PACIFIC SARDINE (*SARDINOPS SAGAX*) ABUNDANCE, DISTRIBUTION, AND ECOLOGICAL RELATIONSHIPS IN THE PACIFIC NORTHWEST

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ABSTRACT

During the 1930s and 1940s, Pacific sardines (*Sardinops sagax*) supported an important fishery in Pacific Northwest waters, but after their population crashed in the mid-1950s, they were rarely observed in this region. Starting in the mid–1990s, sardines resumed migrating into Northwest waters to spawn and feed. Pacific sardines now support a relatively large purse seine fishery centered off the Columbia River. From 1994 to 1998, we identified the abundance and distribution of Pacific sardine eggs and larvae in Northwest waters. The highest egg densities were observed in June 1996. During all years, eggs were associated with surface temperatures between 14° and 15°C. From 1998 to 2004, surface-trawl surveys, primarily on the continental shelf, identified the temporal and spatial distribution and abundance patterns of juvenile and adult Pacific sardines. Adult sardines generally do not over-winter off the Northwest, but migrate north from California in the spring (May–June) when surface temperatures exceed 12°C. However, juvenile sardines over-winter in nearshore coastal waters. During most years, few 0-age juveniles were captured, indicating relatively poor spawning success; however, high densities of 0-age sardines were observed in fall of 2003 and 2004, indicating successful spawning. During the summer, sardines are most abundant on the shelf in cool (<16°C) and high salinity (>30 S) coastal waters, with their highest densities occurring in northern Oregon/Washington waters. Sardines are non-selective planktonic filter feeders; prey include copepods, euphausiids, and phytoplankton. Sardines are important prey of Northwest fishes, such as sharks, salmon, Pacific hake (*Merluccius productus*), and jack mackerel (*Trachurus symmetricus*).

INTRODUCTION

The Pacific sardine (*Sardinops sagax*) is frequently a dominant pelagic fish in the California Current. However, over the last several millennia its abundance has fluctuated greatly due to regime shifts in ocean conditions (Ware and Thomson 1991; Baumgartner et al. 1992; McFarlane et al. 2002; Chavez et al. 2003). During peak abundance periods, this sardine population has supported major commercial fisheries. The main population and fishery are centered off central and southern California, but during periods of high abundance and warmer ocean temperatures, a portion of the population either resides off of, or is a transient visitor to, Oregon, Washington, and British Columbia, with some individuals traveling as far north as southern Alaska (Hart 1973; Wing et al. 2000; McFarlane and Beamish 2001). At these times, commercial fisheries for sardines, or pilchards (another common name), also develop in the Pacific Northwest (PNW) and British Columbia.

Sardines were first landed commercially in Oregon during 1935–36 and a year later in Washington, well after the commencement of sardine fisheries in both California and British Columbia (Chapman 1936; Schaefer et al. 1951). Most sardines were landed in Grays Harbor, Washington and Astoria and Coos Bay, Oregon, and were generally rendered to oil and fishmeal. Following the collapse of the sardine population and fishery in the late 1940s, there were few reports of sardines in the PNW. Reid (1960) reported the catch of a single male in Winchester Bay, Oregon in August of 1957. During coastal purse seine surveys off Oregon and Washington from 1979 to 1985, only five sardines were caught between June and September in 1984 off central Oregon (Brodeur and Pearcy 1986; Pearcy and Schoener 1987). Ermakov and Stepanenko (1996) also reported a few sardines captured from research trawls in the PNW during the 1980s. These sporadic occurrences appear to be associated with warm ocean conditions and the anomalous northward advection of southern species associated with El Niños (Pearcy and Schoener 1987).

In 1992, sardine numbers increased dramatically in the PNW (Hargreaves et al. 1994), apparently in response to the 1992–93 El Niño. They continued to increase in abundance and began spawning in PNW waters (Bentley et al. 1996; McFarlane and Beamish 2001). This abrupt change in sardine abundance and distribution in the PNW followed an apparent ocean regime shift in 1989 (McFarlane and Beamish 2001; McFarlane et al. 2002) and coincided with dramatic changes in the overall pelagic fish biomass off the PNW (Emmett and Brodeur 2000).

Forage fishes, including sardines, anchovies, and other small pelagic fish species, dominate the pelagic ecosystems in many coastal upwelling regions (Crawford 1987). Indeed, pelagic fish can often exert a major control on the trophic dynamics of upwelling ecosystems that fall under the category of midtrophic-level, "wasp-waist" populations (Cury et al. 2000). Sardines are omnivores that feed on both phytoplankton and zooplankton (James 1988, van der Lingen 2002) and can consume a substantial proportion of the primary and secondary production in the southern California Current during years of high abundance (Lasker 1970). However, there have been few studies of the Pacific sardine diet in the northern California Current (e.g., Hart and Wailes 1931, McFarlane and Beamish 2001) and none in the PNW region. During periods of high abundance all sardine life stages are likely to be eaten by a variety of predators that normally consume other forage species. For example, Chapman (1936) showed that sardines were important prey for both coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) when they were abundant in the 1930s. There are presently no studies that have identified sardine predators in the northern California Current during its present population resurgence.

To effectively manage fish stocks, it is necessary to know the basic biological parameters of a stock, such as size, age, feeding habits, and migrational characteristics. Therefore, using a variety of data sources and based on sampling from 1977 to 2004, we describe the abundance, spatial and temporal distribution, size and age composition, life history, and ecological relations of sardines during the recent population increase off the coasts of Washington and Oregon.

DATA AND METHODS

Commercial Catch and Age Distribution, 1999–2003

Both the Oregon and Washington Departments of Fish and Wildlife monitor the amount of sardines landed and collect biological samples from the catch. From 1999 to 2003, each state collected a minimum of three samples per week of at least 25 fish. Because vessels from each state fish in nearly the same location (the fishery operates primarily at the Northern Oregon/Southern Washington state boundary), the two state agencies began a cooperative sampling program in 2004. Each state presently collects three samples per week on alternate weeks during the main fishing period. In addition to collecting biological data on each fish (weight, standard length, sex, and maturity stage), otoliths were extracted and ages were determined by the California Department of Fish and Game. Summary data of Oregon sardine commercial harvest are more fully described in McCrae (2004).

Ichthyoplankton Distribution

The National Marine Fisheries Service (NMFS) conducted an **Ichthyoplankton Survey** off the coast of Oregon and Washington for five years (1994–98). A similar grid of stations was sampled every July, except in 1996 when sampling occurred during June (fig. 1). The sampling was done by vertical tow with a CalVET net (Smith et al. 1985) to a maximum depth of 70 m (Bentley et al. 1996).

Juvenile/Adult Distribution and Size

To describe juvenile/adult sardine distributions, we used catch data from four different fish surveys, which are more fully described in Emmett and Brodeur (2000). The distribution of sampling efforts was mostly at predetermined locations over a number of years. While none of these surveys specifically targeted sardines, sardines were commonly captured.

The first set of surveys, the summertime (July through September) NMFS west coast triennial bottom trawl surveys (**Triennial Survey**), began in 1977. Because the trawls targeted near-bottom species, any sardines captured were likely to have been incidentally caught in mid-water during net deployment and retrieval. We examined catches only from the U.S.-Canada border south to 41.5°N, although many sardines were also caught outside this region (fig. 1). Sardines were counted, measured and weighed, and abundance was calculated using area-swept methodology.[1]

Since 1998, NMFS has conducted three surface trawl surveys of pelagic fish resources off the Northwest: 1) the Bonneville Power Administration (BPA) Columbia River **Plume Survey**, 2) the U.S. Global Ocean Ecosystem Dynamics–Northeast Pacific **(GLOBEC) Survey**, and 3) the **Predator Survey**. During the summer and fall of 1998–2004, the Plume Survey conducted surface surveys for juvenile salmon and associated species along eleven transects off the Washington and Oregon coasts
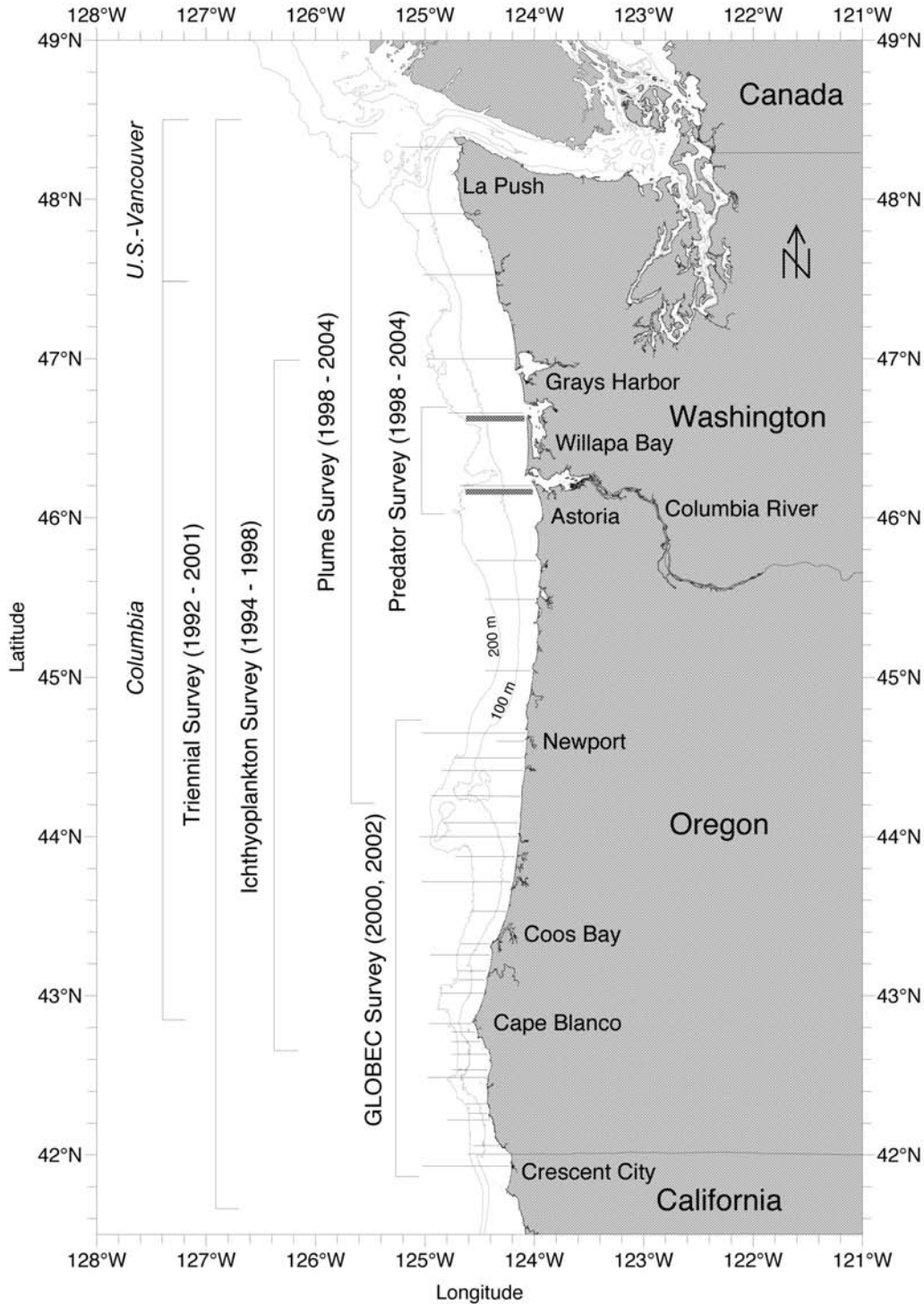
Figure 1.   Location of five survey areas where Pacific sardines (*Sardinops sagax*) were collected. Also shown are 100 and 200 m depth contours. Horizontal lines are transects sampled by the Plume and GLOBEC Surveys. Grey rectangles are two transects sampled by the Predator Survey. Columbia and U.S.-Vancouver regions are designated fishery management areas.

(fig. 1; Emmett and Brodeur 2000). Sampling was conducted generally in late May, June, and September of each year with an additional cruise in November 2003. The GLOBEC Survey sampled during June, and August of 2000 and 2002 and extended from Newport, Oregon to Crescent City in northern California. GLOBEC collections were made along predetermined transects but additional opportunistic samplings were made at various

stations that showed unique oceanographic signals (Brodeur et al. 2004).

All Plume and GLOBEC Survey sampling was during the day or crepuscular periods. Fish were sampled using a Nordic 264 rope trawl (NET Systems[2], Bainbridge Island, WA) fished directly astern the vessel at the surface. The trawl has an effective fishing mouth of 12 m deep and 28 m wide (336 m²) as identified during an early cruise (June 2000) using net mensuration equipment (Emmett et al. 2004). The mouth was spread apart by a pair of 3.0 m foam-filled trawl doors. The trawl was towed with about 300 m of warp for 30 min at 1.5 m sec^{-1}. To fish the trawl at the surface, a cluster of two meshed A-4 Polyform buoys were tethered to each wing tip, and two single A-4 Polyform floats were clipped on either side of the center of the headrope. Mesh sizes ranged from 162.6 cm in the throat of the trawl near the jib lines to 8.9 cm in the cod end. To maintain catches of small fish and squids, a 6.1 m long, 0.8 cm knotless liner was sewn into the cod end.

The Predator Survey consisted of a series of biweekly cruises on two transects near the Columbia River mouth in spring and summer of 1998–2004 (fig. 1; Emmett et al. 2001). Sampling was conducted at night using the same surface trawl gear as in the Plume and GLOBEC Surveys.

Sardines captured in trawls were counted and up to 50 of them were measured to fork length (FL) (mm). However, when there were very large catches a subsample of sardines was measured, counted, and weighed; remaining sardines were mass weighed. Total number of sardines in the haul was then calculated using the known number of sardines/kg. Sardine density was calculated by multiplying the number of sardines in a haul by the volume of water the net fished, which was standardized to number per 10⁶ m³. The volume of water fished was calculated as the trawling distance multiplied by the effective fishing mouth area (336 m²).

Habitat Analysis

We were interested in determining if any environmental factors were related to the distributions of sardine egg, larval, juvenile, and adult stages. During Ichthyoplankton, Plume, and GLOBEC Surveys, temperature (°C; T) and salinity (S) measurements were collected at 3 m depths from each station using a Sea-Bird SBE 19 SeaCat conductivity, temperature, and depth (CTD) profiler. In-vitro chlorophyll *a* (μg/l; C) was measured by filtering water samples collected from 3 m depth, and then examining the filtrate concentrations spectrophotometrically (1994–96) and fluorometrically (1996–98). During GLOBEC Surveys, neuston biovol-

umes were identified from settled plankton volumes collected from a 1 m × 0.3 m neuston net. The neuston net had 0.333 mm mesh and was set out 60 m beyond the vessel's wake and towed at 3 km hr^{-1} for 5 min.

A General Linear Model (GLM) was used to investigate the relationship between average sardine densities during Predator Survey cruises and average 3 m depth temperatures and salinities. Sardine densities were $\log_{10}(x+1)$-transformed before analysis.

We explored the relationships between environmental factors and sardine densities (by life stages and size classes) using General Additive Models (GAM) (Hastie and Tibshirani 1990). We chose this nonparametric method due to the high number of zero catches and the nonlinear relationships between sardine densities (all life stages) and environmental variables.

A Gaussian error model was used in the GAM analysis, with a link identity function based on the following model (Bigelow et al. 1999):

$$\ln(\text{density} + 0.01) = a + \text{lo}(T) + \text{lo}(S) + \text{lo}[\ln(C+1)] + e$$

where a is a constant, e is the error term and $\text{lo}(x)$ is the loess-smoothed independent variable. GAMs were implemented using the mgcv library of R (Wood 2001).

Food Habits

Analyses of sardine diets were synthesized from two studies: the September 1999 Plume Survey and the August 2000 and June and August 2002 GLOBEC Surveys. In both studies, sardines collected for stomach analysis were frozen whole onboard the ship (-20°C), transported to the lab, measured [fork lengths (FL), mm], and weighed (g); then their stomachs were removed and preserved in 10% buffered formalin for a minimum of 10d.

Contents of the cardiac stomach region were identified to the lowest taxonomic level possible, enumerated, and wet weighed (g). Stomach contents in the pyloric stomach region were too digested to identify; therefore, they were not included in laboratory analysis. Stomachs frequently consisted of phytoplankton and microzooplankton too numerous and small to count efficiently. For these stomachs, prey >1.0 mm were removed, identified, measured for length, and wet weighed, and the remaining contents subsampled. To accomplish subsampling, stomach contents were first measured for total settled volume in a volumetric flask, then resuspended and subsampled with a 5.0 ml Hensen–Stempel pipette. Settled volume of the subsample was then measured and examined for prey identification and enumeration. Wet weight of specimens in the flask was calculated from length-weight relationships previously identified for individual prey. The subsample of prey counts and weights was projected to estimate the entire contents of the
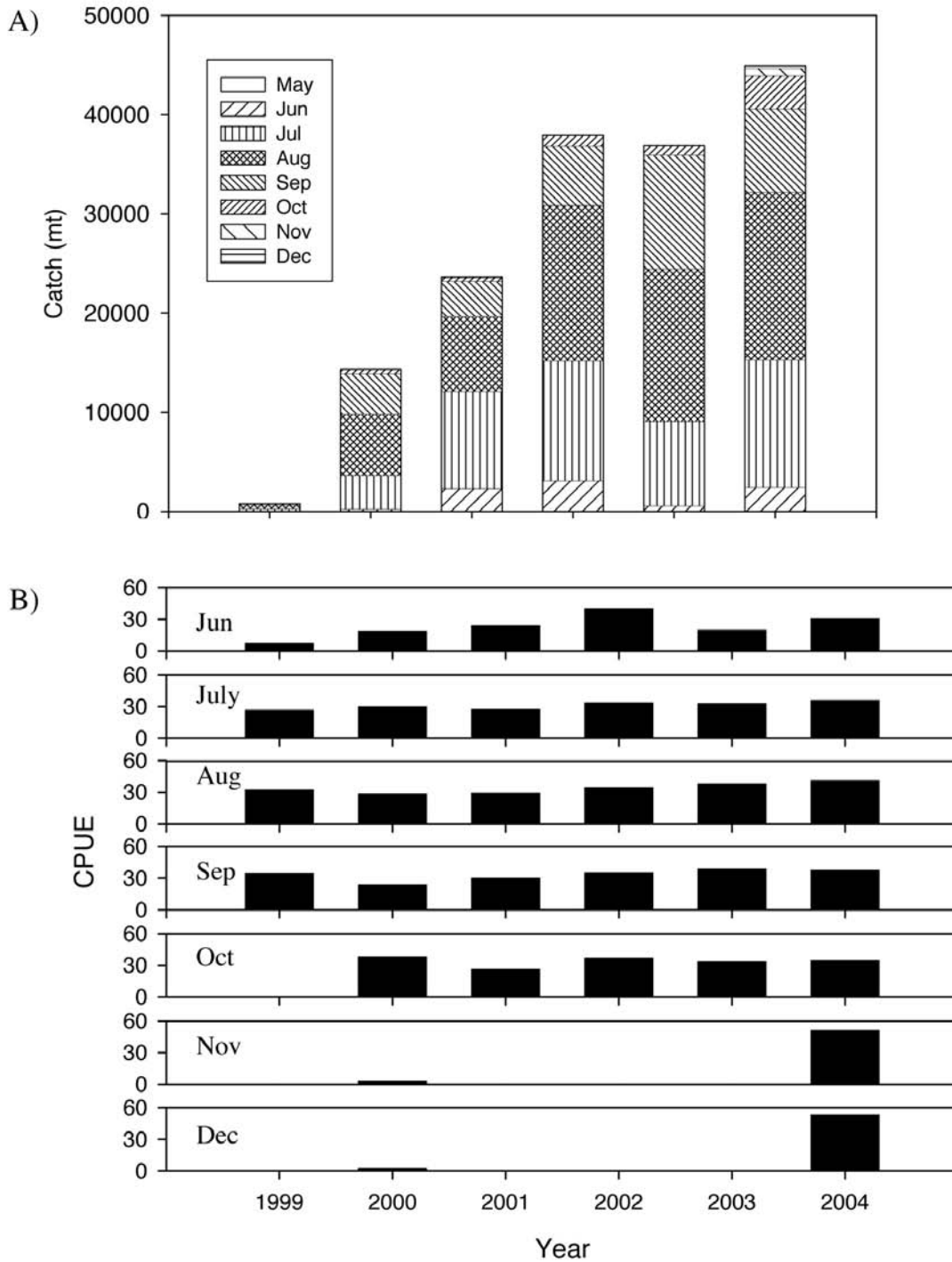
Figure 2. Monthly annual (A) commercial landings and (B) catch per unit effort (CPUE, mt/fishing trip) of Pacific sardine (*Sardinops sagax*) off Oregon/Washington, 1999–2004.

stomach by the multiplier derived from the ratio of sub-sample/stomach total settled volume. Finally, prey >1.0 mm were added to this estimate to give the full diet for that fish. Stomach fullness was defined as the percentage of total stomach prey weight divided by sardine body weight.

Linear regression was used to identify the relationships between stomach fullness, neuston biovolumes, and chlorophyll-*a* concentrations. Stomach fullness was arcsine-transformed and both neuston biovolumes and chlorophyll-*a* concentrations were log-transformed before linear regression analysis. A *t*-test was used to
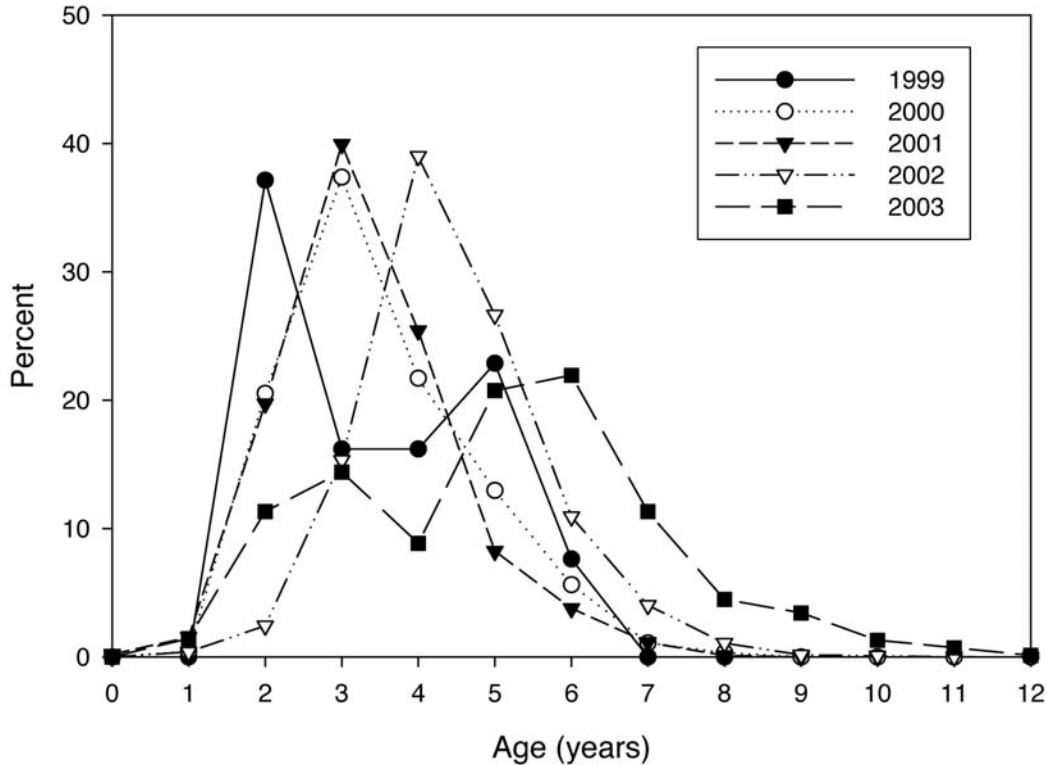
Figure 3. Age distribution of commercially landed Pacific sardine (*Sardinops sagax*) off Oregon/Washington, 1999–2003.

identify differences in stomach fullness between day- and night-caught sardines and to identify differences between nearshore- (<150 m isobath) and offshore- (>150 m isobath) caught sardines.

Identification of Sardine Predators

Sardine fish predators were identified from stomachs collected from the Predator, Plume and GLOBEC Surveys. Most of the fish stomachs examined from the Plume study were from sharks and juvenile and adult salmonids. Predator Surveys provided stomachs from Pacific hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), and chub mackerel (*Scomber japonicus*). The first 30 stomachs were taken from each predator species from each haul during the Predatory study (Emmett et al. 2001). The GLOBEC Survey provided stomach data from more than 20 species of fish and squids, including forage fishes and large sharks.[3] For most of these collections, whole frozen fish were brought back to the laboratory for detailed analysis, although shipboard scans of stomachs were performed on large fishes. Some shark stomach contents were collected by flushing out the contents using a pump, and the sharks were released alive. Overall, 10,000 fish stomachs were examined to identify which species consumed sardine.

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[3]T. Miller, unpubl. data

RESULTS

Commercial Catch and Age Distribution

Recent commercial landings of sardines in the Pacific Northwest started in 1999 when 1,000 mt were landed. By 2004, almost 45,000 mt were landed (fig. 2a), mostly in Astoria, Oregon. Landings generally begin in June and peak in August (fig. 2), with no landings from November through May. However, this seasonal harvest pattern can fluctuate, as some landings continued into December of 2000 and 2004 (fig. 2a). Catch per unit effort (CPUE) averaged between 25 to 36 mt/trip during June through September (fig. 2b), with highest average CPUE occurring in 2004. The unusually calm weather during fall and early winter 2004 allowed a few very successful fishing trips (fig. 2b).

Commercially harvested sardines range from 1 to 12 years old, with the majority being 3 to 5 years old (fig. 3). In most years (1999–2002), the catch has been primarily 2- to 5-year-old fish. However, in 2003 the catch was composed largely of older fish (i.e., 5- and 6-year-olds).

Ichthyoplankton Survey

For the entire five-year Ichthyoplankton Survey period, sardine eggs and larvae were the dominant taxon collected, comprising 26.5% of all ichthyoplankton collected. Sardine abundance exceeded that of the next two
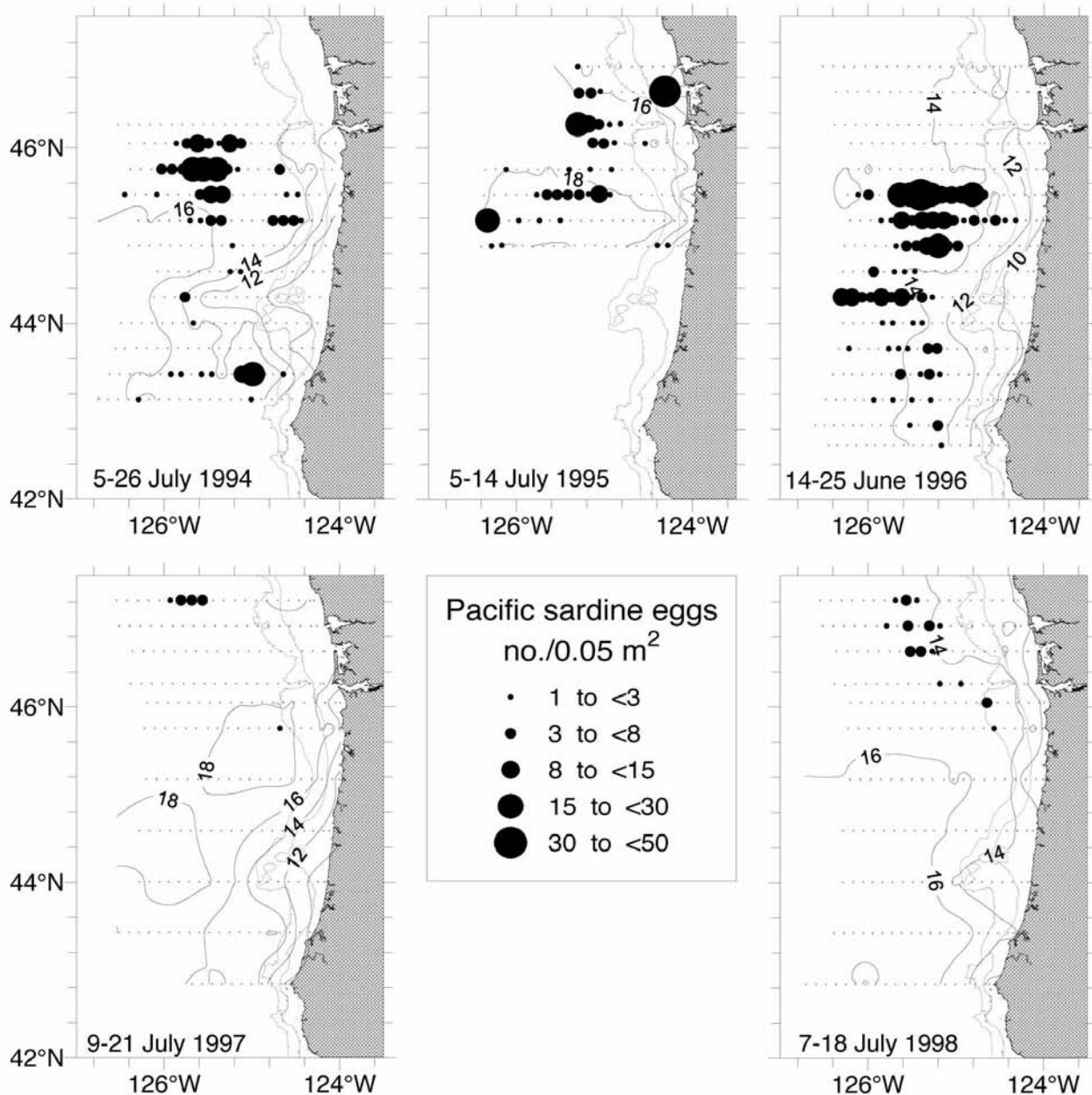
Figure 4. Distribution of Pacific sardine (*Sardinops sagax*) eggs during NMFS ichthyoplankton surveys off Oregon/Washington, 1994–98. Also shown are 3 m depth isotherms and 100 and 200 m depth contours.

species (*Diaphus theta* and *Stenobrachius leucopsarus*) combined. Sardine eggs were distributed over a substantial latitudinal proportion of the study area and well offshore (fig. 4). In some years (e.g., 1995) the entire spawning distribution was probably not effectively sampled because the spawning area went beyond the survey area. Nevertheless, sardine eggs were generally distributed between the 14° and 16°C isotherms (fig. 4). The distribution of sardine larvae was similar to that of eggs, although larvae were slightly farther offshore in most cases (fig. 5).

Triennial Surveys: Juvenile and Adult Spatial Distribution, Abundance, and Size

Sardines were not caught in any of the Triennial Surveys until 1992 (the surveys began in 1977), when high numbers were caught off the Columbia River (fig. 6). During all subsequent surveys, sardines were mainly distributed over the middle- and outer-shelf regions. In 1995, sardines were widely distributed spatially, occurring both farther south and more inshore compared to 1992, although overall abundance was lower. In 1998, catches were again lower and occurred predominantly
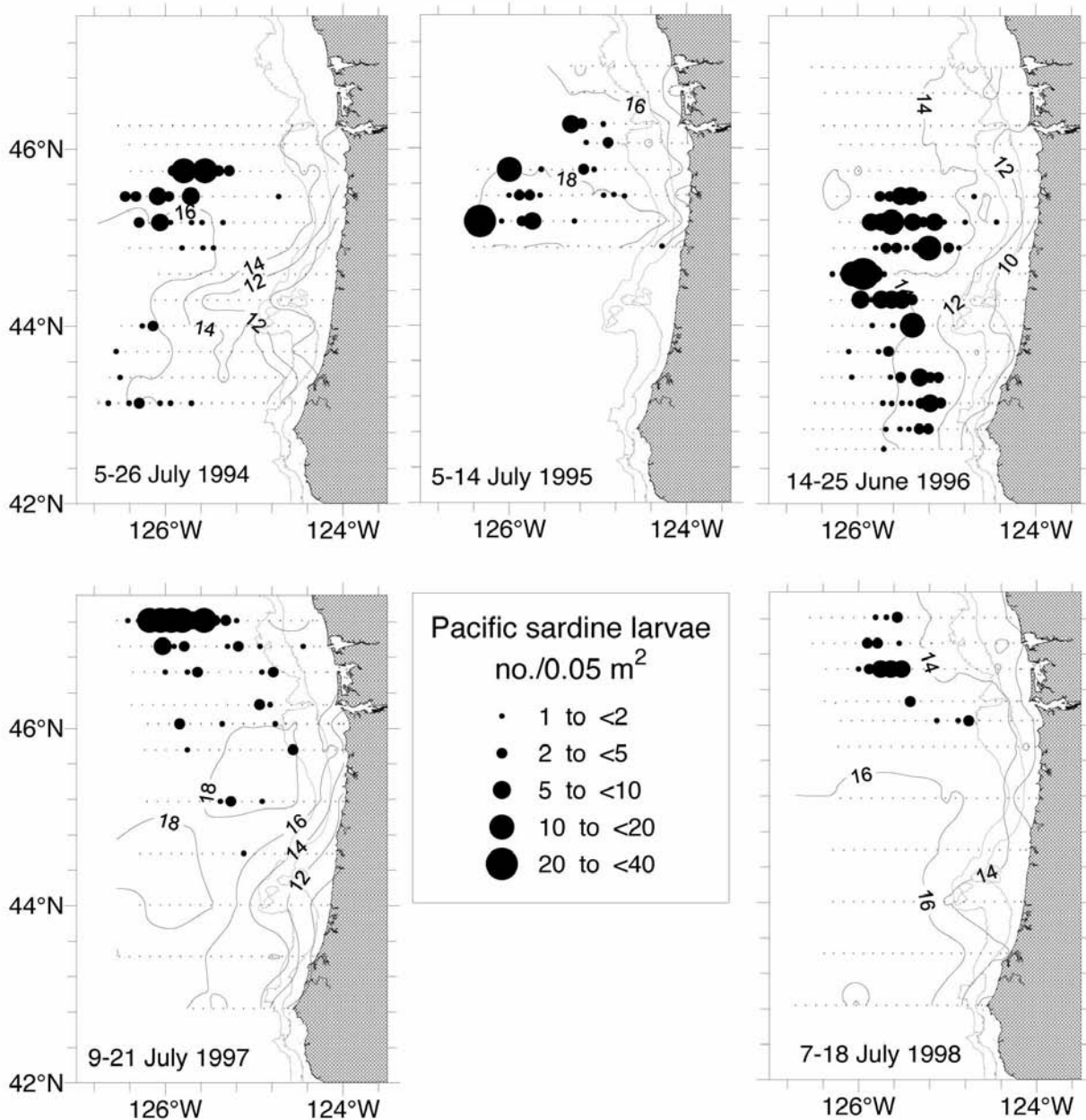
Figure 5.   Distribution of Pacific sardine (*Sardinops sagax*) larvae during NMFS ichthyoplankton surveys off Oregon/Washington, 1994–98. Also shown are 3 m depth isotherms and 100 and 200 m depth contours.

in the vicinity of the Columbia River. In 2001, sardines were more common north and south of the Columbia River mouth (fig. 6). Sardine biomass estimates from these bottom trawl surveys showed a decline in biomass in both the U.S.-Vancouver and Columbia statistical regions from 1992 to 1998 with an increase in 2001 (fig. 7). However, bottom-trawl catches are not efficient estimators of sardine abundance.

Sardines caught during the 1998 Triennial Survey ranged from 120 to 280 mm (FL) (fig. 8). Several size classes were represented in 1998, and sardines were pro-

gressively larger from south to north. There was also a second smaller-sized group, probably primarily 1-year-olds, off northern Washington—evidence that successful spawning and recruitment had probably occurred off the Northwest in 1997 (fig. 8).

NMFS Surface-Trawl Surveys:
Length Frequencies

Fork lengths of sardines captured during the various NMFS surface-trawl surveys ranged from 40 to 368 mm (mean = 158 mm) for all data combined from
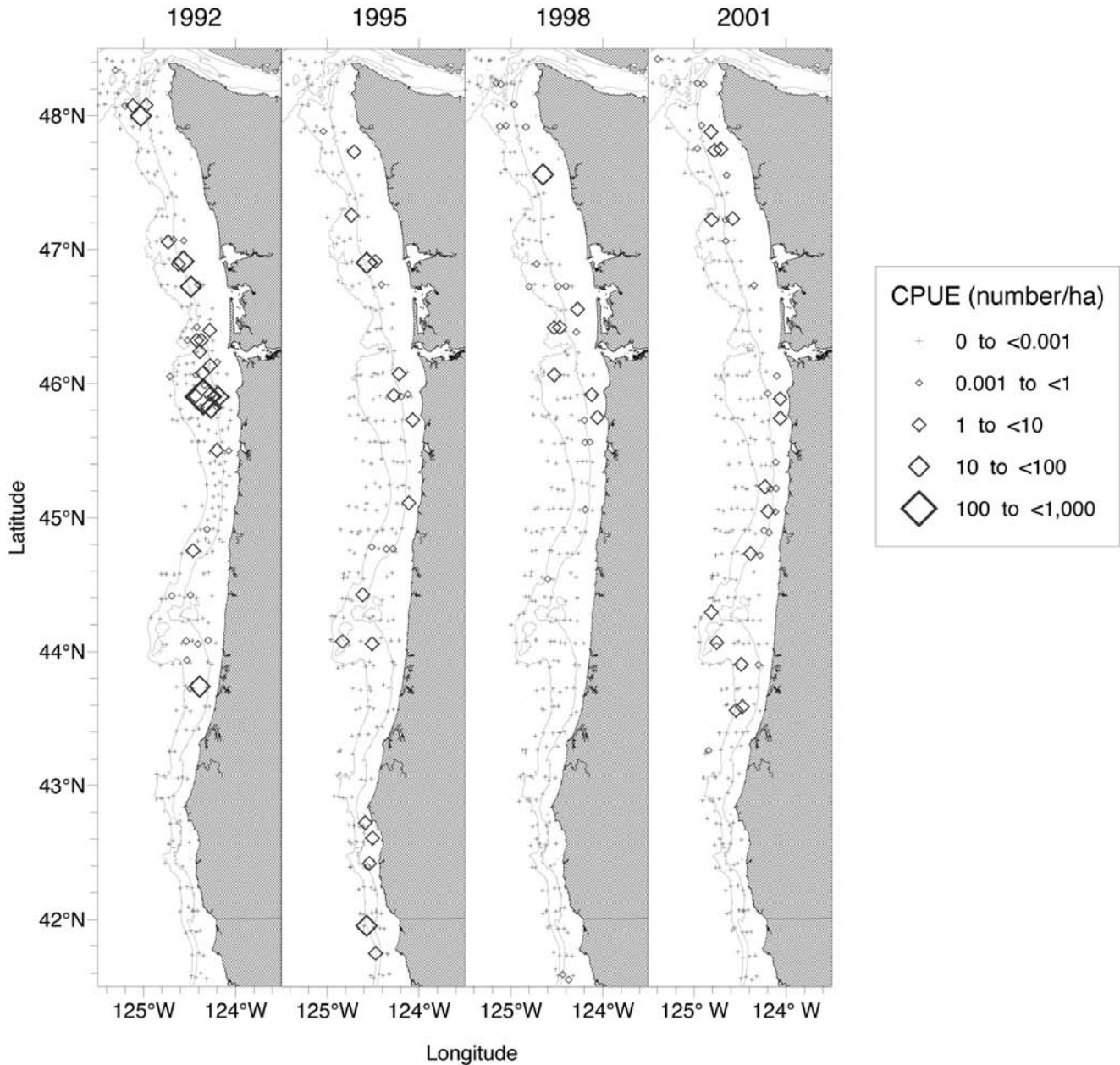
Figure 6. Distribution of Pacific sardine (*Sardinops sagax*) during NMFS 1992, 1995, 1998, and 2001 Triennial Surveys off Oregon/Washington. Also shown are 100 m and 200 m depth contours.

1998 to 2004. Analysis of length frequencies indicated that three size classes of sardines were caught, particularly in September (fig. 9). Length-frequency data from Plume Surveys in September indicate large annual fluctuations in the sizes of sardines inhabiting the PNW coast from 1998 to 2004 (fig. 10). While one or two large size classes are present each year, the small size class (<110 mm FL) is not. These small sardines appear to represent 0-age sardines, those spawned off Oregon and Washington in the summer. They were sparsely present in 1998 and 2001 but strongly represented in

2003 and 2004, years when the ocean was warm. Further analysis, along with considerations of growth and mortality, led us to assign sardines to size classes using lengths by calendar month (tab. 1). Small-, medium-, and large-sized groups were used to examine the spatial distribution of sardine catches and for statistical analysis. Sardines often show a large variance in age versus length (Butler et al. 1996). While we are confident that the small (<110 mm FL) sardines captured in September are 0-age, we are uncertain about the ages of other size classes.
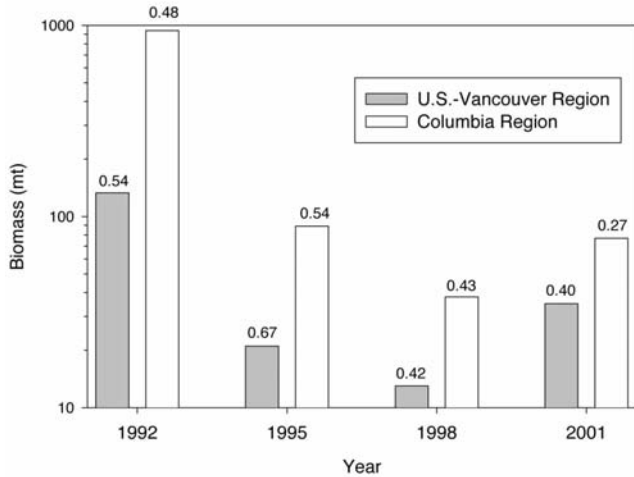
Figure 7. Estimated minimum biomass of Pacific sardine (*Sardinops sagax*) in the U.S.-Vancouver and Columbia fishery management regions from NMFS Triennial Surveys. Numbers above bars are the coefficient of variation of the biomass. Biomass estimates are considered minimums, since the trawl was mainly on the bottom and would not have sampled the sardines effectively.
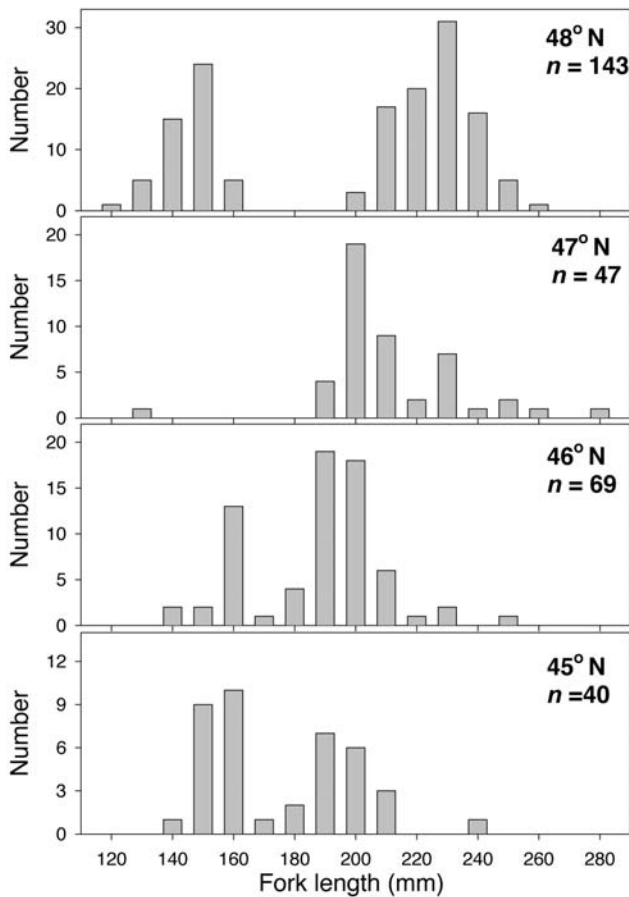

Figure 8. Size distribution of Pacific sardine (*Sardinops sagax*) collected during the NMFS 1998 Triennial Survey by degree of latitude.

Plume and GLOBEC Surveys: Juvenile and Adult Spatial Distribution and Abundance

Juvenile and adult sardines collected during Plume and GLOBEC Surveys showed substantial interannual and seasonal variation in distribution and abundance (fig. 11). During May, when sampling frequency was low, Pacific sardines were caught at only one station in 1999, 2001, and 2002, four stations in 2003, and eight stations in 2004; no sardines were caught in 2000 (fig. 11a). The large catches in May 2004 were primarily medium-sized sardines (fig. 11a). In June 1998, both medium- and large-sized sardines were collected, although at low frequencies. In June 1999, 2000, and 2001, sardines caught were primarily large-sized (fig. 11b) but still relatively uncommon. In 2002, catches of large-sized sardines were common, but only two stations had densities >1,000 10^{-6} m^{-3}. In June 2004, medium-sized (≤160 mm FL) sardines were caught at high densities at most stations (fig. 11b).

In August of 2000 and 2002, mostly large-sized (>180 mm FL) sardines were captured; while densities were generally low, a few hauls captured large numbers. A few sardines were also captured beyond the shelf break at the end of transects (fig. 11c).

During September 1998, sardines were collected at less than half the stations as in September 2003 (fig. 11d). Several stations in September 1999 and 2000 had high densities of both medium- and large-sized sardines. In 2001 small-sized, or 0-age sardines, were caught only along the two southernmost transects; in 2002 they were found at two stations in low abundance. However, in 2003 and 2004 small sardines had high densities at several stations (fig. 11d). In September 2003, most small sardines were caught at offshore stations along three transects, but in September 2004, their spatial distribution was more widespread (fig. 11d). The small juveniles had a more offshore distribution than sardines in the medium-sized group, which showed highest densities within the 100 m isobath (fig. 11d).

In November 2003, many juvenile sardines were caught along the Columbia River transect (46.2°N) and toward the end of other transects sampled (fig. 11c). Similar to September 2003, no medium-sized sardines and only a few large-sized sardines were caught.

Predator Surveys: Juvenile and Adult Abundance

Sardine densities around the mouth of the Columbia River showed very large monthly and annual fluctuations (fig. 12). Only in 1998, a warm El Niño year, were May sardine densities relatively high. Highest average monthly densities generally occurred in July, but not all years. The highest catch density was 2,337 10^{-6} m^{-3} (July 2003), and the lowest densities (zero catch) were in May 1999 and 2000.
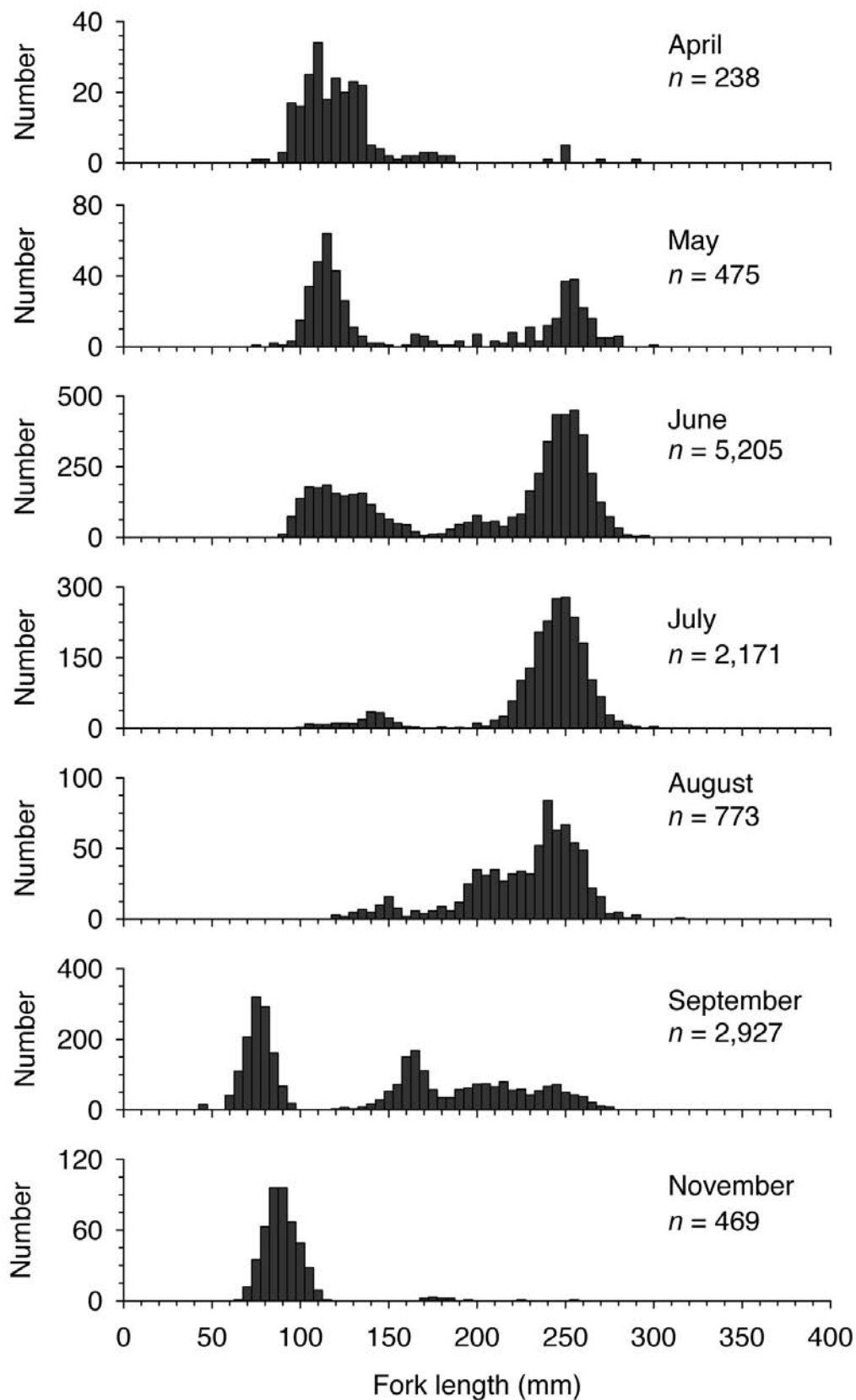
Figure 9.   Monthly length-frequency distribution of Pacific sardine (*Sardinops sagax*) collected during all NMFS 1998–2004 surface trawl surveys.
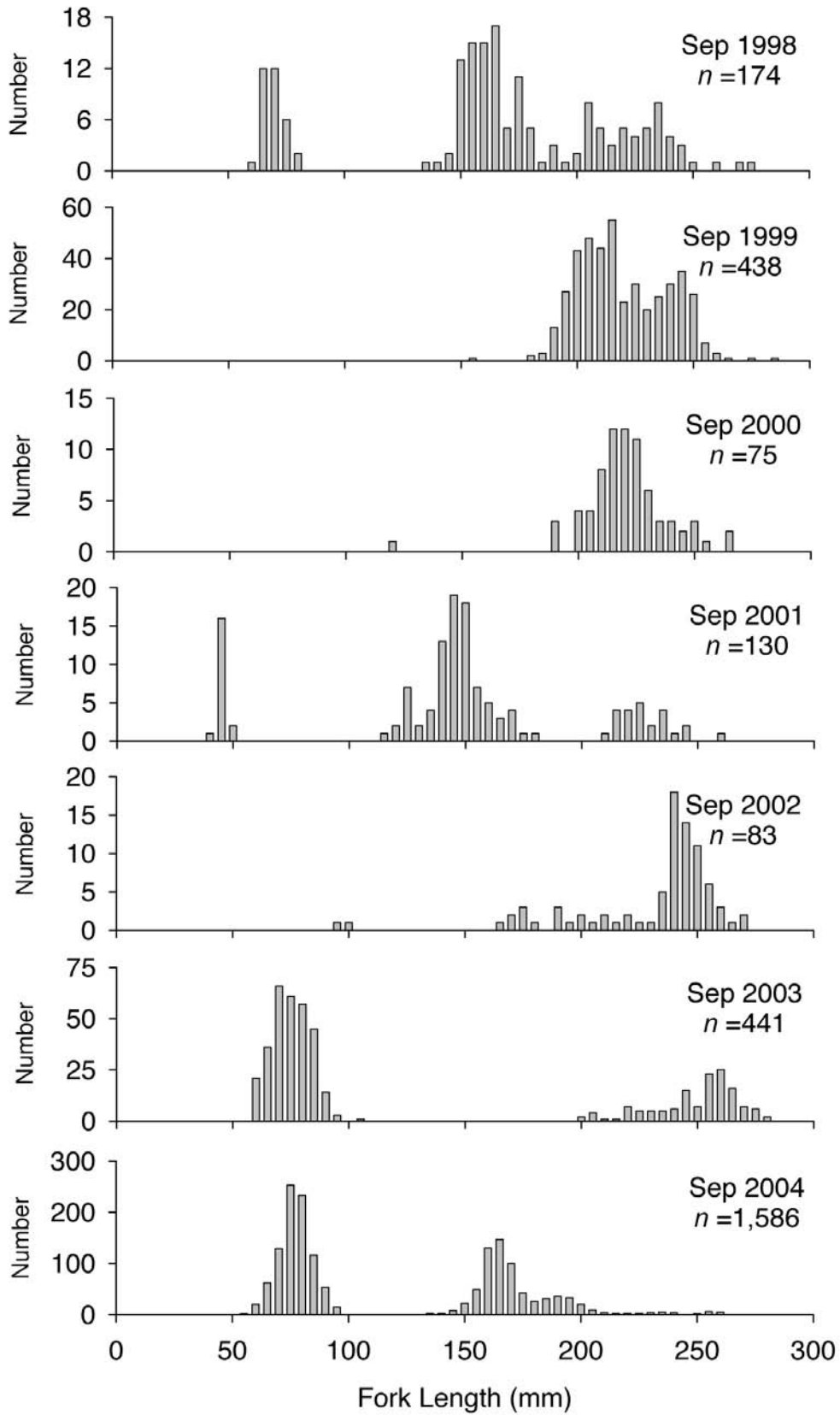
Figure 10.   Length-frequency distribution of Pacific sardine (*Sardinops sagax*) captured during September Plume Surveys off Oregon/Washington, 1998–2004.

Figure 11.   Distribution of Pacific sardine (*Sardinops sagax*) from NMFS 1998–2004 GLOBEC and Plume Surveys off Oregon and Washington during May (A), and June (B). The + signs indicate locations of a surface trawl. Also shown are 100 and 200 m depth contours.
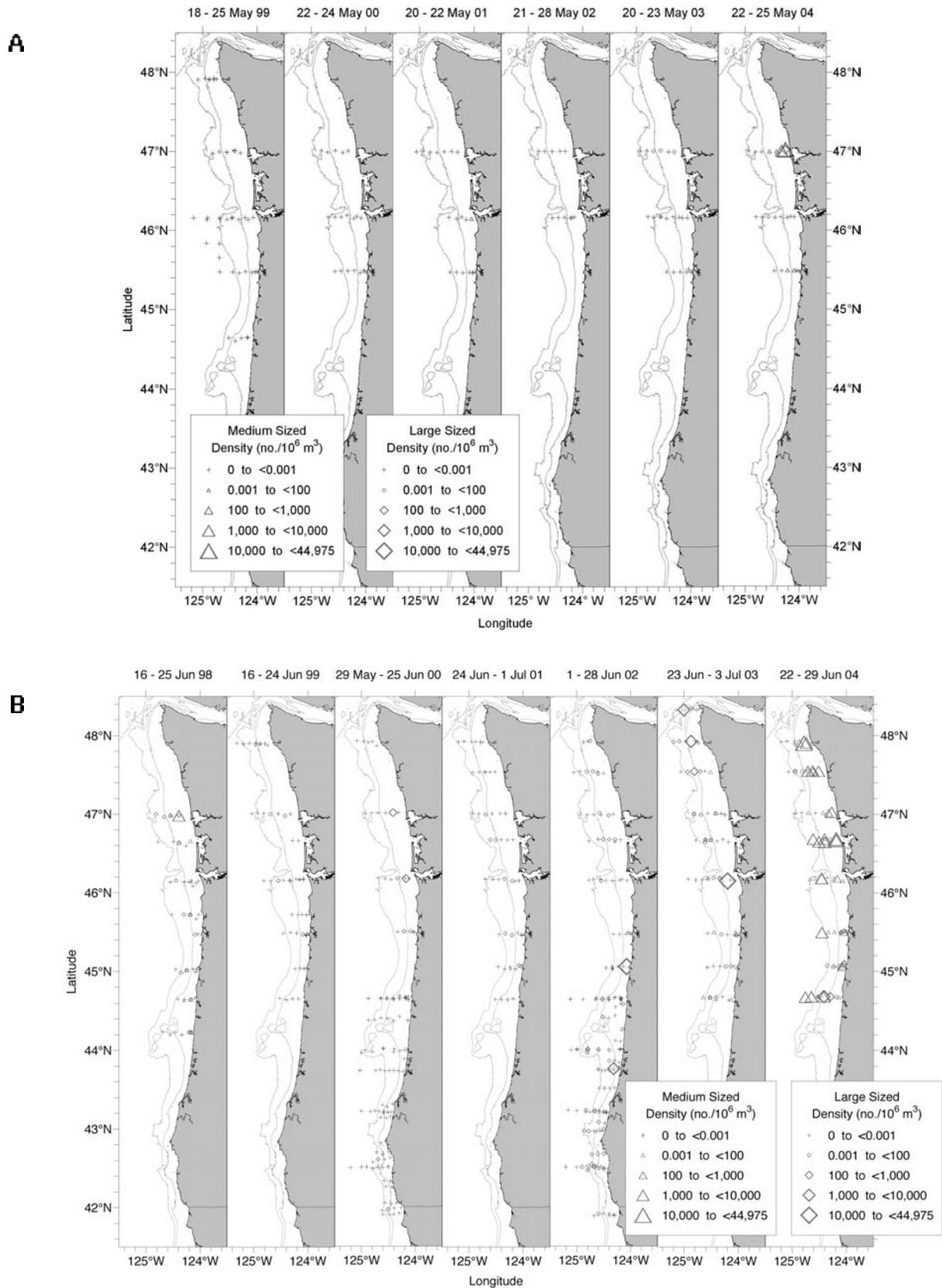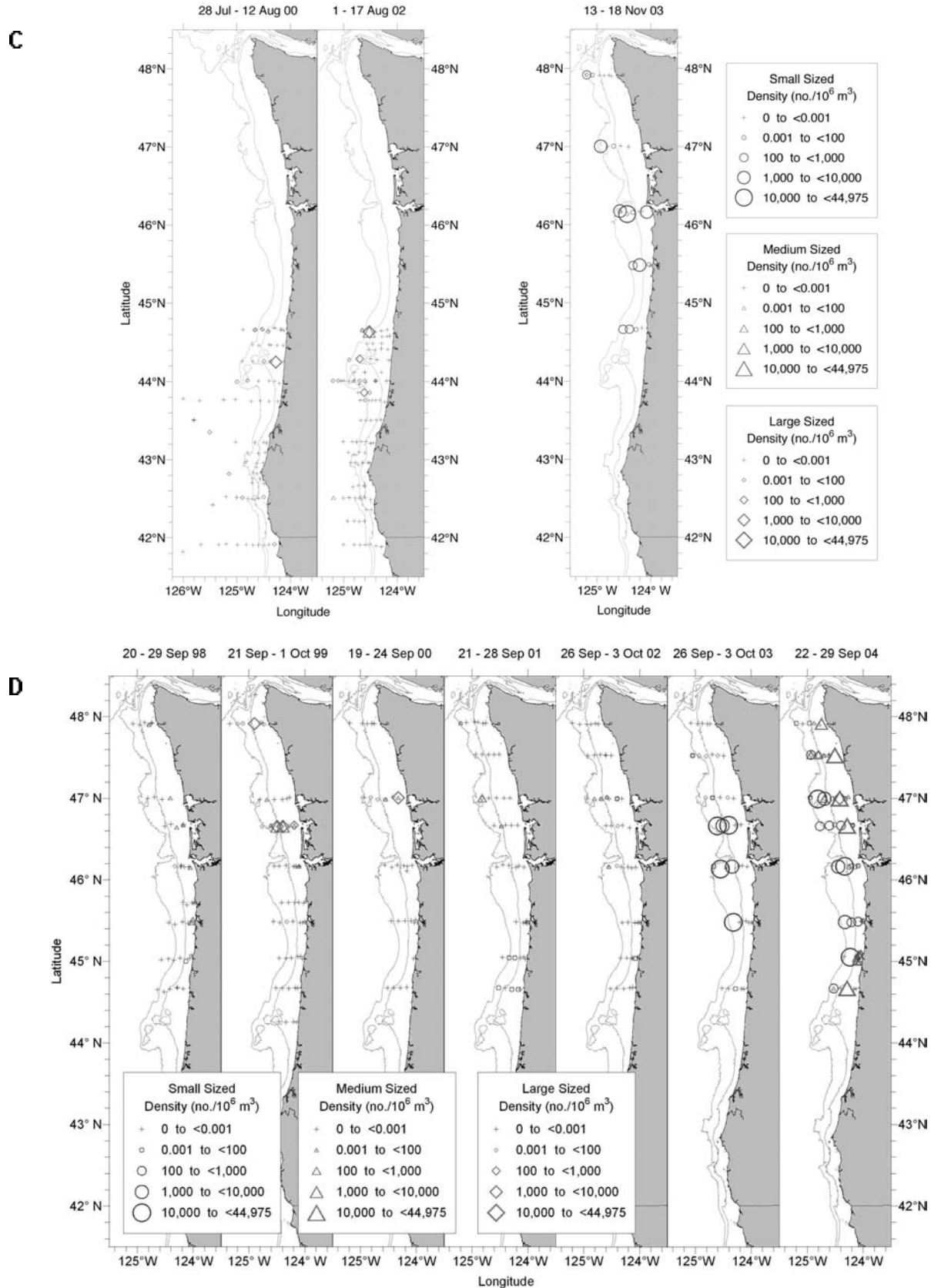
Figure 11.   Distribution of Pacific sardine (*Sardinops sagax*) from NMFS 1998–2004 GLOBEC and Plume Surveys off Oregon and Washington during August and November (C), and September (D). Also shown are 100 and 200 m depth contours.
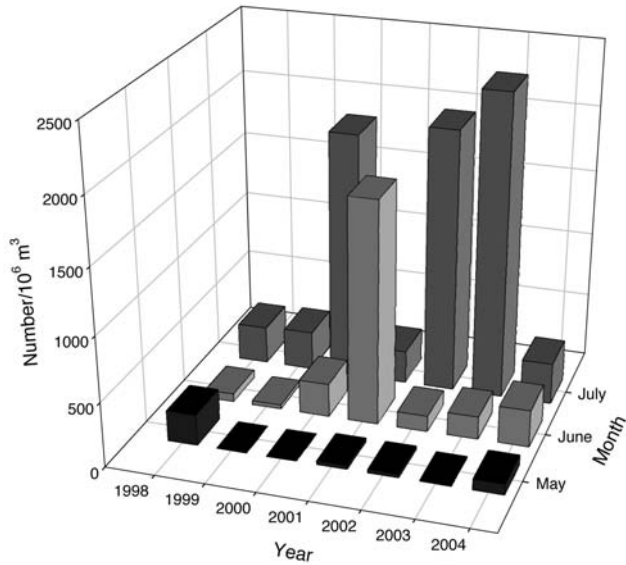
Figure 12. Average monthly densities of Pacific sardine (*Sardinops sagax*) during 1998–2004 NMFS Predator Surveys off the mouth of the Columbia River.
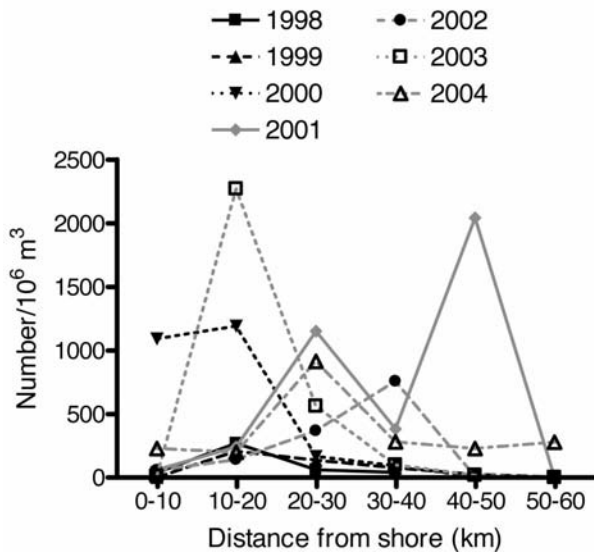

Figure 13. Average annual density of Pacific sardine (*Sardinops sagax*) at different distances from shore during 1998–2004 NMFS Predator Surveys off the mouth of the Columbia River.

TABLE 1
**Fork lengths (mm) of Pacific sardines (*Sardinops sagax*)
used to discriminate size classes of sardines**

Month	Small	Medium	Large
April		≤150	>150
May		≤155	>155
June		≤160	>160
July		≤170	>170
August		≤180	>180
September	<110	110 ≤ x ≤ 195	>195
October	<120	120 ≤ x ≤ 205	>205
November	<130	130 ≤ x ≤ 215	>215

TABLE 2
**Results of General Additive Modeling (GAM) analysis of
the effects of temperature (°C; Temp), salinity (psu; Sal),
and chlorophyll *a* concentrations (µg/l; Chl) on various
life stages of Pacific sardine (*Sardinops sagax*). Shown are
the probability values for the full GAM model for each
variable and all significant *p* values < 0.05 are in boldface
type. The sample size is the number of cases where all
three environmental variables were measured**

Life Stage	Sample size	Variable Temp	Sal	Chl
eggs	744	**0.0338**	0.1429	0.0617
larvae	744	0.7006	0.4956	0.7320
small juveniles	972	**0.0370**	0.2200	**0.0139**
medium juveniles/adults	972	**0.0416**	0.1728	**0.0119**
large adults	972	0.4231	**0.0358**	**<0.0001**

Sardine densities showed little relationship with distance from shore (fig. 13). While in some years the highest average catches were nearshore (<20 km, 2000 and 2003), in other years, the highest catches were offshore (40–50 km, 2001).

Habitat Analysis

Using all data from the NMFS surface-trawl surveys, we found that large- and medium-sized sardines were more frequently captured at lower surface salinities and temperatures than small-sized sardines (fig. 14). Small-sized sardines were most commonly found in warmer temperatures (>12°C) and higher salinities (>28).

For the Ichthyoplankton, Plume, and GLOBEC Surveys, the GAM three-factor models revealed that temperature was significantly related to the abundance of eggs and small- and medium-sized life history stages (tab. 2). The relationship between catch and temperature was positive for all stages. Salinity was a significant indicator for only the large-sized sardines and showed a negative effect. Chlorophyll *a* was an important explanatory variable only for the juvenile and adult stages (tab. 2) and showed a positive coefficient with all three life stages.

Sardine densities from the Predator Survey were highly related to temperature; most fish were caught when the 3 m depth temperature was >12°C (fig. 15). Few sardines were caught at <12°C. The average temperature at 3 m depth explained 50% of the variation (adjusted R^2) (GLM, $p < 0.01$) in average sardine densities per cruise off the Columbia River from 1999 to 2004.

Food Habits

Sardines consumed a variety of prey depending on location and season. In September 1999, sardines off Washington had diets composed primarily of phytoplankton; 84% by weight (tab. 3). Copepods (all stages) and Appendicularia were the primary animal prey items
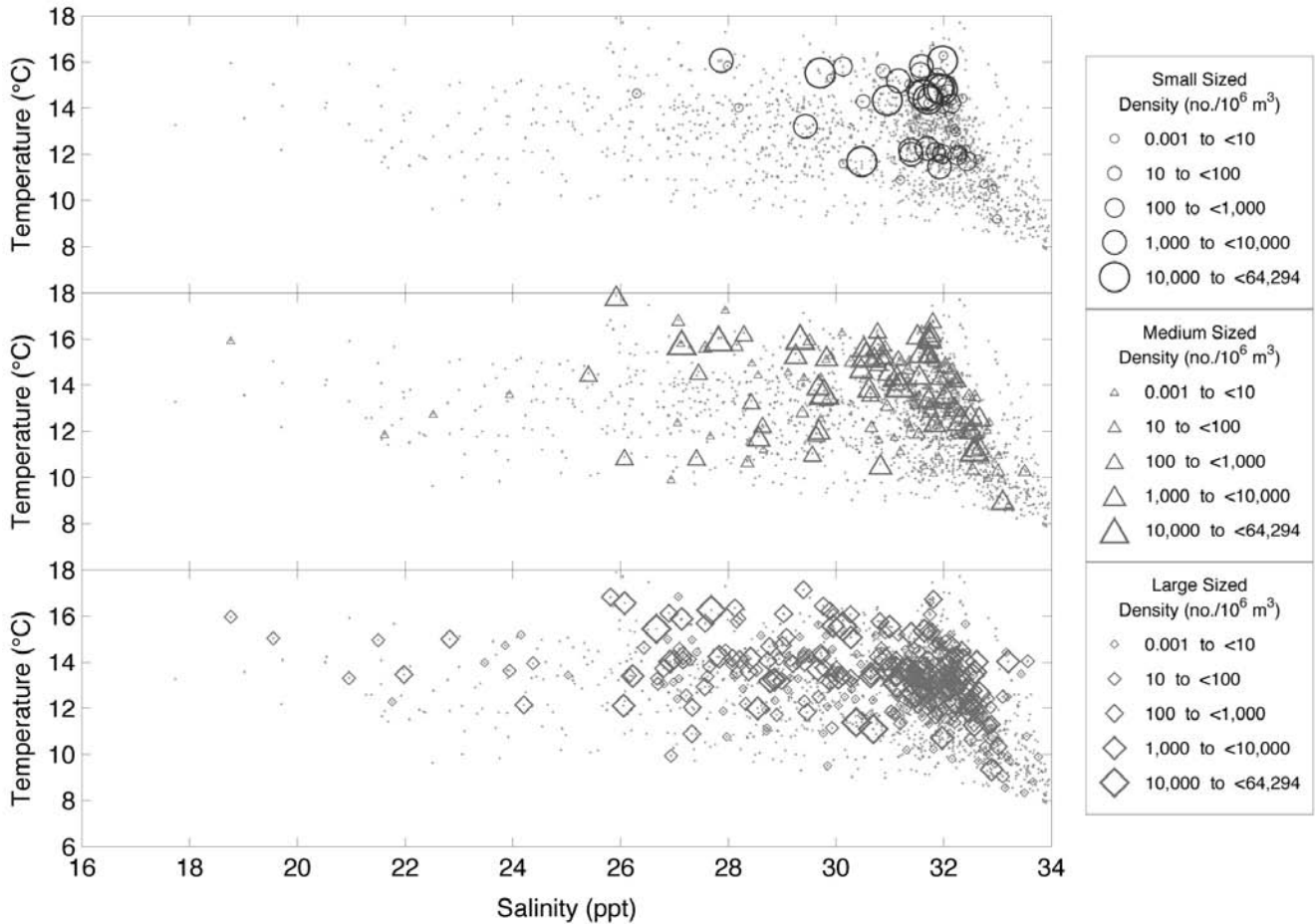
Figure 14.   Densities of three different size classes of Pacific sardine (*Sardinops sagax*) captured during GLOBEC and Plume Surveys in relation to 3 m depth ocean temperatures and salinities. Locations where no sardines were caught are shown as light grey dots. Refer to Table 1 for size class definitions.

(tab. 3). Identifiable copepods in the stomachs were primarily *Acartia* spp. and *Pseudocalanus* spp.

Numerically, adult copepods dominated the diet in August 2000 and June and August 2002, (tab. 3), while euphausiids and copepods were primary prey by wet weight. *Euphausia pacifica* was the most important prey by weight during August 2000, whereas *Thysanoessa spinifera* was the primary prey in August 2002. Most copepods consumed in 2000 and 2002 were at egg, nauplii, or copepodite stages.

Analysis of stomach fullness from sardines collected during the day and night indicated no diel feeding differences (*t*-test, $p = 0.54$). All stomachs were full or distended and had an average stomach fullness of 0.44%±1.23% (SD) of sardine body weight. Stomach fullness was poorly related with neuston biovolume (linear regression, $p = 0.51$). There was also no relationship between phytoplankton abundance in the diet (percent wet weight) and chlorophyll *a* concentrations (linear regression, $p = 0.81$).

Analysis of sardines collected during the GLOBEC Survey showed nearshore/offshore differences in feeding. Sardines in nearshore habitats (inshore of the 150 m isobath) fed primarily on phytoplankton and copepods, whereas those in offshore habitats (>150 m isobath) consumed predominantly adult euphausiids (fig. 16). Nearshore sardines had higher stomach fullness than offshore sardines in August 2000 (*t*-test, $p = 0.002$) but not during June or August 2002 (*t*-test, $p > 0.05$).

Sardine diets from September 1999 and August 2002 contained high proportions of phytoplankton, which coincided with high chlorophyll-*a* concentrations during the two periods (11.7±5.0 and 16.3±7.2 $\mu g \cdot l^{-1}$, respectively). The relatively low contribution of phytoplankton to sardine diets in August 2000 and June 2002 coincided with low chlorophyll-*a* concentrations (4.9±4.1 and 3.5±4.1 $\mu g \cdot l^{-1}$, respectively).

Sardine Predators

We identified seven different fish species that had consumed sardines (tab. 4). Predators included both juvenile and adult stages of coho and Chinook salmon, Pacific hake, jack mackerel and three species of shark.
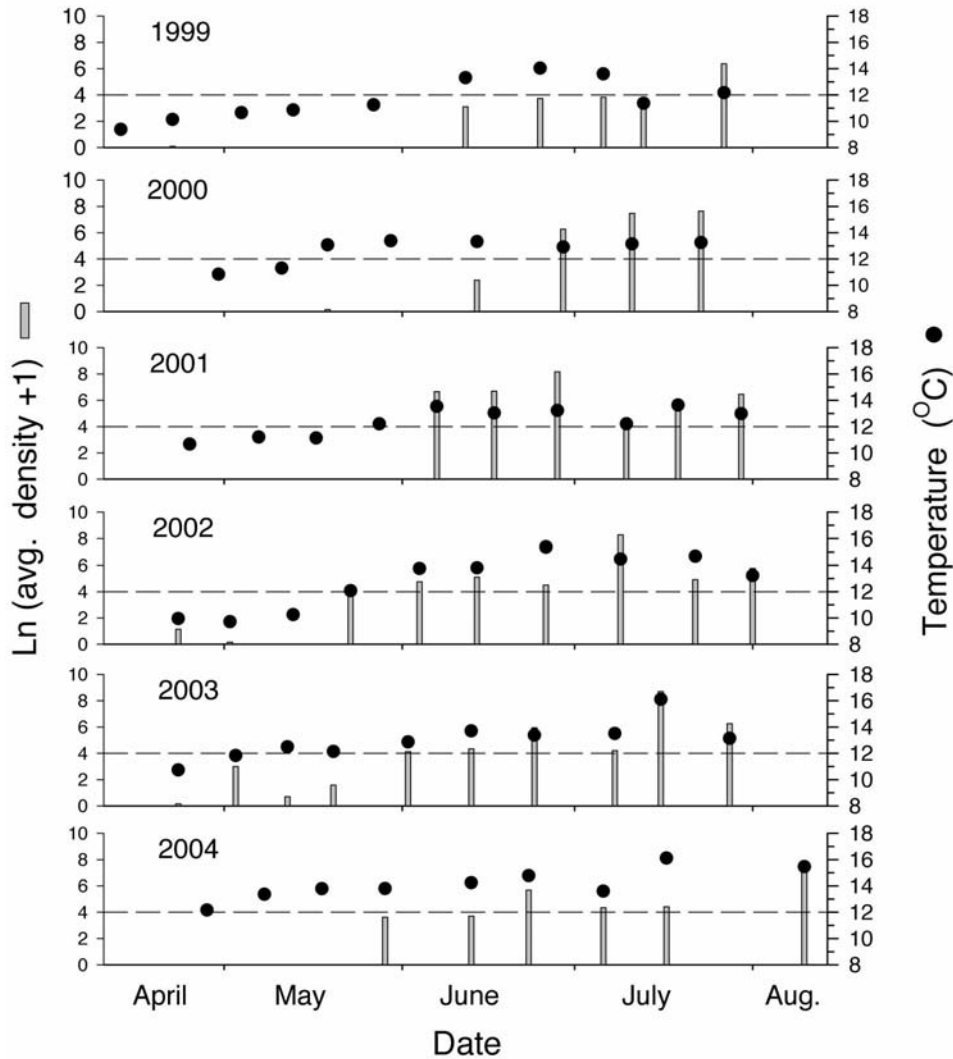
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Figure 15. Average cruise densities of Pacific sardine (*Sardinops sagax*) during 1998–2004 NMFS Predator Surveys off the mouth of the Columbia River in relation to average cruise surface (3 m depth) temperatures.

DISCUSSION

Distribution and Stock Structure

The increase in the commercial sardine catch from 1999 to 2004 off the PNW appears to be related to both more fishing effort and changes in sardine abundance. However, there remains much uncertainty regarding how many sardines reside off the PNW and whether the individuals spawning off Oregon/Washington are a separate population from those that reside in California waters (Smith 2005). If sardines spawning off the PNW (June/July, this study) are not also spawning off California (February–June/July) (Hernandez-Vazquez 1994), then sardines in the PNW may be considered a separate population.

There is presently little information confirming that PNW and California sardines are separate stocks. Radovich (1982), who studied Northwest sardines in the 1930s and 1940s, believed they were separate stocks. However, recent genetic data indicate no identifiable stock differences between PNW and California sardines (Hedgecock et al. 1989; Lacomte et al. 2004), but genetic data may be insensitive to recent population differentiation (Kinsey et al. 1994). The age-class structure of harvested sardines off Oregon/Washington does appear to reflect patterns of local recruitment, suggesting separate stocks. The age-class structure of the commercially caught sardines in the PNW (fig. 3) suggests that many were locally spawned and are possibly a separate population. In 1999, most of the sardines harvested were 2-year-olds (1997-year-class); this year-class was also important in 2000. In 2003, the 1997 year-class was again the primary year-class captured; few younger age-classes were caught. Both 1997 and 1998 were warm years accompanied by successful spawning and recruitment. From 1999 to 2002, the ocean was

TABLE 3
Pacific sardine (*Sardinops sagax*) diets by percent number (%N) and wet weight (%W)

Prey Taxa	1999 September %N	1999 September %W	2000 August %N	2000 August %W	2002 June %N	2002 June %W	2002 August %N	2002 August %W
Chordata								
Osteichthyes egg			<0.1	0.4				
Appendicularia	6.7	2.9	0.2	0.2	0.6	0.3		
Arthropoda								
Crustacea								
Copepoda								
Unidentified egg	42.0	2.3	1.1	<0.1				
Unidentified nauplii	25.5	0.2	7.3	—				
Unidentified copepedite/adult	13.6	4.3	38.0	0.3	75.2	95.0	68.9	1.7
Acartia spp.	6.7	2.7	11.0	0.8	0.1	<0.1		
Calanus spp.			0.4	0.1	2.7	0.5	0.4	<0.1
Centropages spp.			0.6	—				
Oithona spp.			0.5	—				
Pseudocalanus spp.	5.5	3.5	8.8	0.7	17.6	0.4	0.4	<0.1
Cirripedia								
Unidentified nauplii					0.1	<0.1		
Euphausiidae								
Unidentified calyptopis			0.4	<0.1				
Unidentified egg			29.0	0.3	1.6	0.3	9.5	<0.1
Unidentified nauplii			0.9	<0.1	0.1	<0.1	2.6	<0.1
Unidentified furcillia			0.2	0.1	0.4	<0.1		
Euphausia pacifica			1.1	74.7	<0.1	0.3	0.1	0.8
Thysanoessa spinifera					<0.1	0.2	14.8	75.2
Amphipoda								
Hyperiidea			0.1	0.3				
Mollusca								
Unidentified invertebrate egg			0.4	<0.1	1.3	<0.1	3.3	<0.1
Phytoplankton	—[a]	84.1	—	6.0	—	1.7	—	21.1
Unidentified Material			—	15.7	—	0.9	—	0.8
Number Analyzed	20		69		47		48	
Mean Fork Length in mm (SD)	215.2 (19.2)[b]		220.8 (3.1)		238.4 (3.1)		234.6 (2.9)	

[a]Prey item not counted or weighed.
[b]Measurements obtained from field samples (*n*=263) where stomachs were collected for diet analysis.
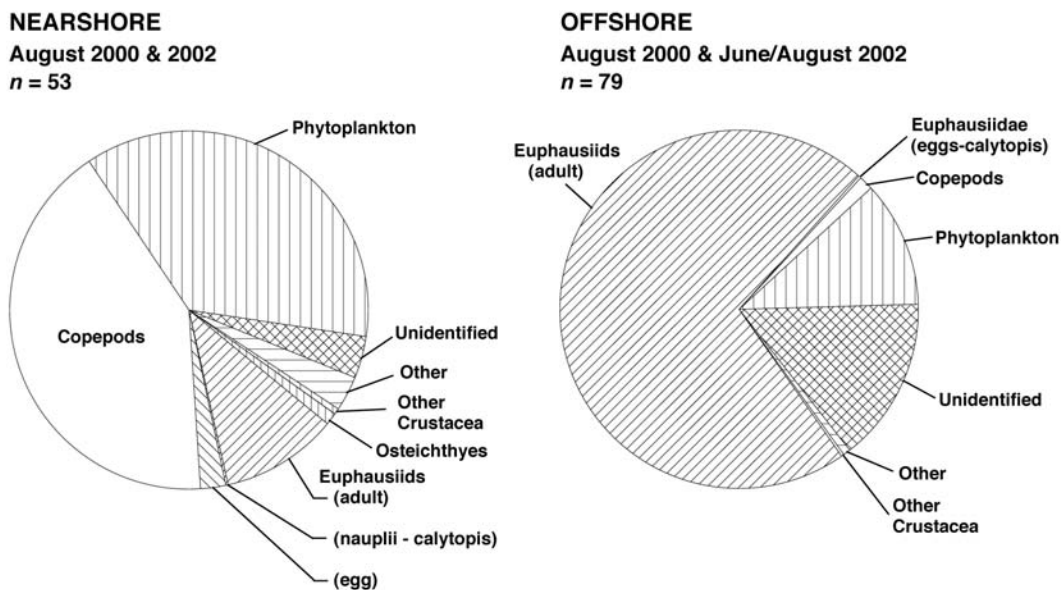

Figure 16. The nearshore (<150 m isobath) and offshore (>150 m isobath) diets (wet weight composition) of Pacific sardine (*Sardinops sagax*) off Oregon from 2000 and 2002 GLOBEC Surveys.

TABLE 4
Fish predators of Pacific sardine (*Sardinops sagax*) off the Oregon and Washington coast

Predator	Scientific name	Size range (mm)	Length type	Length (FL, mm) of sardine eaten	Number of occurrences	Total number
Coho salmon juveniles	*Oncorhynchus kisutch*	252–259	FL	27–86	8	18
Coho salmon adults	*Oncorhynchus kisutch*	532–675	FL	190–205	2	3
Chinook salmon juveniles	*Oncorhynchus tshawytscha*	150–252	FL	20–56	22	38
Chinook salmon adults	*Oncorhynchus tshawytscha*	700–870	FL	125–250	4	4
Pacific hake	*Merluccius productus*	420–720	SL	190–215	9	12
Jack mackerel	*Trachurus symmetricus*	523–573	FL	99–145	9	13
Blue shark	*Prionace glauca*	1160	TL	210	1	1
Soupfin shark	*Galeorhinus galeus*	1360–1750	TL	200–240	2	13
Thresher shark	*Alopias vulpinus*	3200–3900	TL	*		3

*Regurgitated on deck after capture, not quantitative.

cold (Peterson and Schwing 2003) and sardine spawning success off the PNW appeared limited; few 0-age juvenile sardines appeared in the September Plume Surveys (fig. 11). Sardines that spawned from 1999 to 2002 were not abundant in the commercial fishery.

The commercial catch age-class and September size-class structure data suggest that sardines off the PNW consist of a local stock plus fish from California, but additional evidence is needed to identify that PNW sardines are a separate stock. There are many non-genetic techniques that could be used to identify stock differences, including parasites (Marcogliese et al. 2002), meristics (Smith 2005), otolith elemental composition (Milton and Chenery 2001), and morphometric methods (Felin 1954; Kinsey et al. 1994; Cadrin et al. 2005).

Habitat Analysis

Although the GAM analysis identified physical variables that appear to be related to the spatial distributions of sardines at various life-history stages, the amount of variability accounted for by these variables was fairly low. This may be due to the nature of the sampling such that, in some cruises, all habitats sampled may have been within the environmental tolerances of sardine. In addition, the highly contiguous distributions commonly observed with pelagic schooling fishes also present serious statistical problems of analysis. Finally, important mesoscale and fine-scale physical processes, such as fronts or eddies (e.g. Logerwell and Smith 2001; Nishimoto and Washburn 2002), may affect the distribution of all life stages. However, they are not likely to be resolved with our sampling strategy, thereby reducing our ability to identify physical and biological factors that affect sardine distributions. Many pelagic fishes change their behavior and distribution with time of day (Fréon et al. 1993; 1996; Fréon and Misund 1999). Sardines, for example, are known to make diel vertical migrations toward the surface at night (Giannoulaki et. al., 1999). Comparisons between day and night surface trawl catches off Oregon suggest that sardines have higher densities or are more catchable at the surface at night (Krutzikowsky and Emmett, 2005).

Some consistent patterns do emerge from the statistical analyses. Temperature and salinity seem to be important determinants of habitat for early life stages, and there may even be some threshold temperature level needed to induce spawning. Larger sardines appear to show an affinity for the lower salinity Columbia River plume water that may be more productive than oceanic waters. Catch rates of the more mobile juvenile and adult fishes are positively correlated with chlorophyll concentrations, which implies that these fish are migrating into or are maintaining their positions within productive areas necessary for faster growth or reproduction. Our analysis shows that the sardines' habitat requirements or preferences appear to change ontogenetically and that no one variable can explain their distribution throughout their life history.

Diet and Role in Ecosystem

Analysis of PNW sardine diets indicates that sardines consume primarily phytoplankton, copepods, and euphausiids. This is in general agreement with previous studies of sardine diets from British Columbia (Hart and Wailes 1931; McFarlane and Beamish 2001), Southeast Alaska (Wing et al. 2000), Western Pacific (Stovbun 1983; Kawasaki and Kumagai 1984), and the Benguela Current (Van Der Lingen 2002). The proportional importance of primary prey observed in the present study, however, varied spatially and temporally, and coincided with the spatial distribution of prey and the temporal variation in primary (chlorophyll *a*) and secondary production (neuston biovolume).

Sardine diets exhibited spatial heterogeneity in the prey indicative of the onshore/offshore plankton community composition and overall production. Nearshore sardines typically consumed more phytoplankton and copepods whereas offshore sardines consumed more euphausiids. This dietary pattern reflects the typical abundance of copepods and phytoplankton on the shelf

(Anderson 1965; Morgan et al. 2003) and euphausiids on the slope-offshore region (Swartzman 1999).

We did not find correlations between sardine diet (as a percent of body weight), neuston biovolume, proportion of phytoplankton in the diet, and 3 m chlorophyll *a* concentrations. In contrast, Hart and Wailes (1931) observed a moderate correlation (mean = 0.46) between sardine stomach biomass and zooplankton. The apparent lack of correlation between sardine diet and primary and secondary producers implies that sardines are feeding deeper in the mixed layer, possibly just above the thermocline at the chlorophyll maximum. At this depth, phytoplankton, copepods, and euphausiids may be more concentrated (Lamb and Peterson, 2005) and more efficiently obtained. Alternatively, feeding may have occurred at some distance from the capture location, or food resources were sufficiently patchy to yield low statistical correlation. Sardines did show strong seasonal and interannual variation in diet that covaried with changes in primary and secondary production.

The low contribution of copepods and the high amount of phytoplankton in the diet in August 2002 was likely due to the anomalous conditions experienced on the Oregon shelf at the time. During late summer 2002, entrainment of cool, nutrient-rich, subarctic water on the shelf resulted in very high primary productivity (Wheeler et al. 2003) but low copepod abundance (Goericke et al. 2004). The similarities between observed annual/seasonal ocean productivity and sardine diet reveal an important link between the physical oceanographic conditions and sardine trophic responses. Sardines may be an ideal indicator of oceanographic conditions because they filter feed through prey fields (Alamo and Bouchon 1987; James 1988), consuming organisms that are directly influenced by physical shifts in their environment.

Similar to the 1930s, sardines are presently prey for many large piscivorous fishes off the PNW, including adult Chinook and coho salmon (Chapman 1936). Our estimates of fishes that consume sardines are probably minimal because surface trawl nets were inefficient at capturing large, fast-swimming fishes. We suspect, for example, that albacore tuna (*Thunnus alalunga*) and large chub mackerel (*Scomber japonicus*) also eat sardines off Oregon and Washington.

The importance of sardines to PNW salmon life histories is difficult to determine at this time. As sardines have become abundant, salmonid runs in the Columbia River and elsewhere in the PNW have recovered significantly since 1999 (Williams et al. 2005). An increase in forage fish (including sardines) in the Columbia River estuary appears to have reduced Caspian tern (*Sterna caspia*) predation on juvenile salmon smolts.[4] Pacific har-

bor seals (*Phoca vitulina richardsi*), which also prey heavily on juvenile salmonids in coastal estuaries, are now consuming sardines off Oregon (Orr et al. 2004). Besides providing an alternative prey for juvenile salmonid predators (Pearcy 1992), abundant sardine populations may provide adult salmonids with additional calories, allowing them to grow larger, produce larger eggs, and improve hatching and alevin success (Fleming and Gross 1990). The effects of increased sardine abundance on other PNW fishery resources are unclear, but the high sardine biomass is likely to be important food for many different predators in this region.

Relationship to Ocean Conditions

It is believed that the abrupt decline in abundance of Pacific sardines in the late 1940s and 1950s, and the recent resurgence, is largely related to ocean temperature changes linked to climate or ocean regime changes (Jacobson and MacCall 1995; McFarlane et al. 2002; Chavez et al. 2003). During the warm regime of the 1930s–1940s, sardines in the California Current flourished, while during the cold regime of the 1950s–1970s, they declined. In the late 1970s, and perhaps again in the late 1980s, a new warm ocean regime began and sardines in the California Current responded favorably (McFarlane et al. 2002; Chavez et al. 2003). However, in 1999, the Northeast Pacific Ocean appeared to move into a new "cold" regime (Peterson and Schwing 2003), which was evidently not favorable for sardine spawning and recruitment. Our data indicate that this was particularly true for PNW sardines, as few small, 0-age sardines were captured from September 1999–2002 (fig. 11). However, this cool period did not last; both 2003 and 2004 were years with warm sea surface temperatures and apparent successful recruitment of 0-age sardines. If warm ocean conditions continue off the PNW, as expected given the long-term trend of warmer climate and oceans (Levitus et al. 2000), sardines will probably continue to spawn successfully off Oregon and Washington.

Northern anchovy (*Engraulis mordax*) and Pacific sardine populations have been observed to fluctuate out-of-phase with each other, probably because of different temperature preferences (Lluch-Belda et al. 1992; Chavez et al. 2003). However, this has not been observed in the Northwest; both northern anchovy and Pacific sardine populations (and other forage fish populations) have been increasing since 1999[5] and presently represent a substantial proportion of the pelagic nekton abundance off Oregon and Washington (Emmett and Brodeur 2000; Brodeur et al. 2004, 2005). As others (Jacobson and MacCall 1995) have found, our analysis revealed that sea surface temperature strongly influences sardine abun-

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[4]D. Roby, Oregon State University, Corvallis, OR, pers. comm.

[5]Emmett et al. unpub. ms

dance, distribution, and spawning success. Adult sardines, which migrate south to California during the winter, generally do not arrive to PNW coastal feeding grounds until sea surface temperatures exceed 12°C. This arrival usually occurs in July, after they have spawned in warmer (>14°C) waters offshore during June and July. Sardine spawning surveys and surface trawls off Oregon and Washington in July 2003 and 2004 found most adult sardines within 60 nm of shore.[6] Small juvenile sardines, in contrast, do not appear to migrate but over-winter in nearshore coastal waters, including the Columbia River estuary and Willapa Bay. One of us (Bentley) recently observed a die–off of juvenile sardines in the Columbia River estuary in December 2004, which was apparently related to high tides and high freshwater flows causing osmotic stress and death. A similar event was reported in the 1940s (Walford and Mosher 1941).

In conclusion, sardines have returned to the PNW in large numbers and have gone from being nonexistent to one of the dominant pelagic species in the northern California Current (e.g., Brodeur et al. 2004, 2005) in the span of slightly more than a decade. They presently support a healthy commercial fishery and are important prey for many large fishes. Sardines do not appear to have displaced other plankton-feeding pelagic schooling fishes, such as northern anchovy. Sardines may, in fact, play a role in the increase in salmon runs observed in the PNW since 1999. However, additional research needs to be done to confirm this. More importantly for management purposes, we need to determine whether the sardines spawning and residing off the PNW are a separate stock or just an extension of the California population.

ACKNOWLEDGMENTS

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