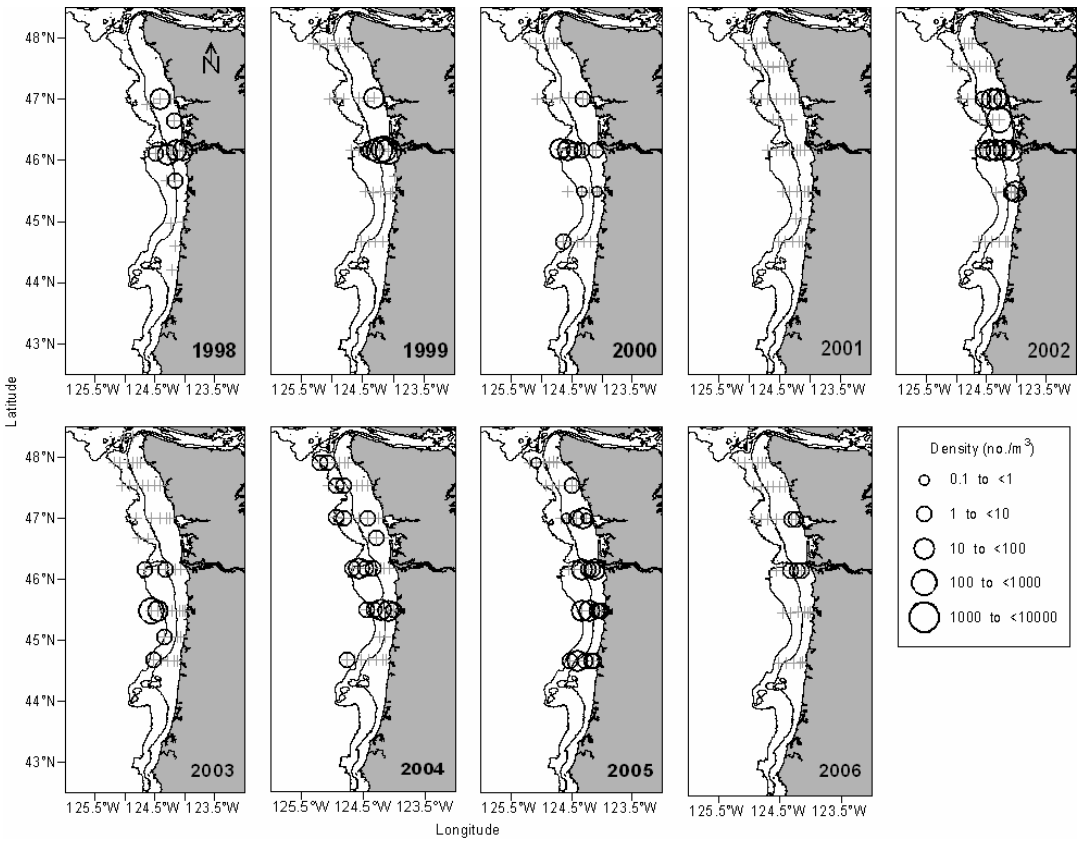

Figure 3.3. Density (standardized to number/m^3) and distribution of northern anchovy (*Engraulis mordax*) eggs collected during June BPA Plume Study cruises off Oregon and Washington 1998-2006. The + symbol signifies stations sampled where no anchovy eggs were caught. Also shown are the 100 and 200m depth contours along the continental shelf.

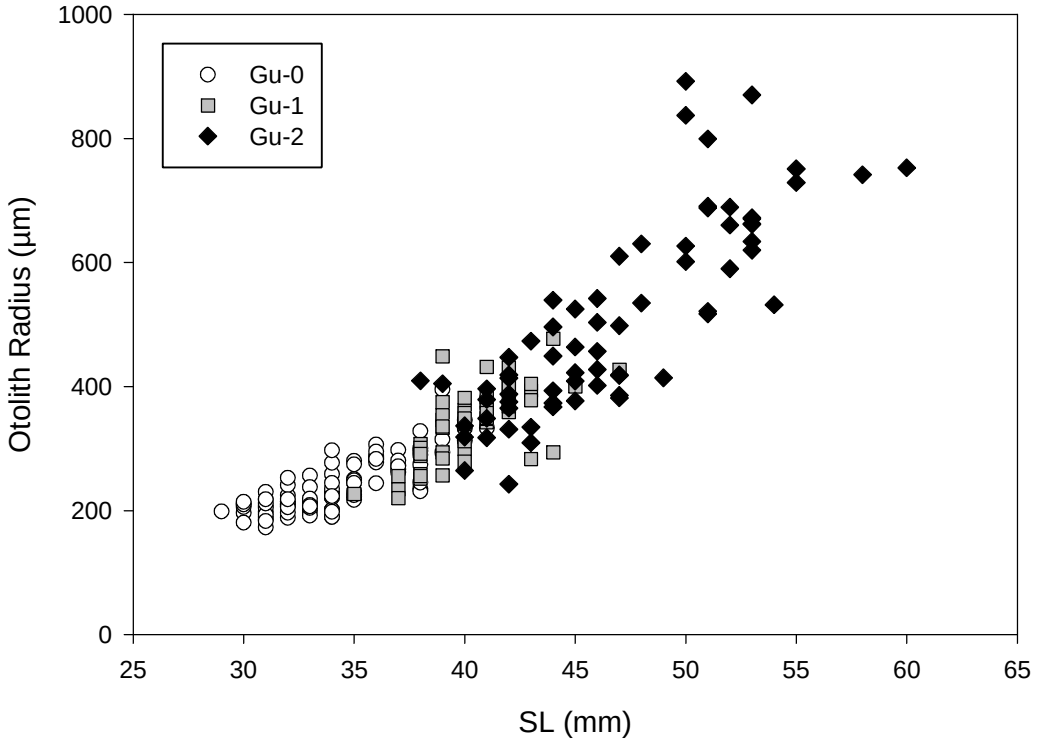

Figure 3.4. Otolith radius (OR in µm) regressed on standard length (SL in mm) for all three developmental stages of northern anchovy (*Engraulis mordax*), late larvae (Gu-0), early juveniles (Gu-1) and juveniles (Gu-2). Fish were assigned to one of three cohorts based on the level of guanine deposition on their surface (see Takahashi and Watanabe 2004c). Exponential growth functions best defined the relationship for Gu-0, Gu-1, and Gu-2 stages.

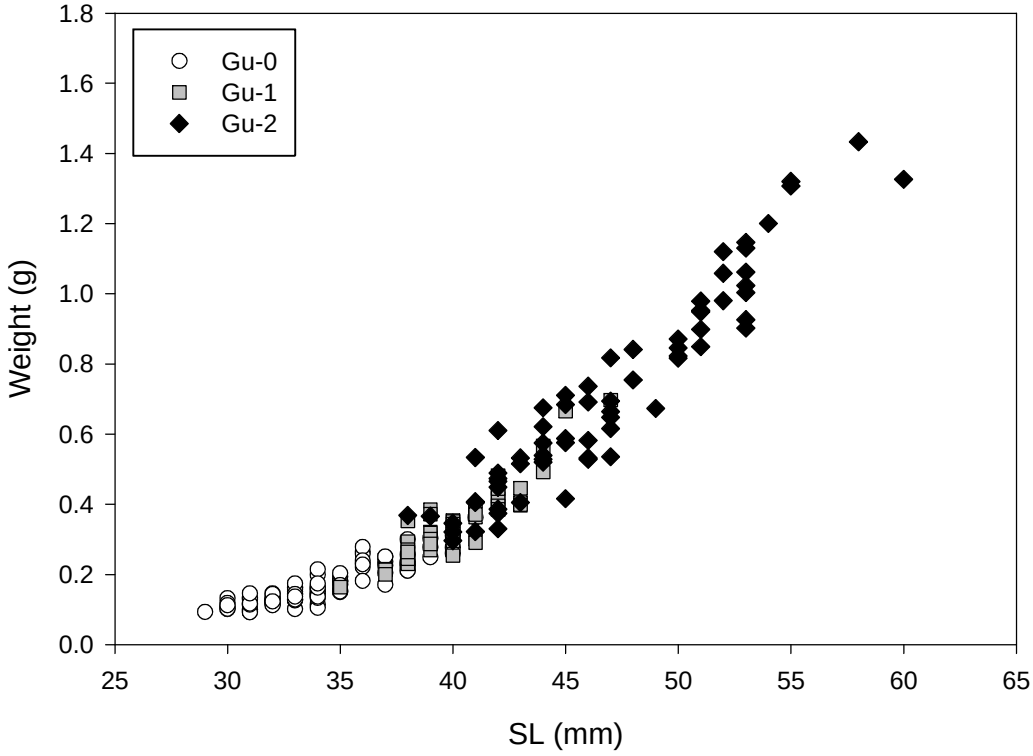

Figure 3.5. Fish weight (W in g) regressed on standard length (SL in mm) for all three developmental stages of northern anchovy (*Engraulis mordax*), late larvae (Gu-0), early juveniles (Gu-1) and juveniles (Gu-2). Fish were assigned to one of three cohorts based on the level of guanine deposition on their surface (see Takahashi and Watanabe 2004c). A linear function best defined the relationship between W and SL for late larvae (Gu-0), but exponential growth functions best fit the relationship between W and SL for juveniles (Gu-1 and Gu-2 stages).

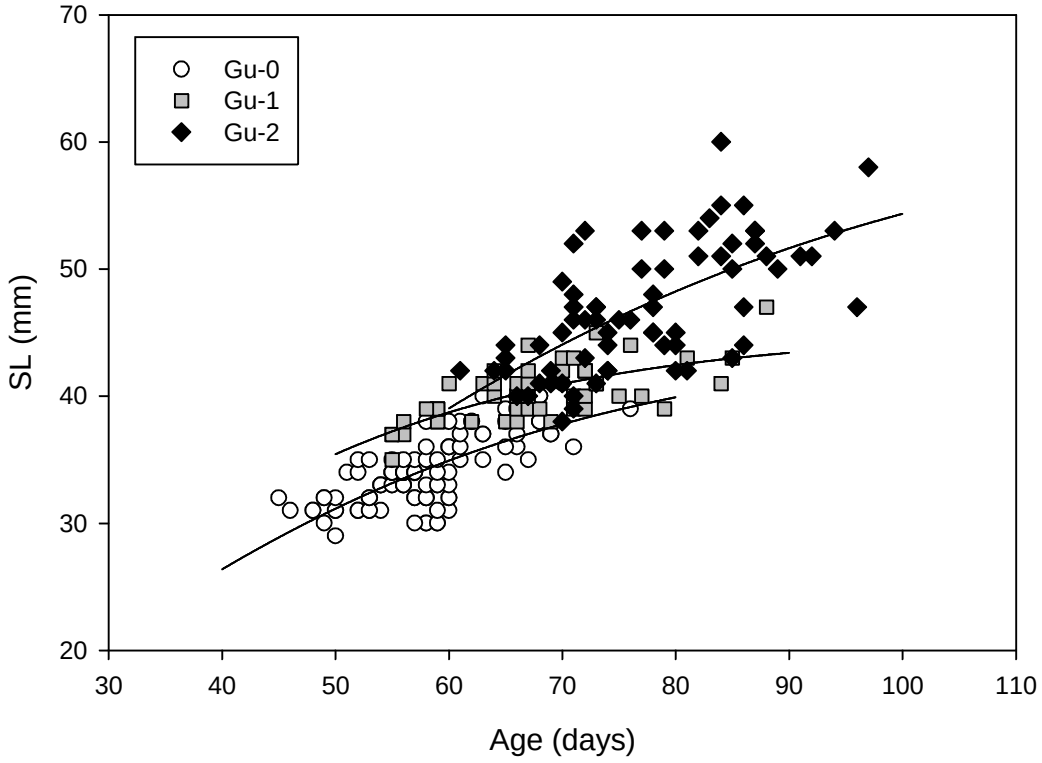

Figure 3.6. Length-at age plot fit to the Gompertz growth model (Zweifel and Lasker 1976) for each of three developmental stages of northern anchovy (*Engraulis mordax*), late larvae (Gu-0), early juveniles (Gu-1) and juveniles (Gu-2). Fish were assigned to one of three cohorts based on the level of guanine deposition on their surface (see Takahashi and Watanabe 2004c).

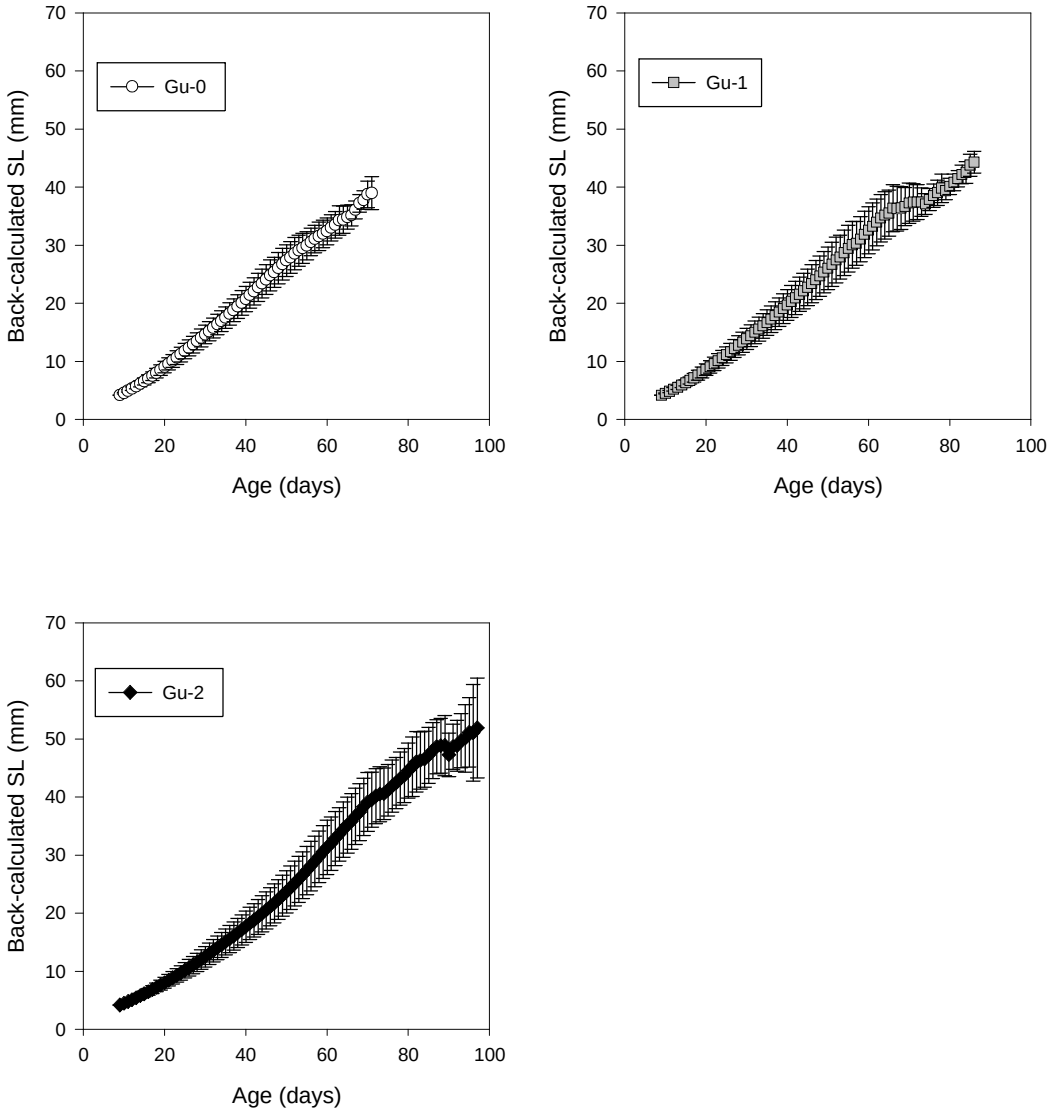

Figure 3.7. Mean ± one standard deviation surrounding the mean (SD) back-calculated standard length-at-age (SL in mm), computed using the biological intercept algorithm (Campana 1990; Campana and Jones 1992) for each of three developmental stages of northern anchovy (*Engraulis mordax*), late larvae (Gu-0), early juveniles (Gu-1) and juveniles (Gu-2). Fish were assigned to one of three cohorts based on the level of guanine deposition on their surface (see Takahashi and Watanabe 2004c).

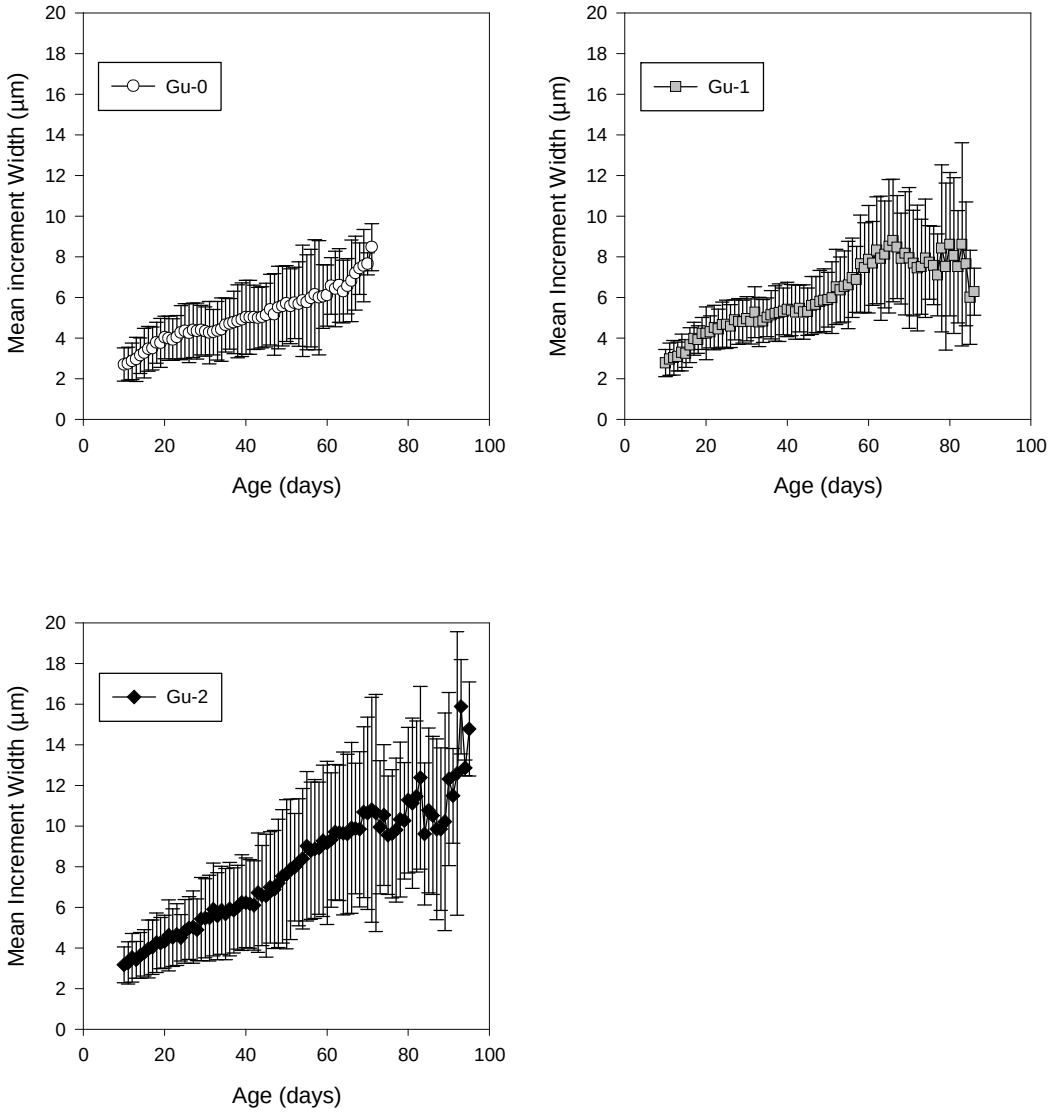

Figure 3.8. Mean ± one standard deviation surrounding the mean (SD) daily increment widths-at-age (IW in µm) measured from otoliths in the three developmental stages of northern anchovy (*Engraulis mordax*), late larvae (Gu-0), early juveniles (Gu-1) and juveniles (Gu-2). Fish were assigned to one of three cohorts based on the level of guanine deposition on their surface (see Takahashi and Watanabe 2004c).

Chapter 4 –Total lipid content and fatty acid composition of common forage fish species off Oregon and Washington under variable oceanographic conditions

ABSTRACT

We determined total lipid content and fatty acid signatures of four forage fish species, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*), which are common in the California Current large marine ecosystem (CCLME). Sampling took place during periods of variable oceanographic conditions in the summers of 2005 and 2006. The summer of 2005 was anomalous because of delayed upwelling conditions that postponed primary productivity until mid-July. In contrast, 2006 was characterized by the early, albeit weak onset of upwelling in May. Strong upwelling-favorable winds blew from July through September, leading to a coast-wide hypoxic region along the Oregon shelf lasting through October. Forage fish densities were low in both years. We observed lowest lipid levels among all species in 2005, and highest lipid levels (26.37% wet mass in Pacific sardine) in 2006. Essential fatty acids, such as docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), are distinctive biomarkers that can only come from the diet and remain unaltered when deposited in adipose tissue. Using ratios of DHA to EPA, we detected a transition from a diet of primarily dinoflagellates in early 2005, to a diet of diatoms by late summer 2005. We also detected higher levels of macrozooplankton carnivory, identified from monounsaturated eicosenoic and erucic fatty acids, in Pacific herring and whitebait smelt, in 2006 relative to 2005. For all fish, lipid levels were negatively

correlated with DHA concentrations, and positively correlated with EPA, demonstrating that delayed upwelling along the eastern boundary of the CCLME can alter forage fish food web structures, and dramatically impact foraging efficiency at multiple trophic levels.

INTRODUCTION

Forage fish off Oregon and Washington, such as northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*) are the prey base for piscivorous predators in the California Current large marine ecosystem (CCLME), including salmonids and other predatory fish, pinnipeds, and seabirds (Livingston and Alton 1982; Brodeur et al. 1987; Brodeur and Pearcy 1992; Riemer and Brown 1997; Roby et al. 2002; Miller and Brodeur 2007). Small pelagic forage fish are mainly planktivorous and occupy a critical link in the food chain, because while biodiversity tends to be large at the bottom and top of marine food webs, only a few forage fish dominate the intermediate level, in a pattern of "wasp-waist" ecosystem dynamics (Cury et al. 2000; Bakun 2006). In upwelling regions, like the eastern boundary current system off the U.S. West Coast, forage fish can also act as alternative prey to endangered juvenile salmonid species (Emmett et al. 2006).

Biological and climatic regime shifts in the Northeast Pacific have been documented on decadal scales, and are generally characterized by fluctuations in anchovy (*Engraulis* spp.) and sardine (*Sardinops sagax*) population sizes, independent

of fishing pressure (Lluch-Belda et al. 1992; Schwartzlose et al. 1999; Chavez et al. 2003). Pacific herring and whitebait smelt likely fluctuate with similar temporal periodicity. Moreover, whitebait smelt may at times be the most abundant forage species in the northern California Current (Emmett et al. 2006), and Pacific herring are a critical component of nearshore and estuarine environments (Ware 1985; Brodeur et al. 2005). Generally speaking, anchovy, Pacific herring and whitebait smelt prefer cold ocean conditions, while sardine prefer warmer ocean conditions.

The Magnuson-Stevens Fishery Conservation and Management Act (as amended in 2007) encourages ecosystem-based fishery management (EBFM), a holistic framework for resource management, conservation, and sustainability (Ecosystems Principles Advisory Panel 1999). Science supporting the implementation of EBFM requires information on species-interactions, climate relationships, and essential habitat requirements for target and non-target species alike (Brodziak and Link 2002; Pikitch et al. 2004; Marasco et al. 2007). In the northern CCLME, it is important to understand linkages between forage fish abundance and distribution, diet, and oceanographic conditions as part of an EFBM approach.

Fatty acids in marine organisms are extremely diverse, and include polyunsaturated fatty acids (PUFA) originating from phytoplankton (Müller-Navarra et al. 2000; St. John et al. 2001). Anomalous ocean conditions during the summers of 2005 and 2006 provided a framework for examining forage fish trophic interactions off Oregon and Washington. For example, 2005 was set apart from other years because of warm surface water temperatures late into the summer, and delayed timing

of the Spring Transition from conditions dominated by downwelling, to summer upwelling (Pierce et al. 2006; Schwing et al. 2006, Barth et al. 2007). In 2005, upwelling-favorable wind stress was the lowest in 20 years, nearshore sea surface temperatures averaged 2°C warmer than normal and surf-zone chlorophyll-α and nutrients were both substantially lower than normal (Barth et al. 2007). In contrast, 2006 was characterized by the onset of upwelling in early May, followed by intense primary production and plankton blooms (Goericke et al. 2007). A subsequent lack of upwelling-favorable winds caused oxygen depleted water (<1.43 ml/L) to build up. Large coast-wide hypoxic regions, or "dead zones" were recorded during both years, but in 2006, the dead zone stretched along the coastal area of central Oregon, and reached 30 miles offshore from mid-June to mid-October (Chan et al. 2008).

Lipids, and especially fatty acids, have long been used as biological markers and gauges of diet in marine ecology (Iverson et al. 2002; Dalsgaard et al. 2003; Iverson et al. 2004; Herman et al. 2005). Fatty acids are the major component of most lipids and in marine organisms, and commonly consist of molecules containing 14 to 24 carbon atoms that are either saturated (contain no double bonds), or unsaturated (contain one to six double bonds). Fatty acids generally remain intact through digestion and become deposited in animal tissues such as cell membranes or neurons with minimal modification (Budge et al. 2006). Most fatty acids can be synthesized in the body, but some (essential fatty acids) can only be obtained through diet, namely phytoplankton or herbivorous zooplankton. Because marine fatty acids are numerous and diverse, they provide the opportunity to investigate trophic interactions in marine

ecosystems, as driven by larger climatic processes in the coastal oceanic environment (Iverson et al. 1997, 2002; Dalsgaard et al. 2003; Budge et al. 2006; Litzow et al. 2006). Laboratory studies have established that the fatty acid composition of fish can be highly affected by their diet (Dalsgaard et al. 2003). It has been suggested (Litzow et al. 2006) that climate-mediated variability in dietary quality plays a role in controlling forage fish regime shifts on long timescales.

In the present study, we use total lipid and fatty acid compositions to detect variability in the diets of common forage fish found off Oregon and Washington under extreme ocean conditions during 2005 and 2006. Our aim is to explore the response of forage fish lipid and fatty acid composition to climate-mediated changes in essential fatty acid (EFA) production by phytoplankton and zooplankton off Oregon and Washington during 2005 and 2006, and to link forage fish fatty acids with environmental parameters and population dynamics. In the Gulf of Alaska, oceanographic conditions structure forage fishes into communities based on lipid content (Abookire and Piatt 2005). In this study, we examine lipid structure under variable oceanographic conditions and test whether EFAs, like omega-3 eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3), vary inter-annually based on forage fish fatty acid profiles. This work represents one of the first attempts to quantify and compare both total lipid content and fatty acid signatures in forage fish of the northern California Current. The quality and quantity of forage available to predators has broad implications for the entire CCLME. This research will provide important information to bioenergetic modelers. Measurements

of whole lipids and fatty acids in forage fish will also be useful to fishery, marine mammal and seabird biologists, facilitating informed resource management decisions consistent with an EBFM approach.

METHODS

Field sampling

In total, we analyzed total lipid content and fatty acid composition of 160 individual forage fish. Ten adults representing four species, northern anchovy, Pacific sardine, Pacific herring, and whitebait smelt, were collected off Oregon and Washington during early summer 2005 and 2006 (ES05 and ES06) and late summer 2005 and 2006 (LS05 and LS06, Table 4.1). Sampling occurred during National Marine Fisheries Service (NMFS) surveys conducted from June 14 through September 21, 2005 and from May 27 through September 26, 2006, and included Bonneville Power Administration (BPA) Plume Study cruises (see Brodeur et al. 2005), Predator Study cruises (see Krutzikowsky and Emmett 2005; Emmett et al. 2006), Stock Assessment Improvement Plan (SAIP) cruises (see Phillips et al. 2007), and LIDAR (laser radar) cruises. Collection stations ranged from 2-40 km offshore and 45° to 48°N latitude (Fig. 4.1). All fish were captured using a Nordic 264-rope trawl (NET Systems, Bainbridge Island, WA) fished behind the vessel at the surface or at midwater (30-50 m depth stratum) for tow durations of 15-30 minutes. The trawl measured 12 m by 28 m (336 m^2) with variable mesh sizes from 162.6 to 8.9 cm, with an additional 6.1 m long, 3-8 mm knotless liner sewed into the cod end. Fish collected

were identified, enumerated and sorted into airtight plastic bags, then frozen immediately at -20°C for transport back to the laboratory.

Lipid extraction

To determine the fatty acid composition of forage fish species, including fatty acid precursors (alcohols or dimethyl acetals), lipids had to be extracted from the samples. In the laboratory, fish were kept at -20° C for less than 12 months, or stored at -80°C until analysis to prevent oxidation. Lipid extractions followed Parrish (1999) and Budge et al. (2006), and employed a modified Folch et al. (1957) procedure, utilizing chloroform ($CHCl_3$) and methanol (MeOH) for the extractions. Each fish was thawed prior to analysis and completely homogenized in a blender. A sub-sample of 0.5-1.5 g was removed and placed in a centrifuge tube with 4 ml chloroform. Each of the centrifuge tubes and collection vials had been previously weighed and solvent-washed to remove any lipid residue. The samples were flushed with nitrogen gas, sealed with Teflon®-lined caps, wrapped in Teflon® tape and stored at -80°C for a minimum of 24 hours before extraction. We added 2 ml ice-cold methanol and 1.5 ml chloroform-extracted water to our samples so that the ratio of chloroform:methanol:water equaled 8:4:3. We recapped the sample and sonicated the mixture in an ice-bath for 4 minutes. We then centrifuged the sample for 2-3 minutes at 3500 rpm. Next, we removed the organic (bottom) layer using the double-pipetting technique, which involved placing a 9-inch Pasteur pipette inside a 5¾-inch one. We placed the organic layer into a lipid-rinsed glass test tube, then rinsed both pipettes

with ice-cold chloroform three times, the larger pipette into the organic layer and the shorter pipette into the aqueous layer. We repeated the procedure at least three times, until no more color remained in the organic layer, then evaporated the solvent under a gentle stream of nitrogen, recorded the weight of the lipid extract remaining, and calculated the proportion of total lipid present in the sub-sample, representative of the whole fish.

Determination of fatty acid composition

Fatty acids in forage fish lipid extract were converted into fatty acid methyl esters (FAME) using a modification of the Association of Official Analytical Chemists (AOAC) method 991.39 (AOAC 1998). Briefly, we trans-esterfied the lipid extract in methanolic sodium hydroxide (NaOH) using an acidic catalyst, boron trifluoride (BF_3), at 100°C for 30 minutes in a nitrogen atmosphere. Fatty acid composition was determined by gas chromatography (GC). A Shimadzu GC-2010 (Shimadzu Corp., Kyoto, Japan), equipped with a flame-ionization detector and capillary column (Omegawax^{TM} 250 capillary column, 30 m × 0.25 × 0.25 μm film thickness, Supelco, Bellefonte, PA) was used for analyzing FAME. We used the following parameters for the GC system: injector and detector temperatures of 250°C and 270°C, respectively; column temperature of 170°C with 8 min hold time; gradual heating to 245°C at a rate of 1°C/ min with 2 min hold time; and helium as a carrier gas. The fatty acids were identified and their concentrations calculated by comparison of their retention times

with those of the reference standards (37-component FAME mix and C22:5n-3 standard, Supelco, Bellefonte, PA) according to AOAC method 991.39 (AOAC 1998).

Statistical analysis

We ran all statistical analyses using the S-Plus 6.2 software package (Insightful Corp. Seattle, WA). Results of whole lipid extractions are presented as total percent (wet weight) mean ± one standard deviation (SD) of 10 fish per species for each time period (ES05, LS05, ES06, and LS06). Fatty acids are presented as mass percent of total fatty acid mean ± one standard deviation (SD) of 3 randomly selected fish of the 10 sampled per species replicated for each time period (ES05, LS05, ES06, and LS06). The coefficient of variation (CV) among replicated samples never exceeded 10%. We made statistical comparisons of total whole lipids among species pooled for all sampling periods and individually for each sampling period using one-way analysis of variance (ANOVA), followed by Tukey's pairwise comparisons, adopting a Bonferroni correction factor to account for multiple comparisons. Intra-specific differences in individual fatty acids among sampling periods were compared for each species using one-way ANOVA, following confirmation of normality and equal variance. We used Tukey's honestly significant difference (HSD) post hoc tests to compare means when ANOVAs were significantly different, and for these analyses, alpha was set at 0.05. We also explored trophic and dietary fatty acid tracers by examining ratios of monounsaturated fatty acids (MUFA) eicosenoic acid (C20:1n-9) to erucic acid (C22:1n-9), and ratios of essential fatty acids DHA to EPA. Longer

chained MUFA have higher caloric content than short-chained MUFA, so the proportion of C22/C20 MUFA should distinguish between low- and high-energy lipid content (Scott et el. 2002). Ratios of DHA to EPA have been effectively used to distinguish among diets comprised of dinoflagellates and diatoms (Budge and Parrish 1998). Finally, we tested for correlations between EFA concentrations and total lipid content for all forage species, log-transforming EFA values to assure normality and equal variance.

RESULTS

Abundance and physical measurements

Pelagic forage fish resources off Oregon and Washington, monitored by NMFS BPA Plume Study cruises and Predator Study cruises, increased following the 1997-1998 El Niño, then subsequently declined in density in 2005 (Fig. 4.2). The decline continued through 2006, with forge fish numbers the lowest of the eight-year-time series, presumably because of poor year-class strength in 2005 (Goericke et al. 2007). Average ± SD fork length (FL in mm) and weight (in g) for anchovy equaled 149 ± 10.4 mm and 27.8 ± 6.04 g, and for Pacific sardine equaled 207 ± 15.4 mm and 99.8 ± 24.9 g, respectively. This is within the range reported by Oregon Department of Fisheries and Wildlife (McCrae and Smith 2005) and other studies in the Pacific Northwest (Emmett et al. 2005; Okada and Morrissey 2007). Average ± SD length and weight for Pacific herring equaled 158 ± 22.3 mm and 38.8 ± 17.7 g, consistent with sizes of immature, non-spawning, 1-2 year-old herring (Ware 1985; Tanasichuk 2002;

Huynh 2007). For whitebait smelt, length and weight averages (± SD) equaled 115 ± 4.94 mm and 9.25 ± 2.27 g respectively. While there were no seasonal or annual differences between anchovy and whitebait smelt sizes, we noted larger sardine and herring individuals in 2006 compared to 2005 (Fig. 4.3).

Forage fish lipid content

Total lipid content (% wet mass) of individual forage fish over collections ranged from 0.37 to 26.37%. Mean ± SD total lipid content (% wet mass) across all seasons was 5.31 ± 3.66, 16.27 ± 5.85, 4.94 ± 3.63, and 4.85 ± 1.67 for northern anchovy, Pacific sardine, Pacific herring and whitebait smelt, respectively. Mean lipid content was significantly higher (ANOVA and Tukey test, $p<0.05$) in sardine than in the other forage fish species. However, we did note significant intra- and inter-specific differences in total lipid content among seasons (Fig. 4.4). Mean lipid content was significantly different (ANOVA and Tukey test, $p<0.05$) in all pairwise comparisons of forage species during ES05, except between anchovy and herring (ANOVA and Tukey test, $p>0.05$) and between sardine and whitebait smelt (Fig. 4.4). Mean anchovy, sardine, and herring lipids were significantly lower in ES05 than during any other season (ANOVA, Tukey test, $p>0.05$). During LS05, all pairwise comparisons of lipid content among forage fish were significantly different (ANOVA, Tukey test, $p<0.05$), except between herring and whitebait smelt (ANOVA, Tukey test, $p>0.05$), and whitebait smelt lipids were significantly lower in LS05 compared to any other season (ANOVA, Tukey test, $p<0.05$). Throughout 2006, only sardine lipid values

differed significantly from any other forage fish species (ANOVA and Tukey test, $p<0.05$), with fat content comprising as much as 25% of sardine wet body mass in ES06 (Fig. 4.4).

Fatty acid profiles

Fatty acid composition of total lipids for each of the four forage fish species sampled during ES05, LS05, ES06, and LS06 are presented in Tables 4.2-4.5. In all, we identified and compared 25 fatty acids among sampling periods for each species, from myristic acid (C14:0), a saturated fatty acid (SFA), to nervonic acid (C24:1n-9), a 24-long carbon monosaturated fatty acid (MUFA) chain. High, but variable proportions of omega-3 polyunsaturated fatty acids (PUFA), specifically C20:5n-3 (EPA) and C22:6n-3 (DHA), were present in all forage fish lipid sampled. The most abundant fatty acids generally included C14:0, C16:0, C16:1n-7, C18:0, C18:1n-9, C20:5n-3, and C22:6n-3. Seasonal and inter-annual differences in individual fatty acids were observed in each species (Tables 4.2-4.5). In general, we saw a seasonal increase in SFA and MUFA between early and late summer for all species, and a decrease in PUFA as the summer progressed.

Saturated fatty acids (SFA)

Saturated fatty acids (SFA) accounted for 38.09 to 42.77% of northern anchovy FA composition (Table 4.2), with palmitic acid (C16:0) the most abundant saturate, ranging from a low of 22.28% in ES06 to 29.27% in ES05. C16:0 has been

shown to be a source of potential metabolic energy in fish during growth, and particularly during sexual maturity in females (Henderson et al. 1984). SFA accounted for 39.89 to 43.19% of total sardine fatty acids, again with C16:0 as the most abundant SFA, but contributing the lowest fraction (24.37%) in ES06, and the highest fraction (25.56%) in LS05 (Table 4.3). Total sardine SFA reported here are slightly above those recorded for the same stock off Oregon and Washington by Okada and Morrissey (2007). SFA ranged from 33.02 to 37.91% of total fatty acids in herring, and the highest levels of C16:0 ranged from 19.55% in ES06 to 24.30% in LS05 (Table 4.4), consistent with herring SFA profiles reported north of the California Current (Iverson et al. 2002; Huynh et al. 2007). The exact same trend was observed in whitebait smelt (Table 4.5), whose SFA fraction ranged from 33.97 to 41.67%, with C16:0 contributing the most, but lowest in ES06 (20.00%) and highest in LS05 (22.10%). Other SFA of notable abundance in all forage fish were butyric acid (C14:0), which increased in abundance from 2005 to 2006 in all fish but sardine, and stearic acid (C18:0), which increased in abundance from 2005 to 2006 in all fish but northern anchovy.

Monounsaturated fatty acids (MUFA)

Monounsaturated fatty acids (MUFA) constituted anywhere from 16.51% to 43.19% of total fatty acids, demonstrating considerable inter-specific and seasonal variability, especially among Pacific herring (Table 4.4). In northern anchovy, MUFA were less present than in any other forage fish species, accounting for only 16.51% of

all fatty acids in ES05 to 22.19% in ES06 (Table 4.2), compared with Pacific sardine MUFA concentrations, which rose from 39.89 to 43.19% in ES05 to LS05, respectively (Table 4.3). Pacific herring MUFA constituted 20.76 to 41.54% of total fatty acids (Table 4.4), which was highly variable, but consistent with herring fatty acid profiles reported elsewhere (Iverson et al. 2002; Huynh et al. 2007). Whitebait smelt MUFA ranged from 30.16% in LS05 to 36.08% in LS06 (Table 4.5). In all species sampled, palmitoleic (C16:1n-7) and oleic (C18:1n-9) acids were the most abundant MUFA present (Tables 4.2-4.5). C16:1n-7 has reliably been tracked in the field and laboratory as a diatom biomarker (Graeve et al. 1994; 2005; Thompson et al. 1992; St John et al. 2001). C18:1n-9 is considered a Prymnesiophyceae, or Haptophyceae biomarker (Tang et al. 2001; Rossi et al. 2006). However, during ES06, 20-22 MUFA, like eicosenoic (C20:1n-9) and erucic (C22:1n-9) acids were also present in high amounts (11.03 and 12.91% respectively) of Pacific herring lipids (Fig. 4.5a). These two MUFA have been associated with carnivorous feeding on calanoid copepods (Budge et al. 2006; Huynh et al. 2007). C20-22 MUFA in herring lipid are the product of oxidized C20:1 and C22:1 fatty alcohols of wax esters that are the primary constituent of cold-water copepods (Graeve et al. 1994), and synthesized *de novo*. C22/20 MUFA ratios (Fig. 4.5b) showed no seasonal patterns, but typically measured about 2:3 in all forage fish, consistent with the findings of Ackman and Eaton (1966). Pacific herring, followed by whitebait smelt, had the highest proportions of C22 to C20 MUFA, indicating that herring consumed prey with greater caloric

content than anchovy or sardine, and despite having the highest total lipid content, sardine had the lowest C22/20 fraction.

Polyunsaturated fatty acids (PUFA)

Polyunsaturated fatty acid (PUFA) concentrations came primarily from two sources of omega-3 EFAs: eicosapentaenoic acid (EPA, C20:5n-3) and docosahexaenoic acid (DHA, C22:6n-3). Organisms cannot effectively synthesize EFAs, yet they are required for cell membrane, hormone and neural tissue development, and must be obtained through diet (Tocher 2003). PUFA content ranged from 35.38% of total fatty acids in LS05 to 42.57% in ES05 for northern anchovy (Table 4.2), and from 34.95% in LS05 to 39.95% of total fatty acid content in LS06 for Pacific sardine (Table 4.3). PUFA concentrations comprised only 25.31% of total fatty acids in LS06 for Pacific herring, but were 45.83% of total fatty acids in ES05 (Table 4.4). In the lipids of whitebait smelt, PUFA accounted for a minimum of 25.25% total fatty acids in LS06 and a maximum of 35.87% in LS05 (Table 4.5).

Generally speaking, PUFA concentrations were lower in 2005 than 2006 and decreased from early to late summer during both years. We observed considerable seasonal shifts in relative contributions of EPA and DHA to total PUFA composition (Tables 4.2-4.5). Anchovy EPA concentrations ranged from 9.99% of total fatty acids in ES05 to 20.06% in ES06 (Table 4.2), while DHA contributions ranged from 27.39 to 11.28% of total fatty acids during the same two periods (Table 4.3). EPA concentrations varied little in Pacific herring, ranging from10.55% of total fatty acids

in LS06 to 12.31% in LS05, but DHA concentrations were highly variable: 9.50% in ES06 to 30.60% in ES05 (Table 4.4). Similarly, the EPA concentration of total fatty acids in whitebait smelt only slightly varied from 10.73% in ES05 to 13.08% in LS05, while DHA concentrations ranged from 9.25% in ES06 to 18.27% in LS05 (Table 4.5). Based on extensive phytoplankton fatty acid analyses, EPA is typically regarded as a diatom biomarker, whereas DHA signals dinoflagellate productivity (Sargent et al. 1987; Graeve et al 1994; 2005; Viso and Marty 1993). The ratio of DHA to EPA (Fig. 4.6) represents a shift in the phytoplankton community (Budge and Parrish 1998), from one dominated by dinoflagellates in 2005 to one dominated by diatoms in 2006, although this ratio is most effectively used as a biomarker in strictly herbivorous species, and must be regarded with caution (Dalsgaard et al. 2003).

Other PUFA of particular concern to our forage fish sampled, although occurring at low levels, were linoleic and linolenic acids (C18:2n-6 and C18:3n-3, respectively), which are considered to be fatty acid markers of terrestrial origin (Budge and Parrish 1998; Dalsgaard 2003). Both of these C18 PUFA were present in higher abundance in 2006 than during 2005, with the largest values recorded in all fish during LS06 (Tables 4.2-4.5), confirming that coastal and estuarine ecosystems can receive considerable inputs of terrestrial organic matter.

Correlations between lipids and essential fatty acids

Quantitative mean (% fatty acid mass) values of DHA and EPA were significantly related to total lipid (% wet mass) content (see Figs. 4.7a-b). General

linear models with lipid content as the explanatory variable and EFA as the dependent response showed that lipid had a significant effect on both DHA ($R^2 = 0.26$, $F_{1,14} = 5.00$, $p = 0.04$) and EPA composition ($R^2 = 0.40$, $F_{1,14} = 9.17$, $p = 0.01$; Table 4.6). We found that DHA decreased (Fig. 4.7a) as a function of total lipid content, while EPA increased (Fig. 4.7b).

DISCUSSION

The North Pacific Ocean has experienced dramatic environmental shifts in the last few decades (Francis and Hare 1994; Hare and Mantua 2000; Peterson and Schwing 2003), but the summer of 2005 was particularly anomalous because of delayed upwelling, warm sea surface temperatures and decreased productivity lasting through July (Pierce et al. 2006; Schwing et al. 2006; Barth et al. 2007). In 2006, upwelling began in early May off Oregon and Washington, but soon dissipated when strong southwesterly storms moved up the coast. Upwelling remained weak through late June, but winds were strong and persistent enough through September to sustain strong, albeit late, upwelling (Goericke et al. 2007). Large hypoxic events recorded in 2005 and 2006 highlighted the sensitivity of the CCLME to discontinuous change (Chan et al 2008). Zooplankton (Mackas et al. 2006) and forage fish densities (see Fig. 4.2) decreased dramatically in shelf waters off Oregon and Washington from 2004 to 2005. Forage fish densities continued their decline in 2006, which was hypothesized to be the result of delayed productivity and poor year-class strength in 2005 (Goericke et al. 2007).

Variations in whole lipids

Intra- and inter-specific variations in total whole lipids were caused by natural variations in food available during early and late summer 2005 and 2006, but were likely influenced by the maturity schedules of fish sampled. Generally speaking, lipids increased from early summer to late summer, and were typically larger in fish during 2006 compared to 2005. However, each of the forage fish sampled had different reproductive strategies, and these were reflected in seasonal variations of whole lipids. Northern anchovy and Pacific sardine spawn off Oregon and Washington during late spring and early summer (Laroche and Richardson 1980; Richardson 1981; Emmett et al. 2006). Pacific herring spawn off the Pacific Northwest in early spring (Ware 1985; Huynh et al. 2007). Presently, we do not know exactly where and when whitebait smelt spawn (Miller and Lea 1972; Hart 1973), but whitebait larvae captured in estuaries of the Pacific Northwest during fall (Misitano 1976; Bottom and Jones 1990) suggest that they may be late summer spawners. From early to late summer, we recorded total lipid increases in northern anchovy and Pacific sardine, no change in Pacific herring, and decreases in total lipid concentrations of whitebait smelt (Fig. 4.4). Increases in northern anchovy and Pacific sardine lipid stores over the summer demonstrated that these species recovered from lipid demands during spawning through active feeding and weight gain. Both species spawned in spring and summer, and then increased their lipid stores towards the end of the upwelling season. Conversely, whitebait smelt lipids decreased as the summer progressed. This was

probably due to reallocation of lipids for reproductive activity in late summer. Pacific herring lipid stores did not change during the summer. One explanation is that the fish sampled had sizes and weights consistent with immature, non-spawning sub-adult 1-2 year olds (Huynh et al. 2007). Sampling of individual tissues would have elucidated more information about the maturity schedules of individual fish.

Although researchers have recorded seasonal trends in total lipid content and fatty acid profiles for forage fish species in the North Pacific (Hayashi and Takagi 1977; 1978; Shirai et al. 2002), most studies only looked at variations in one year. This study incorporated sampling from two years of contrasting oceanographic conditions to detect inter-annual and seasonal differences. We believe that our ES05 sardine lipid profile was small compared to ES06 (see Fig. 4.4) because of the combined factors of active spawning and low food supply (Mackas et al. 2006). Seasonal increases in total lipid content were documented off Oregon and Washington for Pacific sardine in 2005 (Okada and Morrissey 2007). However, sampling never occurred prior to active sardine spawning in the spring. Lipid stores have been shown (Huynh 2007) to be greater in non-spawning Pacific herring, compared to spawning herring, which may explain the seasonal trends we observed in forage fish lipid content over the summer. Prior to spawning, gonadal development utilizes lipid stores of the muscle and liver tissue (Hayashi and Takagi 1977; 1978). ES06 Pacific sardines were captured in late May, nearly three weeks earlier than in ES05. Sardines in ES06 were both longer and heavier than conspecifics in ES05. It is possible that the larger, heavier ES06 sardines contained more lipids because they were in a pre-spent

condition, although we were not able to confirm this. Nevertheless, overall lipid content was greater in 2006 than in 2005 in all species, suggesting that spawning and food supply equally contribute to lipid stores.

Saturated and monounsaturated fatty acids

We used intra-specific variations in individual fatty acids to detect climate-mediated variations in diet under contrasting oceanographic conditions in 2005 and 2006. SFA and MUFA collectively accounted for over two-thirds of fatty acids in all of the forage fish sampled. The most abundant saturated fatty acid in all forage fish, C16:0, has been noted as being a predominant source of potential metabolic energy during growth, and especially during female sexual maturation (Dalsgaard et al. 2003). However, we did not see any of the same seasonal patterns in C16:0 concentrations that we did in total lipid content. This was probably because we sampled unknown ratios of female to male fish, and also because some of the fish sampled, such as Pacific herring, were sexually immature.

MUFA profiles were linked to zooplankton abundance in the northern California Current. Elevated levels of MUFA, particularly C20:1n-9 and C22:1n-9 are effective tracers of copepod carnivory in forage fish (Dalsgaard et al. 2003; Budge et al. 2006), and provide evidence of wax ester synthesis (Tocher 2003) from the oxidation of C20:1 and C22:1 fatty alcohols in the lipids of copepods. Zooplankton anomalies were observed off central Oregon in 2005, and were characterized principally by decreased amounts of euphausiids and lipid-rich, northern boreal

copepods (Mackas et al. 2006, Goericke et al. 2007), which are especially high in unsaturated fatty acids (Davis and Olla 1992). During 2005, the zooplankton community was made up of mostly warm-water species (Mackas et al. 2006), similar to 1997 and 1998, when forage fish densities were at record lows (Fig. 4.2). All four species of forage fish sampled consume zooplankton as part of their regular diet, but Pacific herring and whitebait smelt typically graze most heavily on calanoid copepods and larger zooplankton, like euphausiids (Brodeur et al. 1987; Brodeur and Pearcy 1992; Miller and Brodeur 2007). Euphausiid egg abundances off Newport Oregon was 4 times greater in ES06 compared to ES05, and over 20 times greater in LS06 than LS05 (Goericke et al. 2007). In 2006, 20-22 MUFA concentrations were larger in all species of forage fish, especially for Pacific herring, than during 2005 (Fig. 4.5a), lending weight to observations of an anomalous, lipid-poor zooplankton community off Oregon and Washington during 2005 (Mackas et al. 2006).

Essential fatty acids

Essential fatty acids (EFAs) are the most effective biochemical markers of natural oceanographic variability because they come only from diet. Forage fish in the CCLME are primarily planktivorous (Brodeur et al. 1987; Brodeur and Pearcy 1992; Miller and Brodeur 2007), and they must obtain EFAs like DHA and EPA, directly by feeding on either phytoplankton or zooplankton. DHA and EPA are both important components of cell membranes, and when limited, cause a host of problems in fish, including decreased fecundity, impaired growth, decreased survival of early life

phases, impaired vision, and impaired schooling behavior (Tocher 2003; Litzow et al. 2006), which can ultimately lead to population decline (Bradford and Cabana 1997). PUFA, like DHA and EPA, but also arachidonic acid (ARA, C20:4n-6) are the major sources of metabolic energy, influencing individual and population growth rates and reproduction (Copeman and Parrish 2002; Tocher 2003). ARA is often neglected in fish because it occurs at low concentrations, but studies (Tocher and Sargent 1987; Cejas et al. 2004) have shown that it may also be an important precursor of various eicosanoids and contribute to osmoregulation and cardiovascular function. Bottom-up oceanographic processes, like upwelling and sea surface temperature, regulate the phytoplankton community in the northern CCLME, thus indirectly determining EFA concentrations up the marine food web.

In 2005, delayed coastal upwelling during the summer decreased nutrient supply and chlorophyll production, and it is generally accepted that 2005 was a highly anomalous year (Barth et al. 2006; Pierce et al. 2006; Schwing et al. 2006). Forage fish were captured at very low levels (Fig. 4.2), and seabirds like the Cassin's auklet suffered reproductive failure, leading researchers to hypothesize that in 2005 there was a mismatch of food availability to higher trophic levels (Brodeur et al 2006; Sydeman et al. 2006; Henson and Thomas 2007). Forage fish sampled in this study during early summer 2005 had diets comprised almost exclusively of dinoflagellates, or of dinoflagellate origin, as suggested by high DHA to EPA ratios (Fig. 4.6). In the absence of upwelling, huge pools of warm water piled up along the eastern boundary current region off Oregon and Washington, depressing the thermocline and reducing

the availability of nutrients (Hickey et al. 2006). Under scenarios like these, ciliates, flagellates, coccoid cyanobacteria and small diatoms would tend to dominate the phytoplankton community (Sherr et al. 2005). Not until a biological shift caused by upwelling leads to blooms dominated by large diatoms can large ecosystems be supported along the Oregon-Washington coast (Barth et al. 2006).

In ES05, we detected bottom-up mechanisms influencing fatty acid profiles in forage fish, by way of high DHA to EPA ratios, evidencing dinoflagellate-dominated primary and secondary productivity (Fig. 4.6). Our results show that lipid concentrations negatively correlated with weight mass percent of DHA, and positively correlated with EPA (Fig. 4.8), further lines of evidence that delayed upwelling and subsequent low levels of productivity influenced the marine food chain in 2005. In 2006, the diet of forage fish sampled in this study shifted to more intense grazing on diatom markers (Fig. 4.6). The increased proportion of diatoms in the diet was signified by the lower DHA to EPA ratio, corresponding to increased productivity in the CCLME (Goericke et al. 2007). Higher concentrations of C18 PUFA in 2006 provided evidence of larger terrestrial input into the diets of forage fish sampled in this study, probably due to nutrient loading in the Columbia River. Higher flow rates were recorded in 2006 compared to 2005. However, we expect that lipid levels and EPA concentrations during a highly productive year, such as 2003 (see Fig. 4.2), would greatly exceed any measurements made during this study.

Conclusions

In conclusion, we detected seasonal and annual differences in total lipid content within and among four species of forage fish: northern anchovy, Pacific sardine, Pacific herring and whitebait smelt during the summers of 2005 and 2006 in the northern CCLME. We also detected how bottom-up mechanisms influenced feeding ecology in forage fish during 2005 compared to 2006 through changes in fatty acid compositions. The lowest lipids were measured in ES05 in northern anchovy, when lipids comprised <0.5% (wet mass) of total body weight, and fatty acids had the largest (>2.5) DHA to EPA ratio, denoting a diet rich in dinoflagellate markers. The highest lipids were measured in 2006 in Pacific sardine, at >20% (wet mass), with DHA/EPA ratios around 1, suggesting optimal ratios of essential fatty acids (Kainz et al. 2004). Decreases in whitebait smelt lipids over the summer were probably related to summer spawning, although further studies are required to confirm this. The greatest seasonal differences in total lipids were noted in anchovy and sardine between early and late summer 2005, corresponding with delayed coastal upwelling along the Oregon-Washington coast, and decreases in population densities of all fish (Fig. 4.2). In fact, population densities were low during both years of this study (Fig. 4.2). Nonetheless, our results fail to show overwhelming support of a biological regime shift caused by essential fatty acid limitation, as suggested by Litzow et al. (2006), made all the more difficult because we only had two years of data. However, our results do show that low productivity in the coastal environment in 2005, as a result of delayed coastal upwelling, was manifested as high DHA and low EPA concentrations

in forage fish lipids, and that high lipid content was negatively related to DHA and positively related to EPA in all fish sampled. This information should contribute significantly to time-series observations of lipids and fatty acid signatures in the CCLME.

The distribution of PUFA in forage fish sampled during this study demonstrates that EFA transfer to higher trophic levels will likely vary with the size and taxonomic composition of planktonic organisms consumed. Pacific herring and whitebait smelt displayed high levels of macrozooplankton carnivory during 2005, and especially during 2006, suggested by the high levels of 20-22 MUFA (Fig. 4.4a). However, it has been hypothesized (Kaintz et al. 2004) that the essential fatty acid DHA may still be limited even when planktivorous fish consume the largest zooplankton. Directed studies examining species- and size-specific EFA physiological requirements among forage fish should be the next step in evaluating the biochemical signatures of forage fish in the CCLME. Our general findings on the patterns of forage fish lipid content and fatty acid composition during anomalous ocean conditions should still be useful from a EBFM approach, but will be more valuable if we can determine stronger causative links between physical oceanography, diet and population dynamics.

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Table 4.1. Summary of National Marine Fisheries Service (NMFS) studies conducted during early and late summer 2005 and 2006 (ES05, LS05, ES06, and LS06), where forage fish were collected for use in this study, including the Bonneville Power Administration (BPA) Plume Study, the Stock Assessment Improvement Plan (SAIP) Study, the Predator Study, and the LIDAR Study. Date of collection and station information, denoted by the adjacent land structure and distance from shore (in nautical miles) are listed, along with gear type and number of individuals (*n*) sampled.

Time	Species	Date	Study	Station	Gear	*n*
ES05	Northern anchovy	6/14/05	BPA	La Push 17	Surface	10
	Pacific sardine	6/14/05	BPA	La Push 09	Surface	10
	Pacific herring	6/18/05	BPA	Willapa Bay 05	Surface	10
	Whitebait smelt	7/11/05	SAIP	Willapa Bay 10	Midwater	10
LS05	Northern anchovy	9/21/05	SAIP	Columbia River 20	Midwater	10
	Pacific sardine	8/12/05	Predator	Willapa Bay 23	Surface	10
	Pacific herring	8/11/05	Predator	Willapa Bay 05	Surface	10
	Whitebait smelt	8/1/05	Predator	Columbia River 07	Surface	2
	Whitebait smelt	8/23/05	BPA	Columbia River 07	Surface	2
	Whitebait smelt	8/27/05	BPA	Cascade Head 01	Surface	6
ES06	Northern anchovy	6/07/06	LIDAR	Grays Harbor 06	Surface	10
	Pacific sardine	5/27/06	Predator	Columbia River 15	Surface	10
	Pacific herring	7/17/06	Predator	Willapa Bay 05	Surface	10
	Whitebait smelt	7/17/06	Predator	Willapa Bay 05	Surface	10
LS06	Northern anchovy	9/26/06	BPA	Cape Meares 03	Surface	10
	Pacific sardine	9/22/06	BPA	Queets River 10	Surface	10
	Pacific herring	9/21/06	BPA	La Push 04	Surface	10
	Whitebait smelt	8/15/06	Predator	Willapa Bay 05	Surface	10

Table 4.2. Fatty acid composition (mean % ± one standard deviation of total fatty acids) of northern anchovy (*Engraulis mordax*) sampled during early and late summer, 2005 and 2006 (ES05, LS05, ES06, and LS06). Each mean value comes from the fatty acid profile of 3 fish replicated using gas chromatography (GC). Values in each row that do not share a common superscript are significantly different (One-way ANOVA, Tukey's honestly significant difference test, $p<0.05$). Summaries of total saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA) and omega-3 polyunsaturated fatty acids (n-3) are also presented.

Northern anchovy	**ES05**		**LS05**		**ES06**		**LS06**	
Compounds	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C14:0	4.51^{a}	0.79	8.52^{bc}	0.46	9.00^{b}	0.43	7.55^{c}	0.90
C15:0	0.42^{a}	0.11	0.47^{a}	0.11	0.58^{a}	0.23	0.51^{a}	0.19
C16:0	29.27^{a}	2.94	25.84^{b}	0.35	22.28^{c}	0.54	27.24^{ab}	1.23
C17:0	0.15^{a}	0.04	1.44^{b}	0.08	1.25^{b}	0.39	0.70^{c}	0.14
C18:0	6.23^{a}	0.77	6.38^{a}	0.82	4.79^{b}	0.57	5.74^{ab}	1.24
C20:0	0.05^{a}	0.08	0.02^{a}	0.00	0.05^{a}	0.04	0.05^{a}	0.06
C23:0	0.29^{a}	0.04	0.10^{b}	0.00	0.14^{c}	0.03	0.17^{c}	0.02
SFA	40.92^{a}	2.88	42.77^{a}	0.45	38.09^{a}	0.87	41.98^{a}	1.26
C14:1n-5	0.00^{a}	0.00	0.04^{bc}	0.00	0.03^{ab}	0.04	0.07^{c}	0.03
C16:1n-7	5.27^{a}	0.33	9.82^{b}	0.67	9.99^{b}	0.67	6.98^{c}	0.58
C17:1n-9	0.78^{a}	0.26	1.79^{b}	0.26	1.52^{bc}	0.65	1.03^{ac}	0.30
C18:1n-9	7.11^{a}	0.70	7.75^{a}	0.33	6.13^{b}	0.34	7.80^{a}	0.66
C20:1n-9	1.37^{a}	0.27	1.33^{a}	0.13	2.44^{b}	0.88	2.63^{b}	0.32
C22:1n-9	0.94^{a}	0.24	0.90^{a}	0.11	1.90^{b}	0.91	1.54^{ab}	0.25
C24:1n-9	1.05^{a}	0.59	0.21^{b}	0.03	0.19^{b}	0.03	0.40^{b}	0.08
MUFA	16.51^{a}	0.64	21.85^{a}	0.86	22.19^{a}	0.34	20.45^{a}	0.95
C18:2n-6	1.75^{a}	0.23	1.73^{a}	0.05	1.74^{a}	0.45	2.47^{b}	0.15
C18:3n-6	0.13^{a}	0.23	0.42^{b}	0.11	0.48^{b}	0.12	0.28^{ab}	0.07
C18:3n-3	0.53^{a}	0.19	0.61^{a}	0.03	0.81^{a}	0.30	1.29^{b}	0.14
C20:2n-6	0.06^{a}	0.10	0.05^{a}	0.04	0.31^{b}	0.17	0.11^{a}	0.09
C20:3n-6	0.05^{a}	0.08	0.01^{a}	0.02	0.08^{a}	0.10	0.13^{a}	0.11
C20:3n-3	0.00^{a}	0.00	0.00^{a}	0.00	0.02^{a}	0.04	0.08^{b}	0.05
C20:4n-6	0.34^{a}	0.03	0.38^{a}	0.19	0.51^{ab}	0.12	0.64^{b}	0.03
C20:5n-3	9.99^{a}	1.02	19.37^{b}	0.61	20.06^{b}	2.19	14.65^{c}	0.58
C22:2n-6	0.17^{a}	0.03	0.59^{b}	0.02	0.63^{b}	0.10	0.48^{c}	0.02
C22:5n-3	2.16^{a}	0.36	2.24^{a}	0.26	3.79^{b}	0.69	1.94^{a}	0.18
C22:6n-3	27.39^{a}	2.24	9.99^{b}	0.13	11.28^{b}	2.02	15.49^{c}	1.27
PUFA	42.57^{a}	3.57	25.38^{a}	0.82	39.72^{a}	0.78	37.57^{a}	1.98
n-3	40.06^{a}	3.34	32.21^{a}	0.86	35.97^{a}	0.92	33.45^{a}	1.87

Table 4.3. Fatty acid composition (mean % ± one standard deviation of total fatty acids) of Pacific sardine (*Sardinops sagax*) sampled during early and late summer, 2005 and 2006 (ES05, LS05, ES06, and LS06). Each mean value comes from the fatty acid profile of 3 fish replicated using gas chromatography (GC). Values in each row that do not share a common superscript are significantly different (One-way ANOVA, Tukey's honestly significant difference test, $p<0.05$). Summaries of total saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA) and omega-3 polyunsaturated fatty acids (n-3) are also presented.

Pacific Sardine	**ES05**		**LS05**		**ES06**		**LS06**	
Compounds	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C14:0	9.19^{a}	0.85	9.15^{a}	0.91	8.61^{a}	2.35	7.32^{a}	0.56
C15:0	0.49^{a}	0.16	0.33^{a}	0.14	0.52^{a}	0.12	0.54^{a}	0.15
C16:0	24.37^{a}	1.70	25.56^{a}	0.86	24.68^{a}	1.10	24.78^{a}	1.33
C17:0	1.17^{ab}	0.26	1.42^{a}	0.14	1.01^{b}	0.29	1.21^{ab}	0.27
C18:0	4.52^{a}	0.65	6.61^{a}	1.54	6.27^{a}	2.15	6.10^{a}	0.94
C20:0	0.03^{a}	0.01	0.03^{ab}	0.00	0.07^{ab}	0.07	0.09^{b}	0.02
C23:0	0.12^{a}	0.02	0.09^{a}	0.01	0.19^{b}	0.04	0.14^{a}	0.04
SFA	39.89^{a}	1.54	43.19^{a}	1.55	41.35^{a}	1.78	40.16^{a}	1.72
C14:1n-5	0.01^{a}	0.02	0.01^{a}	0.02	0.04^{a}	0.03	0.04^{a}	0.00
C16:1n-7	11.62^{a}	1.03	10.32^{ac}	1.01	5.52^{b}	2.11	8.23^{c}	0.98
C17:1n-9	1.37^{a}	0.34	1.74^{a}	0.36	1.50^{a}	0.68	2.00^{a}	0.35
C18:1n-9	6.14^{a}	0.63	7.77^{b}	0.65	6.77^{ab}	1.14	6.55^{ab}	1.01
C20:1n-9	0.90^{a}	0.33	1.20^{ac}	0.44	2.69^{b}	0.81	2.13^{bc}	0.66
C22:1n-9	0.32^{a}	0.33	0.34^{a}	0.21	1.78^{b}	0.78	1.26^{ab}	0.94
C24:1n-9	0.43^{a}	0.12	0.48^{a}	0.12	0.40^{a}	0.12	0.40^{a}	0.10
MUFA	20.79^{a}	1.10	21.86^{a}	1.39	18.70^{a}	1.86	20.62^{a}	0.64
C18:2n-6	1.60^{a}	0.33	1.53^{a}	0.11	2.26^{a}	0.94	2.02^{a}	0.35
C18:3n-6	0.39^{a}	0.03	0.50^{b}	0.03	0.41^{ab}	0.10	0.62^{c}	0.05
C18:3n-3	0.78^{ab}	0.31	0.52^{a}	0.06	0.81^{ab}	0.32	0.99^{b}	0.22
C20:2n-6	0.42^{ab}	0.32	0.66^{a}	0.11	0.35^{ab}	0.22	0.29^{b}	0.16
C20:3n-6	0.24^{a}	0.20	0.13^{a}	0.04	0.16^{a}	0.14	0.14^{a}	0.02
C20:3n-3	0.21^{a}	0.14	0.00^{b}	0.00	0.05^{b}	0.05	0.04^{b}	0.04
C20:4n-6	1.17^{a}	0.19	0.36^{b}	0.40	0.56^{b}	0.42	1.18^{a}	0.25
C20:5n-3	20.88^{a}	2.72	19.14^{a}	2.13	18.04^{a}	1.22	18.80^{a}	0.90
C22:2n-6	0.61^{a}	0.05	0.65^{a}	0.03	0.62^{a}	0.08	0.77^{b}	0.02
C22:5n-3	3.29^{a}	0.08	3.54^{ab}	0.15	3.43^{ab}	0.46	3.77^{b}	0.16
C22:6n-3	9.72^{ac}	1.78	7.92^{a}	1.35	13.25^{b}	1.61	10.59^{c}	1.75
PUFA	39.32^{a}	1.72	34.95^{a}	2.26	39.95^{a}	1.47	39.22^{a}	1.99
n-3	34.88^{a}	1.69	31.11^{a}	2.57	35.58^{a}	1.62	34.19^{a}	1.66

Table 4.4. Fatty acid composition (mean % ± one standard deviation of total fatty acids) of Pacific herring (*Clupea harengus pallasii*) sampled during early and late summer, 2005 and 2006 (ES05, LS05, ES06, and LS06). Each mean value comes from the fatty acid profile of 3 fish replicated using gas chromatography (GC). Values in each row that do not share a common superscript are significantly different (One-way ANOVA, Tukey's honestly significant difference test, $p<0.05$). Summaries of total saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA) and omega-3 polyunsaturated fatty acids (n-3) are also presented.

Pacific Herring	**ES05**		**LS05**		**ES06**		**LS06**	
Compounds	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C14:0	4.27^{a}	0.64	4.87^{a}	0.24	7.99^{b}	1.44	5.30^{a}	0.53
C15:0	0.37^{a}	0.11	0.26^{a}	0.03	0.25^{a}	0.10	0.26^{a}	0.08
C16:0	24.28^{a}	1.54	24.30^{a}	1.40	19.55^{b}	1.51	21.89^{c}	0.39
C17:0	0.28^{a}	0.10	0.44^{a}	0.10	0.91^{b}	0.18	0.93^{b}	0.15
C18:0	4.06^{a}	0.39	4.00^{a}	0.68	4.22^{a}	1.10	9.40^{b}	1.48
C20:0	0.00^{a}	0.00	0.04^{a}	0.06	0.04^{a}	0.02	0.03^{a}	0.02
C23:0	0.15^{a}	0.08	0.14^{a}	0.01	0.05^{b}	0.04	0.10^{ab}	0.00
SFA	33.41^{a}	1.83	34.04^{a}	1.33	33.02^{a}	1.41	37.91^{a}	1.24
C14:1n-5	0.04^{a}	0.10	0.00^{a}	0.00	0.03^{a}	0.02	0.01^{a}	0.02
C16:1n-7	6.74^{a}	1.21	8.39^{b}	0.96	7.85^{ab}	0.94	7.75^{ab}	0.60
C17:1n-9	0.45^{a}	0.12	0.55^{a}	0.08	1.16^{b}	0.11	1.56^{c}	0.40
C18:1n-9	5.84^{a}	1.11	10.19^{b}	1.08	8.11^{c}	1.12	11.17^{b}	0.85
C20:1n-9	3.05^{a}	1.96	3.76^{a}	1.54	11.03^{b}	0.74	7.35^{c}	0.98
C22:1n-9	3.72^{a}	1.87	4.46^{a}	1.90	12.91^{b}	1.49	8.13^{c}	1.32
C24:1n-9	0.93^{a}	0.48	0.84^{a}	0.21	0.44^{a}	0.22	0.80^{a}	0.19
MUFA	20.76^{a}	3.96	28.19^{ab}	3.37	41.54^{b}	1.20	36.78^{ab}	2.74
C18:2n-6	1.23^{a}	0.13	1.29^{a}	0.28	1.26^{a}	0.23	1.42^{a}	0.11
C18:3n-6	0.00^{a}	0.00	0.39^{b}	0.37	0.15^{ab}	0.08	0.24^{ab}	0.04
C18:3n-3	0.48^{a}	0.09	0.54^{ab}	0.19	0.70^{b}	0.11	0.54^{ab}	0.03
C20:2n-6	0.08^{a}	0.12	0.14^{a}	0.12	0.14^{a}	0.03	0.15^{a}	0.11
C20:3n-6	0.00^{a}	0.00	0.08^{b}	0.06	0.04^{ab}	0.05	0.09^{b}	0.02
C20:3n-3	0.00^{a}	0.00	0.00^{a}	0.00	0.05^{a}	0.01	0.08^{a}	0.19
C20:4n-6	0.30^{a}	0.06	0.38^{ab}	0.02	0.45^{b}	0.03	0.28^{a}	0.12
C20:5n-3	11.71^{ab}	0.52	12.31^{a}	0.94	11.34^{ab}	0.74	10.55^{b}	0.92
C22:2n-6	0.17^{a}	0.08	0.25^{b}	0.03	0.38^{c}	0.03	0.35^{c}	0.02
C22:5n-3	1.27^{a}	0.21	1.34^{a}	0.05	1.42^{a}	0.16	1.40^{a}	0.10
C22:6n-3	30.60^{a}	3.32	21.05^{b}	1.69	9.50^{c}	0.87	10.21^{c}	1.20
PUFA	45.83^{a}	3.11	37.78^{a}	2.64	25.45^{a}	1.66	25.31^{a}	2.33
n-3	44.06^{a}	3.14	35.24^{a}	2.52	23.01^{a}	1.54	22.78^{a}	2.09

Table 4.5. Fatty acid composition (mean % ± one standard deviation of total fatty acids) of whitebait smelt (*Allosmerus elongatus*) sampled during early and late summer, 2005 and 2006 (ES05, LS05, ES06, and LS06). Each mean value comes from the fatty acid profile of 3 fish replicated using gas chromatography (GC). Values in each row that do not share a common superscript are significantly different (One-way ANOVA, Tukey's honestly significant difference test, $p<0.05$). Summaries of total saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA) and omega-3 polyunsaturated fatty acids (n-3) are also presented.

Whitebait Smelt	**ES05**		**LS05**		**ES06**		**LS06**	
Compounds	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C14:0	5.77^{ac}	0.41	5.27^{a}	0.66	6.38^{bc}	0.61	7.32^{b}	0.82
C15:0	0.29^{a}	0.06	0.10^{b}	0.11	0.21^{ab}	0.05	0.19^{ab}	0.01
C16:0	21.52^{a}	0.50	22.10^{a}	1.15	20.00^{b}	0.61	20.95^{ab}	1.09
C17:0	0.62^{a}	0.05	0.47^{a}	0.15	0.95^{b}	0.24	0.96^{b}	0.17
C18:0	6.00^{a}	0.88	5.87^{a}	2.44	14.01^{b}	1.95	9.17^{c}	1.56
C20:0	0.02^{a}	0.02	0.03^{a}	0.06	0.02^{a}	0.00	0.02^{a}	0.01
C23:0	0.14^{a}	0.01	0.13^{ab}	0.03	0.10^{b}	0.00	0.07^{c}	0.04
SFA	34.37^{a}	1.09	33.97^{a}	3.04	41.67^{a}	1.79	38.67^{a}	1.45
C14:1n-5	0.06^{a}	0.08	0.00^{a}	0.00	0.02^{a}	0.02	0.03^{a}	0.03
C16:1n-7	11.06^{a}	0.46	8.57^{b}	0.64	10.18^{a}	0.70	11.15^{a}	0.74
C17:1n-9	0.82^{ab}	0.28	0.55^{b}	0.19	0.95^{a}	0.23	1.05^{a}	0.23
C18:1n-9	13.49^{a}	0.57	17.02^{ab}	3.99	16.57^{ab}	1.64	18.19^{b}	1.54
C20:1n-9	3.25^{a}	0.28	1.89^{b}	0.61	2.80^{ab}	1.14	3.31^{a}	0.30
C22:1n-9	2.48^{a}	0.14	1.31^{b}	0.43	1.85^{c}	0.10	1.98^{c}	0.33
C24:1n-9	0.86^{a}	0.08	0.82^{a}	0.26	0.33^{b}	0.03	0.37^{b}	0.07
MUFA	32.02^{a}	0.70	30.16^{a}	2.72	32.70^{a}	1.95	36.08^{a}	1.68
C18:2n-6	1.31^{ab}	0.51	1.05^{b}	0.11	1.61^{a}	0.02	1.58^{a}	0.04
C18:3n-6	0.17^{a}	0.05	0.16^{a}	0.09	0.20^{a}	0.06	0.11^{a}	0.06
C18:3n-3	0.58^{a}	0.26	0.34^{a}	0.07	0.43^{a}	0.25	0.40^{a}	0.23
C20:2n-6	0.20^{a}	0.02	0.09^{a}	0.16	0.21^{ab}	0.20	0.03^{a}	0.05
C20:3n-6	0.11^{a}	0.01	0.02^{b}	0.04	0.12^{a}	0.07	0.08^{ab}	0.06
C20:3n-3	0.05^{a}	0.04	0.00^{b}	0.00	0.04^{ab}	0.03	0.01^{ab}	0.02
C20:4n-6	0.42^{a}	0.03	0.32^{b}	0.07	0.40^{a}	0.03	0.42^{a}	0.02
C20:5n-3	10.73^{a}	0.40	13.08^{b}	1.31	10.79^{a}	0.22	10.81^{a}	0.38
C22:2n-6	0.27^{a}	0.00	0.31^{a}	0.04	0.41^{b}	0.01	0.38^{b}	0.02
C22:5n-3	1.60^{a}	0.10	2.24^{b}	0.25	2.17^{b}	0.07	2.01^{b}	0.15
C22:6n-3	18.17^{a}	1.26	18.27^{a}	4.53	9.25^{b}	0.39	9.42^{b}	0.88
PUFA	33.62^{a}	1.43	35.87^{a}	4.09	25.63^{a}	0.64	25.25^{a}	1.59
n-3	31.13^{a}	1.78	33.93^{a}	4.36	22.68^{a}	0.71	22.65^{a}	1.53

Table 4.6. Regression coefficients showing the effect of lipid content (% wet mass) on docosahexanoic acid (DHA), and eicosapentanoic acid (EPA) concentrations in four species of pelagic forage fish off Oregon and Washington used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax),* Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*). Both essential fatty acids are significantly correlated with lipid content (ANOVA, $p<0.05$), although DHA is negatively correlated and EPA is positively correlated.

Variable	**DHA**	(*n*=16)		**EPA**	(*n*=16)	
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	1.25	0.07	0.00	1.05	0.04	0.00
Lipid	-0.02	0.01	0.04	0.01	0.00	0.01

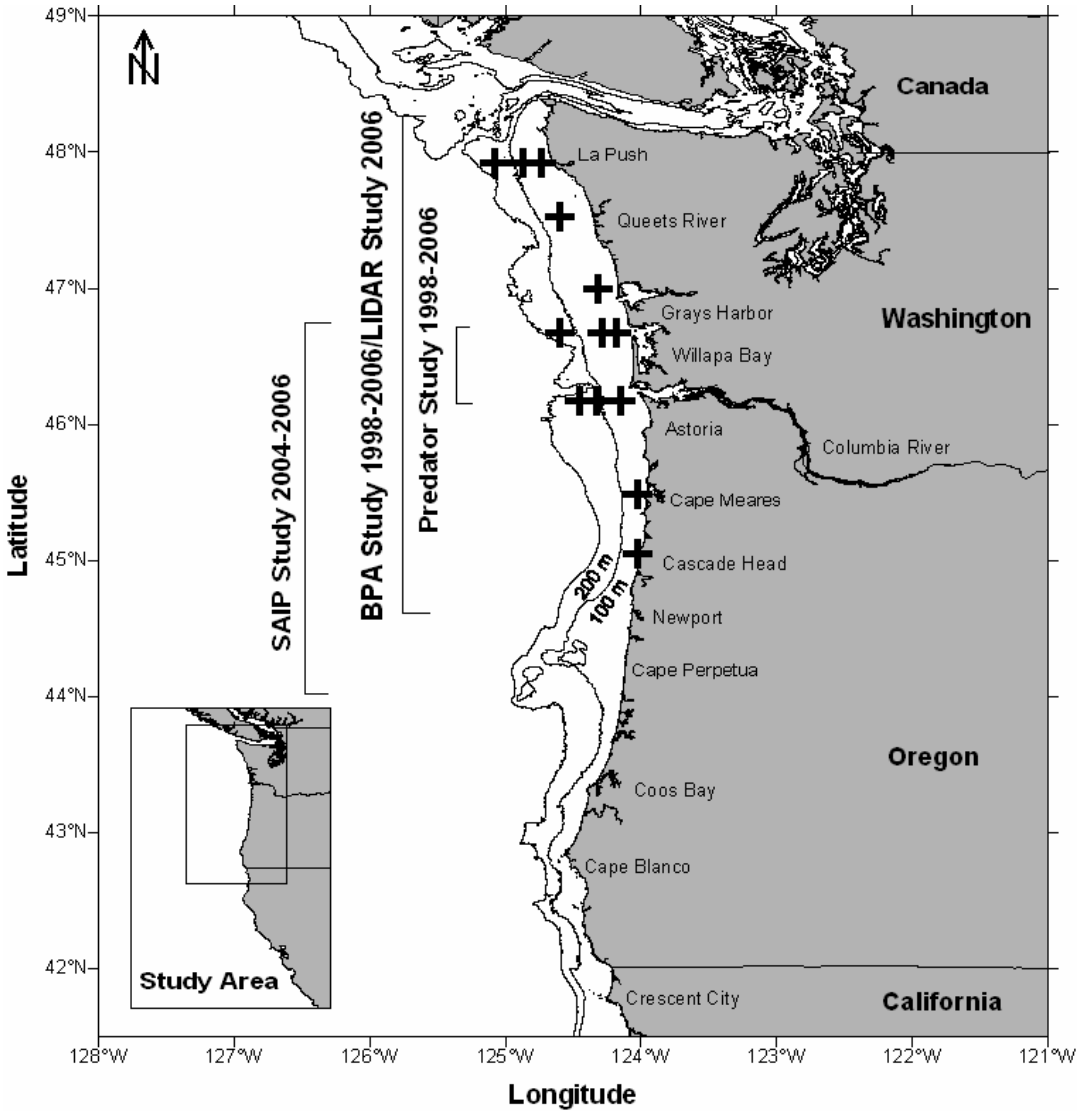

Figure 4.1. Map displaying the collection sites for forage fish used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax)*, Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*). We relied on four National Marine Fisheries Service (NMFS) sampling studies (Predator, BPA Plume, LIDAR, and SAIP) during 2005 and 2006 to obtain our fish. Stations where fish were collected are denoted with a + sign. Also shown are the 100 and 200m depth contours.

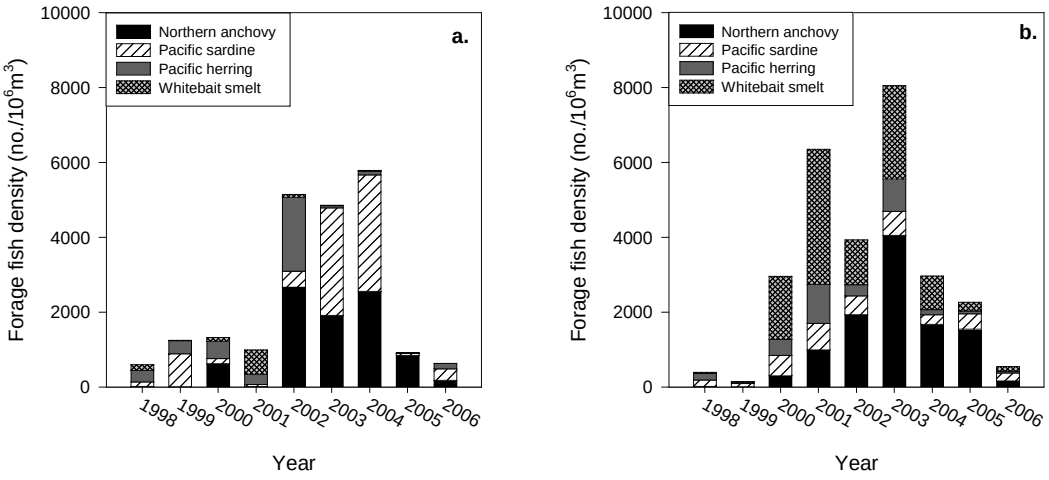

Figure 4.2. Mean annual densities (standardized to number/10^6m^3) of the four species forage fish used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax),* Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*) from 1998-2006. These data are recorded catches from (**a**) National Marine Fisheries Service (NMFS) BPA Plume Study cruises (May, June and September); and (**b**) NMFS Predator Study cruises (April-August). Although both studies utilized the same surface trawl gear to catch fish, the Plume Study sampled during the day, while the Predator Study sampled at night.

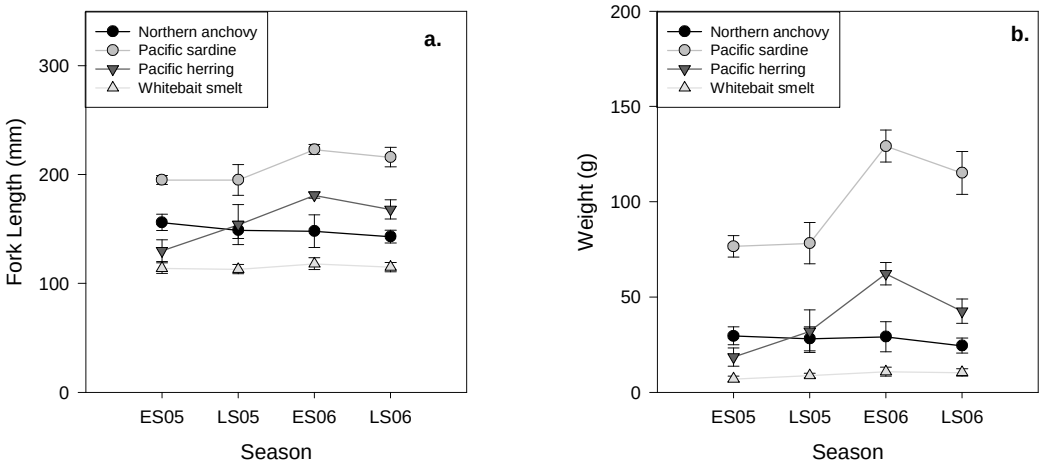

Figure 4.3. Mean ± SD (**a**) fork lengths (FL, in mm) and (**b**) weights (in g) of the four species of forage fish used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax),* Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*) sampled during early and late summer 2005 and 2006 (ES05, LS05, ES06, and LS06). Values come from 10 individuals of each species sampled during each time period.

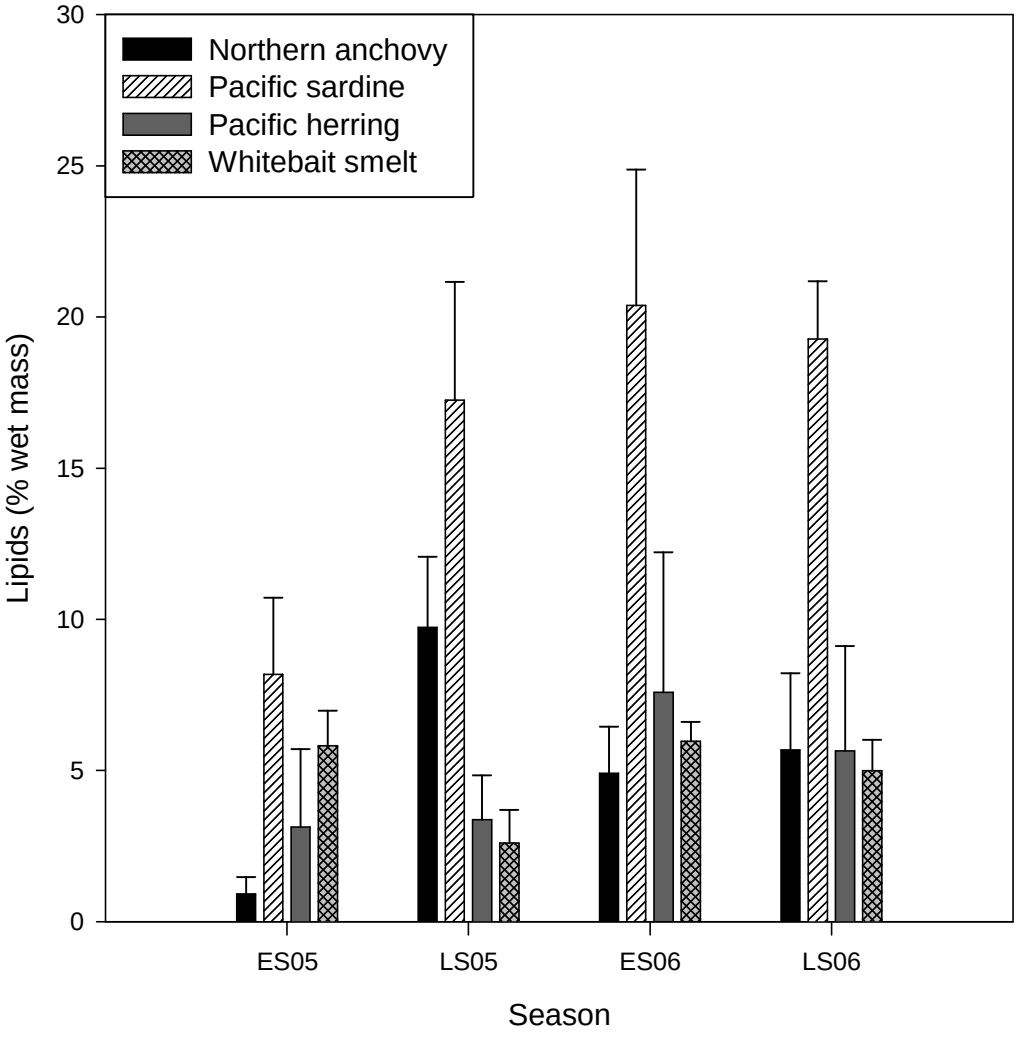

Figure 4.4. Mean ± one standard deviation surrounding the mean (SD) total lipid content (% wet mass) of four species of forage fish used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax),* Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*). Values come from total whole lipids extracted from 10 individuals of each species during each of four time periods: early and late summer 2005 and 2006 (ES05, LS05, ES06, and LS06).

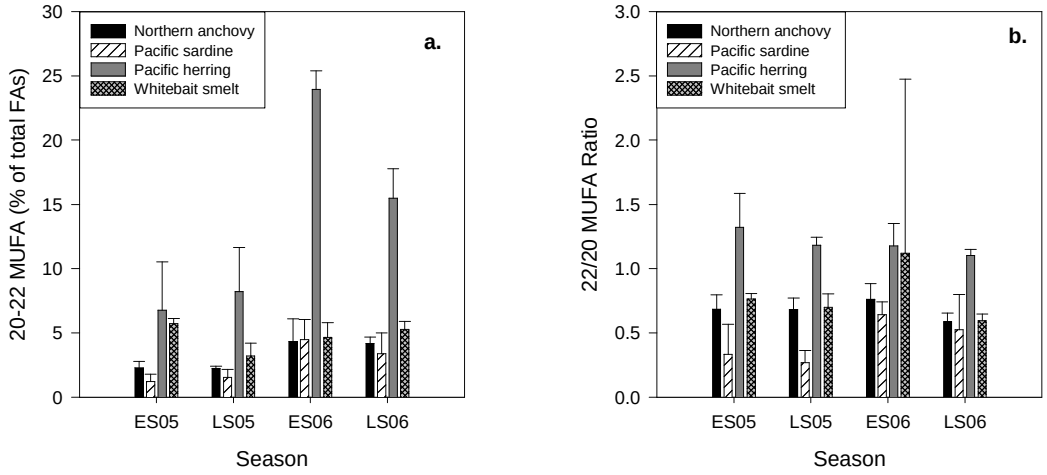

Figure 4.5. Fatty acid markers representing copepod carnivory and wax ester synthesis, calculated from the fatty acid profiles of four species of forage fish used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax),* Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*), during early and late summer 2005 and 2006 (ES05, LS05, ES06, and LS06). Shown are (**a**) mean ± one standard deviation surrounding the mean (SD) content of eicosenoic (C20:1n-9) and erucic (C22:1n-9), both monosaturated fatty acids (MUFA), and (**b**) mean ± SD ratios between the MUFA. Values come from 3 individuals replicated once during each time period.

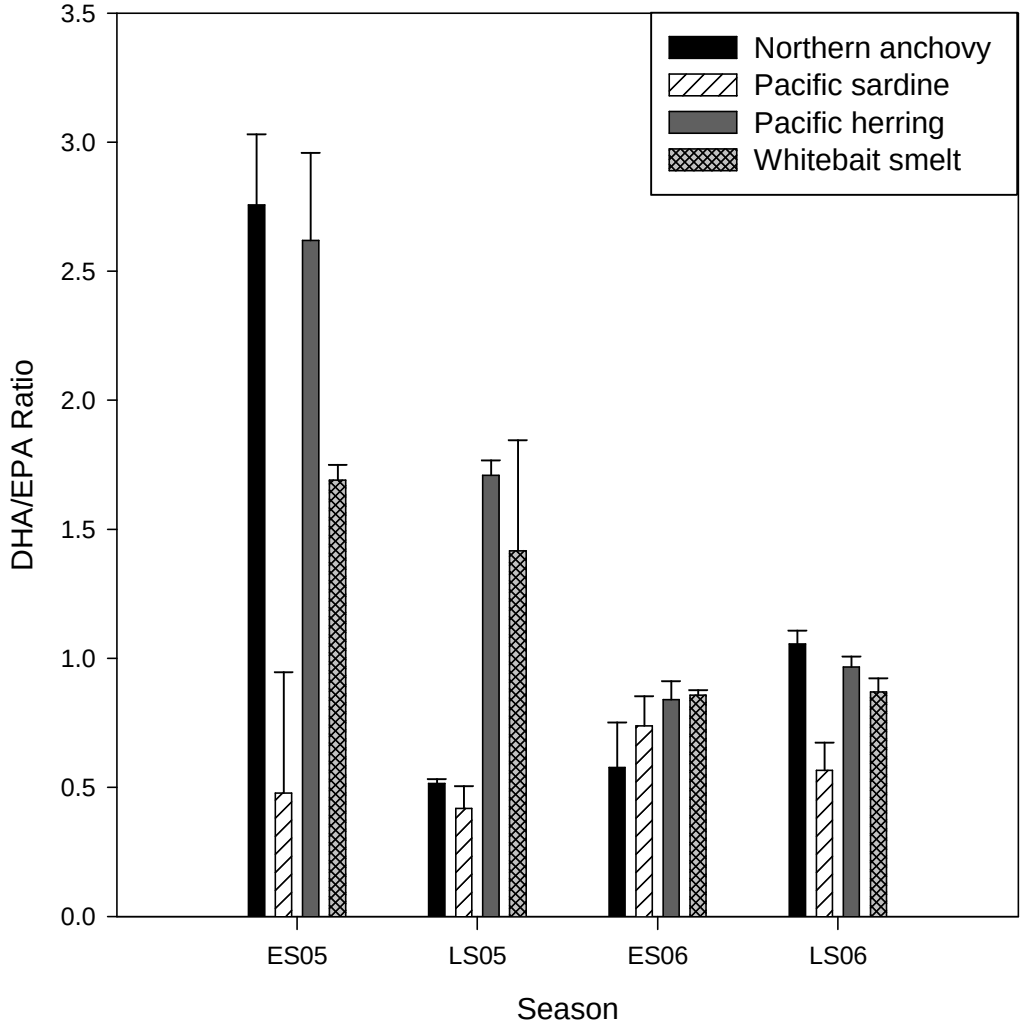

Figure 4.6. Fatty acid markers indicating the proportion of dinoflagellates to diatoms in the diet, calculated from the fatty acid profiles of forage fish used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax),* Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*), during early and late summer 2005 and 2006 (ES05, LS05, ES06, and LS06). Mean ± one standard deviation surrounding the mean (SD) polyunsaturated fatty acid (PUFA) ratios between essential fatty acids, docosahexanoic acid (DHA), and eicosapentanoic acid (EPA) are shown. Values come from 3 individuals replicated once during each time period.

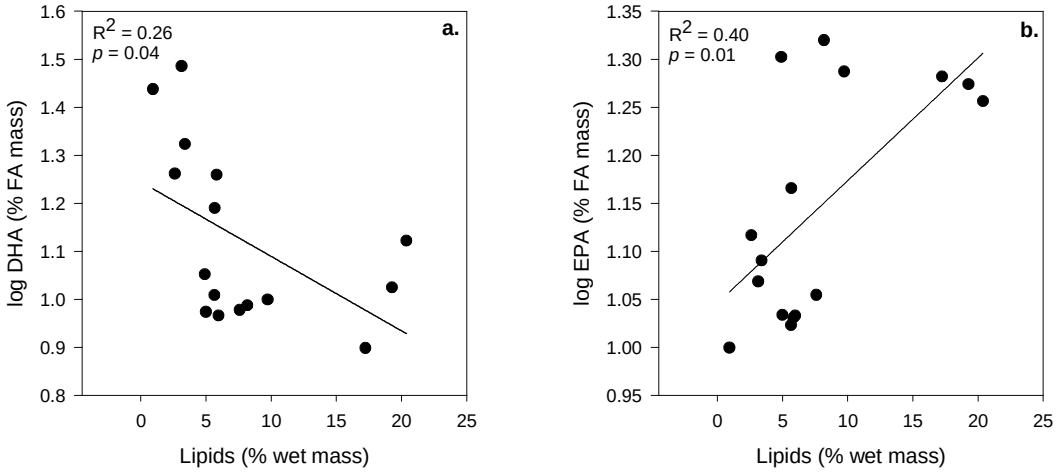

Figure 4.7. The relationship between total lipid content (% wet mass) and essential fatty acid (EFA) content (% fatty acid mass), namely (**a**) docosahexanoic acid (DHA), and (**b**) eicosapentanoic acid (EPA) for the four species of forage fish used in this study, northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax),* Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*), during early and late summer 2005 and 2006. EFA content values were log-transformed prior to analysis. See Table 6 for a full summary of significance as determined by ANOVA.

Chapter 5 – General Conclusion

This research examined ecology of the northern subpopulation of northern anchovy (*Engraulis mordax*) in the California Current large marine ecosystem (CCLME), by evaluating patterns in abundance, distribution, age structure, recruitment, and foraging success from data collected during four major National Marine Fisheries Service (NMFS) surveys from 1977-2006. I successfully developed methods to determine associations between northern anchovy and their physical habitat at meso- and macro-scales, and to determine annual/daily growth, and spawning timing. I also utilized biochemical procedures to examine natural variability in forage fish food quality over contrasting years (2005 and 2006). I then used these methods to explore (1) inter- and intra-annual variation in anchovy distribution and its relationship to oceanographic variables, (2) growth rates of juvenile anchovy that indicate the timing of major spawning events and changes in mortality rates, and (3) changes in whole lipids and fatty acid profiles to determine food sources in years of contrasting oceanographic conditions.

This work was driven by lack of ecological information pertaining to the northern subpopulation of northern anchovy, despite anchovy being one of the most abundant forage species in the CCLME. The importance of anchovy as prey for piscivorous predators cannot be underestimated, particularly with the recommendation by a variety of advisory panels for a more effective and holistic ecosystem-based fishery management (EBFM) approach to fishery management (Pikitch et al. 2004). From an EBFM perspective, adequate knowledge of commercially exploited

populations and trophic interactions are required for sustainable exploitation of marine resources in the CCLME (Marasco et al. 2007).

In the CCLME, and elsewhere in the Pacific Ocean, anchovy productivity has varied over periods of about 20-50 years (Baumgartner et al. 1992; Lluch-Belda et al. 1992; Schwartzlose et al. 1999; Rodriguez-Sanchez et al. 2002; Chavez et al. 2003). Hypotheses tested in this thesis were developed to contribute to discussions about anchovy population fluctuations on decadal timescales. In Chapter 2, I hypothesized anchovy abundance and distribution would be related to cool oceanographic conditions. This was supported by both physical and biological oceanographic time-series observations, after careful consideration of population age structure. Northern anchovy demonstrated high affinity for nearshore (0-10 km) habitats off Oregon and Washington. Anchovy density (standardized to number/$10^6 m^3$) appeared to be positively related to sea surface temperature (SST), but when corrected for age, the relationship proved to be negative. Increases in anchovy density were preceded by a year (or years) of cooler than average SST. In addition, northern anchovy year-class strength was highly correlated with, and presumably driven by, the abundance of cold-water copepods. This is important, because it provides researchers with a measurable indicator of northern anchovy population size.

In Chapter 3, I attempted to resolve contradictory reports of spawning timing for the northern subpopulation of northern anchovy, by determining hatch date and growth rates in three distinct developmental stages of young-of-the-year (YOY) anchovy captured in September 2006. For this study, I used otolith microstructure

analysis. I hypothesized that northern anchovy spawned earlier in the upwelling season (juveniles) would exhibit faster growth rates than those spawned in later months (late larvae and early juveniles), leading to higher probability of survival. My results confirmed protracted spawning in the northern subpopulation of northern anchovy from mid-June through early August 2006. Late-stage larvae grew quickly in their first 50 days, obtaining significantly larger sizes-at-age than juveniles. But beginning at metamorphosis from the larval to juvenile phase at 60 days (or ~35mm standard length), older fish gained more weight and grew faster than younger fish. Older juveniles also had wider mean increment widths, and higher mean and recent growth rates (0.56 and 0.78 mm/day respectively) than younger congeners, supporting my hypothesis that anchovy spawned earlier in the upwelling season have faster growth rates. This is important for the fact that the identification of ecological mechanisms that determine juvenile survival of fish can contribute to better prediction of recruitment (Campana 1996). Over time, our understanding of these mechanisms will allow us predict the consequences of environmental perturbations, like delayed upwelling. Further monitoring of YOY hatch-date and size-at-age is recommended for northern anchovy in the CCLME.

It has been proposed that biochemistry plays a role in structuring forage fish populations on decadal timescales (Litzow et al. 2006). Bottom-up oceanographic processes are thought to limit essential fatty acids (EFAs) necessary for optimal physiological functioning. In Chapter 4, I examined total lipid content and fatty acid signatures of northern anchovy and three other forage fish species common to the

CCLME, during two years of contrasting oceanographic conditions (summers of 2005 and 2006): Pacific sardine (*Sardinops sagax*), Pacific herring (*Clupea harengus pallasii*), and whitebait smelt (*Allosmerus elongatus*). I hypothesized that EFAs were limited in early summer 2005, corresponding with low forage fish densities and anomalous ocean conditions, characterized by delayed upwelling, warm SSTs, and low primary productivity. Lipid levels were lower in 2005 when compared to 2006 in all species. I confirmed lower EFA concentrations during early summer 2005, namely in the availability of eicosapentaenoic acid (EPA). Ratios of docosahexaenoic acid (DHA) to EPA provided evidence of a planktonic food web dominated by dinoflagellates in early summer 2005. Diatom-based production and higher macrozooplankton carnivory were detected (from DHA/EPA ratios and monounsaturated fatty acids, respectively) in forage fish fatty acids in 2006 compared to 2005, although forage fish densities remained low. Lipid levels were positively correlated with EPA concentrations, and negatively correlated with DHA concentrations.

The results of Chapter 4 corroborate our findings in Chapter 2 that climate-mediated, bottom-up processes influence northern anchovy population dynamics in the CCLME. Translated up the food web, this has implications for piscivorous predators in the CCLME. However, I recognize that ecological top-down processes, such as predation, may also be acting on northern anchovy, contributing to inter- and intra-annual population density variability. Continued monitoring of northern anchovy in relation to oceanographic and atmospheric environmental variables in the CCLME off

Oregon and Washington is recommended for understanding how northern anchovy are positioned and related within the trophic web. This is consistent with an EBFM approach for the CCLME.

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