

AN ABSTRACT OF THE DISSERTATION OF

Amanda May Kaltenberg for the degree of Doctor of Philosophy in Oceanography
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Title: Bio-physical Interactions of Small Pelagic Fish Schools and Zooplankton Prey in
the California Current System over Multiple Scales.

Abstract approved: _____
Kelly Benoit-Bird

Small pelagic fish represent a critical trophic link between plankton and large predators in marine upwelling ecosystems such as the California Current System. Populations of these fish are highly variable over time and are characterized by extreme fluctuations in abundance, which have significant ecosystem impacts. The causes driving this instability are not well understood, but several climactic and ecological factors have been hypothesized. This research investigated the linkages between habitat, plankton prey resources, and the abundance and behavior of small pelagic fish at various temporal and spatial scales (i.e., daily, weekly patterns of wind-driven upwelling, and seasonal) to understand how changes in physical and prey habitats influence trophic interactions. This research utilized a combination of stationary and shipboard acoustics, net sampling, and physical oceanography sampling approaches. A comparison of diel schooling behavior and zooplankton availability off Oregon and Monterey Bay, California revealed that changes in fish aggregation behaviors were caused by different timings of zooplankton availability in each region attributable to the extent of zooplankton diel vertical

migrations. An analysis of the spatial relationships of acoustic scatterers across ocean fronts caused by wind-driven coastal upwelling indicated that upwelling may lead to a spatial mismatch between small plankton prey and schooling fish that select habitat based on their preference of warmer temperatures. The temporal patterns of zooplankton and pelagic fish abundance near the Columbia River plume were identified, finding that the seasonal appearance of small pelagic fish occurred very abruptly. The timing of fish arrival was poorly correlated with zooplankton abundance but was strongly linked with temperature, salinity, and river flow. Zooplankton abundance was highly variable with very large spikes occurring with the passage of tidally-driven river fronts. This research on the ecological and environmental factors between habitat, plankton, and small pelagic fish has revealed that both the physical habitat and prey fields play an important role in determining these interactions. Variability in the trophic interaction between small pelagic fish and zooplankton over varying scales has important ecosystem consequences, including the potential availability of these prey resources to larger predators, as well as impacts for management.

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Bio-physical Interactions of Small Pelagic Fish Schools and Zooplankton Prey in the
California Current System over Multiple Scales

by
Amanda May Kaltenberg

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Dean of the Graduate School

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

Amanda May Kaltenberg, Author

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CONTRIBUTION OF AUTHORS

Dr. Kelly J. Benoit-Bird contributed to the data, analysis, and writing of all chapters. Dr. Robert Emmett contributed to the data, analysis and writing of chapter 4.

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DEDICATION

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Bio-physical Interactions of Small Pelagic Fish Schools and Zooplankton Prey in the California Current System over Multiple Scales

Chapter 1. Introduction

Small pelagic fish including sardines, anchovies, herrings, and smelts are an important intermediate trophic group in marine ecosystems, representing a link between primary producers and top predators. In the coastal regions of eastern boundary currents, where wind-driven coastal upwelling causes productivity to be generally very high, small pelagic fish are especially important for supporting a variety of predators, including larger fish, marine mammals, and seabirds. The California Current System is one the four major coastal upwelling systems of the world, where fish communities are dominated by small pelagic schooling fish. The primary species present in the California Current System are Pacific sardine *Sardinops sagax*, northern Anchovy *Engraulis mordax*, Pacific herring *Clupea pallasi*, and whitebait smelt *Allosmerus elongatus* (Brodeur et al., 2003). The distributions of these species are seasonal, as well as the abundance and distribution of their prey, with productivity typically highest during the summer months when wind-driven coastal upwelling enhances nutrient concentrations in the euphotic zone (Huyer, 1983).

Populations of small pelagic fish species are characterized by high natural variability with unstable populations (Baumgartner et al., 1992; Cury et al., 2000). Coupled with increasing intensity of fishing pressure over the past century, small pelagic fish species have undergone extreme fluctuations and population crashes. Recent studies have linked these population crashes with shifts in species composition,

with sardines and anchovies oscillating out of phase with each other (Chavez et al., 2003; Lluch-Belda et al., 1992). When shifts like these occur in multiple species simultaneously, they are referred to as regime shifts (Bakun, 2001). One example of a recent regime shift occurred when the Pacific sardine *Sardinops sagax* dominated with California Current System in the early 1900's until the population crashed in the 1950's, which was linked to intense fishing pressure. That event was also associated with a change in the Pacific Decadal Oscillation, in which conditions turned cooler than average and the abundance and range of northern anchovy *Engraulis mordax* expanded (Rodriguez-Sanchez et al., 2002). Within the past decade sardines have returned to moderately high abundances.

Mechanisms driving the ecological interactions of small pelagic species that may lead to unstable population biology are not well understood, yet have significant ecological and socio-economic impacts. Examination of the factors influencing the dynamics of behavioral and ecological interactions of small pelagic fish over a range of temporal and spatial scales is necessary to understand their role in coastal upwelling ecosystems.

One complication for understanding these small pelagic fish is that they are highly aggregative. All species of small pelagic fish are obligate schooling species, meaning they spend the majority of their lives in organized fish schools (Pitcher and Parrish, 1993). Schooling behavior in fishes provides several advantages increasing survival, including reduced predation, increased efficiency in detecting prey in a heterogeneous environment, and increased hydrodynamic efficiency when swimming

(Cushing and Harden Jones, 1968; Magurran, 1990; Pitcher and Parrish, 1993; Radakov, 1973). However, fish schools, as well as many other animal aggregations, are highly dynamic phenomena, constantly and methodically responding to environmental cues with all individuals within the group following the same patterns (Bertrand et al., 2006; Parrish and Turchin, 1997). Although schooling has been shown to increase the efficiency of the school finding a prey patch, it also increases competition for limited prey within the patch. Schooling therefore is an ecological tradeoff between the group finding food quickly, while having to share that food with everyone within the group leading to high inter-school competition. For schooling to be a successful anti-predation strategy, it must also allow for individuals to effectively obtain their required amount of prey. The abundance and distribution of prey as well as the characteristics of its patchiness are important in determining this trade-off.

Because one of the advantages of schooling is to reduce predation by visual predators, the other side of the schooling trade-off is partially controlled by the daily light cycle. The threat of predation by visual predators is highest during the daytime and lowest during nighttime low-light conditions. Therefore the typical pattern of schooling observed is fish dispersing at nighttime and reforming into organized schools as light levels increase at daytime (Radakov, 1973). Several studies have documented this schooling pattern (Azzali et al., 1985; Cardinale et al., 2003; Fréon et al., 1996; Pitcher and Parrish, 1993). However, a pattern opposite to one described solely by these trade-offs has also been observed for some schooling fish when prey availability becomes more important than the risk of predation (Bertrand et al., 2006).

Another challenge important to understanding the abundance and distribution of small pelagic fish is the factors that regulate the availability of their prey. Small pelagic fish are important grazers in these systems, feeding on large phytoplankton and mesozooplankton. Our knowledge regarding the interaction between these trophic groups is limited due to the difficulty to directly observe their behaviors and the high variability of the abundance of prey. The biomass of zooplankton prey is not uniformly distributed in time or space due to behavioral and advective influences, which may lead to varying behavioral responses by foraging fish. Diel vertical migration is a behavioral factor determining the distribution of zooplankton prey. It is nearly ubiquitous among zooplankton, reducing grazing by small pelagic fish in the surface waters during the day by migrating to depth (Hays, 2003; Lampert, 1989). This represents a challenge to predators that rely on vertically migrating animals as prey by reducing the amount of time their distributions overlap.

The distribution of prey in coastal upwelling systems is highly dynamic and driven by advection associated with wind-driven upwelling. There is strong seasonality in wind velocity in the California Current System, with winds typically from the north in the summer and from the south in the winter. Typical wind-driven upwelling conditions are manifest in the coastal hydrography as slightly decreased sea surface height, shoaling of the pycnocline, and decreased sea surface temperature near the coast (Huyer, 1983). An upwelling front develops on the continental shelf (Austin and Barth, 2002). Surface currents are typically southward, as an equatorward jet results from geostrophic balance of the upwelling pressure gradient (Kosro, 2005). Within the

upwelling season, there is a near-weekly pattern of wind variability, resulting in wind-induced upwelling events followed by brief reversals in wind direction and relaxation of these shelf upwelling conditions. These seasonal and sub-seasonal patterns of upwelling are the critical drivers of the intensity and cross-shelf distribution of primary productivity, which in turn drives the distribution and abundance of secondary productivity.

Abundance of the coastal zooplankton community in the northern California Current System is highest in the summer upwelling season (Peterson and Miller, 1977), and is dominated with northern-associated copepods in the summer and southern-associated copepods in the winter, as the source water of the alongshore current switches direction seasonally (Peterson and Miller, 1977). Zooplankton composition varies inter-annually due to events such as El Niño and La Niña (Peterson and Keister, 2002). Zonally, the zooplankton community composition is broken in distinct groups divided by the shelf break (~180 m water depth) for copepods (Morgan et al., 2003; Peterson and Keister, 2002) and euphausiids (Gómez-Gutiérrez et al., 2005), with highest abundances observed on the shelf. The species present in the northern California Current System must be adapted to living in this highly advective environment, with life history strategies adapted through ontogenetic shifts in the vertical and cross-shelf distributions (Lu et al., 2003; Peterson, 1998a). Several studies have observed euphausiid aggregation at the shelf break (Genin, 2004; Mackas et al., 1997; Simard et al., 1986), and in strong correlation with surface chlorophyll concentration (Ressler et al., 2005). Pacific hake *Merluccius productus* also tend to aggregate near the shelf break

in response to their euphausiid prey (Mackas et al., 1997). Less information is known about the effect that these upwelling fronts have on the cross-shelf distribution of zooplankton prey, and their influence on small pelagic fish distributions.

In this dissertation, I examine aspects of the interaction between small pelagic fish and zooplankton populations over scales ranging from daily to seasonal in the northern California Current System. The objective is to examine behavioral interactions between small pelagic fish predators and zooplankton prey, and to determine how these interactions are influenced by environmental variability in the upwelling ecosystem. The dissertation is organized into three data chapters examining the relationship between small pelagic fish schools and zooplankton prey at the diel, (near weekly) upwelling-event, and seasonal temporal scales. The goal is to provide a better understanding of the factors controlling small pelagic fish schooling behavior and distribution, and their role in the coastal upwelling ecosystems.

**Chapter 2: Diel behavior of sardine and anchovy schools in the
California Current System**

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ABSTRACT

Fish schools containing Pacific sardine *Sardinops sagax* and northern anchovy *Engraulis mordax* were observed in 2 regions within the California Current System in 2 years using a combination of moored and shipboard acoustics and net sampling. Schools of sardines and anchovies off the Oregon coast followed typical diel patterns consistent with antipredator behavior, dispersing at nighttime, rapidly reforming into discrete schools at sunrise, and maintaining schooling behavior throughout daylight hours. Discrete schools containing primarily sardines in Monterey Bay, California, were observed during both day and night in addition to layers and loose aggregations at nighttime, with a peak in the formation of schools occurring several hours before sunrise. Transitions between daytime and nighttime behaviors occurred more gradually in Monterey Bay than off the Oregon coast. The 2 regions experienced different prey environments, with acoustic indices for zooplankton abundance in Monterey Bay much higher than off Oregon. Due to the shallower water column, prey availability was fairly consistent throughout daytime and nighttime in Monterey Bay. However, prey availability was highly variable at the Oregon site, where diurnally migrating zooplankton were only available to fish in the surface region at night. The combined effects of prey availability and the water column depth may influence the efficiency of school formation, leading to the differences in diel patterns of schooling that were observed among the 2 regions. These environmental influences on schooling behavior likely have significant consequences for predators that rely on sardine and anchovy schools as prey as well as the commercial fisheries in both regions.

INTRODUCTION

In coastal upwelling regions, wind-driven upwelling brings nutrient-rich waters to the surface, which can support enhanced primary productivity as compared to other coastal or oceanic biomes (Huyer, 1983). In the major coastal upwelling regions of the world, small pelagic schooling fish are an ecologically and commercially important group that serves as important prey for larger fish, marine mammals, and seabirds (Brodeur et al., 2005; Emmett et al., 2005). Sardines *Sardinops* spp. and anchovies *Engraulis* spp., 2 dominant fish species in upwelling ecosystems, are generalist planktonic grazers that feed on phytoplankton, copepods, and euphausiids, and are significant consumers of both primary and secondary production (Cunha et al., 2005; Emmett et al., 2005; Lasker, 1970; Robinson, 2000).

Sardines and anchovies are obligate schoolers, meaning they spend most of their lives swimming in coherently organized schools (Breder, 1967). Fish schools, like those observed in sardines and anchovies, display synchronized and polarized behavior, making them one type of aggregated social assemblage, more generally referred to as fish shoals (Pitcher and Parrish, 1993). Schooling fish generally display a behavior of forming into dense schools during the day and dispersing at night (Azzali et al., 1985; Cardinale et al., 2003; Fréon et al., 1996; Fréon and Misund, 1999). This diel behavior is believed to be regulated by a balance between the pressures of predation and the needs of individuals to eat. Nighttime dispersal may also benefit schooling fish by decreasing predation by nocturnal predators (Radakov, 1973). Nocturnal predators that do not rely on vision for prey detection have an increased predation rate on schooling

fish when they are aggregated in schools compared to when they are dispersed (Pitcher and Parrish, 1993). Schooling may also be hindered by decreased light level at nighttime in some species that rely on vision to maintain orientation within the group. Anchovy, however, are able to maintain schooling at very low light levels (Hunter and Nicholl, 1985; O'Connell, 1963), and saithe *Pollachius virens* are able to school with no light relying solely on lateral line senses (Pitcher et al., 1976).

The specific forces driving the formation and dispersal dynamics of schools are not well understood, with a number of studies reaching contradictory results regarding the rate of school dispersal and formation at dusk and dawn. Azzalli et al., (1985) modeled the diel patterns of schooling and suggested that nighttime school dispersion is sudden while the reforming of schools at dawn is a gradual process. In situ acoustic observations of schools by Fréon et al. (1996) indicated the opposite pattern, that school dispersal at nighttime is slow, whereas the dawn reformation was rapid. Weston & Andrews (1990) also observed rapid dispersal at dusk with more gradual formation at dawn, and also found seasonal shifts in timing and speed of dispersal and formation linked to seasonal light patterns. The combined results of these previous experiments have lead to the hypothesis that the dynamics of school formation and dispersal are driven by a combination of factors that may include light, prey density, and individual fish energy requirements. For example, once individuals have eaten enough so that foraging is no longer their top priority during nighttime, individuals may rejoin a group as a refuge from predation (Radakov, 1973), assuming the low light level permits for schooling. The amount of time fish spend in aggregated or dispersed behavior during

dark hours may therefore be a function of prey density in addition to predation risk, as food availability determines how much effort must be expended for effective foraging.

The purpose of the present study was to investigate the diel patterns of pelagic fish schooling behavior by quantifying the timing and rate of school formation and dispersal relative to prey availability. The west coast of the United States is adjacent to the California Current System, an eastern boundary current driven by coastal upwelling, and supports large populations of small, pelagic schooling fish usually dominated by Pacific sardine *Sardinops sagax* and northern anchovy *Engraulis mordax*. Fishery grounds on the west coast of the United States are generally located adjacent to processing facilities. To target the areas of high ecological and commercial interest, the present study took place in 2 of these major fishery grounds, 1 near Monterey, California, and 1 off Astoria, Oregon. Continuous observations with moored and shipboard acoustics of fish schools and mesozooplankton prey provided extensive information on school behavior and prey availability. These acoustic observations were supplemented with oceanographic measurements. Data from bottom-mounted, upward-looking acoustic moorings may provide advantages over sampling from shipboard spatial survey data alone (Axenrot et al., 2004). (1) Bottom-mounted moorings are able to provide data from the depth region very near the surface that is within the blind zone of hull-mounted transducers, typically at least 3 to 5 m. A significant portion of small schools may be located entirely within this zone. (2) Potential ship-avoidance behaviors observed in other studies (Fréon and Misund, 1999; Soria et al., 1996; Vabø et al., 2002) are eliminated since moorings are mounted on the seafloor at a distance from the

targeted animals. (3) Moorings can be easily deployed and recovered from small boats that need to visit the site only once at the beginning and end of the study period, providing extended data sets that might not be possible to collect otherwise. However, stationary moorings alone cannot measure the horizontal dimension of fish schools. We have combined moored and shipboard acoustic data to investigate the temporal and spatial patterns of school behavior, providing further information on schooling behavior that would not be available by either method alone.

METHODS

Data collection

Fish schools were acoustically observed in a northern and southern region of the California Current System in 2005 and 2006 (Figure 2.1). The northern site, near the mouth of the Columbia River between the border of Oregon and Washington, was studied in August 2005 and June 2006. The Oregon and Washington coast is characterized by relatively simple topography, a narrow shelf, and a straight coastline. Wind conditions in summer are generally upwelling-favorable with brief relaxation events between upwelling and downwelling conditions (Huyer, 1983). The southern site was located in Monterey Bay, California, and was studied in July 2005 and July to August 2006. Monterey Bay is a large, shallow bay with the exception of a long, deep canyon running through the center. Commercial purse seine fishing for sardines occurs on the shallow shelf regions of the bay. Like the Oregon coast, the hydrology and circulation in Monterey Bay in the summer months (March to August) is characterized

by wind-driven upwelling conditions. Circulation within the bay is also influenced by bathymetric upwelling due to the interaction of flow and the canyon walls and the advection of cold, upwelled water from the adjacent region to the north outside of the bay (Graham and Largier, 1997; Rosenfeld et al., 1994). Local study sites within each region were selected in areas of high fish abundance based on either pre-deployment surveys or the location of high commercial fishing efforts at the time. Bottom-mounted 200 kHz bio-acoustic moorings, WCPs (Water Column Profiler, ASL Environmental Sciences), were deployed in either a straight line or a box pattern at each site (Figure 2.1). The WCPs had a 3 dB beamwidth of 10 degrees. The pulse rate and vertical bin size of WCPs were set to maximize the resolution for each study length and water depth (Table 2.1). Each WCP was attached directly to sandbag anchors so that the transducer was approximately 1 m off the seafloor with substantial floatation under the transducer to keep the instrument stable. This stability was confirmed using readings from a logging tilt and roll sensor in each instrument. No floats or lines were deployed above the instrument package to limit unintended acoustic returns and the aggregation of fish that is sometimes observed around surface floats. Recovery of each WCP was accomplished using acoustic releases that permitted the instrument package to float to the surface and be retrieved, sacrificing the sandbag anchors.

Ship-board spatial surveys were conducted both day and night in Monterey Bay and primarily during the daytime for Oregon sampling. Surveys were conducted surrounding the area of each mooring array using split-beam Simrad EK60 echosounders at 38 and 120 kHz (Table 2.2) surveying at speeds between 3 and 5 knots.

The 120 kHz transducer had a 7° conical beam and the 38 kHz transducer had a 12° conical beam. Transducers were mounted 1 m below the surface using a rigid pole-mount over the side of the R/V New Horizon in Monterey Bay in 2005 and over the side of the R/V Thomas Thompson in Monterey Bay in 2006. Transducers were mounted on a towfish that was towed approximately 1 m below the surface alongside the F/V Frosti during the Oregon 2005 and 2006 sampling. All echosounders were calibrated using an indirect procedure incorporating a 38.1 mm diameter tungsten carbide reference sphere as prescribed by Foote et al. (1987).

Daytime fish sampling was conducted by collaborators from the Northwest Fisheries Science Center during the Oregon study in 2005 and 2006 from the F/V Frosti near the WCP moorings as part of a study integrating acoustic and net trawl sampling (Brodeur, unpubl. data). A Nordic 264 rope trawl (12 m deep x 28 m wide) (Net Systems) was towed at the surface astern the vessel at 1.5 ms^{-1} for 30 min per tow. Mesh size of the net ranged from 162.6 cm at the mouth to 8.9 cm at the cod end. Abundance data of small schooling species collected from net samples taken at sampling stations within 25 km of the moorings were used for ground-truthing and interpretation of the acoustic data, more detailed results from the net tows will be presented elsewhere (Reese and Brodeur, in prep).

Fish sampling by conventional net tows was not possible in Monterey Bay. However, alternative methods were employed to provide as much quantitative information as possible on fish species composition near the study site. Commercial fishery landings in California are documented in detail in the Fish Bulletin Series of the

Division of Fish and Game of California (<http://www.dfg.ca.gov>). Monthly data for the Monterey region were used to quantify commercial landings of pelagic schooling fish species. Results of the dominant species are reported as a percentage of the total biomass of all pelagic schooling species including northern anchovy *Engraulis mordax*, Pacific herring *Clupea pallasi*, Pacific mackerel *Scomber japonicus*, jack mackerel *Trachurus symmetricus*, Chinook salmon *Oncorhynchus tshawytscha*, and Pacific sardine *Sardinops sagax*. Visual observations were also made during acoustic survey cruises of schooling fish very near the surface and in the mouths of diving seabirds and sea lions. Visual observations were made at sampling intervals of 5 min during all daytime sampling by an individual experienced with identifying fish species found in Monterey Bay. Finally, daily interviews were conducted during 2006 sampling with local purse-seine fishermen as they returned to shore. They provided daily information on the location of fishing efforts, the species caught, and the timing of their fishing efforts.

Zooplankton net tows took place during daytime and nighttime in both years of Monterey Bay sampling and for the 2006 Oregon sampling. In 2005, sampling off Oregon took place during daytime only. Samples were collected using either a 0.5 m diameter vertically towed net (200 µm mesh) from 100 m to the surface in deep water or 5 m off the bottom (when water depth was <100 m), or a Bongo Net (200 µm mesh) towed obliquely. Plankton samples were preserved in 10% buffered formalin and later counted for relative abundance measurements of each species or lowest possible taxonomic group in the lab, except during the Oregon 2006 study when Bongo plankton

samples were frozen and later thawed and immediately preserved in 10% buffered formalin before being sorted in the lab.

Local times for day and night categorizations were based on the time of sunrise and sunset provided by the US Naval Observatory database. Transition periods, within 1 h of sunrise and sunset, were not included in daytime or nighttime periods. Data on moon phase were also used and was provided by the US Naval Observatory database. Fraction of the moon's face illuminated was used to characterize nighttime illumination (i.e. 1 = full moon, 0 = new moon).

Acoustic characterization of fish schools

Data from the 38 and 120 kHz shipboard echosounders and from the stationary 200 kHz WCPs were used to characterize school behavior. Acoustical schools, characterized as acoustically unresolved multiple fish or plankton aggregations and with discrete edges (Kieser et al., 1993), are strong acoustic scattering targets with a broad frequency response observable at both 38 and 200 kHz. Acoustic schools were detected using a modified method of the schools detection module (Barange, 1994) in Echoview (Myriax software). To detect fish schools, first a minimum threshold criterion of -60 dB was applied to all data to remove low-intensity targets and noise. Then, to determine if a potential acoustical patch was a school, it needed to meet length and height criteria (if from shipboard data) or a comparable duration and height criteria (from WCP mooring data). For shipboard data, acoustic schools exceeded a minimum length of 5 m and a minimum height of 2 m. Schools that were not connected by adjacent bins but were very close to each other were considered one school if the horizontal distance separating

them was less than 6 m ('max horizontal linking distance' in Echoview) and the vertical distance was less than 3 m ('max vertical linking distance'). Finally, a potential school made up of combined linked schools was considered a positive detection if the school had a total horizontal dimension of at least 10 m ('minimum total length') and total vertical dimension of 5 m ('minimum total height'). Data from stationary WCPs represents time and depth rather than distance and depth as in shipboard data. The duration that a school can be detected in the acoustic beam depends on the size of the school and the speed of movement through the beam. To detect schools in stationary WCP data, the same vertical criteria were used as with shipboard data (minimum of 2 m), but duration was used instead of the length measurements of shipboard data for the horizontal parameters. To be classified as a school, an aggregation must have exceeded a minimum duration equivalent to 24 s, horizontal linking distance must have been less than 12 s, vertical linking distance less than 3 s, and total horizontal duration was at least 18 s and total vertical distance was at least 5 s.

These criteria settings for shipboard and stationary data were selected to include all true fish schools including small schools. Acoustic fish schools in echograms can be visually characterized as strong scattering features with discrete and continuous edges, and are distinct from dispersed aggregations of fish or layers of fish (Figure 2.2). Efforts were made to avoid false positive detections of schools in the data by visually searching through all of the detected schools in the echograms. Schools that were suspected of false positive detections such as those that did not have discrete edges were categorized as layers or loose aggregations and were not included in the analysis. Schools that had

skewness or kurtosis values significantly different from the mean (greater than the mean $\pm 95\%$ confidence interval) were excluded from the analysis. Similarly, attempts were made to include incorrectly missed schools that did not meet the automated detection criteria. Again, the acoustic echograms were visually searched for suspected missed schools. If a suspected school was consistent with the acoustic characteristics of a true fish school defined above, it was manually defined as a school region using Echoview's region tool and analyzed along with other detected schools.

Each identified school was characterized by several parameters; date and time of the school, lunar phase as percent of moon illumination for that date and location, depth of school, water column depth, skewness, kurtosis, school NASC (nautical area scattering coefficient, which is the integrated acoustic backscatter from within the school in units of $m^2 \text{ nmi}^{-2}$), school length (for schools detected from EK60 surveys), and duration of the school (for schools detected by WCPs). School length measurements were used as a description of school behavior, since school expansion generally occurs more in the horizontal plane rather than in the vertical or omnidirectional for most clupeoids (Blaxter and Hunter, 1982; Soria et al., 2003; Zwolinski et al., 2007). School length measurements were based on the start and end difference of GPS position from shipboard surveys corrected to account for beam width as suggested by Diner (2001). For schools smaller than the width of the beam, the uncorrected lengths were used since correction could lead to negative values. Similarly, duration for schools detected by the moored instruments was based on the start and end

time of each school and was corrected for changes of beam width with depth, using the following equation;

$$\text{Corrected School Duration} = (\text{time}_{\text{start}} - \text{time}_{\text{end}}) / (2 \times \text{depth mean of school} \times \tan(\theta/2))$$

Where, θ is the 3 dB beamwidth of the echosounder, which in this case was 10 degrees. The rate of school formation and dissolution were calculated based on the difference between the mean number of schools observed at one hour and the previous hour for each study.

Acoustic characterization of zooplankton

Acoustic zooplankton prey abundance was measured using mooring data from each study. Acoustic backscatter from acoustic schools as well as regions consistent with fish but not defined as schools including layers or fish aggregations were subtracted from the total signal. High intensity backscatter near the surface corresponding to air bubbles as afternoon winds picked up were observed in Monterey Bay (Holliday and Greenlaw, 2008). The signal was usually within 1 m of the surface and was subtracted from the total signal. Relative abundance data, nautical area scattering coefficient (NASC), were binned into hourly intervals and integrated over 20 m vertical depth bins. Since fish schools were primarily observed in the upper 20 m only, this upper layer was used to quantify the availability of zooplankton to fish for the Oregon site. For the Monterey Bay site, the entire water column was integrated since the water depth was near 20 m.

Hourly chlorophyll sampling took place in Monterey Bay in 2005 near the WCP mooring and in 2006 near 2 of the 4 WCP mooring stations using an autonomous bottom-up profiler (Donaghay, 2004) (Sullivan & Donaghay, unpubl. data). Chlorophyll samples were integrated from 0.5 m water depth below the surface to the seafloor (<20 m). Daytime and nighttime integrated chlorophyll samples were compared to assess the relative availability of phytoplankton prey to foraging fish.

Statistical analysis

Descriptive parameters of each school detected from shipboard surveys and acoustic moorings were analyzed using statistical analysis software (SPSS). To investigate the diel patterns of schools observed, the number of schools detected was binned into hourly counts (schools h⁻¹) based on the start time for each school. The effect of hour (h) of the day (24), site (Monterey Bay, Oregon), and year (yr) (2005 and 2006) on the number of schools h⁻¹ was tested using an ANOVA model:

$$\text{Schools h}^{-1} \sim \text{Site} + \text{yr} + \text{h}$$

The characteristics of schools were described by testing the schools h⁻¹ against the mean hourly school length (m) obtained from shipboard data, mean hourly school duration (s) from acoustic mooring data, and mean hourly school area scattering (NASC (m² nmi⁻²)) from acoustic mooring data using a generalized least squares model:

$$\text{Schools h}^{-1} \sim \text{m} + \text{s} + \text{NASC} + \text{m:s} + \text{m:NASC} + \text{s:NASC} + \text{m:s:NASC}$$

A linear regression analysis was used to test the relationship between lunar phase and schools h⁻¹ during nighttime hours for both sites and years.

RESULTS

Fish species composition

The 7 daytime fish trawls that were collected by collaborators in 2005 near the moorings showed that northern anchovy *Engraulis mordax* were numerically the most abundant species (76% of the total fish catch), followed by 16% Pacific sardine *Sardinops sagax*, and 2% Pacific herring *Clupea pallasi* (Brodeur, unpubl. data). In 2006, 7 daytime trawls near the moorings indicated that northern anchovy (45%) and Pacific sardine (46%) were the dominant species and present in nearly equal abundances.

Commercial fish landings for August and September, 2005 in Monterey Bay indicated that sardines were the dominant species, representing 85% of the total catch of pelagic schooling fish by weight. Pacific herring were second at 9%, and northern anchovy was third at 3%. Visual observations of schools at the surface and being foraged on by seabirds and sea lions, supported these landings data with the dominant fish species in Monterey Bay during 2005 sampling being Pacific sardine. Interviews with commercial purse seine fishermen targeting fish schools in the area of Monterey Bay adjacent to the moorings confirmed that they were also catching both sardines and anchovies.

In 2006 Pacific sardine was the dominant species landed in Monterey Bay in July and August at the time of this study, representing 72% of the total catch of schooling by weight. Northern anchovy was second at 26%, while Pacific herring was

third at 2%. Observations and interviews were also in agreement with landing data that Pacific sardines were dominant over Northern anchovy by about 3 to 1 numerically.

Hourly patterns of schooling

Acoustic schools consistent with sardine or anchovy schools were observed almost exclusively in the upper 20 m of the water column at the Oregon site (depth 75 to 130 m). Acoustic aggregations that were not consistent with sardine or anchovy schools based on their frequency response from shipboard data were typically observed near bottom during day and vertically migrated to the surface and dispersed at night. These schools were stronger acoustic targets at 120 kHz than 38 kHz, and likely represent krill swarms and were omitted from the analysis of fish schools. Acoustic schools of fish in Monterey Bay were observed throughout the water column (depth < 21 m). Very low differences in the mean skewness and kurtosis were observed between daytime and nighttime schools for both sites and in both years indicating that the criteria used for defining acoustic schools resulted in statistically similar schools between years and over the daily cycle. An ANOVA test for a difference in means of school skewness on data pooled into 3 categories, day, night, and transition hours, found no significant difference in school skewness ($df = 2$, sum of squares = 0.67, mean square = 0.34, $F = 0.55$, $p = 0.58$).

The frequency of schools detected (schools h^{-1}) for each hour of the day determined from acoustic moorings for each study is shown in Figure 2.3. An ANOVA for the effects of site, year, and hour on the number of schools indicated that hour of the day had a significant effect on schools h^{-1} in all 4 studies ($p < 0.001$). In Monterey Bay,

the peak number of schools was observed from 02:00 to 05:00 h local time in both years, with a secondary peak observed at 15:00 h in 2006. The hour during the peak formation of schools is based on the change in the number of schools observed from one hour to the next (Figure 2.3). The period of the greatest formation of schools was 02:00 h local time in both 2005 and 2006. The number of schools generally decreased throughout the day in 2005, while in 2006 a secondary peak in school formation was observed in the afternoon at 15:00 h and then dispersed after sunset.

The Oregon acoustic mooring sampling in 2005 observed almost no schools at night. The period of greatest school formation at 07:00 h coincided with the timing of sunrise, and the greatest period of school dispersal occurred at 21:00 h, just after sunset. In 2006 off Oregon, a similar pattern of school formation was observed, with the peak of school formation occurring the hour before sunrise at 04:00 h and declining throughout the daylight hours with a minimum between 01:00 h and 03:00 h local time. Again, relatively few fish schools were observed at night off Oregon.

To explore the diel characteristics of schools, the number of schools h^{-1} observed ($N = 24$) was tested for a correlation between the mean length (m), duration (s), and integrated backscatter (NASC) of schools using a generalized least squares model including each parameter and their interactions (Table 2.3). Schools were not observed during many nighttime hours in mooring data in Oregon, so only hours where there were enough schools observed were tested for an effect (primarily daytime hours). No significant effects of school length, duration of schools, and integrated school NASC were found on the number of schools for the Oregon observations. Schools were

highly abundant and observed during all hours in Monterey Bay in both years. A significant negative effect of mean school length was found on the number of schools h^{-1} in 2005, indicating that as more schools were observed they tended to cover less horizontal distance and when fewer schools were observed the schools were larger horizontally. School length each hour of the day from shipboard acoustic surveys in each study is shown in Figure 2.4. In 2006 in Monterey Bay, duration showed a significant negative relationship with schools h^{-1} , indicating that when a greater number of schools were observed, their duration over the moorings was shorter. The mean duration of schools from moorings in each hour of the day is shown in Figure 2.5. In Monterey Bay 2006 sampling, there was also significant interaction between duration and school NASC. The mean hourly NASC per school observed by acoustic moorings is shown in Figure 2.6 for each study.

A linear regression analysis indicated that schools h^{-1} between local sunset and sunrise was not significantly related to the moon phase in Monterey Bay ($p = 0.35$ in 2005, 0.31 in 2006). Not enough nighttime schools were observed during Oregon observations for an analysis of lunar illumination effects on schools.

The prey environment

Zooplankton from Monterey Bay was numerically dominated by copepods (Table 2.4). The most abundant genera were *Calanus*, *Ctenocalanus*, and *Acartia* (mean body length \pm SD in mm: 1.35 ± 0.27 , 0.88 ± 0.09 , and 0.95 ± 0.07 , respectively). Zooplankton off Oregon had a similar composition, dominated by copepods during daytime including *Acartia* and *Clausocalanus* (mean length in mm \pm SD: 1.23 ± 0.20

and 1.33 ± 0.23) (Table 2.4). However, nighttime samples in 2006 also included relatively many *Euphausia pacifica* (mean length 10.33 ± 6.8 mm).

Analysis of mesozooplankton abundance from acoustic mooring data revealed diel vertical migration towards the surface at night and towards the seafloor at day in both sites (Figure 2.7). The mean acoustic scattering from zooplankton was higher at night than day for all 4 studies, based on an ANOVA test to compare means between the pooled daytime and nighttime intervals with transition periods excluded ($p<0.001$). The shift between daytime and nighttime abundance in Oregon was very distinct and coincided with sunrise and sunset times (Figure 2.8). In Monterey Bay, the shift between daytime and nighttime abundance was more gradual (Figure 2.8). Assessment of the timing of the vertical migration of prey out of or into the surface waters was based on the greatest positive or negative change in zooplankton abundance from one hour to the next (Figure 2.8). In Monterey Bay in 2005, the greatest decrease of zooplankton acoustic scattering corresponding with the diel migration out of the surface waters occurred at 03:00 h local time with the greatest increase occurring at 21:00 h. In Monterey Bay in 2006, the greatest decrease in zooplankton abundance occurred twice during the morning, at 01:00 h and 05:00 h, with the ascending migration at 21:00 h. The timing and the intensity of these diel patterns of zooplankton were more distinct at the Oregon site where the water column was deeper. In 2005, the greatest decrease in zooplankton occurred at 04:00 h and peak increase occurred at 21:00 h. In Oregon in 2006, the descending migration out of the surface occurred at 05:00 h, with the ascending migration at 21:00 h.

Hourly, vertically integrated chlorophyll data was collected during Monterey Bay sampling only (Sullivan & Donaghay, unpubl. data). Binned daytime and nighttime chlorophyll data indicated a significant difference between daytime and nighttime water-column integrated chlorophyll based on a t-test, with higher concentrations observed during daytime in both years ($t= 1.97$, $p < 0.001$ for 2005; $t= 1.97$, $p < 0.001$ for 2006).

DISCUSSION

Diel patterns of schooling

Analysis of the diel patterns of fish behavior in Monterey Bay and Oregon revealed that schools dispersed and re-aggregated throughout the diel cycle at both sites, although there was variability in the timing and rates of these behaviors between sites and years. Acoustic observations of schooling at the Oregon site detected almost no schooling at night. During night hours, layers or loose fish aggregations were also not observed, and single small pelagic fish were dispersed both horizontally and vertically throughout this upper region of the water column. The formation of schools at dawn and their dispersal at dusk were rapid processes that generally took place within an hour of the local sunrise and sunset. Rapid dispersal of schooling fish beginning close to sunset has been described previously (Axenrot et al., 2004; Azzali et al., 1985; Zwolinski et al., 2007). Diel schooling in Oregon was consistent with the traditional view for obligate schoolers, in which fish schools expand at night resulting from a release of predation by visual predators (Parrish and Hamner, 1997; Radakov, 1973). During

night, while fish were highly dispersed, zooplankton abundance was several orders of magnitude higher in the upper 20 m than during the day due to the strong effect of diel vertical migrations of zooplankton.

Fish schools in Monterey Bay also displayed diel formation and dispersal with the peak in formation and the number of schools occurring 3 to 4 h before sunrise. The formation and dispersal of schools occurred more gradually in Monterey Bay than at the Oregon site. Distinct schools were often observed at nighttime, and when dispersed, fish were generally aggregated in layers or loose groups that could still be defined as aggregations but did not meet our criteria for schools. Fréon et al (1996) observed a similar pattern of sardine diel behavior, with limited dispersal of schools at night resulting in aggregations with highly skewed distributions of cross-sectional area and volume backscattering coefficient as compared to daytime schools. The number of schools observed here was linked to the average length of schools, as well as to the combined effects of length and duration in Monterey Bay in 2005, implying a change in average swimming speed as schools broke up into a greater number of smaller schools. In 2006, when more schools were detected, they tended to have shorter duration times over the moorings. Shorter duration times could be expected when observing either smaller schools or schools that are swimming at greater speeds. Our results from Monterey Bay suggest that as schools broke up into a greater number of smaller schools, they also tended to swim at faster speeds. We did not find significant relationships between the number of schools and school length or duration for the Oregon study, likely due to lack of schooling at night and the rapid transitions that

prevented gradients in these relationships from being resolved. For each hour, schools tended to be either present or absent, and average schooling characteristics such as length were fairly constant throughout daytime.

The 2 sites studied here differ substantially in water depth, which may provide an explanation for the differences observed in schooling behavior. The Oregon site was much deeper than the typical vertical range of schools, which were generally within the upper 20 m of the water column. The study site in Monterey Bay was only about 20 m, which may have restricted individuals from dispersing more vertically. We speculate that the combined effects of greater abundance of individuals in Monterey Bay and constrained water depth may have facilitated organization of individuals into schools because they were in closer proximity.

These results suggest that the availability of prey likely influenced schooling behavior. A diel pattern in zooplankton prey in Monterey Bay was observed with higher abundances at nighttime (Figure 2.8). This pattern was likely due to the migration of organisms very near the bottom and below the instrument about 1 m off the seafloor (Axenrot et al., 2004). However, the water was too shallow to allow diel vertical migrations of zooplankton to have a significant influence on the availability to fish. Fish schools were observed throughout the water column, and at times, particularly large schools were observed spanning the entire water column. So even if zooplankton vertically migrated to the bottom at the Monterey Bay site, they were likely still accessible to schooling fish in the lower portion of the water column. Diel differences were also observed in vertically integrated chlorophyll concentrations in Monterey Bay.

However, these changes were due to reverse diel vertical migrations of dinoflagellates over short distance near the surface that was typically above the vertical range of the instrument used (<3 m) (Cheriton et al., 2009). These small movements of phytoplankton could influence availability to foraging fish, especially if fish avoid the very near surface area because of high predation by seabirds.

The availability of zooplankton at the Oregon site had a much stronger diel pattern than those observed in Monterey Bay (Figure 2.8). The daytime vertical migrations to near the bottom at the Oregon site allowed zooplankton to descend out of the daytime range of fish schools, which were primarily observed in the upper 20 m. These zooplankton migrations were very distinct, with the timing corresponding to sunrise and sunset. Visual analysis of acoustic echograms indicated that most of the zooplankton biomass typically migrated to lower regions of the water column and were occasionally observed as layers.

Schooling behavior by small pelagic fish increases foraging encounters on heterogeneous prey patches (Pitcher and Parrish, 1993). However, when the water depth allows for zooplankton to avoid schooling predators by diel vertical migration out of surface waters, the foraging advantages associated with schooling may be decreased or absent. Searching by schooling fish for patches of prey that vertically migrate would be more advantageous at nighttime when their habitats overlap. Schools of South Pacific jack mackerel *Trachurus murphyi* have displayed ‘atypical’ schooling behavior, with schooling at night and dispersing during day in order to take advantage of vertically migrating mesopelagic prey during their foraging migration along the Chilean coast

(Bertrand et al., 2006). We observed only a slight diel variability in the availability of mesozooplankton prey in Monterey Bay, but schooling at night or early morning hours could provide an advantage for foraging when prey were heterogeneously distributed as observed in other studies.

Both sites observed here contained mixed-species assemblages primarily containing primarily sardines and anchovies. The proportion of each species present varied by site and year. Sardines were numerical dominant in Monterey Bay in both years. Anchovies only made up about 25% of the total small pelagic species catch in 2006 and 3% in 2005, with herring making up 9%. Trawl sampling in Oregon indicated that anchovy were relatively more common during our sampling periods, with anchovies being the dominant species in 2005, while in 2006 sardines and anchovies were present in nearly equal abundances. These differences in species composition could suggest different foraging behaviors. Forage fish are able to shift between filter feeding and particle feeding modes in different prey environments and their diets have linked with the ambient prey concentrations (Cunha et al., 2005; Garrido et al., 2008; James, 1987). Schooling fish can filter feed while swimming in schools but schooling fish have been observed dispersing and disorientating with neighboring fish when shifting to particulate feeding (Garrido et al., 2007; James and Findlay, 1989). The shift between these behaviors is initiated at different particle sizes for each species. Sardines filter feed on prey items between 4 and 724 μm and particulate feeding on prey items greater than 780 μm , while anchovies filter feeding on prey between 93 and 710 μm and particulate feed on prey greater than 720 μm in size (James and Findlay, 1989). The

relative distribution of size classes of potential prey particles were not measured in this study. However, the higher relative proportion of anchovies at the Oregon site means that in general, the fish schools observed in Oregon were capable of particle feeding on smaller items than schools observed in Monterey Bay, which would be more conducive to dispersing.

Based on our results, we speculate that schooling fish at the Oregon site followed the typical schooling behavior, with dispersal at night in a region where diel vertical migration of zooplankton limited particle feeding during the day while relying on filter feeding on small prey while in schools. During the night, foraging may depend on ambient light as vision limits particle feeding. If light is limited, these fish might rely primarily on filter feeding both day and night. However, comparison of daytime and nighttime stomach content of sardine conducted near the Oregon study site found no difference in stomach fullness and no relationship between phytoplankton abundance in the diet and chlorophyll a (chl *a*) concentrations (Emmett et al., 2005). The same study did find a seasonal and spatial effect on sardine diet composition, with inshore sardines (<150 m isobaths) consuming primarily copepods and phytoplankton, but did not investigate the diel pattern of diet composition. To confirm our hypothesis, a future study would be needed to investigate the diel patterns of forage fish diet composition simultaneously with the diel schooling behaviors to test if fish are in fact switching feeding modes when transitioning to dispersed behavior at night.

Conclusion

The sites in this study represent 2 different regions of important commercial fishing grounds for sardines and anchovies in the California Current System. Variability in schooling dynamics of these important commercial species can have significant implications for the fishery. The difference between dispersed individuals and distinct schools or aggregations determines the availability of fish to the fishery and the type of gear that will be most effective at catching them (Fréon and Misund, 1999; Parrish, 1999). The timing of fish behavior is also an important factor in capture as well as assessment for management. Sardines and anchovies are typically fished in Monterey Bay and off the Oregon and Washington coasts by purse seine operations. The sardine fishery in Astoria, Oregon, near our study site, fishes primarily during the day, relying on spotter planes to direct boats to the large schools of fish that can be observed at the surface. In Monterey Bay, the fishery on sardines and anchovies occurs during both day and night, with individual vessels making multiple trips per day. These patterns of fishing efforts are consistent with the diel patterns of schooling observed for each region.

Water column observations from stationary moorings allowed us to investigate the diel patterns of schooling behavior. The continuous observations from these moorings provided an extensive and unique data set of fish schooling behavior devoid of the effects of avoidance behaviors and a near-surface blind zone that are usually associated with ship-based surveys. By combining these temporal-based observations with spatial-based observations from ships, we were able to obtain new insight into the

diel behaviors of schools in their natural habitat. Diel patterns of schooling are dependent on several variables in addition to daylight or night conditions and prey availability may play a key role in the foraging behaviors for these pelagic fish schools.

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<u>Region</u>	<u>Year</u>	<u>Dates</u>	<u>Deployment Duration (days)</u>	<u>Number of Moorings</u>	<u>Water Depth (m)</u>	<u>Pulse Rate (Hz)</u>	<u>Vertical Bin Resolution (m)</u>
Monterey Bay	2005	Aug. 9 - Sept. 14	35	1	21	0.08	0.125
Monterey Bay	2006	July 12 - July 29	17	4	16.4, 17.8, 18.9, 20.5	0.25	0.125
Oregon	2005	Aug. 9 - Aug. 25	16	2	75, 110	0.016, 0.06	0.125
Oregon	2006	June 2 - June 7	5	4	118, 123, 125, 131	0.25	0.25

Table 2.1 WCP mooring data collection; instrument frequency 200 kHz, pulse length 156 μ s.

Table 2.2 Shipboard spatial surveys data collection; instrument frequencies 38/120 kHz, pulse lengths 256/64 µs, respectively.

<u>Region</u>	<u>Year</u>	<u>Dates</u>	<u>Ship</u>
Monterey Bay	2005	Aug. 20 - Sept. 8	R/V New Horizon
Monterey Bay	2006	July 11 – Aug. 9	R/V Thomas Thompson
Oregon	2005	Aug. 23 - Aug. 26	F/V Frosti
Oregon	2006	June 2 - June 7	F/V Frosti

	Oregon				Monterey Bay			
	2005		2006		2005		2006	
	df = 6	df = 17	df = 24	df = 24				
	<u>Coeffiecient</u>	<u>p-value</u>	<u>Coeffiecient</u>	<u>p-value</u>	<u>Coeffiecient</u>	<u>p-value</u>	<u>Coeffiecient</u>	<u>p-value</u>
(Intercept)	1.71	0.40	0.11	0.98	2.23	0.08	5.79	0.02*
Length	-0.03	0.43	-0.01	0.96	-0.19	0.02*	-0.15	0.52
Duration	0.00	0.39	0.00	0.99	0.00	0.64	-0.06	0.01*
NASC	0.00	0.83	0.01	0.68	-0.01	0.26	-0.02	0.07
Length:Duration	0.00	0.63	0.00	0.98	0.00	0.03*	0.00	0.39
Length:NASC	-	-	0.00	0.98	0.00	0.12	0.00	0.77
Duration:NASC	-	-	0.00	0.73	0.00	0.53	0.00	0.03*
Length:Duration: NASC	-	-	0.00	0.94	0.00	0.09	0.00	0.67

Table 2.3 Summary of a generalized least squares test for effects on the number of schools h^{-1} observed during each study. School length was measured from shipboard surveys. Duration and school NASC were measured from acoustic moorings. Significant test results are marked *, (df = degrees of freedom). Schools were not detected during several nighttime hours during Oregon sampling, limiting the degrees of freedom to hours when schools were detected.

	<u>OR2005</u>	<u>OR2006</u> N = 11 (6) *Bongo Net	<u>MB2005</u> N = 8 (13)	<u>MB2006</u> N=10 (2)
Calanoid Copepods				
Acartia	980.4 (--)	99.2 (78.8)	19.0 (126.3)	17.4 (3.6)
Calanus	51.3 (--)	391.1 (352.3)	58.4 (1.9)	262.6 (110.5)
Clausocalanus		98.1 (159.7)	2.2 (0.64)	263.5 (758.8)
Psuedocalanus	189.1 (--)		2.1 (108.8)	
Augaptilidae	10.0 (--)			
juvenile calanoid copepods	955.2 (--)	17.9 (1.8)	125.4 (105.4)	43.5 (534.2)
Total Calanoid Copepods	2427.7 (--)	608.7 (593.8)	132.5 (364.6)	587 (1411.5)
Cyclopodia Copepods				
Oithonia	615.3 (--)	1.9 (1.2)	18.7 (3.6)	67.6 (76.1)
Total Cyclopodia Copepods	615.3 (--)	1.9 (1.2)	19.4 (6.4)	67.6 (76.1)
Poecilostomatoida				
Copilia			9.8 (0)	
Corycaeus		1.1 (0.7)	0 (11.6)	0.2
Total Poecilostomatoida		1.1 (0.7)	9.8 (11.6)	0.2 (0)
Cladocerans				
Total Cladocerans		2.6 (4.2)	0 (6.2)	113.5 (159.3)

Table 2.4 Results of mesozooplankton sampling. Densities, in Individuals m⁻³, are shown for day samples, with night samples in parentheses.

	<u>OR2005</u>	<u>OR2006</u>	<u>MB2005</u>	<u>MB2006</u>
Euphausiia				
Euphausia Pacifica				
- adult		12.0 (15.1)		
Euphausia pacifica				
- juvenile	103.9 (--)	24.2 (56.7)		6.3 (37.1)
Thysanoessa spinifera				
-juvenile	23.2 (--)			
Total Euphusia	127.1 (--)	36.2 (71.9)	36.0 (29.5)	6.3 (37.1)
Chaetognatha				
Total Chaetognatha	3.3 (--)	2.6 (1.5)	0.25 (13.6)	2.8 (1.8)
Crab zoea				
Total Crab Zoea		0 (0.1)	33.7 (6.6)	
Appendicularia				
Total Appendicularia		0.2 (0.4)	5.3 (116.3)	26 (89.6)
Calycophoran siphonophore				
Total Siphonophore			27.1 (24.3)	7 (51.6)
Pteropods				
Total Pteropods		55.0 (62.1)	0.6 (1.4)	0.3 (0.9)

Table 2.4 (Continued)

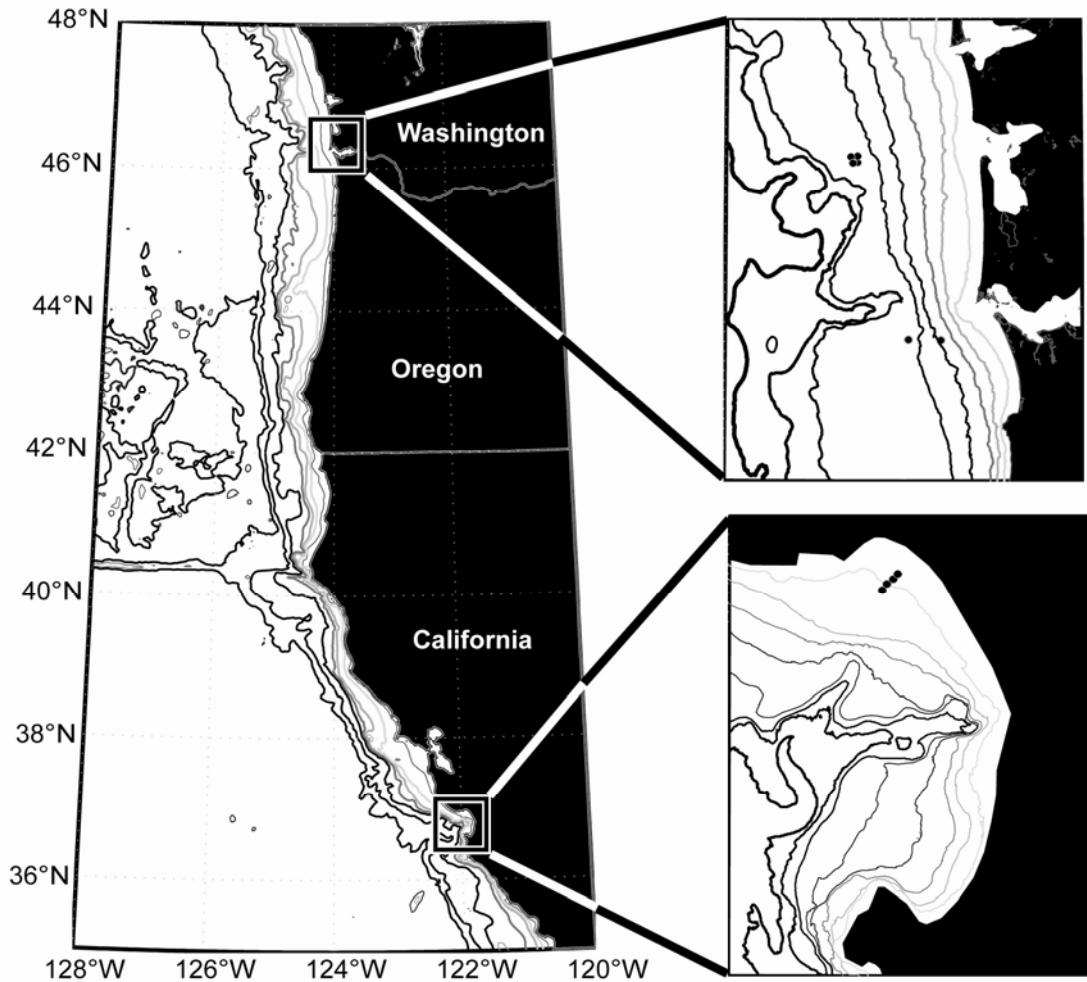


Figure 2.1 The two study regions in the California Current Systems showing the 50, 100, 200, 500, 1000, 2000, and 5000 m isobaths. Inset maps of the Oregon and Monterey Bay study regions show the placement of acoustic moorings (●), and the 20, 40, 60, 80, 100, 200, 500, 1000, and 2000 m isobaths.

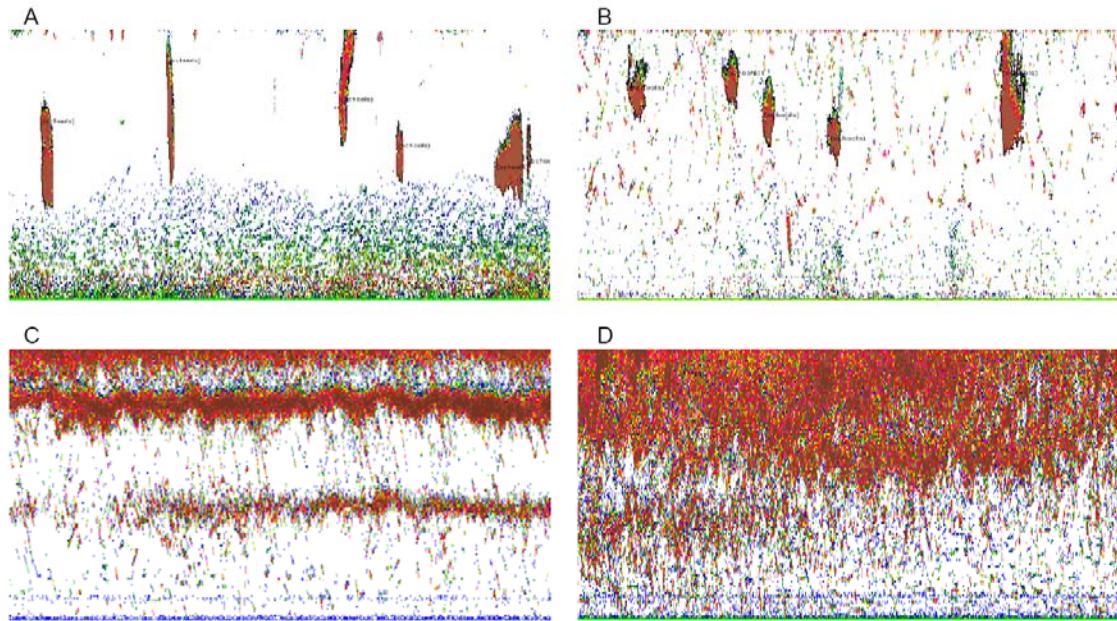


Figure 2.2 Echograms of fish behavior. Each panel represents 1 hour of time (x-axis) for data collected from WCP acoustic moorings in Monterey Bay over the water column depth of 20 m (y-axis). (A) Daytime fish schools (this example was observed from local time 11:00 to 12:00). (B) Nighttime fish schools (02:00 to 03:00). (C) Layered fish behavior (22:00 to 23:00), and (D) dispersed aggregation of fish (23:00 to 00:00).

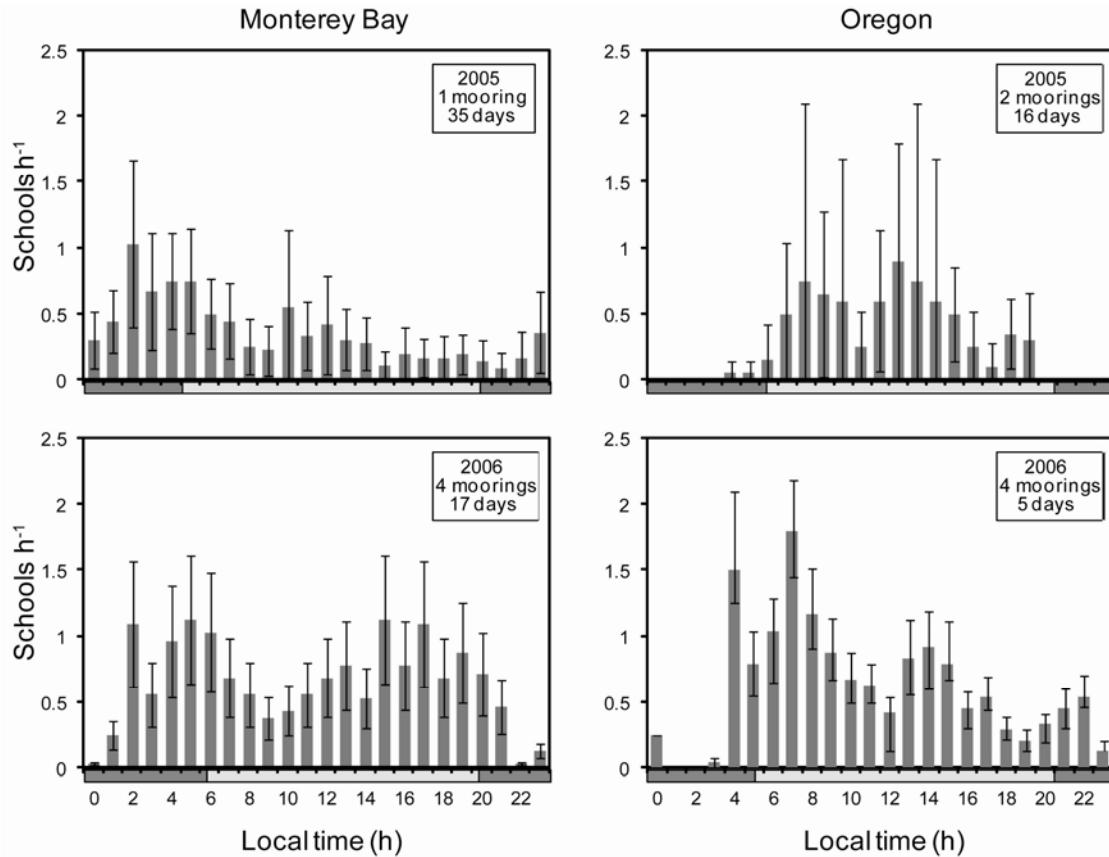


Figure 2.3 Mean schools h^{-1} detected during each study $\pm 95\%$ confidence interval. Local sunrise and sunset times are indicated by the black/gray bar on the x-axis.

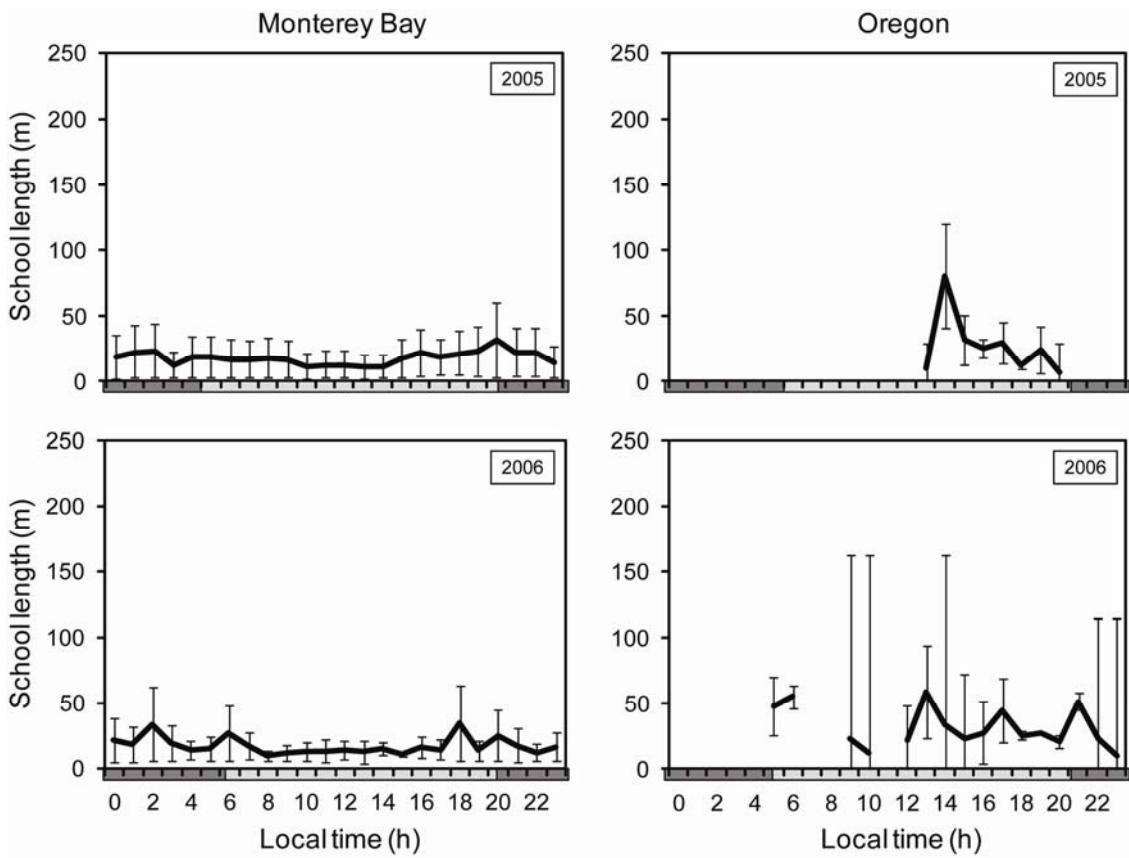


Figure 2.4 Mean school length $\pm 95\%$ confidence interval collected from shipboard spatial surveys. Sunrise and sunset times are indicated by the black/gray bar along the x-axis.

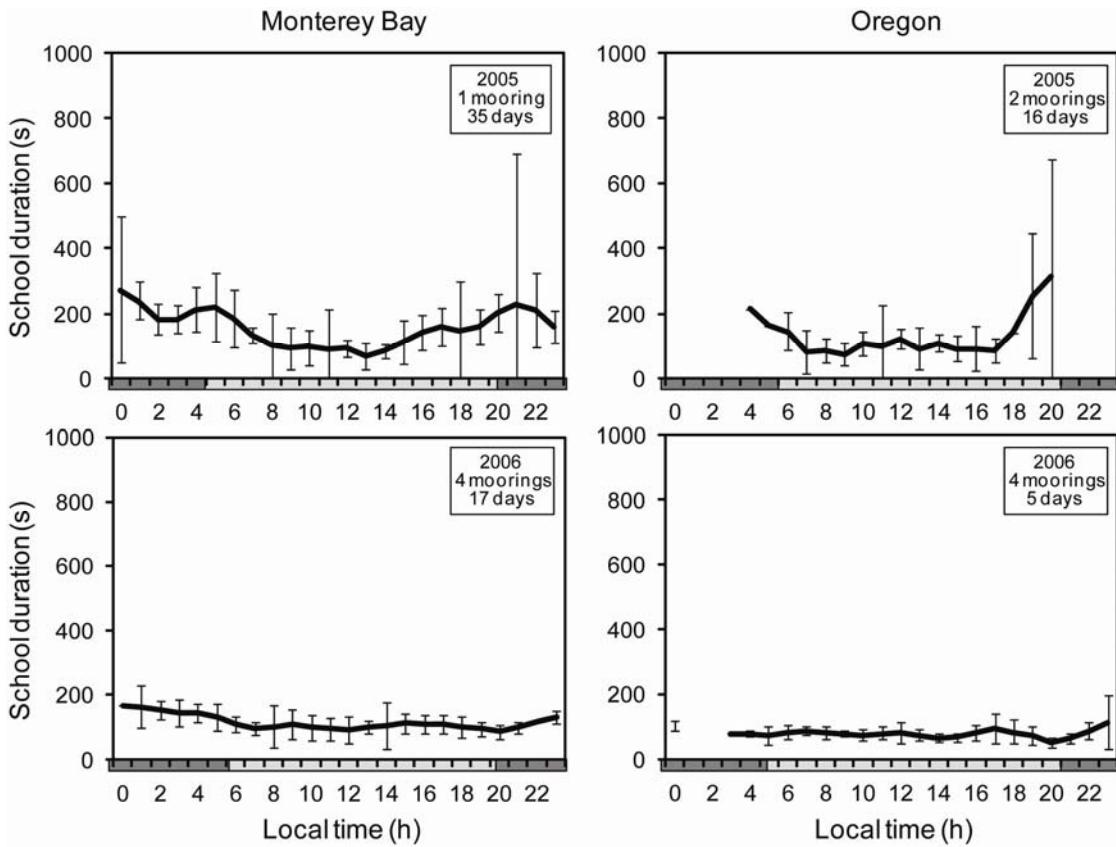


Figure 2.5 Mean school duration (s) detected over stationary moorings $\pm 95\%$ confidence interval. Duration calculations were corrected for changes of beam diameter with depth. Sunrise and sunset times are indicated by the black/gray bar along the x-axis.

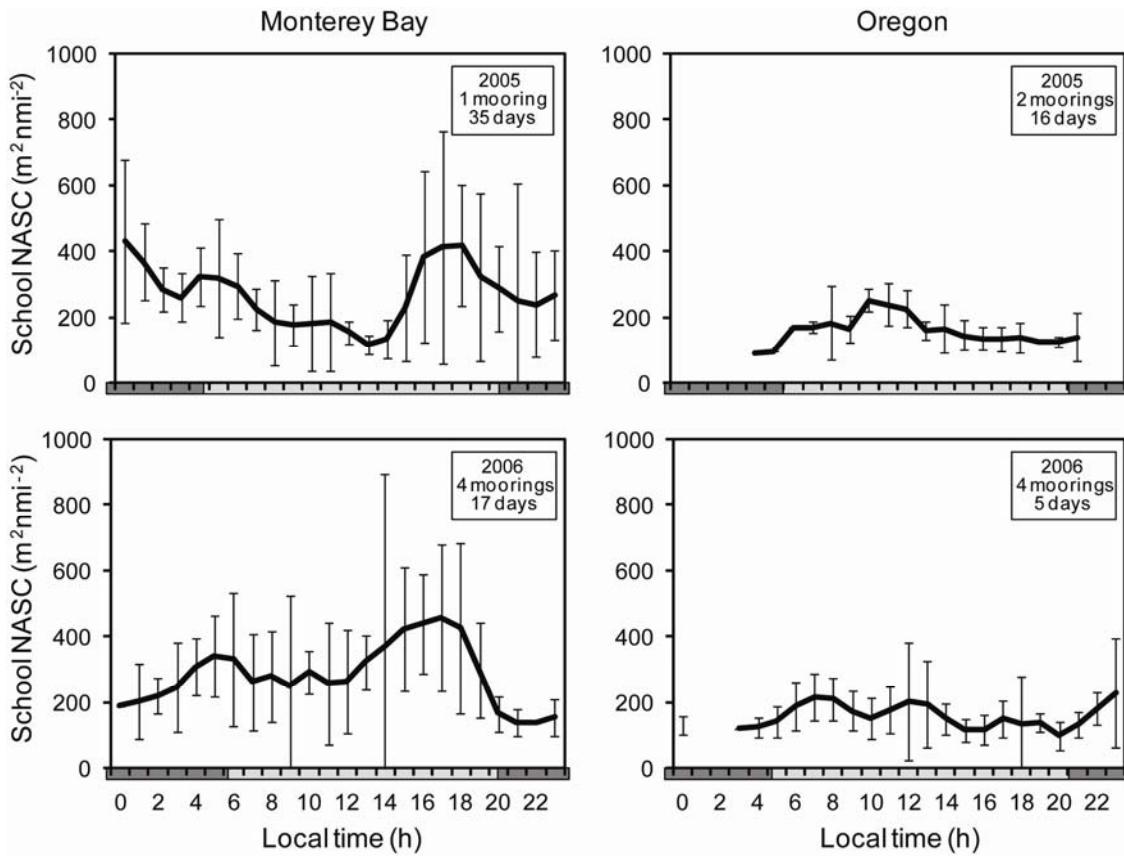


Figure 2.6 Mean school nautical area scattering coefficient (NASC) $\pm 95\%$ confidence interval. Local sunrise and sunset times are indicated by the black/gray bar on the x-axis.

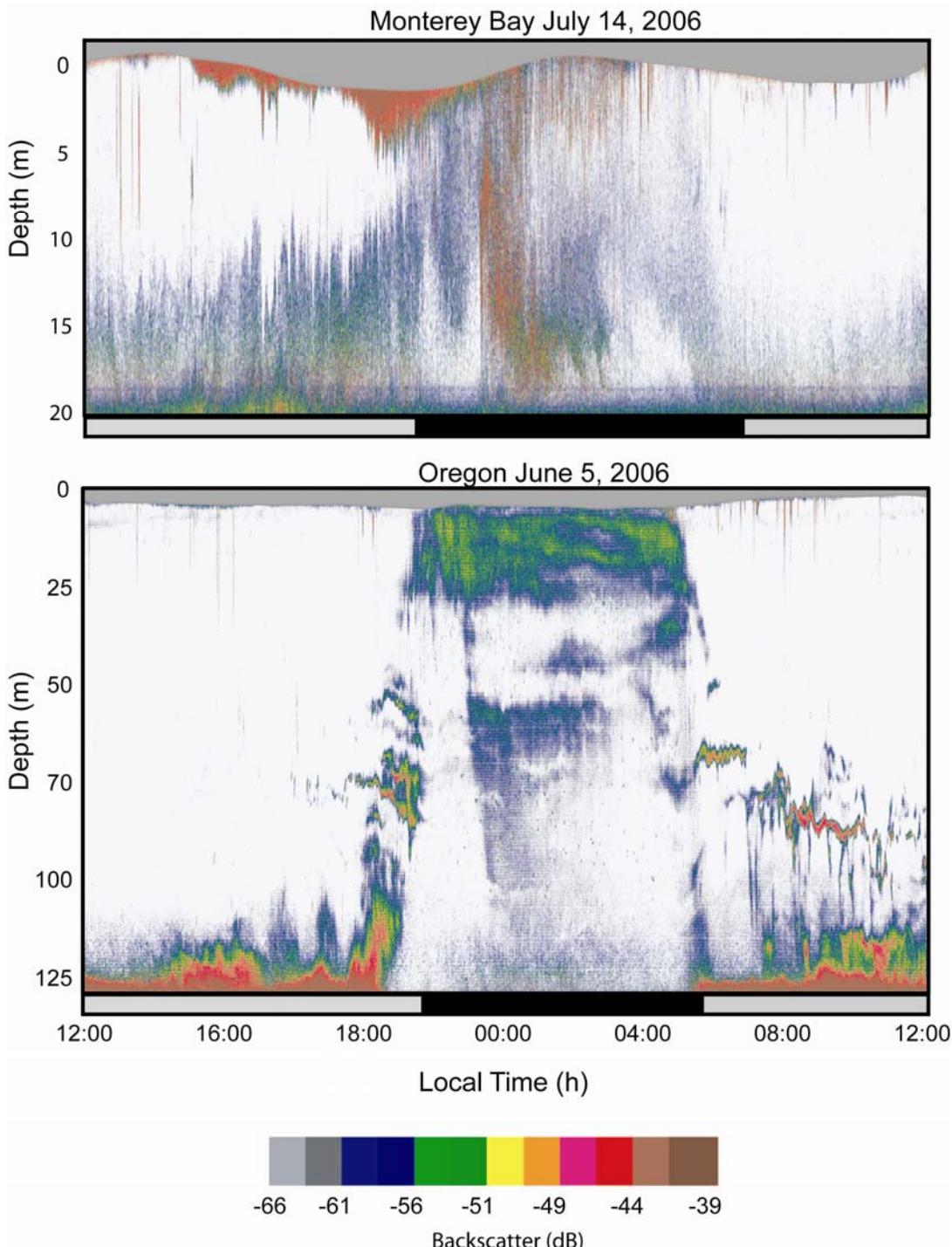


Figure 2.7 Representative daily echogram of acoustic backscatter from WCP moorings for each study site. Note the different y-axes indicating different water depths. Sunrise and sunset times are indicated by the black/gray bar along the x-axis.

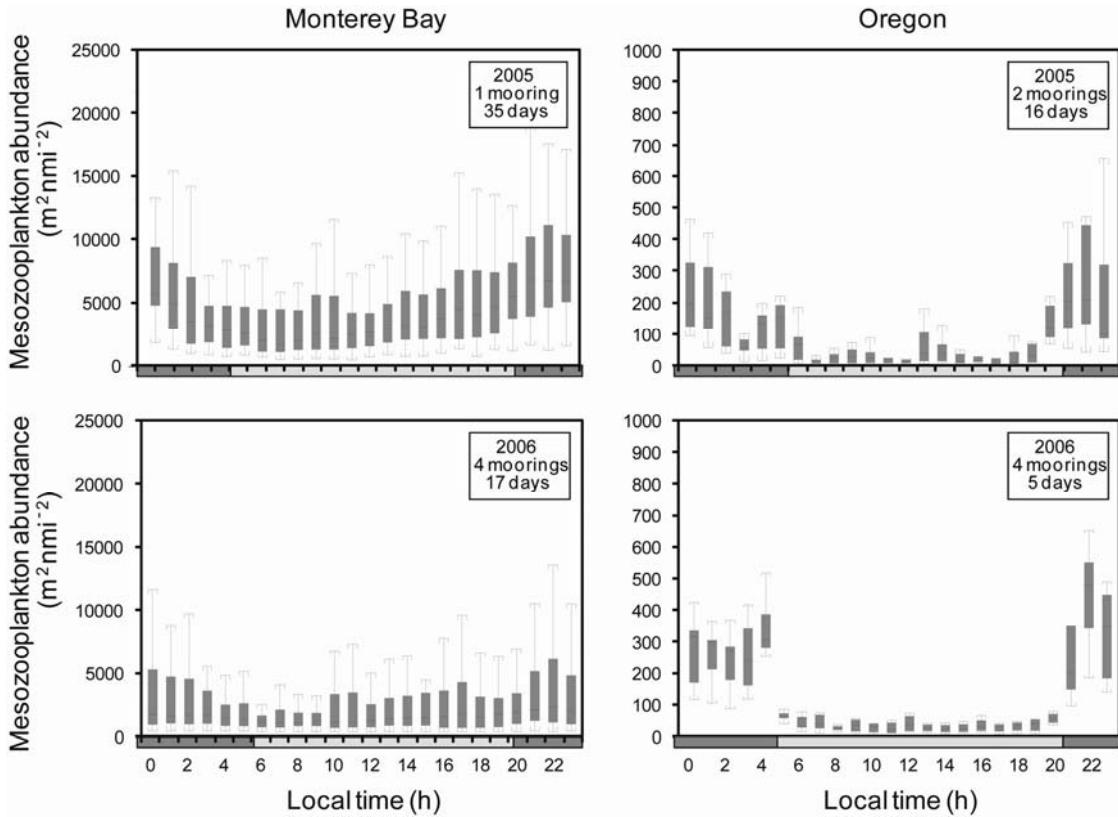


Figure 2.8 Mesozooplankton abundance (NASC) in the upper 20 m of the water column for each study $\pm 95\%$ confidence interval.

**Chapter 3: Mismatched zooplankton and pelagic schooling fish distributions
caused by temperature effects of a coastal upwelling front and bathymetry**

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ABSTRACT

Cross-shelf bio-acoustic scattering in the northern California Current System off Oregon was sampled using ship-board split-beam echosounders at 38, 120, 200 kHz to determine the relationship of backscatter to coastal upwelling fronts and seafloor bathymetry. Acoustic sampling was conducted across a developing upwelling front between August 23 and September 2, 2008, concurrently with underway flowthrough CTD and acoustic Doppler current profiler measurements to determine the distance of acoustical aggregations to upwelling fronts. Over the course of the study, conditions shifted from downwelling-favorable winds to strong upwelling-favorable winds, which had a significant effect on the shelf distributions of zooplankton and pelagic schooling fish. Acoustic scattering at 200 kHz, associated with small zooplankton, accumulated in the upwelling plume within 5 km of the front, while no front effect was found on larger zooplanktonic scatterers at 120 kHz, which were consistently aggregated at approximately 120 to 150 m water depth. As the plume developed, the pelagic schooling fish community responded by moving further offshore, away from the accumulation of prey at the front, maintaining their position where sea surface temperatures were between 14.9 and 15.6°C, higher than the temperatures associated with the fronts at 14.0 to 14.14°C. This behavioral response of moving to deeper, warmer waters as the upwelling plume developed created a spatial mismatch between fish schools and zooplankton aggregations observed in high abundance near upwelling fronts.

INTRODUCTION

Pelagic organisms are non-uniformly distributed in space and time (Haury et al., 1978) and only organisms overlapping in their spatial and temporal distributions can trophically interact. In the ocean, circulation patterns create a heterogeneous environment where regions of divergence often provide enhanced primary productivity resulting from localized upwelling of deep, nutrient-rich waters into the euphotic zone. These regions may attract a variety of large predators, creating biological hotspots (Reese and Brodeur, 2006; Sydeman et al., 2006a). In contrast, convergent regions between water masses are associated with downwelling of surface waters, low nutrient concentrations, and low primary productivity. However, when coupled with the vertical migrations of some zooplanktonic species, these confluence regions may serve as a mechanism to retain buoyant or swimming particles (Franks, 1992; Genin et al., 2005; Morgan et al., 2005). As a result, confluence regions formed at oceanic fronts are also often associated with increased biovolumes of zooplankton relative to surrounding waters, attracting larger predators to these regions as well.

Ocean fronts are manifest in a variety of hydrographic properties over space as sharp gradients in temperature, salinity, density, chlorophyll, velocity, or turbidity (Belkin et al., 2009). Several physical mechanisms exist for the creation of fronts in the coastal ocean such as the boundaries between major ocean currents, mesoscale eddies, tidal mixing, riverine plumes, and wind-driven coastal upwelling. The biological response to these features depends on their persistence and the sharpness of the hydrographic gradient. River fronts are an example where very sharp gradients are

observed in hydrography, with high contrasting salinity and turbidity making them easily detected and are often visible at the surface. Recent studies in the northern California Current System have described the accumulation of plankton at river fronts (Morgan et al., 2005; Peterson and Peterson, 2008) and shown the potential of river fronts to serve as a mechanism for the cross-shelf transport of passive or diel vertically migrating zooplankton (Peterson and Peterson, 2009).

Wind-driven coastal upwelling creates an along-shore upwelling front driven by wind shear at the ocean-atmosphere interface. The near-shore surface region is characterized by cold, nutrient-rich waters, advected offshore by Ekman transport, while an equatorward jet forms in geostrophic balance. The position of the front is determined by seasonal evolution and a flow-topography interaction (Barth et al., 2005). Coastal upwelling regions are characterized by decreased surface temperatures, high salinity and density waters, and shoaling of the pycnocline and thermocline depths (Huyer, 1983). When sustained upwelling conditions persist and this nutrient-rich water continues to enter the euphotic zone, primary productivity increases and phytoplankton biomass accumulates. The more time that upwelling winds persist, the greater this enhancement of primary production and greater chance for these effects to transfer to higher trophic levels either in secondary production or as a behavioral attraction to regions of increased food availability.

Plankton-feeding pelagic schooling fish are an important component of these highly productive upwelling systems, supporting a variety of large predators as well as commercial fisheries. These fish, which include sardines, anchovies, herring, and

smelts, are opportunistic grazers, feeding on both phytoplankton and zooplankton (Blaxter and Hunter, 1982; Emmett et al., 2005; Lasker, 1970). Distributions of pelagic fish schools are seasonal, with ranges expanding in response to temperature during the summer upwelling season when prey availability is high (Emmett et al., 2006; Kaltenberg et al., in Review).

Enhancement of the zooplankton prey of these schooling fish in response to upwelling fronts can occur either through increases in production at the front, retention of particles, or through behavioral attraction of zooplankton to regions of increased food availability (Belkin et al., 2009; Franks, 1992). Large zooplankton (i.e., adult euphausiids) are diel vertical migrators that travel from the surface at night to deep waters during the day. However, horizontal current velocities are typically much stronger than zooplankton swimming speed, leaving the horizontal distribution patterns driven by advection. Zooplankton may be able to maintain their horizontal position at a favorable prey environment by taking advantage of contrasting current directions at different depths (Genin et al., 2005). Small zooplankton (i.e., juvenile euphausiids, copepods, etc.) may make vertical migrations over shorter vertical extents, so their horizontal distribution patterns are subject to a greater influence by surface layer advection.

The objective of this study was to characterize the cross-shelf distribution of acoustic scatterers in the coastal ocean during the wind-driven upwelling season to determine the influence of an upwelling front and seafloor bathymetry on the distribution of various sizes of acoustic scatterers. This approach provides a better

understanding of the role of upwelling fronts on the trophic interaction between zooplankton scatterers and small pelagic fish.

METHODS

Front detection

Shipboard hydrographic sampling took place from 26 August to 2 September, 2008 on the R/V Wecoma using a flow-through conductivity, temperature, depth sampling system. Water from 3.5 m below the surface was sampled for conductivity, temperature, and fluorescence at a rate of 0.5 Hz. Density was calculated from temperature and salinity using the equation of state for seawater (Poisson et al., 1980), and a 2-minute running average filter was applied to the data. A 600 kHz acoustic Doppler current profiler (ADCP) was used to determine the east-west and north-south components of current velocity from just below the instrument to the seafloor.

Sampling was conducted during 26 transects taking place along cross-shelf or zig-zag lines between 44°N and 45°N, primarily centered along the Newport Hydrographic Line (44.6°N), between the 40 m and 300 m isobaths (Figure 3.1). Individual transects lasted between 3 and 6 hours and were categorized into daytime, nighttime, or transition periods (within 1 hour before or after sunrise and sunset times), based on the local sunset and sunrise times obtained from the US Naval Observatory database.

Upwelling fronts were identified using hydrographic data from the shipboard flow-through CTD. A positive front detection was identified if the difference in density

was greater than 0.1 kg m^{-3} over 1 km traveled. ADCP data was used to verify the locations of the upwelling fronts, which were usually visible as a shift in the current velocity field and to determine the depth of the frontal influence (Figure 3.2). For transects containing a front, the distance to the front for all points along each transect was calculated so that all locations inshore of the front had negative values and locations offshore of the front had positive distances.

Bio-acoustic sampling

A Simrad split-beam EK60 system (operating at 38, 120, and 200 kHz) acoustically sampled the water column during cross-shelf hydrographic transect surveys. The transducers were mounted 1.5 m below the surface over the port side of the ship using a rigid pole-mount. The 38 kHz transducer had a 12° conical split beam while the 120 kHz and 200 kHz transducers each had a 7° conical split beam. All three frequencies used a pulse length of 256 μs . Each transducer was calibrated before sampling began using a 38.1 mm diameter tungsten carbide reference sphere following the procedure suggested by Foote et al. (1987). Surveys took place both daytime and nighttime, sampling along cross-shelf transects at ship speeds from 1.5 to 2.5 m s^{-1} (approximately 3 to 5 knots). Transects including transition periods (within one hour before and after the local sunrise or sunset times) were not used due to the high variance in abundance as organisms changed position during their diel vertical migrations.

Acoustic data were analyzed using Echoview software (Myriax). Schooling fish were detected using the 38 kHz data by a combination of Echoview's school detection module and visual scrutiny (Kaltenberg & Benoit-Bird, 2009). Data for all three

frequencies after fish schools were removed was resampled using 0.5 m vertical bins and 6-second time bins. This resampling helped to reduce noise in the data while preserving the biological signal. Processed data at each frequency was then binned into 500 m horizontal bins along the ship transect and integrated from 10 m from the surface to the minimum of either 3 m above the bottom or 100 m when the water depth was greater than 100 m.

Ancillary Data

Oceanographic data was obtained from the National Data Buoy Center (NDBC) for station 46050 located at 20 nmi from shore along the Newport Line (44.64°N, 124.50°W) (Figure 3.1). Data used included sea surface temperature, sea surface salinity, and wind velocity. These oceanographic data were smoothed using a 24-hr running average filter. The north-south wind velocity component was used to characterize the influence of upwelling-favorable conditions preceding sampling and during the sampling cruise.

Daily composite sea surface temperature data was obtained from the Advanced Very-High Resolution Radiometer satellite provided by NOAA. These data had a spatial resolution of 1.25 km. Daily sea surface temperature maps were used to further help identify the location and type of fronts detected by the shipboard data.

Data Analysis

To distinguish between the effects of hydrographic fronts and potential accumulations associated with particular depths, the biomass of acoustic scatterers was visually compared to the bottom depth using the nautical area scattering coefficient

(NASC, in $\text{m}^2 \text{nmi}^{-2}$) at each frequency, a proxy measure for biomass of a given size class. Only transects that did not contain a sharp surface gradient in hydrographic characteristics were used in order to distinguish between accumulation at depth and accumulation at sharp gradients. Transects containing sharp gradients associated with hydrographic fronts were not included to avoid biases in biomass distribution not caused by bottom depth, and daytime transects were not used because most transects conducted during daytime were in areas with bottom depths less than 100 m.

Analysis of the distribution of acoustic biomass in relation to sharp surface gradients at upwelling hydrographic fronts was conducted. NASC for 10 km centered around the sharpest gradient (i.e., at the front) was used to determine the distribution of biomass in relation to the front. In order to use both daytime and nighttime transects, acoustic abundance was normalized by scaling NASC as a percentage of the maximum observed along the 10-km portion of the transect.

RESULTS

Hydrographic conditions

The sampling period coincided with the spin-up of upwelling conditions, marked by a reversal of wind velocity that shifted from downwelling-favorable (southerly), conditions to increasingly upwelling-favorable (northerly) winds (Figure 3.3). An associated response of the sea surface temperature was evident from data collected at the NDBC buoy as well as from satellite data (Figure 3.3). Sea surface temperature at the buoy decreased from approximately 16°C at the start of the study to

approximately 12°C by the end of the study. During this time, a front associated with the upwelling plume developed and began to travel offshore as it evolved (Figure 3.3).

Of the 26 cross-shelf transects sampled, 9 transects contained a front crossing. Most of these front crossings occurred over the second half of the cruise, as the front developed and began to move offshore, and all of these front crossings occurred at water depths less than 100 m (Figure 3.4).

Distribution of acoustic scatters in relation to bathymetry and fronts

Transects took place over bottom depths ranging from 40 m to 300 m. The highest acoustic backscatter intensities integrated through the water column (NASC) were observed at 200 kHz, with the lowest at 38 kHz (Figure 3.4). For transects that did not cross a front (e.g. those that occurred during the first half of the cruise), a peak in NASC was observed at 120 and 200 kHz between 120 m and 150 m water depth (Figure 3.4). No clear peak was present at 38 kHz (with schools removed from the signal) with respect to bottom depth (Figure 3.4), but some localized clusters of relatively higher abundances were observed at roughly 50 m, 100 m, and 140 m water depth.

A peak in 200 kHz NASC occurred on the inshore side of each front (negative distance values) at a distance of approximately 1000 m from the front (Figure 3.5). There was no effect of distance to each front on NASC at 120 and 38 kHz (Figure 3.5).

Distribution of pelagic schooling fish

Over all sampling transects, pelagic fish schools showed a strong preference towards water depths less than 100 m (Figure 3.6), based on a t-test for a difference in means between depth over all transects and the depth where schools were found

($p<0.001$, d.f.=2521). The mean depth of the location of schools occurred at 51.0 m (95% Confidence Interval = 44.6 to 52.9) with the mean depth of all transects at 92.1 m (95% Confidence Interval = 85.7 to 93.8). Note that a higher proportion of schools were observed over the first half of the study period than the second half.

Of the 9 transects (3 daytime, 2 nighttime, 4 transition) that crossed a hydrographic front, only 1 of those (13%) (a transition period transect), contained pelagic fish schools in the region near the front (within 5 km). Of the 16 transects not containing a front, 11 (69%) contained pelagic fish schools (primarily those conducted during the daytime), indicating that fish schools were not found preferentially near fronts. In fact, along transects with fronts, almost all schools (95%) were located on the offshore side of the front and at large distances from the front edge, with only 1 school found within the upwelling plume and 2 schools within 5 km of the front (Figure 3.6).

Schooling fish observed over all transects showed preferential selection for temperature based on a one-way ANOVA test for difference in mean temperature across all transects, the locations of fish schools, and the region within 5 km of hydrographic fronts ($F=345.6$, d.f.= 2, $p<0.001$). Fish school distributions occurred over a much narrower range of temperatures than was sampled during all transects, and occurred primarily in only the warmest temperatures sampled (Figure 3.7). The mean temperature over all transects was 14.6°C, while the mean temperature within 5 km of hydrographic fronts was 14.1°C (Table 3.1). The mean temperature observed at the locations of fish schools was 15.2°C, significantly lower than the temperatures over all transects as well as the temperature at fronts (Table 3.1).

There was no significant correlation between fish school abundance and chlorophyll fluorescence from ship-board flow-through CTD, indicating that fish were not selecting for habitat based on chlorophyll (t-test for difference in means, p-value=0.9).

DISCUSSION

The multi-frequency acoustic methods used in this study provided high-resolution sampling of the spatial distributions of acoustic scatterers across an evolving upwelling front. The sampling period aligned with a transition event marked by a shift from downwelling wind conditions to very strong upwelling-favorable conditions. This timing made it possible to test the influence of a developing front on the distributions of zooplankton and pelagic schooling fish. Across transects that did not cross a front, water column-integrated acoustic scatterers at 200 and 120 kHz were aggregated at between 120 and 150 m water depth. This depth was shallower than the typical depth of zooplankton aggregations often observed at the shelf break, defined between 180 and 200 m (Mackas et al., 1997; Ressler et al., 2005; Simard and Mackas, 1989).

Accumulation of acoustic scattering across a developing upwelling front was observed at 200 kHz, the highest sampling frequency used. The front was characterized by strong gradients in several hydrographic parameters, and was occasionally visible from the deck of the ship. Although net sampling was not conducted, high scattering at 200 kHz is consistent with small zooplankton (i.e. copepods, juvenile euphausiids, etc). Enhanced scattering across the front was not observed at 120 kHz or 38 kHz,

frequencies that are associated with larger zooplankton (i.e. adult euphausiids) and fish. This difference in the influence of the front across frequencies likely indicates accumulation of the smallest-sized organisms with poor swimming abilities and diel vertical migrations that may contribute to their accumulation at fronts (Franks, 1992). Larger zooplankton (i.e. adult euphausiids) that are typically highest acoustic scatterers at 120 kHz have greater swimming capabilities with diel vertical migrations taking place throughout the entire water column, which may prevent them from accumulating at the front. Migration through the upwelling plume to deeper waters in this case would mean that they also occupy environment with flow characteristics different from the surface (upper 15 m) (based on current velocity data, Figure 3.2), which would further create separation from the front.

Pelagic fish schools detected at 38 kHz showed a preference for water depths less than 100 m, significantly shallower than all depths sampled (40 to 300 m). Although this depth preference spatially overlapped with the range of depths that fronts were observed, it did not overlap temporally with fish distributions shifting as the front developed and was pushed offshore. A higher proportion of the total schools detected occurred early in the sampling cruise before the upwelling of cold waters was detected at the surface. Only a few schools were observed by the end of the cruise and these schools occurred only at relatively large distances from the front. The pattern of school distributions observed could be explained solely by their preferential selection for temperatures warmer than those observed at fronts or the temperature within 5 km of the front, the likely range of influence for frontal accumulation of small scatterers based

on the accumulation effect observed at 200 kHz. As the plume developed and covered more of the shelf, schools likely migrated to follow the warmer surface waters located in waters deeper than the primary area sampled. Other than 2 outliers, all pelagic schools were observed at sea surface temperatures between 15°C and 16°C (Figure 3.7).

This study provides evidence for a significant effect of coastal upwelling fronts on the cross-shelf distributions of the pelagic community that temporally varies over a scale of days to weeks and is driven by local winds. These results showed that the combined effects of bathymetry preference and upwelling front may at least temporarily create a spatial mismatch in the distributions of pelagic schooling fish and small zooplankton that may serve as their prey, which are influenced by localized accumulation at hydrographic fronts. In this case, the avoidance or failure to utilize this region of enhanced prey caused by the preferential selection by pelagic fish schools for temperatures warmer than those observed within the upwelling plume or the adjacent region suggests that fish distributions are limited by the cold temperatures of upwelling plumes. Temporary decoupling of predator-prey interactions has important ecosystem consequences. Pelagic schooling fish species are efficient grazers, able to take advantage of a variety of prey types as they become available, including large phytoplankton and small zooplankton. However, accumulation of prey that cannot be grazed by these fish because of environmental conditions may lead to increased export from the pelagic environment or an increase in prey availability to alternative predators.

This result has important implications for understanding the role of small pelagic fish in upwelling ecosystems as well as the dynamics of zooplankton prey

availability. The near-shore region influenced by coastal upwelling plumes off Oregon in the summertime is regularly below 15°C, which may mean that the avoidance of these regions by small pelagic fish as observed in this study could be fairly common. Avoidance of upwelling fronts and offshore displacement from surface upwelling plumes by pelagic fish schools likely impacts the predators that depend on these fish as prey, including larger fish, seabirds, and marine mammals. Some of these predators may be able to switch foraging habits to utilize different prey, such as the smaller zooplankton that are accumulated at upwelling fronts, while other predators may be impacted by having to travel further offshore to continue to forage on their schooling fish prey. Alterations of the foraging behavior of the California sea lion *Zalophus californianus* have been observed in response to pelagic fish distributions when anomalous conditions in 2005 caused northward displacement of fish schools that they forage on. Sea lions traveled greater distances offshore to forage (Brodeur et al., 2006; Weise et al., 2006). A similar pattern of predator behavior is likely to be expected from offshore displacement of pelagic fish schools caused by the cold water of upwelling plumes.

Localized enhancement of plankton biomass is a common effect at convergence zones, such as those associated with upwelling fronts, mesoscale eddies, river fronts, internal waves (Rogachev et al., 1996), tropical instability waves (Yoder et al., 1994), and other oceanic currents (Belkin et al., 2009). Hydrographic fronts such as these are often viewed as biological hotspots due to their attraction of a variety of predators that utilize the enhanced plankton or larger predators that take advantage of the aggregation

of smaller grazers on that plankton. Upwelling fronts differ from longer-lasting oceanic fronts by their duration and stability. Upwelling fronts are driven by wind variability with periodicity of only several days to weeks. Additionally, frequent reversals in wind direction are observed that may act to reset the system. Any accumulation of plankton at fronts is likely short in duration, limited by the consistency of wind direction. The cooler temperatures associated with the upwelling plume expands and contracts with these wind events, allowing for fish and zooplankton distributions to overlap as they also are reset, which could minimize the impacts of these mismatches between predator and prey.

The dynamic nature of upwelling systems make it difficult to observe the mechanisms driving biological responses. For small pelagic schooling fish in the upwelling system off Oregon, the primary mechanism driving distributions is temperature, despite warmer temperatures having lower abundances of small acoustic scatters consistent with their prey. Spawning distributions of sardines and anchovies in the California Current System are also linked with sea surface temperature (Lluch-Belda et al., 1991), and temperature and salinity are also the major driver of sardine, anchovy, and jack mackerel in the Humbolt Current system (Castillo et al., 1996). In contrast, upwelling fronts and bathymetry are important mechanisms driving aggregations of zooplankton in upwelling systems. These different impacts on the cross-shelf distributions of fish and zooplankton across upwelling fronts are important in determining their spatial and temporal overlaps and opportunity for trophic mismatches.

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Table 3.1 Temperature distributions across all transects sampled, the locations of positive fish school detections, and the region within 5 km of hydrographic fronts.

<u>Group</u>	<u>Mean Temp.</u>	<u>Standard Deviation</u>	<u>Standard Error</u>	<u>Lower 95% Conf. Int.</u>	<u>Upper 95% Conf. Int.</u>
Transects	14.66	0.99	0.02	14.62	14.69
Fish	15.22	0.83	0.17	14.87	15.57
Fronts	14.07	0.74	0.01	14.05	14.10

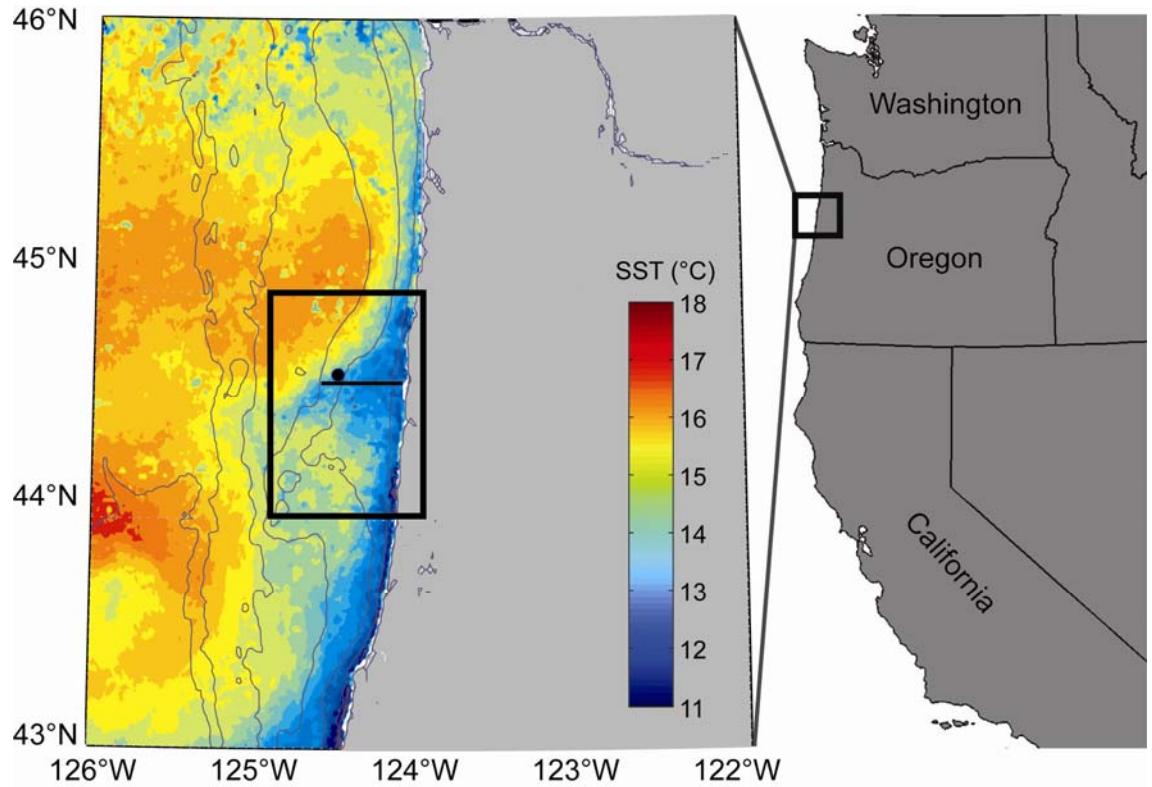


Figure 3.1 The study area along the United States west coast. The sampling area is highlighted with a rectangle in the inset SST map. A total of 26 cross-shelf and zig-zag pattern transects were conducted within the study area. The Newport Hydrographic line and NDBC buoy locations are plotted for reference, and the 50, 100, 200, 1000, and 2000 m isobaths are shown.

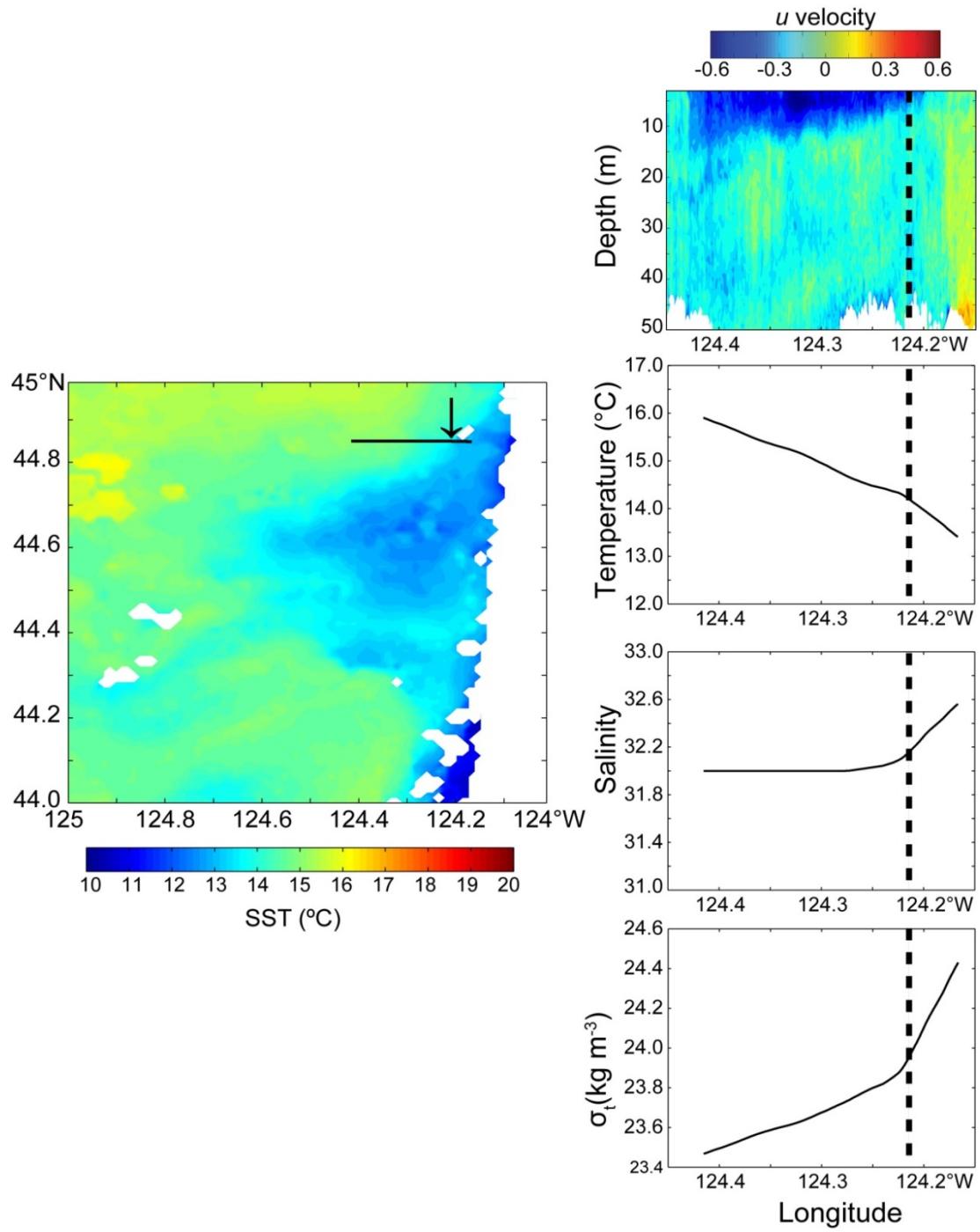


Figure 3.2 Sea surface temperature from satellite (left). An example cross-shelf transect surveyed on Sept. 1, 2008 is illustrated by the bold line. Shipboard ADCP and flow-through data (right) were used to identify strong gradients in current velocity, temperature, salinity, and density associated with crossing an upwelling front. In this example, the ship crossed a front at 124.23°W, indicated by the arrow and dashed line.

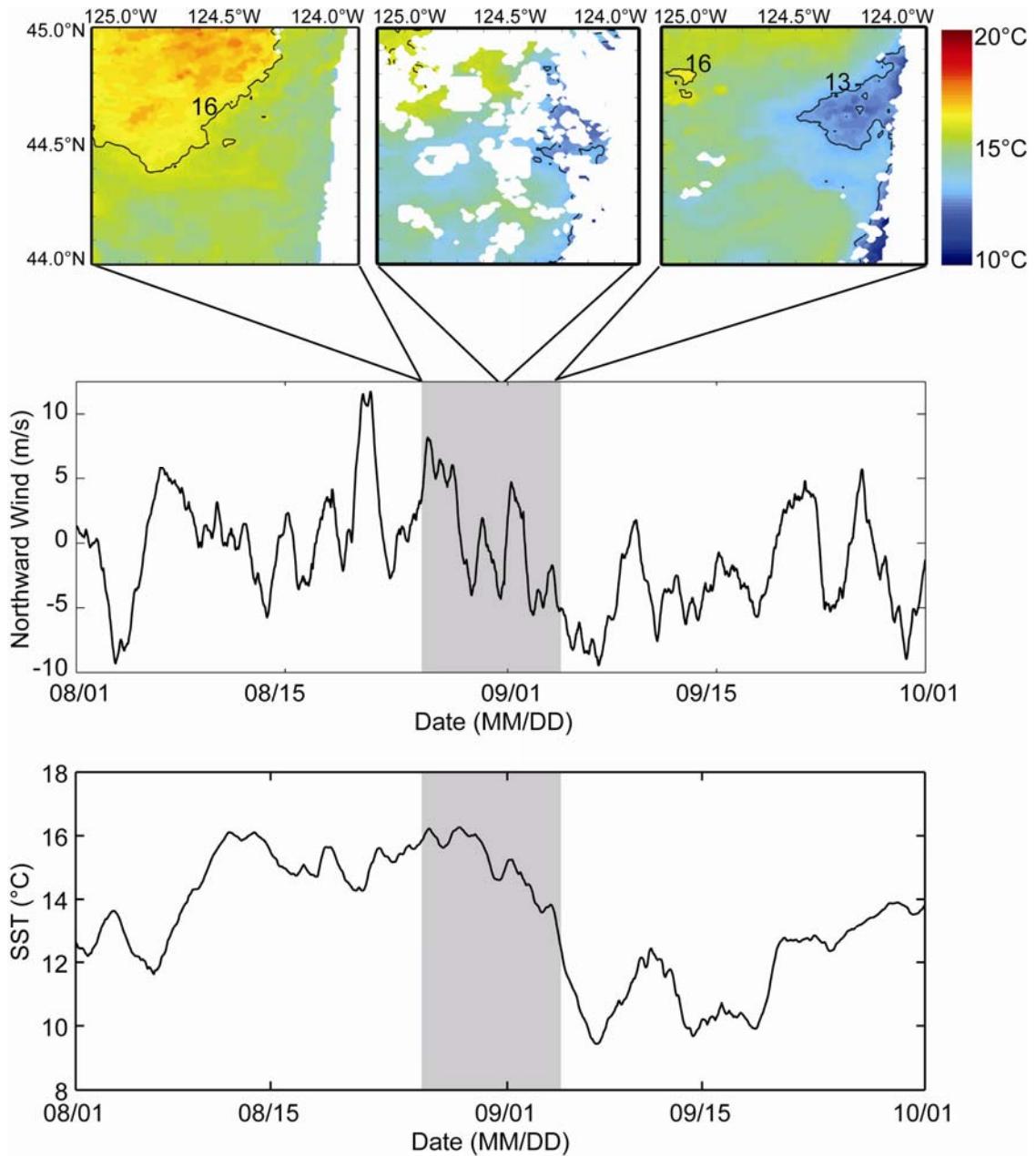


Figure 3.3 Sea surface temperature from satellite composite data for Aug. 8, Aug. 31, and Sept. 2, 2008 (top) with the 13 and 16°C isotherms. Wind velocity (middle) and sea surface temperature (bottom) data are from NDBC buoy. Sampling dates are indicated in the shaded region. During this time, winds shifted from downwelling to upwelling-favorable conditions. Sea surface temperature responded by declining throughout the sampling period as the upwelling plume was pushed further offshore.

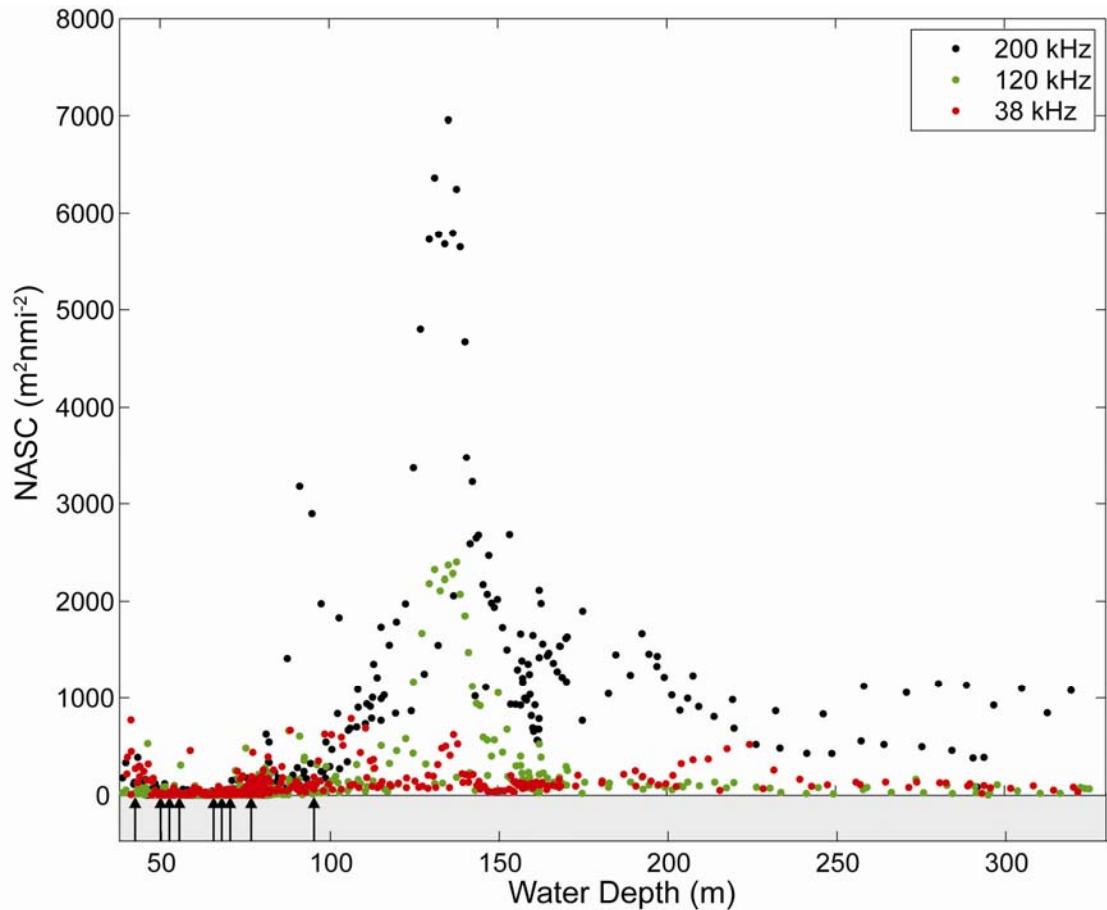


Figure 3.4 Water column-integrated acoustic scattering in relation to water depth along all transects that did not cross a hydrographic front. Depth of fronts sampled along other transects are indicated with arrows.

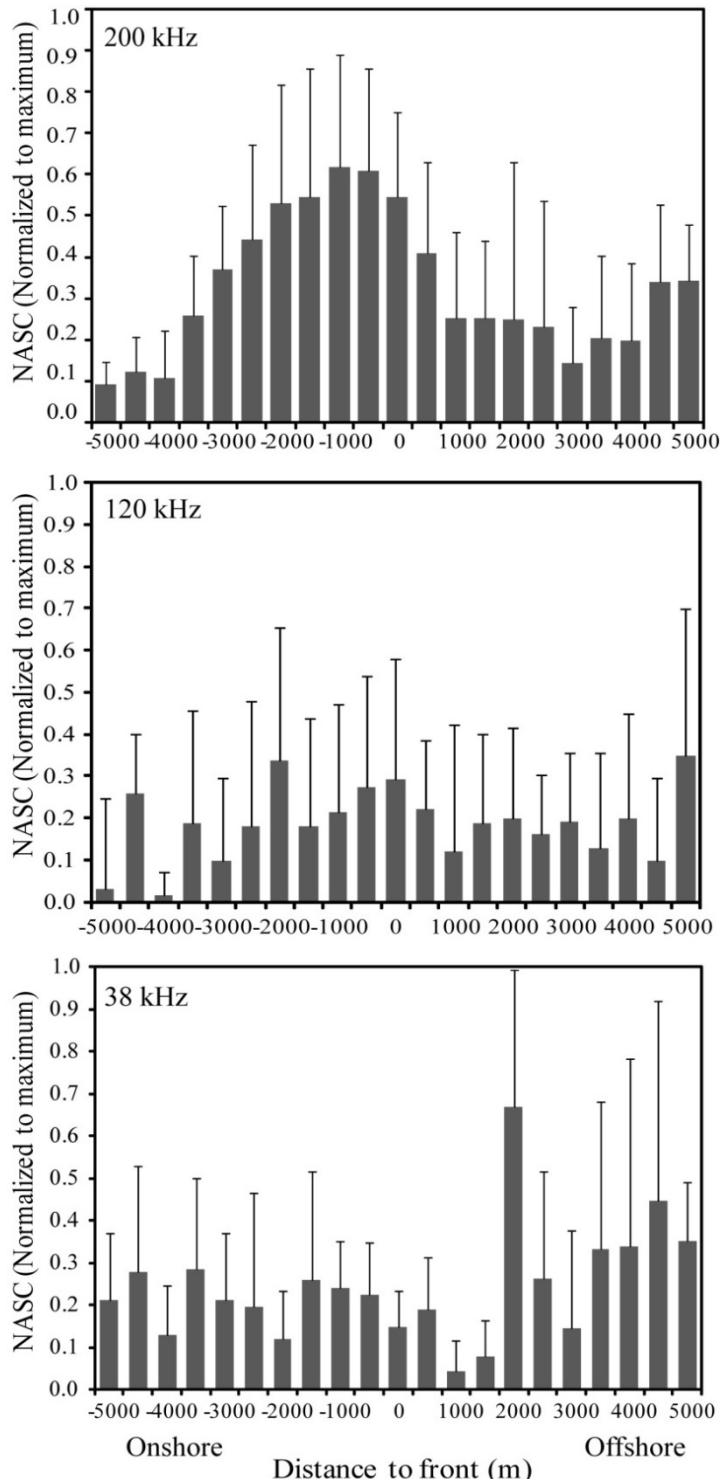


Figure 3.5 Normalized NASC in relation to distance to front. Negative distances are closer to shore and positive values are on the offshore side of the front. The 95% confidence intervals are shown.

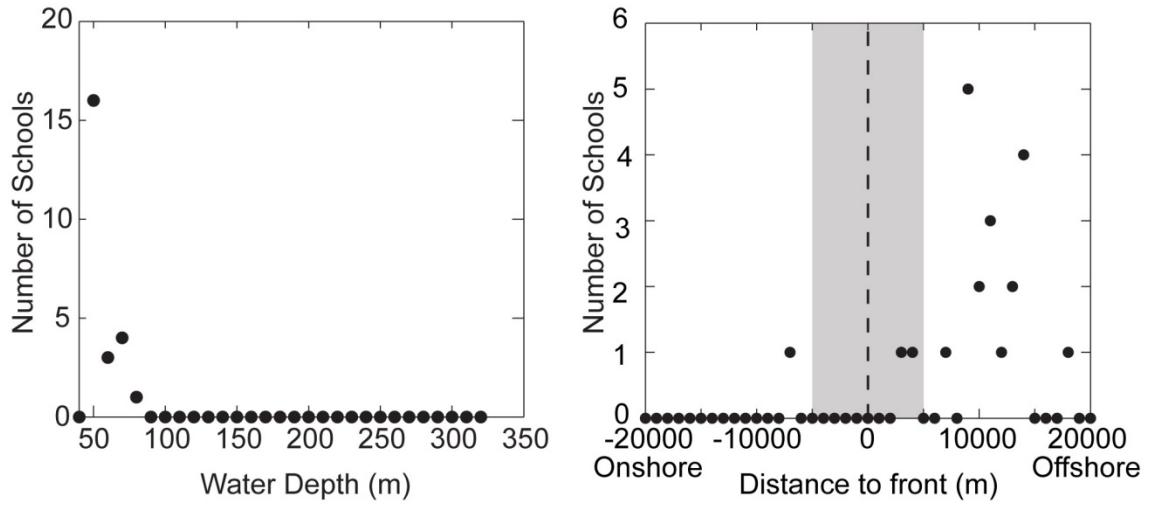


Figure 3.6 Distribution of fish schools in relation to water depth (left) and distance to front (right). Schools showed a strong preference for shallow water depths (< 100 m) and the offshore side of fronts as indicated by positive distance values. Note, the x-axis on the right panel has been expanded to 20 km from the front. The 5-km region near the front is shaded in gray.

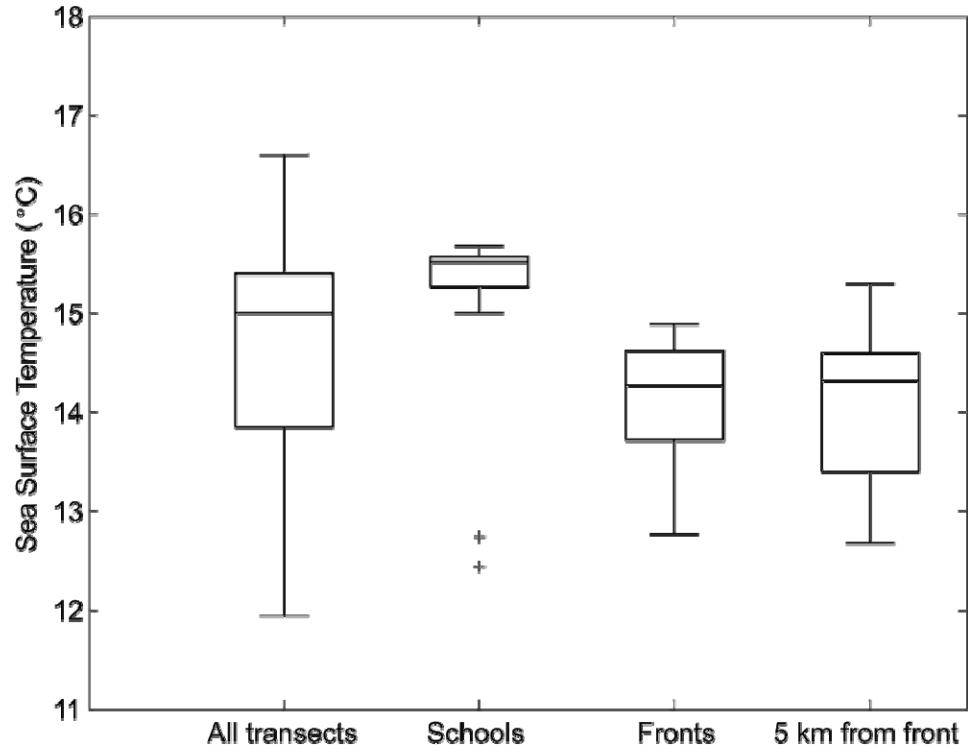


Figure 3.7 Distribution of sea surface temperature obtained from ship-board flowthrough CTD for all transects sampled, the location of schools, the locations of fronts, and the region within 5 km from the fronts.

**Chapter 4: Timing of forage fish seasonal appearance in the Columbia River
plume and link to ocean conditions and zooplankton variability**

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ABSTRACT

This study describes the timing and patterns of variability of forage fish and mesozooplankton populations near the Columbia River plume. Our objective was to identify the timing of the seasonal appearance of forage fish and to characterize the temporal patterns of abundance in relation to ocean conditions and zooplankton variability. Fish and mesozooplankton were observed continuously throughout the transition period from winter to summer upwelling conditions in 2008 and 2009 at two stations using bottom-mounted, 200-kHz bio-acoustic moorings. These observations were supplemented with nighttime surface net sampling to identify fish species, and the oceanographic habitat was characterized using sea surface temperature, salinity, and wind velocity data obtained from nearby buoys. Acoustic mooring observations revealed that the seasonal timing of forage fish schools containing primarily northern anchovy *Engraulis mordax*, whitebait smelt *Allosmerus elongatus*, and Pacific sardine *Sardinops sagax* occurred very abruptly, with specific dates of appearance identified at each station in mid-May in both years. 2008 and 2009 represented very similar years for the timing and strength of wind-driven coastal upwelling. The timing of forage fish appearances were linked with ocean temperature and salinity, but poorly correlated with mesozooplankton abundance, which was highly variable and extreme fluctuations were observed over a period of hours to days as salinity fronts passed the sampling stations. Fluctuations in zooplankton and forage fish populations drive many trophic interactions, including juvenile salmon, seabirds, and large predators (e.g. adult salmon) that rely on

the timing and abundances of these populations, having significant implications for ecosystem-based management.

INTRODUCTION

Fish communities in coastal upwelling regions of the world are generally dominated by a few species of very abundant small schooling forage fish. In these ‘wasp-waist’ ecosystems (Cury et al., 2000), species diversity is high in the upper and lower trophic levels but low at the intermediate levels, where small pelagic fish represent a significant portion of the total biomass. Forage fish, including sardines, anchovies, herring, and smelts, are generalist planktonic grazers that opportunistically feed on phytoplankton, copepods, and euphausiids, (Brodeur and Pearcy, 1992; Emmett et al., 2005; Robinson, 2000) and are significant consumers of primary and secondary production (Emmett et al., 2005; Lasker, 1970). Forage fish are an important prey resource in these ecosystems, supporting a variety of predators including larger fish, marine mammals, and seabirds, and serve as a critical link between plankton resources and upper trophic levels. In the northern California Current upwelling system, the abundance of forage fish is seasonal. Pacific sardine *Sardinops sagax* typically appear on the Oregon and Washington coasts beginning in May, peak in August, and are absent by the end of October, while the peak in northern anchovy *Engraulis mordax* catches typically occurs earlier (May or June) and closer to shore than sardines (Emmett et al., 2006).

The abundance and timing of forage fish populations in the coastal region play a significant role in a number of ecosystem interactions, including the timing and success of seabird breeding performance (Anderson et al., 1982; Anderson et al., 2007; Hedd et al., 2006; Safina and Burger, 1988), and the ecology of sea lions (Sinclair and Zeppelin, 2002; Weise et al., 2006; Womble and Sigler, 2006; Womble et al., 2005), killer whales (Similae and Holst, 1996), and minke whales (Macleod et al., 2004). The timing of forage fish presence is also hypothesized to be an important factor in determining juvenile salmon marine survival by providing alternative prey for large piscivorous fish, marine mammals, and seabirds (Pearcy, 1992). There is a trend for juvenile salmon survival to be high when forage fish populations are high, and in years when sardine and anchovy populations have been low, salmon survival has been low (Emmett and Sampson, 2007). Therefore, the temporal and spatial dynamics of forage fish may be critical variables determining these ecosystem interactions.

The Columbia River plume region adjacent to the Washington-Oregon border is an important transition area for a large number of juvenile salmon of the west coast of the United States and provides habitat for many commercially important species (salmon, sardines, Dungeness crab *Cancer magister*, albacore tuna *Thunnus alalunga*, etc). Oceanographic conditions in this area are strongly influenced by the interaction of Columbia River flows, winds, and tides, and often has a bi-directional surface plume of fresh river water (Hickey et al., 2005). This plume may extend up to 400 km offshore and along the entire Washington and Oregon coast. Upwelling conditions facilitate the

offshore and southward transport of the river plume, whereas downwelling conditions push the plume northward and tight to the coast.

Zooplankton distributions in the Columbia River plume appear to be driven by these ocean conditions and wind patterns, creating a retention mechanism for vertically migrating coastal zooplankton (Lamb and Peterson, 2005; Peterson, 1998b). Sardine and anchovy schools are highly mobile and can quickly respond to changing local conditions to select their preferred habitat. However, zooplankton are much less mobile, and increased abundances have been associated at convergence zones with strong gradients in density and current velocity (Morgan et al., 2005; Woodson et al., 2005). Increased zooplankton biovolume has been observed at the Columbia River front and at depths near the base of the plume (Peterson and Peterson, 2008), which may provide a mechanism for the cross-shelf transport of zooplankton (Peterson and Peterson, 2009).

Surface trawl surveys from this region indicate that the pelagic fish community is typically dominated by Pacific sardine, northern anchovy, Pacific herring *Clupea pallasi*, and whitebait smelt *Allosmerus elongatus* (Brodeur et al., 2003). These species are obligate schooling fish, meaning they spend most of their lives in coherently organized schools (Breder, 1976). These schools typically exhibit strong diel behavior with discrete schools present during daytime, which disperse horizontally and vertically throughout the water column at nighttime (Azzali et al., 1985; Cardinale et al., 2003; Fréon et al., 1996; Fréon and Misund, 1999; Kaltenberg and Benoit-Bird, 2009).

All forage species have high levels of interannual variability, particularly sardines and anchovies (Baumgartner et al., 1992; Hsieh et al., 2006). However,

oceanographic mechanisms driving this high natural variability are poorly understood. Variability of forage fish populations has been linked to decadal-scale oscillations of atmospheric forcing (Lluch-Belda et al., 1992), interannual patterns of wind stress curl (Rykaczewski and Checkley, 2008), and ocean conditions (Brodeur et al., 2005). However, little information is available to examine the effects of more localized and frequent sources of variability such as upwelling events and riverine influences on forage fish abundance. Local patterns of population variability determine the degree of spatial and temporal overlap between the forage fish population and other ecosystem groups that rely on them as either prey (e.g., adult salmon, marine mammals, and seabirds) or as alternative prey to mutual predators (e.g., juvenile salmon).

The objective of this study was to characterize the local patterns of variability of zooplankton and forage fish near the mouth of the Columbia River and to determine how oceanographic variables influence the seasonal timing of these patterns.

METHODS

Bio-acoustic moorings

Bio-acoustic moorings were deployed at two stations near the mouth of the Columbia River to collect fish and zooplankton abundance data (Figure 4.1). The inshore station was located 6 nautical miles from shore at 40 m water depth (46.17°N, 124.12°W), and an offshore station was 13 nautical miles from shore at 95 m depth (46.04°N, 124.25°W). These specific station sites were selected within the study region because they were within the area utilized by the commercial forage fish fishery and

they are adjacent to OGI (Oregon Graduate Institute) oceanographic buoys maintained by Clatsop Community College, Astoria, OR. These buoys provided surface expressions of equipment and a deterrence to trawl fishermen, with reduced chances of instrument interference. The moorings were placed on the seafloor just outside of the swing radius of the surface buoys to prevent contamination of the acoustic data. Previous sampling utilizing these moorings has shown that there is a high correlation among moorings placed in the corners of a 1 square nautical mile box pattern, indicating that one mooring station provides daily abundance data representative of sampling over a spatial scale of at least 1 nmi² (Kaltenberg and Benoit-Bird, 2009).

Sampling took place from March 31 to June 27, 2008, and from April 10 to June 21, 2009 using moored, upward-looking, 200-kHz echosounders (Water Column Profiler, ASL Environmental Science). The echosounders had a 3 dB beamwidth of 10° and were sampling with a transmitted pulse length of 156 µs. Acoustic backscatter data was collected over 60 m and 115 m at the shallow and deep stations, respectively. In 2008, moorings were set to sample with a vertical resolution of 0.5 m with a pulse rate of 0.125 sec⁻¹ and recorded on an internally stored drive. In 2009 the vertical resolution was increased to 0.25 m, with a pulse rate was 1 sec⁻¹, when data was recorded to replaceable compact flash cards with a larger storage capacity. In 2008, the moorings were replaced once mid-study on May 14, however the mooring at the shallow site was not recovered (i.e., missing). In 2009, one set of moorings were used throughout the entire sampling period.

Moorings were deployed from the M/V Forerunner by lowering the instrument

attached to sandbag anchors to the seafloor before releasing the deployment wire with an acoustic release. The upward pointing transducer was positioned 1 m above the seafloor and orientated upward using sandbag anchors. Floats were attached to each instrument below the transducer to keep the instrument stable. This stability was confirmed using an internal logging tilt and roll sensor in each instrument. No floats or lines were placed above the instrument package to prevent unintended acoustic returns or fish aggregations near the instruments. The design of the instrument package has been previously tested during prior sampling on the Oregon coast, and is further described in Kaltenberg and Benoit-Bird (2009). The moorings were recovered at the end of the sampling period in both years by the F/V Piki using an acoustic release that allowed the instrument package to float to the surface, sacrificing the sandbag anchors.

Physical oceanography

The oceanographic habitat was characterized using data from two nearby oceanographic buoys. Hourly data was obtained from the NOAA National Data Buoy Center (NDBC) buoy 46029 moored at 46.14°N 124.51°W, 20 nautical miles from the mouth of the Columbia River at 135 m water depth (Figure 4.1). This buoy is equipped with meteorological sensors that recorded wind speed and direction at 5 m above the sea surface. It also recorded sea surface temperature and sea surface salinity at 0.6 m below the surface. An oceanographic buoy operated by OGI was located at the deep acoustic mooring station during our sampling period in 2008 (Figure 4.1). This buoy measured sea surface temperature and sea surface salinity data from 0.8 m below the surface once every 2 minutes. Data from the NDBC and OGI buoys were available only for 2008 and

not available during 2009 sampling. For the 2008 oceanographic data, a 24-hour running average low-pass filter was applied to all meteorological and oceanographic data to remove diurnal variability. Wind vector data were left un-rotated since the coastline in this region has a north-south orientation. The historical dataset for sea surface temperature, available from 1984 to 2007, was used to determine and remove the seasonal trend to calculate the daily sea surface temperature anomaly.

Columbia River flow (daily discharge volume data ($\text{m}^3 \text{ s}^{-1}$)) was collected at Beaver Army Terminal, near Quincy, Oregon, (located 86.6 kilometers upstream from the river mouth) by the United States Geological Service (available at <http://waterdata.usgs.gov/nwis>). This site represents approximately 97% of the total river flow at the Columbia River mouth during summer conditions (Bottom et al., 2001). Historical flows were also obtained for 1991 through 2007 and used to determine the seasonal trend and calculate the flow anomalies in 2008 and 2009.

Daily upwelling indices were obtained from NOAA's Pacific Fisheries Environmental Laboratory, Environmental Research Division, which are based on estimates of offshore Ekman transport ($\text{m}^3 \text{ s}^{-1}$) driven by geostrophic wind stress (Bakun, 1973). Values were derived from mean atmospheric pressure field at 45°N , 125°W (available at <http://www.pfeg.noaa.gov>). The date of the spring transition was determined using the cumulative upwelling method, which is defined as the date of minimum cumulative upwelling from the beginning of the year after a 10-day running average filter was applied to the daily upwelling index values (Schwing et al., 1996). The spring transition is an event marking a shift from predominantly downwelling

conditions in the winter to predominately upwelling conditions in the summer. This method has been commonly used to characterize the spring transition and is appropriate for the northern California Current where there is a relatively large contrast between winter and summer wind conditions (Bograd et al., 2009; Holt and Mantua, 2009).

Fish sampling

The pelagic fish community was sampled during a series of sampling cruises that took place as part of the NOAA Predator Study (Emmett et al., 2006). Stations at 7, 10, 15, and 20 nmi from the mouth of the Columbia River were sampled from the F/V Picky, but only those stations closest to each acoustic mooring station were used (i.e., 7 and 15 nmi) for comparison of acoustic and total fish density and to identify the dominant species for each region (Figure 4.1). The trawl station CR7 was located 2.4 km from the shallow acoustic mooring station, and trawl station CR15 was located 15.2 km from the deep mooring station. Sampling took place approximately once every two weeks in May and June in both years. Sampling dates were May 26, June 14, and June 23 in 2008, and May 11, May 25, June 8, and June 22 in 2009. Trawls were conducted using a Nordic 264 rope trawl (30 m wide by 20 m high) with 3 m foam-filled Lite doors towed astern of the vessel at approximately 2.6 m s^{-1} (5 knots). Trawls were conducted at nighttime, when schools are typically near the surface and dispersed. Nighttime samples also minimize net avoidance behaviors (Fréon and Misund, 1999). Density estimates were calculated for each species based on the area-swept by the net.

Analysis of bio-acoustic data

Bio-acoustic mooring data were converted from echo intensity into volume backscattering strength (S_v , dB re 1 m^{-1}) by the sonar equation (Urick, 1983), using the manufacturer's calibrations before being analyzed using the acoustic processing software Echoview (Myriax). Minimum and maximum data thresholds of -65 dB and -30 dB were applied before the identification of acoustic features. Acoustical schools, defined as acoustically unresolved multiple fish or plankton aggregations (Kieser et al., 1993), were detected using a modified method of the school detection module (Barange, 1994) of Echoview combined with visual scrutiny (Kaltenberg & Benoit-Bird, 2009). Low threshold settings were used to include all possible aggregations. Each aggregation was then categorized into one of 5 categories based on visual characteristics; fish school, fish aggregation, fish layer, zooplankton aggregation, and zooplankton swarm (Figure 4.2). Fish schools were distinct, rounded features (i.e., not layers), and relatively homogeneous within the region (in contrast to other aggregations).

Data from the 2009 moorings were used to compare the 5 aggregation categories (i.e., fish school, fish aggregation, fish layer, zooplankton swarm, and zooplankton aggregation) detected by the visual scrutiny with a statistical detection method to test the robustness of visual identifications. All aggregations (5 categories) were exported from Echoview for analysis and the categories were statistically tested using a 2-step cluster analysis (using SPSS statistical software) with a fixed number of clusters set to 5. Fourteen aggregation descriptor variables (Table 4.1) were used to assign each aggregation to a cluster group. The statistically-determined groupings were then

compared with the visually-determined groups. Only school regions that were detected both visually and statistically were used for analysis of forage fish abundance (300 statistically-detected schools out of 304 visually-detected schools). The integrated nautical area scattering coefficient, NASC, ($\text{m}^2 \text{nmi}^{-2}$) for each school was binned to obtain a daily index for forage fish abundance. This combined technique of visual scrutiny with a statistical classification ensured confidence that the acoustic school aggregations were distinctly different from other aggregations and represented forage fish schools while excluding other aggregations.

To quantify the abundance of the mesozooplankton availability to the surface-oriented forage fish, daily acoustic backscatter from the moored echosounders was analyzed from the surface to 20 m depth. Regions defined as fish schools or aggregations were removed from the total acoustic backscatter. The remaining data was binned into a daily index of zooplankton abundance (NASC), removing the diel pattern due to diel vertical migrations of zooplankton into and out of the surface layer. These daily indices for zooplankton and forage fish abundances were tested for correlation with each other and with ocean conditions using the non-parametric Kendall's tau correlation test (Table 4.2). An Analysis of Variance test for a difference in means was used to test for an effect of year and site on the daily forage fish abundance, and a multiple linear regression test was used to identify relationships between zooplankton and the various oceanographic variables.

RESULTS

Upwelling and river flow

In both 2008 and 2009, winds became upwelling-favorable in March. In 2008, the spring transition occurred on March 27. This was a typical date for the spring transition compared to the spring transition date for the previous 5 years, which has ranged from March 15 in 2007 to May 23 in 2005 (Figure 4.3). The spring transition date was slightly earlier in 2009, occurring on March 23, and the strength of seasonal upwelling after the transition was slightly less in 2009 than was observed in 2008 (Figure 4.3).

Columbia River flows increased during the first half of each study year, with peaks observed at the end of May in both 2008 and 2009 (Figure 4.4). River flows were lower in April 2008 than in 2009, but increased rapidly in May 2008 (Figure 4.4).

Fish schooling

Forage fish schools were observed primarily during the daytime and very close to the surface (mean depth=4.96 m, standard deviation=4.55, Table 4.1). A cluster analysis of all categories of aggregations indicated that schools could be distinguished from other aggregations based on their statistical parameters. These statistically-determined schools were in very high agreement with the visual classifications (98.6% of visual schools were also determined statistically). Schools typically had lower skewness (mean=0.24, standard deviation=0.96) and kurtosis (mean=-0.50, standard deviation = 2.37) values than other aggregations, indicating that they had higher internal homogeneity in density than other aggregations (Table 4.1). Schools also tended to have

lower values for Image Compactness (mean=23.37, standard deviation=14.27), meaning that they were more rounded than other aggregations, and had a lower Coefficient of Variation (mean=92.45, standard deviation=33.55), meaning that individuals are more evenly distributed within the school than in other aggregations (Table 4.1).

Timing of forage fish appearance

Continuous acoustic data of forage fish abundance at the two stations in 2008 and 2009 is shown in Figure 4.5. Very few forage fish schools were detected in April and the first half of May at both mooring sites and in both years (note the shorter sampling period at the shallow station in 2008, beginning on May 14). One large spike in abundance was observed at the shallow station in 2008 just after the second deployment began (May 18), but it otherwise followed similar patterns with the other moorings with school abundance becoming high by the end of May and in June. The distinct timing for forage fish appearance (when schools appeared and were consistently detected over multiple days) were pinpointed to specific days; May 24 and May 15 at the deep station in 2008 and 2009, respectively, and May 17 and May 16 at the shallow station in 2008 and 2009, respectively. An ANOVA test for a difference in means indicated that the year had no effect on forage fish abundance ($d.f.=1$, $F=0.07$, $p=0.791$), but site did have a significant effect ($d.f.=1$, $F=9.56$, $p=0.002$), with higher abundances of forage fish observed at the deep mooring station than the shallow station. There was no significant interaction effect between year and site on forage fish abundance ($d.f.=1$, $F=2.47$, $p=0.12$).

Fish species composition

Trawl sampling indicated that there were differences in fish species composition by density for each species, both temporally and between sampling stations (Table 4.3). Sampling near the shallow mooring station in 2008 and 2009 indicated that northern anchovy and smelts (Osmeridae) were the 2 dominant species present (Table 4.3). However, smelts were absent from all samples at the deeper trawl station, where the most common species were northern anchovy and Pacific sardine.

Temporal patterns of zooplankton abundance

Acoustic mooring data indicated that there was generally much higher zooplankton abundance observed at the deep site than the shallow site when integrated throughout the entire water column (daily mean NASC = $4,396 \text{ m}^2 \text{ nmi}^{-2}$ at the deep station, daily mean NASC = $281 \text{ m}^2 \text{ nmi}^{-2}$ at the shallow station). However, since schooling fish were acoustically observed only within 20 m from the surface, zooplankton abundances were analyzed from the surface to 20 m depth (Figure 4.6). No clear seasonal trends were detected for surface zooplankton abundance during the sampling period. However, very large spikes were observed, which generally lasted from 1 to 3 days (Figure 4.6).

One example of these large fluctuations of abundance was observed at the deep site on 22 April, 2008 followed by a sudden drop to very low abundance on 23 April (Figure 4.6). Meteorological and hydrographic measurements indicated that the strong spikes in zooplankton abundance were associated with the timing of a reversal in wind direction. Strong upwelling-favorable winds were observed for a period of 8 days

before the reversal from upwelling-favorable to downwelling-favorable winds occurred on April 22 (Figure 4.7, top). This event appears to have also marked the passage of a salinity front, characterized by a rapid increase in sea surface salinity as oceanic water was drawn nearshore (Figure 4.7, bottom). The salinity stayed high over a duration of several days until the wind reversed again, however the spike in zooplankton abundance was observed only for one day, indicating that the region of high biomass was associated with the front and not the oceanic water mass.

A multiple linear regression test indicated a strong link between zooplankton abundance in 2008 at the deep mooring site and the interaction of alongshore wind and river flow ($R^2=0.52$, $p<0.001$). At the shallow site, the multiple linear regression test indicated that there was a significant relationship between zooplankton abundance and sea surface temperature anomaly ($R^2=0.14$, $p<0.001$), and alongshore wind velocity ($R^2=0.22$, $p<0.001$). The relationship between zooplankton abundance at the shallow site and sea surface salinity was not significant ($R^2=0.01$, $p=0.42$), nor the relationship between zooplankton abundance and river flow ($R^2=0.05$, $p=0.13$).

Forage fish and ocean conditions

Daily forage fish abundances in 2008 were not significantly correlated with surface mesozooplankton abundance (shallow station=-0.04, $p=0.73$, $n=44$; deep station=0.09, $p=0.26$, $n=88$) based on a Kendall's tau correlation test (Table 4.2). However, in 2009 forage fish abundance was significantly correlated with zooplankton abundance at each station, but the correlation patterns were opposite at the two stations (shallow station=0.21, $p=0.03$, $n=72$; deep station=-0.22, $p=0.01$, $n=72$).

A correlation test was conducted between the observed forage fish abundance and the ocean condition variables that were available for each year (SST and SSS were available in 2008 but were not available in 2009). In 2008, forage fish at the shallow station was significantly correlated with the daily upwelling index but not correlated with temperature or salinity measured at the OGI buoy at the deep station or with river flow (Table 4.2). Forage fish abundance at the deep station in 2008 was correlated with sea surface temperature, sea surface salinity, river flow, and river flow anomaly, but not related to the daily upwelling index (Table 4.2).

In 2009, a correlation test found no significant relationship between forage fish abundance and the daily upwelling index at either station (shallow station=-0.02, p=0.84, n=72; deep station=0.02, p=0.78, n=72). However, forage fish abundance in 2009 was positively correlated to river flow at both stations (shallow station=0.35, p<0.001, n=72; deep station=0.477, p<0.001, n=72), as well as the river flow anomaly (shallow station=0.25, p=0.007, n=72; deep station=0.32, p<0.001, n=72).

DISCUSSION

Continuous observations from acoustic moorings provided an effective method to identify the timing of movements of forage fish and mesozooplankton in the northern California Current. The appearance of forage fish schools were very distinct events at each sampling station and we were able to identify a specific day during each year when forage fish schools appeared and consistently remained for the remainder of the sampling period. A few small periods of school abundance were usually observed prior

to the transition day. These schools that were not visually or statistically different from other schools were limited to only a few occasions and did not persist over adjacent days, indicating that they were single events not associated with the arrival of a large number of forage fish into the study area. The timing of schools appearance in the two years were very similar to each other for both the deep station (May 24 in 2008, May 15 in 2009) and the shallow station (May 17 in 2008, and May 16 in 2009). We should note that only 2 days of fish absence preceded the appearance of fish at the shallow station in 2008, since the data record began on May 15. It is not possible to know if forage fish were present before that date, but the brief period of 2 days with very low abundance followed by a large spike was similar to the pattern observed in 2009.

Net sampling was conducted near the mooring stations during bi-weekly sampling cruises in May and June each year as part of the NOAA ‘Predator Study’. These trawl samples indicated that there were differences in the dominant species of forage fish at the shallow (40 m) and deep (100 m) mooring stations. Trawls conducted near the shallow station consisted of either northern anchovy or whitebait smelt, while trawls near the deep station were dominated by northern anchovy and Pacific sardine (Table 4.3). The samples also suggested that there were temporal shifts in species composition at these sites from anchovies in May to smelts in June at the shallow station and sardines becoming more abundant in June at the deep station. The dates that were defined as the appearance of forage fish schools in the acoustic data record likely correspond to the timing of the earliest migrating species, which would likely be anchovy and whitebait smelts. Another important point to note is that the trawl

sampling dates were not exactly the same in both years due to weather, logistics, etc. This difference in sampling dates could have lead to different monthly proportions of species when comparing the 2 years, especially given that the results presented here show that day-to-day variability to total forage fish can be very high. Relative forage fish abundance estimates determined acoustically were in high agreement with total fish density determined from trawl surveys (Figure 4.8). The four trawl sample points available during the acoustic time series resolved a similar pattern in total fish abundance, however often missed high variability that occurred between sampling dates (Figure 4.8). Routine net sampling even with bi-weekly frequency did not resolve the short-term variability of forage fish populations at these sampling stations, or identify the distinct timing when schools appeared. Additionally, weather conditions near the Columbia River plume often limit ship-board sampling, especially in April and May, making it even more difficult to address questions regarding the timing of forage fish appearance. The stationary acoustic moorings in the study demonstrated the effectiveness of adding acoustic moorings to net sampling programs to identify daily fluctuations of zooplankton and fish abundance. Future sampling designs for studies involving the timing of ecosystem events in regions with seasonal presence of forage fish would benefit from the incorporation of continuous sampling platforms, such as acoustic moorings, to identify fish and zooplankton variability.

The timing of forage fish appearance in the Columbia River plume region is likely driven by forage fish responding to a combination of factors and selecting their preferred physical and prey environments. Wind-driven coastal upwelling

characteristics during the 2 sampling years were slightly different in the timing of the spring transition, but they were much more similar to each other when compared with the previous 5 years (ranging from March 15 in 2007, to May 24 in 2005) (Figure 4.3). The cumulative strength of upwelling from the spring transition was also very similar over these 2 years relative to other previous years (Figure 4.3). We speculate that the similar timing in forage fish appearance at the mooring stations during these two years may have been linked with the similarity in the timing and strength of physical upwelling characteristics experienced during these years. More sampling of the timing of school appearance over a number of years under variable upwelling conditions would be needed to observe how these patterns are influenced by variability in the timing of seasonal upwelling.

Variability in the timing and strength of upwelling between years has previously been shown to have extensive impacts on the ecosystem with cascading effects observed throughout the entire food web. The anomalously late upwelling in 2005 (approximately 50 days later than the average) was associated with warmer than average sea surface temperatures throughout the northern California Current System (Barth et al., 2007; Kosro et al., 2006; Pierce et al., 2006; Schwing et al., 2006). A shift in the normal spawning distribution of forage fish species was observed, with spawning activity occurring farther north and onshore than typical (Brodeur et al., 2006). California sea lions *Zalophus californianus* altered their foraging behavior in 2005 as they traveled farther during foraging trips to utilize offshore species of forage fish (Weise et al., 2006). The planktivorous auklet *Ptychoramphus aleuticus* had almost a

complete reproductive failure off central California and southern British Columbia in 2005 due to a lack of their euphausiid prey (Sydeman et al., 2006). It appears that the ecosystem consequences of delayed upwelling strongly influence the abundance and distribution of forage fish.

Forage fish distribution biology is strongly linked to ocean temperatures in the California Current (Lluch-Belda et al., 1992) as well as in other coastal upwelling systems (Castillo et al., 1996). The appearance of forage fish schools at the deep and shallow mooring sites in 2008, during the period when we were able to obtain consistent temperature data, occurred shortly after a sharp rise in sea surface temperature to about 13°C. This pattern is consistent with other observations linking sardine and anchovy spawning distributions to specific sea surface temperatures. Sardines spawn in the California Current between 13 °C and 25°C, and anchovies spawn between 11.5°C and 16.5°C (Lluch-Belda et al., 1991). We found a significant correlation between forage fish abundance at the mooring sites and sea surface temperature anomaly within the sampling period, suggesting that the local (short-term) patterns of forage fish distributions were linked with fluctuations in sea surface temperature over the daily to weekly time scales as physical features passed over the mooring locations.

The short term variability in abundance observed at the stationary sampling locations is related to the spatial distributions of fish as they select preferred habitats. Combining the information from oceanographic sensors with information on the variability in fish abundance observed at the mooring site provides insight into what

factors forage fish schools were selecting for. We found no significant correlation between forage fish and mesozooplankton abundance in 2008. However, in 2009 this relationship was significant, but opposite, at the two stations, with forage fish and mesozooplankton abundance positively correlated at the shallow station and negatively correlated at the deep station. The abundance of mesozooplankton in the surface layer (0 – 20 m from the surface) at the two sampling stations was dominated by high frequency variability, with strong peaks usually lasting between 1 and 3 days. These peaks were linked to the timing of wind reversals and the passage of sea surface salinity fronts (i.e., the Columbia River plume).

This region is strongly influenced by the low salinity, high temperature Columbia River plume (Hickey et al., 2005). Currents and tides determine the position and extent of the plume and drive variability in the position of river fronts. Our observations of large spikes in zooplankton abundance with the passage of the river front were consistent with other studies showing aggregation of zooplankton at the Columbia River plume front (Morgan et al., 2005; Peterson and Peterson, 2008; Peterson and Peterson, 2009). Zooplankton aggregations at the river front were also observed closer to the surface (within 10 m of the surface) at the fronts than in regions without fronts (within 25 m of the surface) (Peterson and Peterson, 2008), which may be important in attracting or retaining larger predators. Increased forage fish abundances in this region have been associated at thermal fronts (Reese et al., in review).

High variability of zooplankton abundance due to variability of the river front may be a possible explanation for the lack of a consistent correlation between forage

fish and mesozooplankton abundance sampled during this study. The mesozooplankton community sampled by the acoustic moorings also represents only a portion of the total prey items available for the diet of forage fish. Forage fish feed opportunistically on a variety of plankton groups, and may switch between filter feeding on phytoplankton and particle feeding on zooplankton depending on availability of prey items (Garrido et al., 2008; Garrido et al., 2007). Forage fish abundance has been shown to reflect changes in zooplankton concentrations on an inter-annual scale, but lag zooplankton abundance by 1 year (Emmett et al., 2006). Garrido et al (2008) also showed a correlation between phytoplankton contribution in sardine diets and satellite-derived chlorophyll concentration. Stomach content analysis of sardines collected during day and night sampling in the Columbia River plume region were conducted by Emmett et al. (2005). In this study, all sardine stomachs analyzed were full, indicating that prey might not be limiting to individual fish during this transition period. Further, sardine stomach content was poorly related with neuston biovolume, and phytoplankton composition did not reflect the ambient chlorophyll a concentrations, which may be further evidence that forage fish in this region select their habitat based primarily on physical conditions because ambient prey concentrations during spring are generally not limiting.

In 2008, when ocean temperature data were available throughout our sampling period at the deep mooring station, forage fish abundance at the deep station was highly linked with sea surface temperature, sea surface salinity, river flow, and river flow anomaly. These same variables were not significantly correlated with the forage fish abundance at the shallow station. The shallow station is more strongly impacted by the

river plume, and likely is within the plume most of the time, especially during summer upwelling conditions. Therefore, the conditions in the surface layer at the shallow station are dominated by river flows.

The distribution of forage fishes in the northern California Current is seasonal. Pacific sardines appear to migrate to Oregon, Washington, and British Columbia, Canada to forage during summer months from their spawning grounds off California (Clark and Janssen, 1945). However, anchovy, smelts, and herring do not migrate to California but they over-winter by moving offshore to deep water habitats (Hernandez-Vazquez, 1994). Regardless of their wintering locations, the seasonal presence of forage fish in the coastal region has important ecosystem effects on many groups that depend on them as predators, prey, or co-prey. For example, a recent study found that the timing of salmon smolt arrival to the ocean may determine their marine survival (Scheuerell et al., 2009). We suspect that forage fish presence plays a significant role in early marine survival of juvenile salmon, by acting as competitors or by serving as alternative prey to mutual predators (Beamish and Mahnken, 2001; Emmett et al., 2006; Pearcy, 1992). The outmigration of juvenile salmon from the Columbia River takes place in spring (April-June), during our study period, for coho *Oncorhynchus kisutch*, yearling Chinook *Oncorhynchus tshawytscha*, sockeye *Oncorhynchus gorbuscha*, and chum salmon *Oncorhynchus keta*, and steelhead trout *Oncorhynchus mykiss*. Smolt outmigration timing may be regulated by timing the release of hatchery smolts and controlling the river flow through dams. Understanding the factors controlling the timing of forage fish presence in the Columbia River plume could be used to increase

the effectiveness of these salmon management efforts. This may be particularly important in the face of anticipated anthropogenic changes in global temperatures, as the timing and strength of seasonal upwelling are also expected to change. These changes are expected to lead to shifts in the timing and strength of coastal wind-driven upwelling, leading to disruptions in the overlap of predator-prey relationships in these regions ('match-mismatch hypothesis') (Cushing, 1990), and a number of recent studies have demonstrated the ecological effects of these phenological shifts (Sydeman and Bograd, 2009).

Forage fish represent a critical link in coastal upwelling ecosystems and their temporal and spatial distribution patterns are important ecosystem variables. The results of this study have significant implications for ecosystem-based management efforts. Currently, Chinook and coho salmon populations are supplemented with the addition of hatchery-reared smolts that are released into the Columbia River prior to entry into the ocean. This study shows that if forage fish populations play a role in determining marine juvenile salmon survival, then the timing of ocean entry by juvenile salmon is critical due to the abrupt appearance of forage fishes. The ocean conditions that juvenile salmon inhabit one day may be very different than the conditions that they face the following day. The timing of forage fish appearance was poorly related to zooplankton prey conditions, but were much more strongly related to abiotic conditions (i.e., temperature, salinity, and upwelling index). These variables are monitored in this region by a number of sources that have data available to managers in near real-time (e.g., NDCB, OGI, etc.). Furthermore, the use of near real-time biological indices of forage

fish abundance off the Columbia River (through the incorporation of bio-acoustic instrumentation) could improve marine juvenile salmon survival by optimizing ocean entry timing (i.e., salmon would enter the ocean when forage fish are abundant and environmental conditions are best).

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<u>Variable</u>		<u>Aggregation</u>	<u>Fish Ag.</u>	<u>Swarm</u>	<u>Schools</u>	<u>Fish Layer</u>	<u>Combined</u>
	N	737	300	233	300	47	1617
S _A (Area Scattering)	Mean	1744.25	2172.51	3796.28	4036.59	7436.87	2710.15
	SD	1629.21	1921.80	4845.29	3008.59	8949.29	3292.86
Skewness	Mean	1.24	0.90	2.48	0.24	1.76	1.19
	SD	1.04	0.96	2.29	0.96	2.03	1.46
Kurtosis	Mean	1.94	0.67	14.30	-0.50	9.13	3.24
	SD	4.44	3.61	22.91	2.37	18.34	10.98
Corrected Length ^a	Mean	137.91	151.79	371.59	152.28	1122.47	205.44
	SD	90.65	120.17	253.66	103.22	846.66	263.83
Corrected Thickness	Mean	5.84	5.62	14.33	9.17	26.83	8.25
	SD	3.29	3.60	7.45	5.03	11.63	6.58
Corrected Perimeter ^a	Mean	401.02	452.68	1337.69	460.47	4386.67	672.45
	SD	266.15	351.32	731.05	319.14	3044.85	964.63
Corrected Area ^a	Mean	463.89	486.21	2351.66	872.14	10869.62	1118.24
	SD	429.72	551.54	1601.83	915.05	6380.26	2255.67
Image Compactness ^a	Mean	34.58	44.76	79.21	23.37	177.89	44.99
	SD	25.41	39.74	63.31	14.27	174.89	53.75
Coefficient of Variation	Mean	118.65	109.87	151.29	92.45	125.15	117.05
	SD	35.34	33.22	70.67	33.55	53.03	45.52
Horizontal Roughness Coefficient	Mean	1.20E-05	1.10E-05	8.65E-06	5.09E-06	5.34E-06	9.84E-06
	SD	1.22E-05	8.23E-06	8.49E-06	4.04E-06	3.44E-06	1.00E-05

Table 4.1 Summary of 5 aggregation categories determined by cluster analysis of 14 aggregation descriptors. Only school categories were included in the analysis of forage fish abundance.

<u>Variable</u>		<u>Aggregation</u>	<u>Fish Ag.</u>	<u>Swarm</u>	<u>Schools</u>	<u>Fish Layer</u>	<u>Combined</u>
Vertical Roughness Coefficient	Mean	1.75E-05	2.30E-05	9.45E-06	4.14E-06	6.22E-06	1.46E-05
	SD	2.00E-05	2.31E-05	9.47E-06	3.37E-06	6.11E-06	1.84E-05
3D School Area ^a	Mean	3573.00	4061.62	20393.44	6183.68	107235.28	9584.80
	SD	3451.27	4762.19	14400.87	6790.93	96471.94	25126.13
3D School Volume ^a	Mean	1755.95	1775.75	16324.66	5790.49	120904.36	8070.60
	SD	2529.20	3120.55	16481.43	8784.91	132189.00	31016.24
Mean Depth	Mean	17.48	20.16	20.12	4.96	17.25	16.03
	SD	13.03	14.50	12.77	4.55	10.74	13.27

^a variables typically determined by school length

Table 4.1 (Continued)

		<u>Upwelling</u>	<u>SST</u>	<u>SSS</u>	<u>CR</u>	<u>CR Flow</u>	<u>Zooplankton</u>
		<u>Index</u>	<u>SST</u>	<u>anomaly</u>	<u>Flow</u>	<u>anomaly</u>	<u>abundance</u>
<u>Shallow station</u>	N	44	44	44	44	44	44
	correlation	0.27*	0.16	0.1	-0.08	0.08	-0.04
	significance	0.01*	0.15	0.38	0.47	0.49	0.73
<u>Deep station</u>	N	88	88	88	88	88	88
	correlation	0.08	0.4*	0.07	-0.33*	0.39*	0.38*
	significance	0.35	<0.01*	0.36	<0.01*	<0.01*	<0.01*

Table 4.2 Results of Kendall's tau correlation test between ocean conditions and forage fish abundance measured by bottom-mounted acoustic echosounders at the shallow and deep mooring stations located off the Columbia River April-June, 2008. Significant results are marked with *. CR= Columbia River, SST = sea surface temperature, SSS = Sea surface salinity.

Date	Station	Total Density Individuals 10^6 m^{-3}	California market squid	Chinook salmon	Coho salmon	Northern anchovy	Osmeridae (larvae)	Pacific hake	Pacific herring	Pacific sanddab	Pacific sardine	Pacific tomcod	Rockfishes YOY	Whitebait smelt
<u>2008</u>														
26-May	CR7	112.55	7.50	0	0	0	85.0	0	0	0	0	17.51	0	0
3-Jul	CR7	122.05	0	4.98	0	4.98	0	0	2.49	22.4	19.93	2.49	14.95	49.82
26-May	CR15	56.29	0	0	0	31.52	0	18.01	2.25	0	0	2.25	0	0
14-Jun	CR15	498.10	0	3.23	1.08	356.1	0	60.24	0	0	77.46	0	0	0
23-Jun	CR15	262.82	0	1.37	0	0	0	5.48	1.37	1.37	232.71	19.16	0	0
3-Jul	CR15	77.65	0	2.25	2.25	2.25	0	39.39	1.13	0	12.38	0.00	12.38	0
<u>2009</u>														
11-May	CR7	5380.9	1.06	24.30	0	236.71	0	0	3.17	0	0	0	0	5114.56
25-May	CR7	243.35	1.14	0	0	137.60	1.14	0	0	1.14	0	0	0	102.34
8-Jun	CR7	2825.7	0	0	0	0	0	0	23.57	0	0	0	0	2802.09
22-Jun	CR7	28.37	1.89	1.89	0	0	0	0	0	0	7.56	0	3.78	11.35
11-May	CR15	9.32	0	0	0	8.28	0	0	0	0	0	0	0	0
25-May	CR15	533.42	0	1.29	0	521.77	0	0	7.77	0	0	0	0	0
8-Jun	CR15	197.81	0	0	0	0	0	0	0	0	195.44	0	0	0
22-Jun	CR15	84.58	0	1.21	0	19.33	0	0	0	0	60.41	1.21	1.21	0

Table 4.3 Fish density by species from nighttime trawl samples collected at 2 trawl stations nearest the acoustic mooring stations.

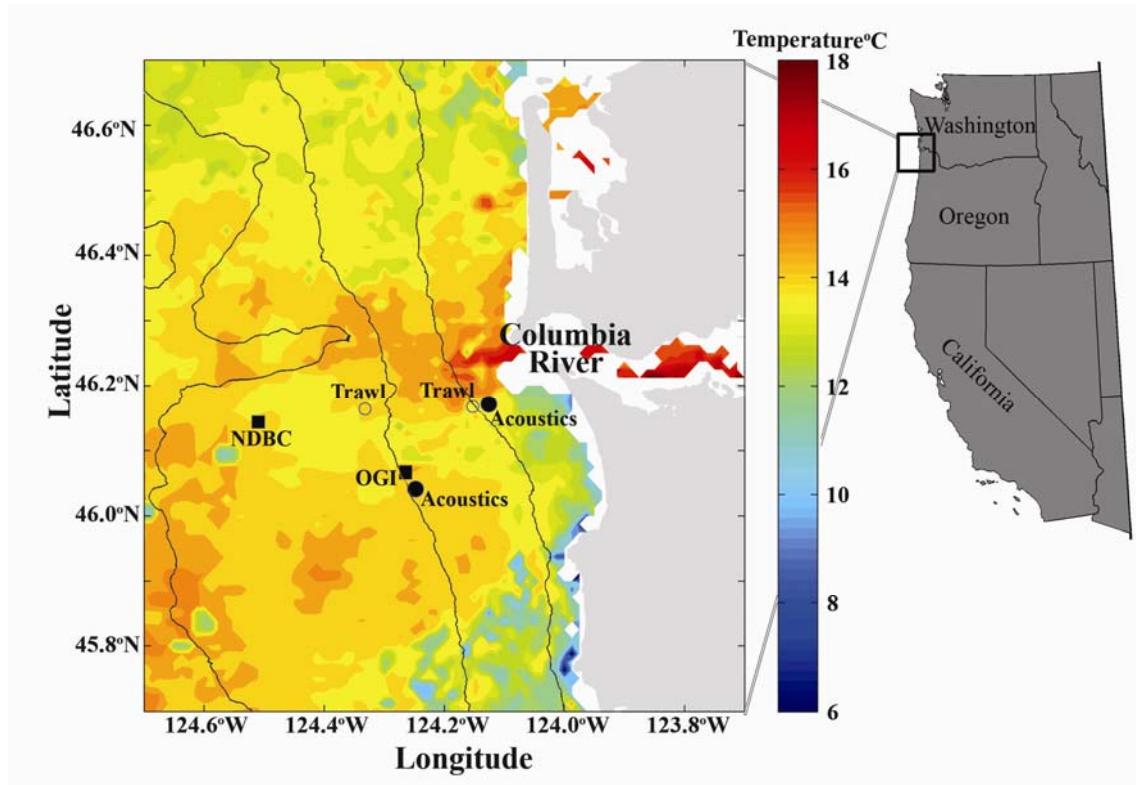


Figure 4.1 Location of the study area and sampling sites showing sea surface temperature from MODIS (Moderate Resolution Imaging Spectroradiometer) on the *Aqua* satellite from the period June 15-30, 2008. The 50, 100, 150, and 200 m isobaths are shown. The National Data Buoy Center (NDBC) buoy is 20 nautical miles from shore (■), and an Oregon Graduate Institute buoy is located at the deep acoustic mooring station (■). The two sampling stations consisting of bottom-mounted acoustic moorings are 6 and 13 nautical miles from shore (●). Trawl sampling stations are shown at 7 and 15 nautical miles from shore (○).

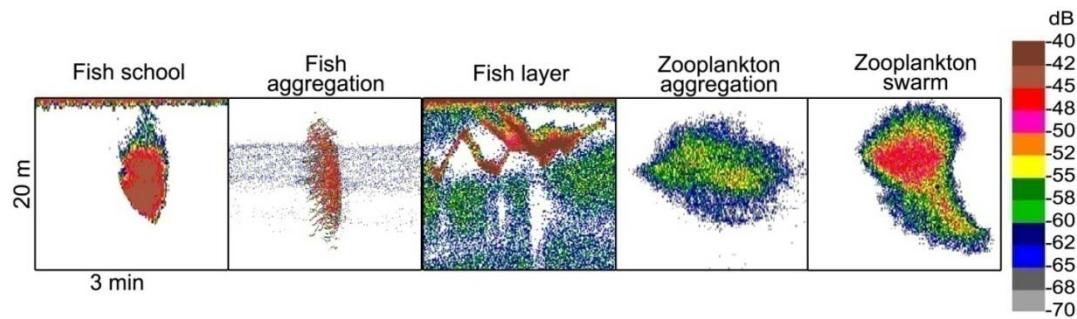


Figure 4.2 Example echograms for each classification of aggregations detected visually and statistically. Each panel represents 20 m (vertical axis) recorded over 3 min duration (horizontal axis).

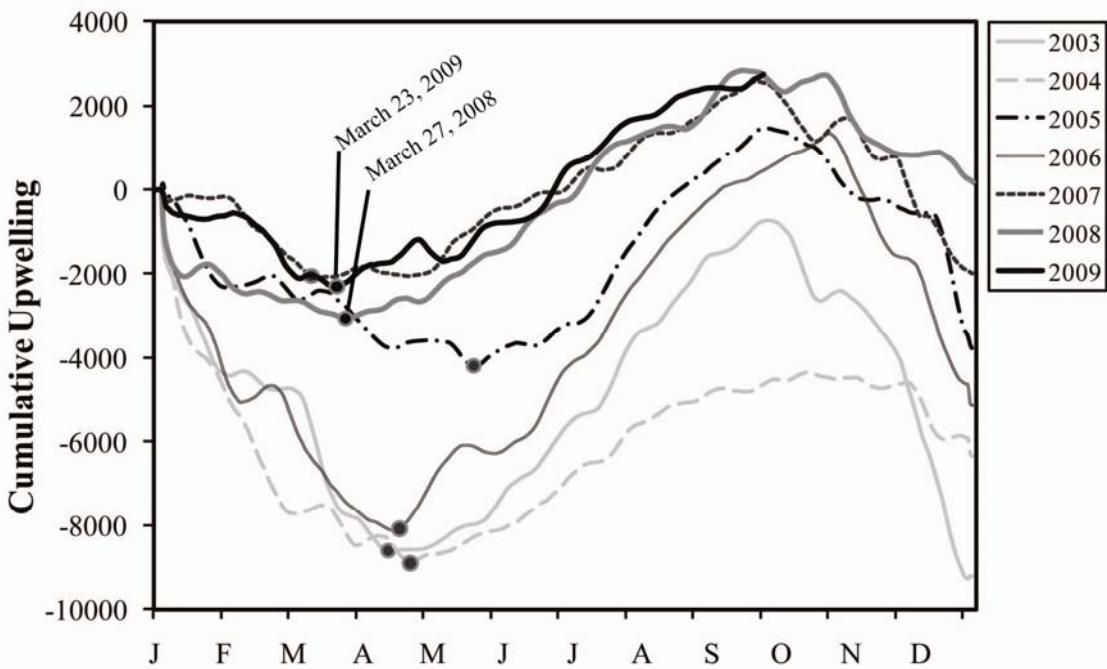


Figure 4.3 Cumulative upwelling index at 45°N , 125°W for each year, 2003 to 2009, from the Pacific Fisheries Environmental laboratory (www.pgeg.noaa.gov). Data were smoothed with a 10-day running average. Decreasing cumulative upwelling indicates downwelling and increasing values indicate upwelling. The circle marks the date of the spring transition for each year and is the date of minimum cumulative upwelling. The spring transition dates for 2008 and 2009 are indicated with arrows.

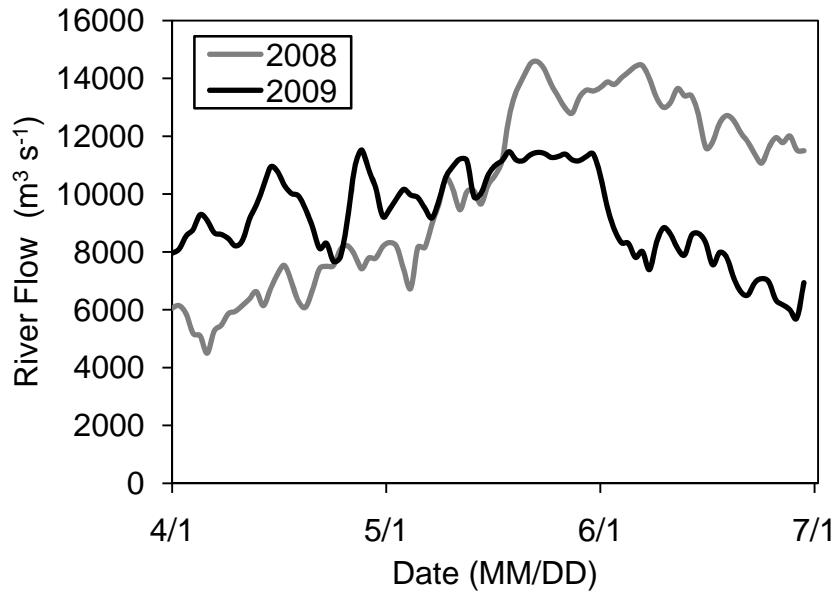


Figure 4.4 Columbia River flow at Beaver Army Station, located 86.6 km upstream of the Columbia River mouth in 2008 and 2009. Peak flows in 2008 occurred on May 23, and several peak flows were observed in 2009, but the maximum peak occurred on May 8.

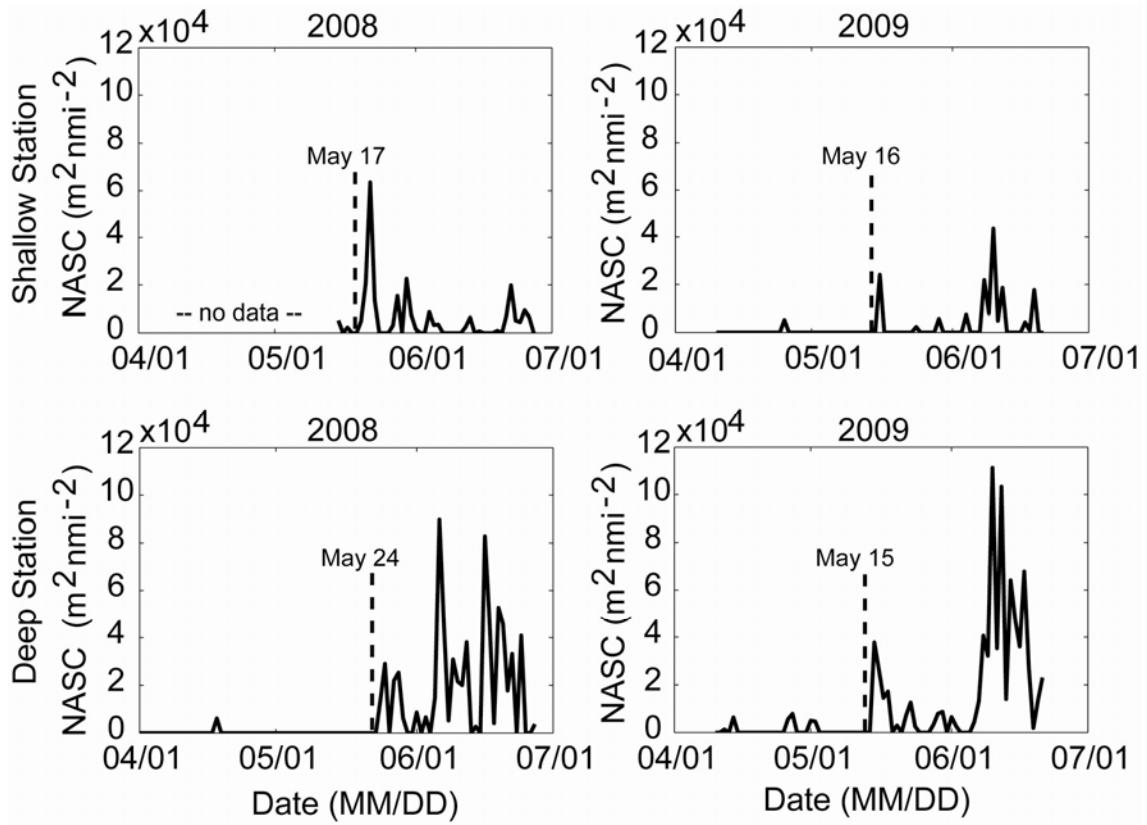


Figure 4.5 Daily forage fish abundance, NASC (the nautical area scattering coefficient, a proxy for forage fish abundance), is shown for the shallow mooring station (top row), and the deep station (bottom row). The dates of forage fish appearance at each station are marked by the dashed line.

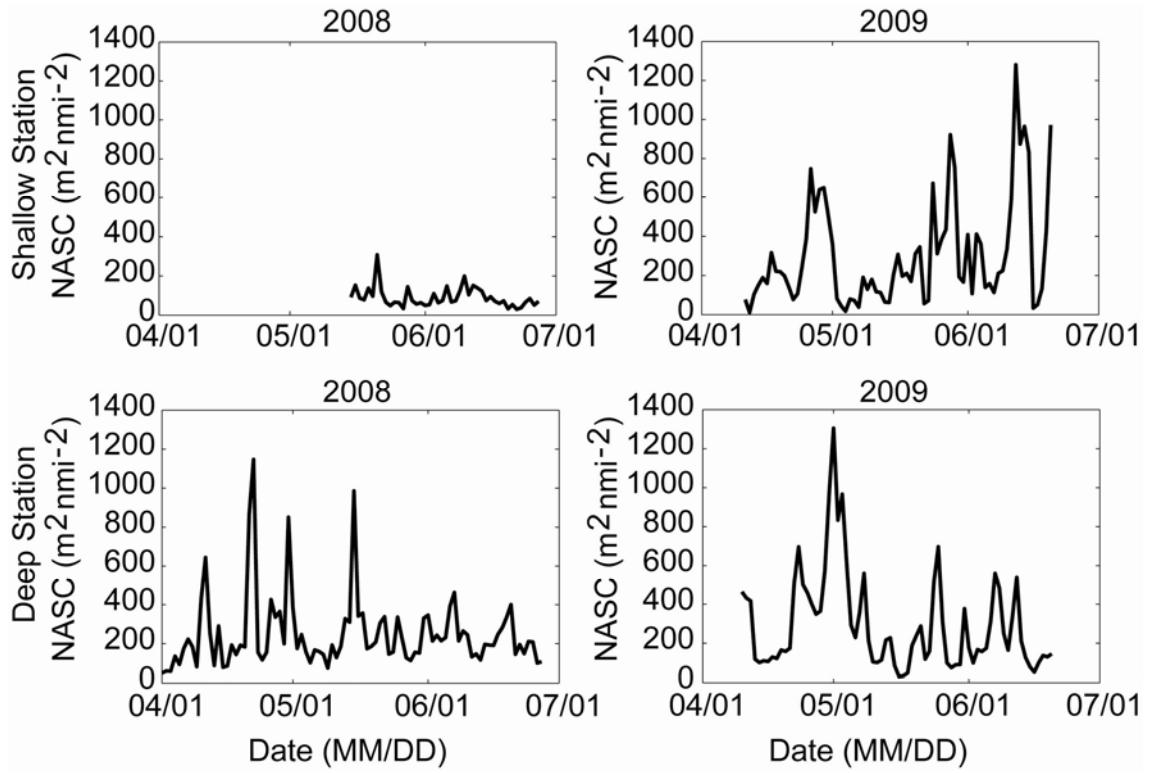


Figure 4.6 Daily zooplankton abundance observed between the surface and 20 m at the shallow (top) and deep (bottom) mooring stations in 2008 and 2009. Note the high-frequency variability, with very large spikes in abundance usually lasting 1 to 3 days. These spikes were usually associated with a reversal in winds and the passage of a temperature or salinity front over the mooring site.

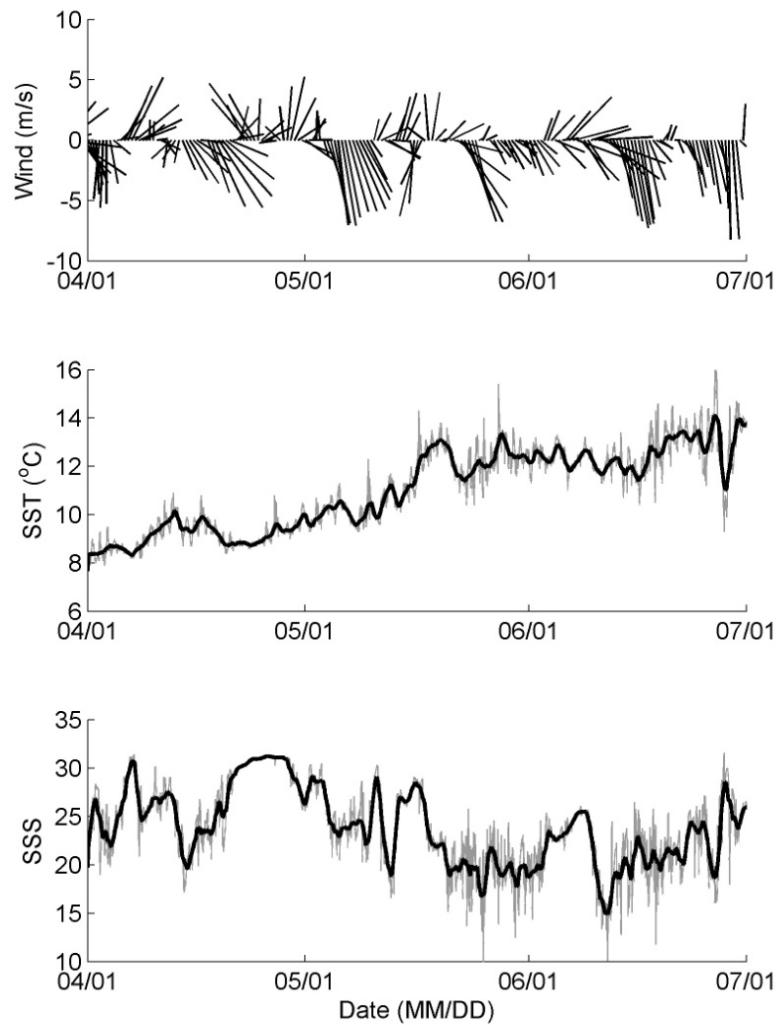


Figure 4.7 Wind velocity data (top) from 2008 collected at National Data Buoy Center buoy #46029. Negative wind values indicate winds from the north (upwelling-favorable). Sea surface temperature data (middle panel) collected at the Oregon Graduate Institute (OGI) buoy at the deep acoustic mooring station, and collected once every 5 minutes (gray line). The black line is 24-hour smoothed temperature data. Sea surface salinity data (bottom panel), also collected from the OGI buoy at the deep mooring station with the 5-minute values (gray line) and the 24-hour averaged (black line).

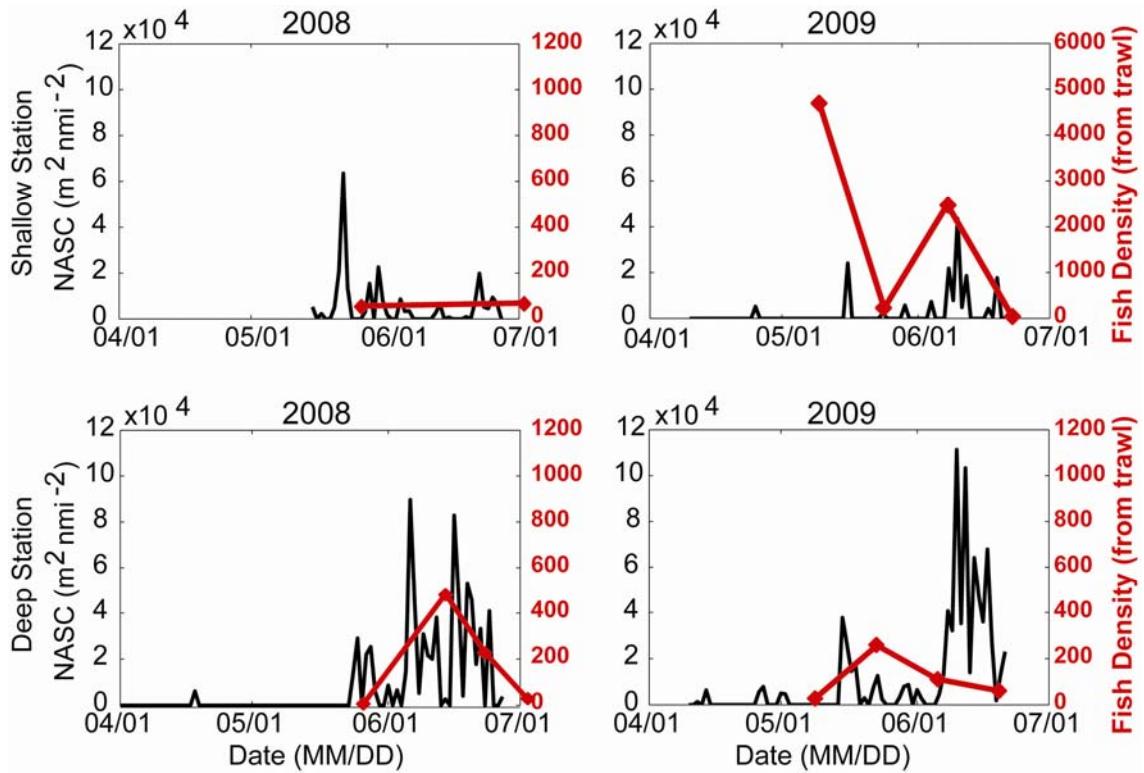


Figure 4.8 Comparison of acoustic time series with fish density collected in trawl samples at the nearest trawl station. Trawl sample y-axes were scaled to match acoustic samples for relative comparisons.

Chapter 5: Review of the bio-physical interactions of small pelagic fish schools and zooplankton prey in the California Current System over multiple scales

In this dissertation, I have focused on the predator-prey interaction between small pelagic fish schools and zooplankton prey over multiple scales and some of the impacts that environmental variability has on this interaction. My goal was to provide a better understanding of what controls the behavior and distribution of small pelagic fish, a critical intermediate group of coastal upwelling systems, and to determine the impacts that these behaviors have on the biology of their ecosystems.

The dynamics of pelagic schooling behavior are regulated by a balance between the pressures of predation and the need by individuals to eat, which usually results in a strong circadian pattern with schools present during the day and dispersed in loose aggregations at night (Fréon and Misund, 1999). While individuals may passively filter feed in schools, individuals within schools are unable to maximize foraging in a limited prey environment because of the high density of fish that increases competition between individuals for prey items (Bertram, 1978). When schools disperse into loose aggregations, they are able to forage at a more optimal density as well as selectively feed on larger or preferred prey items.

The ‘typical’ and ‘atypical’ schooling behaviors described in Chapter 2 documented both of these behaviors for sardines and anchovies in relation to prey availability, a first in the literature. These schooling patterns have important implications for understanding the role of small pelagic fish as prey to larger predators in the California Current System, and can have a significant impact on the success of

foraging predators. For example, studies in other systems have shown that in years when herring schools were larger and deeper than years when they were shallower, the seabird *Brachyramphus marmoratus*, commonly known as the marbled murrelet, switched from feeding on herring schools to alternative prey that had easier accessibility (Ostrand et al., 2004). The accessibility of schooling fish as prey to larger predators is highly dependent on their aggregation behaviors. Schooling fish have adapted complex predator-evasion maneuvers to reduce individual risk of predation such as flash expansion, when densities rapidly increase in all directions, and the hourglass effect, when schools change their shape in response to the position of a predator (Pitcher and Parrish, 1993). For other predators that are able to more easily utilize fish in schools, schooling provides an advantage to the predator because it concentrates a large amount of prey into a small area. Some marine mammals like killer whales *Orcinus orca* use tactics like releasing bubbles, tail slapping, and herding to scare schools into compressing even further to capture prey (Simila and Ugarte, 1993; Simon et al., 2005). As shown in Chapter 2, prey availability is at least partially responsible for determining the degree of aggregation of fish schools, thus this prey availability-schooling interaction may be important in determining the composition and distribution of large predators present in a given location.

Diel schooling behaviors also play an important role in the techniques used by the commercial fishery. When fish are schooling, they are most easily captured by purse seiners by surrounding the entire school. However, when fish are dispersed, they are more easily captured by trawl nets (Fréon and Misund, 1999). The sardine fisheries off

Oregon and Monterey Bay follow different techniques reflecting those differences observed in schooling behavior. It seems intuitive that the composition and feeding strategies of large predators besides humans in each region must also reflect these differences in schooling behaviors.

In addition to varying at diel time scales, small pelagic fish distributions in the California Current System are highly seasonal, with most species making either latitudinal or cross-shelf migrations driven by biotic and abiotic factors. Based on optimal foraging theory, which states that organisms forage in a way to maximize their energy intake per unit time (Krebs, 1978), we expected small pelagic fish to occupy areas of highest prey abundance, including river and upwelling fronts. However, data from the California Current show the interaction of fish schools and mesozooplankton over medium to large temporal scales (weekly to seasonal) were, in general, not well linked with these fronts. Fish schools were not strongly influenced by the accumulation of small zooplankton observed at upwelling fronts (Chapter 3). Fish schools were also not strongly linked with the very large spikes of mesozooplankton abundance associated with the Columbia River plume (Chapter 4). In both cases, fish schools showed stronger correlations with physical parameters than with these indices of potential prey abundance. These results are consistent with other previous studies that have also shown strong correlation between Pacific sardine abundance and temperature in the California Current (Lluch-Belda et al., 1991) as well as their geographic range and temperature (Rodriguez-Sanchez et al., 2002).

Avoidance of front regions with accumulated prey could possibly benefit intermediate-sized predators, if there is an increased risk of predation present. Front regions have often been associated with increased predators (seabirds, marine mammals, and large fish). By controlling their vertical position in the water column, adult euphausiids and small pelagic fish could optimize the trade-off between enhanced grazing and increased risk of predation by avoiding these regions that have been associated with high predation. In a highly productive region where food is abundant in the adjacent waters, it might be advantageous to avoid these regions that attract a large numbers of predators. Since the effect of predators on small pelagic fish was outside of the scope of this research, this hypothesis wasn't addressed in this study, but should be a focus in future work.

In addition to temporal variation, spatial variation or patchiness is a common characteristics of life in the oceans (Mackas et al., 1985). This patchiness is often enhanced in the coastal ocean at hydrographic discontinuities, such as fronts (Yoder et al., 1994), eddies (Haury, 1984), and internal waves (Lennert-Cody and Franks, 1999). This research has also demonstrated the high degree of heterogeneous distributions of zooplankton and pelagic fish. The combination of mobile and stationary platforms of observations in this study provided greater insight into the patterns of patchiness of these populations than would have been possible to observe with either method alone.

The stationary moorings used in the Columbia River plume documented extreme fluctuations in mesozooplankton abundance (Chapter 4). Peaks usually lasted one day with magnitudes of acoustic abundance several orders of magnitude higher than the

surrounding times (Chapter 4). At 200 kHz, these acoustic echosounders resolved acoustic scatterers most consistent with the size range of copepods. This is the same frequency that measured the strongest effect of hydrographic fronts on biology (Chapter 3). We can conclude that the advective forces in the dynamic upwelling system are most influential on the small, passive zooplankton (e.g., copepods) and appears to not have a strong effect on aggregating larger animals (e.g. adult euphausiids and fish) that are able to swim to varying degrees and overcome the aggregation mechanism of fronts.

The role of small pelagic fish in upwelling ecosystems

Sardines and anchovies are generalist foragers, feeding on both large phytoplankton and zooplankton as they become available in the environment (Cunha et al., 2005; Emmett et al., 2005; Lasker, 1970; Robinson, 2004). This generalization of prey resources is one reason small pelagic fish are an important link between lower and upper trophic levels in highly productive upwelling ecosystems (Cury et al., 2000). Studies have emphasized the significance of the role of small pelagic fish in marine systems through ecosystem models using tools such as Ecopath and Ecosim, which assess the trophic level of each species and determine the impact of one group on others in the system (Christensen and Waters, 2004). These tools have shown that small pelagic fish are the dominant fish group by biomass, and slight changes in their abundance can have large impacts on other trophic groups in the ecosystem (Palomera et al., 2007). When populations of small pelagic fish have extreme fluctuations in abundance, as observed at various temporal scales here, there are significant ecosystem

consequences. These consequences are difficult to predict because the dominant species are often replaced by other, similar species.

The role of pelagic fish schools as a link from plankton to large predators is dependent on the degree of their spatial and temporal overlap with phytoplankton and zooplankton prey resources. Variability in the overlap of these groups is influenced by a number of abiotic factors including; water depth limiting the extent of diel vertical migrations of zooplankton (Chapter 2), temperature effects from upwelling fronts (Chapter 3), and river plume (Chapter 4). Each of these factors has proven critical to determining the interaction of zooplankton and fish schools and their roles in the California Current System.

Implications for sampling methods

The results of this research have important implications on how we sample these organisms and interpret data from traditional net sampling methods. Many sampling programs rely on data collected at fixed sampling stations. A single net tow might be used and the data between successive sampling cruises sometimes weeks or months apart is often interpolated. Data that was collected from acoustic moorings showed very brief and very high fluctuations in abundance. A net trawl conducted between these events would miss a large portion of the total biomass and underestimate the population. However, if the single net sample does happen to sample at the time of the passing front, the results could be overestimated. This research provides a quantitative assessment of the temporal variability of zooplankton and fish school abundance at a

temporal resolution of up to 1 second. It is critical to be aware of extreme fluctuations when interpreting discretely sampled data of animal aggregations.

The results of Chapter 2 also have implications for sampling schooling fish. Net sampling programs that sample schooling fish at night have improved quantitative estimates over day sampling due to the dispersal of schools as well as decreased net avoidance (Fréon and Misund, 1999; Krutzikowsky and Emmett, 2005). Chapter 2 shows that nighttime school dispersal may not always be consistent in different regions with differing depths (Kaltenberg and Benoit-Bird, 2009), leading to inconsistent biases of abundance estimates in different regions.

Implications for management

Variations in schooling behavior and distribution of small pelagic fish are important factors driving many ecological interactions in the California Current System, including the impact that they may have on salmon survival and recruitment (Chapter 4). This research provides information that can help improve the management of small pelagic fish species and ecosystem-based management of coastal upwelling ecosystems. In the two years sampled for the timing of small pelagic fish presence in the Columbia River plume (Chapter 4), the timing of fish appearance was an abrupt event and consistent in seasonal timing between years. This study provided the first of its kind information on the consistency of this timing and characteristics of the appearance of small pelagic fish in the northern California Current System at high temporal resolution. This study emphasizes the importance of understanding timing in predicting ecosystem interactions. The phenology of predators may be tightly linked with this timing of fish

migrations. A number of seabird species are adapted to the timing of small pelagic fish for breeding success (Anderson et al., 1982; Russell et al., 1999; Sydeman et al., 2006b). In years when unusual physical conditions has caused the timing of these interactions to deviate from usual there have been significant ecosystem consequences (e.g., 2005 and 2010 in the northern California Current).

There is a growing emphasis in the management efforts in aquatic systems on an ecosystem-based approach, which relies on the construction of an all-inclusive model containing all components of the ecosystem, including biotic and abiotic parameters. Management of a target species then depends on the fluctuations and health of the entire system. In order for ecosystem-based models for aquatic systems to be successful in the future, there is a need to understand how the various trophic levels interact. This research has shown that these trophic links are not always consistent and may vary with complex aggregating behaviors and with interactions of environmental variability over a range of spatial and temporal scales.

Final conclusions

This work has resulted in several new hypotheses to be further developed and tested to help understand the factors controlling pelagic fish schools and zooplankton prey and their role in coastal upwelling ecosystems. One hypothesis resulting from this work is that the timing of pelagic fish schools appearance to the Columbia River plume is impacted by variability in the spring transition date and timing for ocean conditions. The two years sampled, 2008 and 2009, had very similar dates of spring transition and very consistent arrival times of forage fish schools. This hypothesis is currently being

addressed in collaboration with NOAA fisheries with acoustic mooring sampling that will provide a third year of repeat sampling under varying ocean conditions during a moderate El Niño year in 2010, in which the date of the spring transition is slightly later. A second hypothesis that requires more focus is regarding the role of hydrographic fronts in creating trophic mismatches in upwelling ecosystems by limiting the accessibility of fish in near-shore regions. This effect likely impacts a great number of predators that rely on schooling fish as prey, and it will be important to determine how these predators respond to variable fish and zooplankton distributions across varying shelf characteristics. This dissertation has shown that combined sampling from stationary and mobile acoustic platforms with net trawls provides important information on the ecology and behavior of schooling fish and zooplankton aggregations. Small pelagic fish populations are highly unstable, with high variability in their distributions over time and space, influencing their complex grazing and anti-predation schooling behaviors.

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