EGG PRODUCTION OF PACIFIC SARDINE (*SARDINOPS SAGAX*) OFF OREGON IN 1994

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ABSTRACT

Since the late 1970s, the Pacific sardine (*Sardinops sagax*) population off the west coast of the United States has been increasing. In 1994, an ichthyoplankton survey to assess anchovy biomass was conducted off the Oregon coast from the Columbia River to the Coquille River (just north of Cape Blanco) and out to 190 km offshore. Samples collected during the survey contained numerous Pacific sardine eggs and larvae, which were used to estimate daily egg production (0.42 eggs/0.05 m^2/day) and egg mortality (0.13/day). The spawning biomass of Pacific sardine was calculated to be about 50,000 MT.

There appears to be an association between geographic distribution of sardine eggs and the 14°C isotherm derived from the 1-m to 10-m depth zone. We hypothesize that the isotherm of 14°C forms a distinct boundary for spawning sardine off Oregon and may prove useful for determining boundaries for future spawning surveys.

INTRODUCTION

The Pacific sardine (*Sardinops sagax*) fishery, which ranged from Baja California, Mexico, to as far north as British Columbia, Canada, was the largest commercial fishery in the Western Hemisphere in the early 1900s (Wolf 1992). During that period, sardine evidently spawned throughout most of their range. Spawning occurred during the summer in Oregon and British Columbia waters (Walford and Mosher 1941; Ahlstrom 1948). Since the decline of the sardine population in the 1940s, no landings have been documented in waters off Oregon and Washington (Radovich 1982; Wolf 1992), and to our knowledge no spawning has been documented in waters north of California.

In 1994, the National Marine Fisheries Service (NMFS) conducted an ichthyoplankton survey off the Oregon coast to estimate northern anchovy (*Engraulis mordax*) biomass. During this survey northern anchovy eggs were rarely collected, but Pacific sardine eggs were abundant throughout the study area. Pacific sardine eggs were found as far north as Tillamook Head, Oregon, indicating that the Pacific sardine may again be using northern portions of its historical spawning range. This apparent expansion of spawning range to Oregon waters is consistent with the rates of increase in biomass and spawning area that have been observed off California since the mid-1980s (Deriso et al. 1996).

In this paper, we describe the geographic distribution of Pacific sardine eggs and larvae and estimate egg production and mortality in our study area off Oregon in July 1994. We also provide a crude estimate of Pacific sardine spawning biomass.

MATERIALS AND METHODS

Survey Description

The ichthyoplankton survey used the egg production methods of Lasker (1985) and was conducted aboard the 17.4-m research vessel *Sea Otter* during 5–26 July 1994. Sampling was conducted over a grid of 234 stations along 12 east–west transects, which encompassed an area of 69,308 km^2 (figure 1). Transects extended

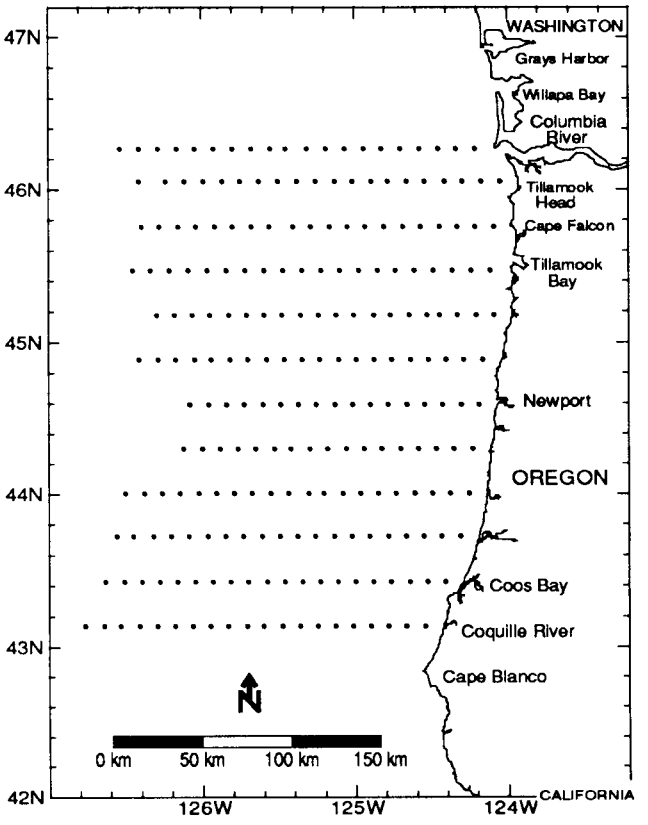

Figure 1. A grid of 234 sampling stations occupied during the ichthyoplankton survey, 5–26 July 1994.

from 9 to 190 km offshore and encompassed a north–south distance of 348 km, from the Columbia River to the Coquille River, Oregon (just north of Cape Blanco). Transects were at 32-km intervals and included 17–20 evenly spaced sampling stations, each about 9 km apart.

Vertical egg tows were made at each station from a depth of 70 m, or just above the bottom, to the surface with a CalVET net that had a mouth area of 0.05 m^2 and a mesh size of 0.15 mm (Smith et al. 1985). In conjunction with each egg tow, temperature and salinity profiles were collected with a Seacat SBE19 profiler. Seawater from the 3-m depth at each station was collected for chlorophyll *a* analysis. Stations were sampled when the boat arrived, regardless of time of day. Vessel speeds of 13–17 km/h between stations allowed for completion of about one transect every 24 h.

Plankton Sample Processing and Egg Identification and Staging

Standard techniques (Smith and Richardson 1977) were used to preserve and sort fish eggs and larvae. Eggs were identified and staged by personnel at the NMFS Southwest Fisheries Science Center in La Jolla, California. Sardine eggs were identified from characters described by Ahlstrom (1943), Miller (1952), and Lo et al. (1996) and assigned to 11 developmental stages based on their morphology.

Egg Mortality and Egg Production

To estimate daily production of age-0 eggs and egg mortality, we first assigned ages to staged eggs from each tow, based on incubation temperature, time of tow, and time of peak spawning. We used a model for temperature-dependent age of each egg stage developed by Lo et al. (1996) to assign an age to each egg stage, aided by a computer program STAGETOAGE (Hewitt et al. 1984; Lo 1985; Picquelle and Stauffer 1985). The peak spawning time for Pacific sardine off California in 1994 ranged from 2000 to 2400 h and was centered at 2100 h (Lo et al. 1996). Silliman (1943) found that most Pacific sardine eggs off California were distributed in the 10-m to 20-m depth zone at temperatures of 14°–16°C, and Ahlstrom (1943) used the mean temperature for this zone to assign an age to each egg based on its stage of development.

Eggs were further grouped by half-day age category (e.g., 4–15 h, 16–27, etc.; table 1), excluding those eggs less than 3 h old or greater than the expected hatching time, which depends on water temperature (3 days, exposed to 15°C waters; Picquelle and Stauffer 1985; Lo et al. 1996). Densities of young eggs, less than 3 h old, tend to be misrepresented because of their contagious distribution and their short duration. Eggs older than the expected hatching time are also biased because of hatching (Lo et al. 1996). Mean number of eggs and mean age in each half-day age group (P_t) were used to estimate daily production of eggs in the sea, P_0, from the following egg mortality equation:

TABLE 1
Observed Egg Densities (Eggs/0.05 m^2/day) and Age Categories (Days) Used to Model the Egg Mortality of Pacific Sardine off Oregon, 1994

Age category (days)	Egg density (eggs/0.05 m^2/day)
0.39	0.170
0.82	0.461
1.42	0.641
1.88	0.435
2.42	0.275
2.83	0.097

$$P_t = P_0 e^{-zt}$$

where P_t = egg production per 0.05 m^2 at age t (day),
P_0 = egg production per 0.05 m^2 at age 0,
z = the daily instantaneous egg mortality rate.

Spawning Biomass

To compute spawning biomass, we used the daily egg production method (DEPM; Lasker 1985). The DEPM computes the spawning biomass as the ratio of estimates of P_0 and daily specific fecundity (number of eggs/population weight/day):

$$B_s = \frac{P_0 A}{Q k}$$

where B_s = spawning biomass (MT),
P_0 = daily egg production per 0.05 m^2,
A = total survey area (in units of 0.05 m^2),
Q = daily specific fecundity (number of eggs/g biomass/day) = RSF/W_f where R is the fraction of mature female fish by weight (sex ratio); S is the proportion of mature females that spawned per day; F is the batch fecundity; W_f is the average weight of mature females (g),
k = constant (g to MT).

Daily specific fecundity (Q) is normally computed from adult samples collected in conjunction with egg sampling. Because no adult sardines were collected during our survey, we decided to use the daily specific fecundity observed for sardine in California in 1994 (11.53 eggs/g biomass/day; Lo et al. 1996; Macewicz et al. 1996) as a crude estimate for adult sardines in our study area. Because of the potential bias in using an estimate for $|Q|$ from California in an estimate for sardine off Oregon, we obtained only the point estimate for the

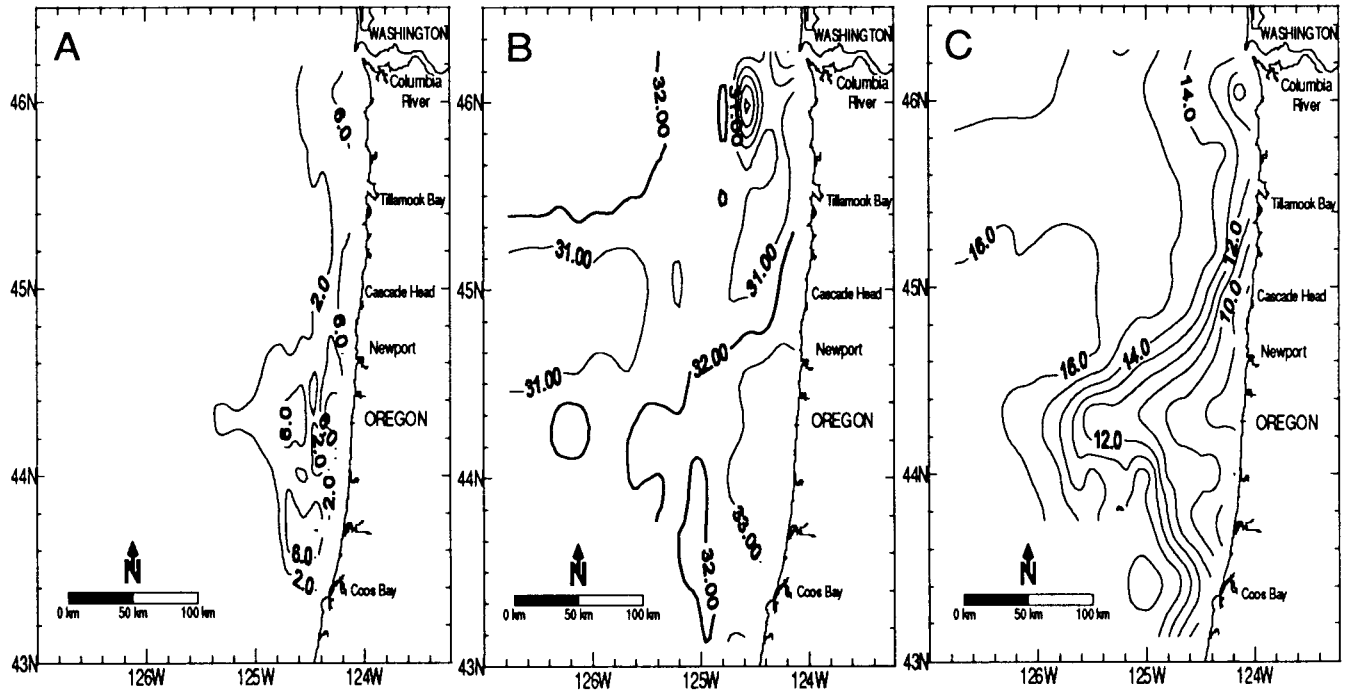

Figure 2. *A*, Chlorophyll *a* (mg/m^3), *B*, salinity (ppt), and *C*, temperature (°C) contours observed during the ichthyoplankton survey off Oregon, 5–26 July 1994. All measurements were taken at the 3-m depth.

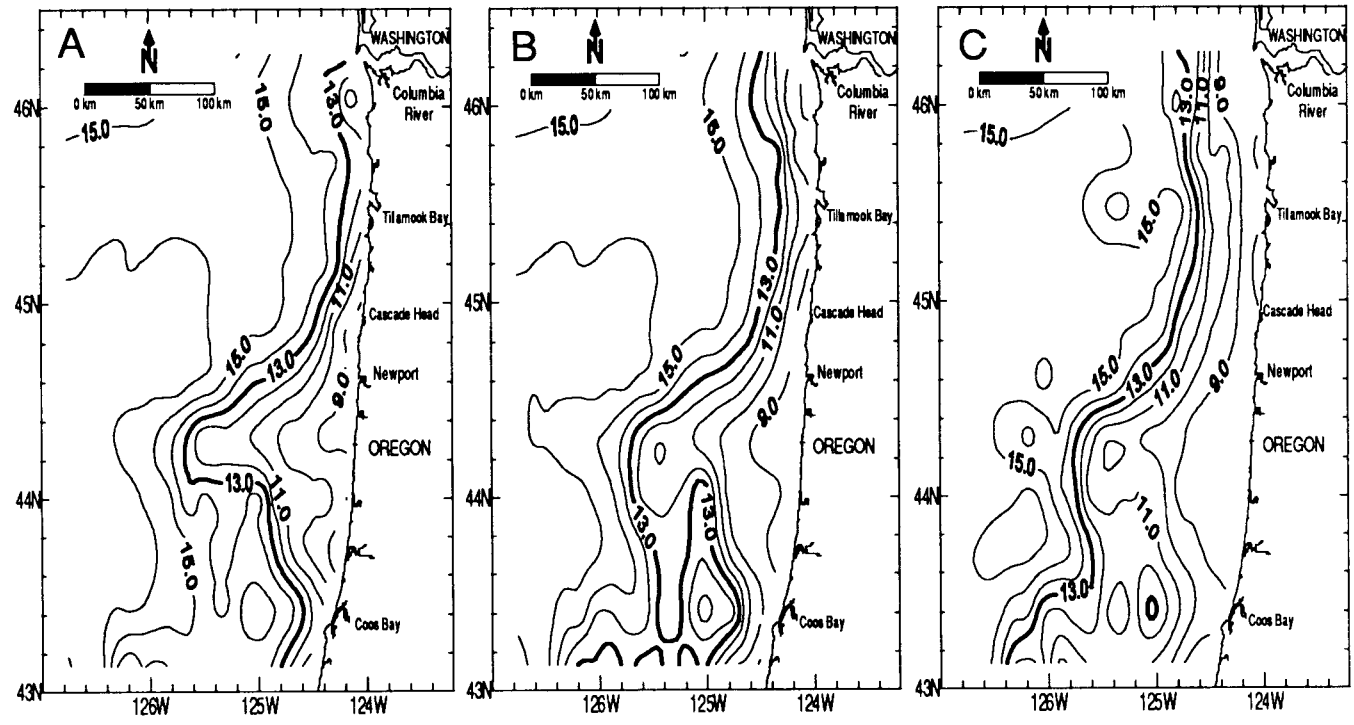

Figure 3. Temperature (°C) contours for the 3-m (*A*), 10-m (*B*), and 20-m (*C*) depths observed during the ichthyoplankton survey off Oregon, 5–26 July 1994.

spawning biomass of sardine off Oregon, and made no attempt to obtain confidence interval estimates for the spawning biomass.

RESULTS

Ocean Conditions

Marine environmental conditions in July 1994 were representative of summer conditions found along the Oregon coast when upwelling, generated by sustained northwesterly winds, causes low ocean temperatures and high salinities in a narrow band along the coast (figure 2; Barnes et al. 1972; Huyer et al. 1975; Huyer 1979). Upwelling calculated for July 1994 at latitude 45°N, longitude 125°W was among the highest on record (data obtained from the Pacific Fisheries Environmental Group, Monterey, Calif.). Low surface temperatures (<10°C) and high surface salinities (>33 ppt) observed along the central Oregon coast were further evidence of strong upwelling. Chlorophyll *a* concentrations reflected the trends in surface temperature and salinity, and increased in areas where nutrient-rich waters were upwelled into the euphotic zone. Highest chlorophyll *a* levels (>10 mg/m^3) were found near shore around the Columbia River mouth and along the central Oregon coast just south of Newport, Oregon.

The 13°C isotherm, the lower limit for successful spawning of Pacific sardine, was observed along the entire coastal portion of the survey grid (figure 3). In the northern half of the survey area, from Newport north to the Columbia River, a mixed layer of 15°C water was observed from about 60 to 190 km offshore and at depths greater than 10 m (figure 4). The Columbia River plume, delineated by lower-salinity surface waters (<32 ppt), usually follows an offshore and southerly direction during the summer (Pearcy and Mueller 1969; Barnes et al. 1972; Hickey and Landry 1989; Fiedler and Laurs 1990), and this pattern was evident during July 1994.

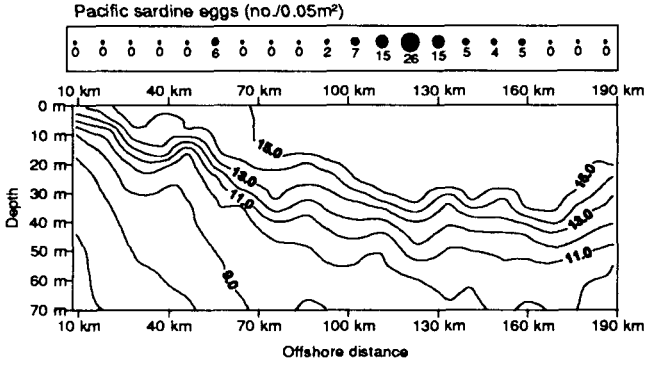

Figure 4. Temperature profile off Cape Falcon, Oregon (45.8°N), and the number of Pacific sardine eggs collected per station.

TABLE 2

A. Summary of Pacific Sardine Egg and Larval Data Collected off the Oregon Coast during July 1994

	Total number	Percent of sampling stations
Number of stations containing:		
Eggs	46	19.6
Larvae	30	12.8
Eggs or larvae	64	27.3
Eggs and larvae	12	5.1
Mean number of eggs/0.05 m^2		
All stations	0.96	
Positive stations	4.87	
Mean number of larvae/0.05 m^2		
All stations	0.38	
Positive stations	3.00	

B. Temperatures (°C) That Eggs May Have Been Exposed to

		Positive tows for eggs	
Depth (m)	Average all tows	Average	Weighted average
1–10	14.16°	15.06°	15.31°
10–20	13.38°	14.39°	14.87°

Egg Identification and Staging

A total of 224 Pacific sardine eggs was collected at 46 (20%) of the 234 stations sampled (table 2). The average number of eggs per tow was 0.96—coefficient of variation (CV) = 0.2—with a maximum of 26 eggs.

Sardine eggs from our samples had a mean size similar to eggs collected off central California during May 1994 (Lo et al. 1996), but they had a slightly higher size variation (table 3; figure 5). We found proportionally more eggs at the high and low extremes of the size range than were found off central California. Also, the oil globule is usually obvious in California sardine eggs but was often difficult to detect in our samples.

Melanostomiid eggs with features similar to those of Pacific sardine (large diameter, wide perivitelline space, segmented yolk, and single oil globule) were found in 24 samples. The size range of these eggs partially overlaps that of sardine (table 3); however, the composition and color of the yolk and size of the oil globule were different from those of sardine eggs. The melanostomiid egg has bright yellow, spherical yolk segments that are smaller than the polygonal, pale orange segments of sardine eggs. Also, the oil globule of the melanostomiid egg (usually dispersed) is at least two times larger than that of sardine eggs. The melanostomiid eggs in our samples were most likely from *Tactostoma macropus*, since this species spawns primarily in summer (Kawaguchi and Moser 1993).

All 11 developmental stages of Pacific sardine eggs were present in our samples, although not all were equally

TABLE 3
Diameters of Sardine Eggs from Oregon and Central California Compared to Those of a Melanostomiid Species from Oregon

Species	Area	Size range (mm)	Mean size	SE ($\times 10^{-03}$)	n
Sardine	California	1.43–2.00	1.75	7.18	150
Sardine	Oregon	1.23–2.00	1.75	9.65	165
Melanostomiid	Oregon	1.32–1.60	1.50	1.13	32

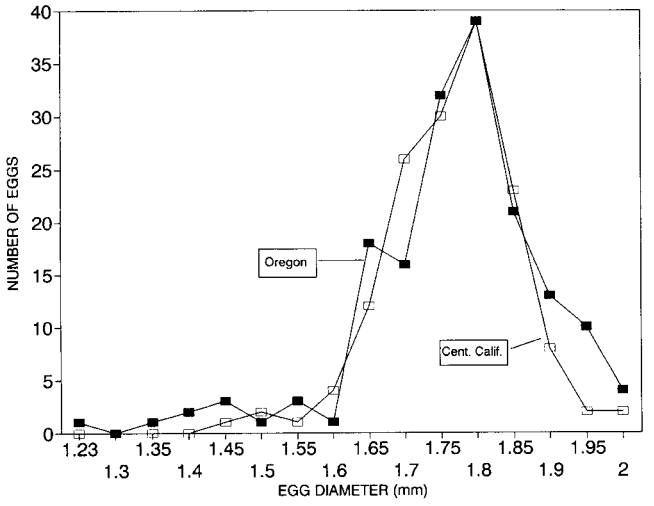

Figure 5. Diameters (mm) of sardine (*Sardinops sagax*) eggs collected off Oregon in July 1994, and off central California in April 1994.

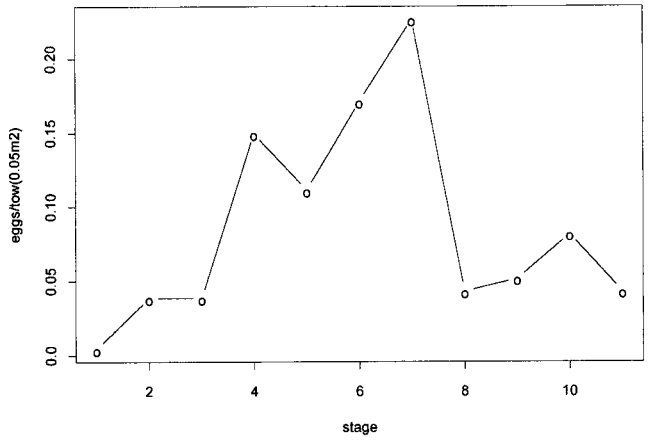

Figure 6. Egg densities categorized by developmental stage for Pacific sardine collected off Oregon, July 1994.

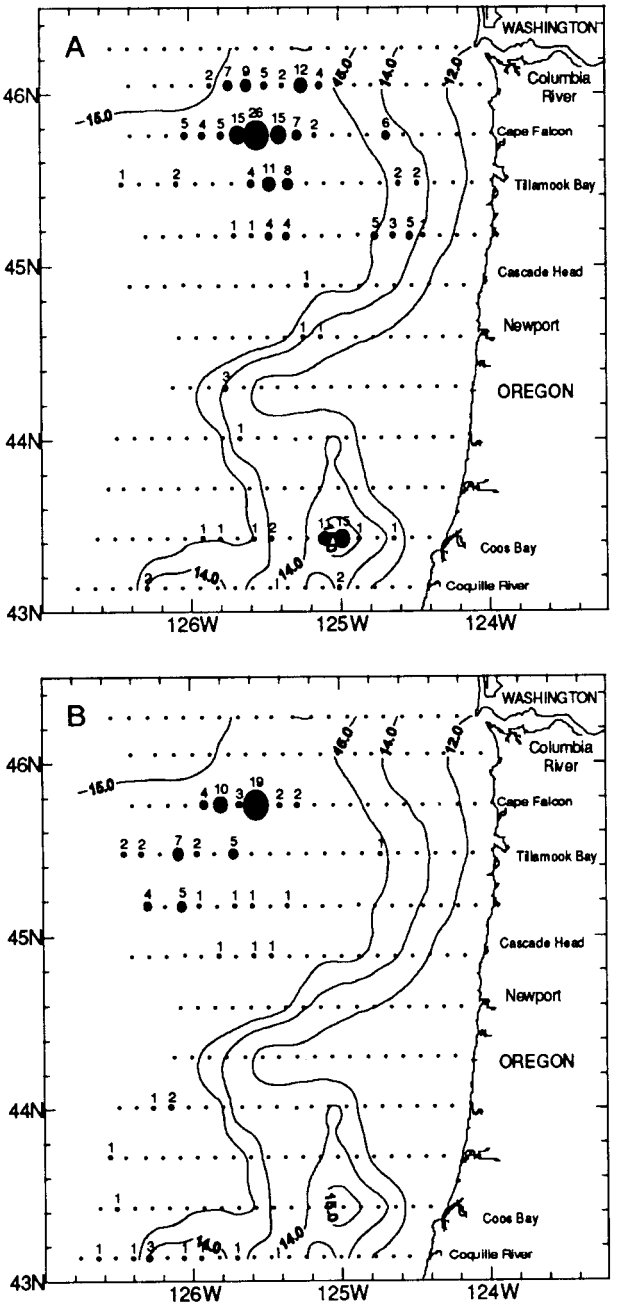

Figure 7. Geographic distribution of Pacific sardine eggs (*A*) and larvae (*B*) collected during the ichthyoplankton survey, 5–26 July 1994. Eggs and larvae are presented as the number per tow (no./0.05 m^2). The 12°, 14°, and 15°C isotherms for the 1-m to 10-m depth profile are also presented.

represented. Due to the contagious distribution and difficulties in sampling young eggs, density was lowest for stage 1, increased with subsequent stages, peaked at stage 7, and decreased thereafter due to mortality and dispersal (figure 6).

Egg and Larvae Distribution

Numerically, Pacific sardine eggs constituted 52.0% of all fish eggs collected. The highest concentration of sardine eggs was found 120 km off Cape Falcon, about 45 km south of the Columbia River, in waters 15°C or warmer (figure 7). Geographically, this is the same region that was preferred by spawning northern anchovy two decades ago, and this region is thought to be strongly affected by the Columbia River plume (Richardson 1981).

Pacific sardine larvae were found less frequently than eggs, occurring at 30 (12.8%) of 234 stations. Sardine

larvae made up about 30% (88/292) of all fish larvae collected. The area of highest concentration (>10 larvae/0.05 m^2) was geographically similar to that of highest egg abundance (figure 7).

Egg Production and Spawning Biomass

The developmental rate of sardine eggs is temperature dependent; thus the temperature of the water column where females lay eggs is essential for estimating egg production. Silliman (1943) documented that the most sardine eggs collected off southern California were found to be within the 10-m to 20-m depth zone at temperatures of 14° to 16°C. However, using this depth criterion, we discovered that about 40% of station temperatures (mostly nearshore) were less than 13°C, a temperature at which little spawning occurs (Hart 1973) and at which newly hatched sardine larvae do not survive (Lasker 1964). For the Oregon survey area we chose to use the average temperature of the upper 10-m depth zone at each tow for age assignments. The overall average temperature in the upper 10-m depth zone, weighted by sardine egg abundance, was 15.3°C.

At 15.3°C, Pacific sardine eggs generally hatch about 3 days after being spawned (Lasker 1964; Lo et al. 1996); therefore, only eggs younger than 3 days were included in mortality estimates. Including eggs 3 days or older would overestimate the mortality rate because decreasing abundance after 3 days is primarily due to hatching rather than mortality.

Egg production (P_0) was estimated to be 0.42 eggs/0.05 m^2/day (CV = 0.51), and instantaneous mortality rate (z) was estimated to be 0.13/day (CV = 2.43). The high CV for the instantaneous mortality rate resulted from low catches of eggs in early developmental stages (figure 6). This is not unusual, because stage 2 and stage 3 eggs are patchy in distribution, and have high variance, in particular when the number of sample tows is small and small-volume plankton nets, which may miss patches, are used (Smith 1973, 1981). The egg mortality model, necessary for estimating P_0 (figure 8), fit poorly to the observed egg abundance data as a result of the low catches of young eggs. On the basis of egg production of 0.42 eggs/0.05 m^2/day, we estimated that the spawning biomass of Pacific sardine in the 69,308-km^2 survey area was 50,493 MT. No standard error of the spawning biomass was computed.

DISCUSSION

There appears to be a close association between the geographic distribution of sardine eggs and the 14°C isotherm derived from the 1-m to 10-m depth zone. A similar phenomenon was observed off California, where sardine eggs were concentrated in a narrow range of sea-surface temperatures between 13.8° and 14.5°C (Lo et al. 1996). On the basis of patterns of occurrence of eggs, depth, and temperature, we hypothesize that the isotherm of 14°C may form a distinct boundary which could be used to determine the vertical distribution of sardine eggs and will be a useful stratifying variable in sampling design for sardine egg surveys off Oregon. Sardine eggs off Oregon may have been concentrated in a shallower area of the water column than sardine eggs off California. Further research on the vertical distribution of sardine eggs off the Oregon coast is needed to test this hypothesis.

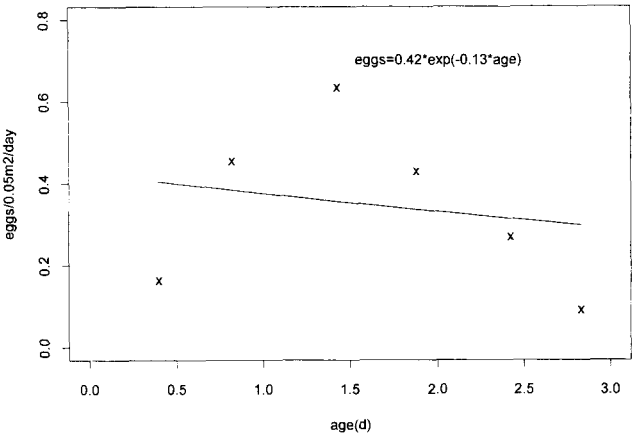

Figure 8. Sardine egg mortality curve and the observed egg density (eggs/0.05 m^2) for each half-day category, July 1994, off Oregon.

The developmental rate of sardine eggs is temperature dependent; thus vertical distribution of sardine eggs and the water-temperature profile are required for estimating egg production. In this study, however, we did not know the vertical distribution of eggs collected, and we assumed that most Pacific sardine were concentrated in the 1-m to 10-m depth zone, in which the temperatures were suitable for spawning and larval survival (i.e., warmer than 13°C; Silliman 1943; Lasker 1964).

The poorly fitted mortality curve is primarily due to the high variances of young eggs (stage 3 and younger). When the sample is small or the population is at a low level, it is common to observe either extremely high or extremely low catches of young eggs because young eggs are patchy (Smith 1973, 1981). A similar phenomenon was observed in the survey for Pacific sardine off California in 1994 (Lo et al. 1996). Other estimation procedures and sampling schemes should be considered for the future. To circumvent the highly variable density of young eggs, Lo et al. (1996) used an embryonic mortality curve which included both eggs and yolk-sac larvae to reduce the variance of the estimates of egg production and egg mortality.

The spawning biomass estimate for the Oregon survey area is speculative, for lack of estimates of adult reproductive parameters, and consequently we did not

calculate the error of the estimate. The greatest potential bias is the assumption that the estimate of Q for California in April was the same as for Oregon in July. Since spawning frequency varies each year from zero to the maximum of 1.6 (Macewicz et al. 1996), any number in between is possible. Batch fecundity is linearly related to fish weight, so the fecundity per gram of female may be similar. Even though there is strong evidence of latitudinal clines in age composition of sardine along the west coast, with the age structure increasing northward (Hart 1973; Butler et al. 1996; Deriso et al. 1996), the difference in fecundity per fish weight between two areas is likely to be negligible.

The estimated egg production off Oregon in July 1994 (0.42 eggs/0.05 m^2/day) was more than twice the production estimated off the California coast in May 1994 (0.169 eggs/0.05 m^2/day; Lo et al. 1996). The percentage of tows that yielded eggs (20%) in our survey was also higher than that observed off California (11%). However, when we compared egg production off Oregon with that of stratum 1[1] off California, the results were similar: stratum 1 was 46% of the total area surveyed in California waters, and the egg production in stratum 1 was 0.37 (= 0.169/0.46), which is similar to the egg production we observed off Oregon. Although the egg mortality rates from both surveys had a high CV, their point estimates were similar. The percentage of tows yielding eggs in stratum 1 off California was 23%, which is also similar to the 20% yield we observed off Oregon.

Pacific sardine spawning off Oregon in July 1994 appeared to occupy the same habitat (Columbia River plume) occupied by the northern subpopulation of northern anchovy in the 1970s (Richardson 1981). Although the occurrence of Pacific sardine eggs was high, northern anchovy eggs were rarely observed in our survey area. Whether this indicates displacement of northern anchovy by Pacific sardine is uncertain, and what effect this would have on regional trophic interactions is unknown. However, northern anchovy have been identified as the primary prey off the Oregon coast for many fish species, including salmonids (Fresh et al. 1981; Brodeur et al. 1987). Although salmonids have been known to feed on sardines in the past (Silliman 1941), displacement of anchovy by sardine would have unpredictable effects on the food habits of salmonids. Sardines grow considerably larger (Hart 1973) and evidently swim faster than northern anchovy. The increasing Pacific sardine population, while perhaps compensating for the reduction in anchovy biomass (unpublished data), may not be prey of adequate size range and may be more difficult to capture than northern anchovy.

Whether the spawning of Pacific sardine off Oregon in 1994 was an anomalous event or part of a long-term northward expansion is uncertain. However, there is evidence that Pacific sardine may have spawned as far north as Vancouver Island, British Columbia, in recent years (Morgan Busby, NMFS, Alaska Fisheries Science Center, pers. comm., Nov. 1995). The shift in oceanic regimes (reduced advection from the north and decreased coastal upwelling) in the North Pacific over the past two decades, and the resulting increased surface temperatures may have created an environment more suited for Pacific sardine (Jacobson and MacCall 1995). A long-term data set for coastal Oregon would identify the mechanisms responsible for the northward expansion of the Pacific sardine's spawning distribution.

[1]In the California survey, the area was poststratified: stratum 1 encompassed the area where eggs were found or were likely to be found based on incidence in surrounding locations, and stratum 0 consisted of the area devoid of eggs.

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