

Abstract—The Pacific sardine (*Sardinops sagax*) is distributed along the west coast of North America from Baja California to British Columbia. This article presents estimates of biomass, spawning biomass, and related biological parameters based on four trawl-ichthyoplankton surveys conducted during July 2003–March 2005 off Oregon and Washington. The trawl-based biomass estimates, serving as relative abundance, were 198,600 t (coefficient of variation [CV]=0.51) in July 2003, 20,100 t (0.8) in March 2004, 77,900 t (0.34) in July 2004, and 30,100 t (0.72) in March 2005 over an area close to 200,000 km². The biomass estimates, high in July and low in March, are a strong indication of migration in and out of this area. Sardine spawn in July off the Pacific Northwest (PNW) coast and none of the sampled fish had spawned in March. The estimated spawning biomass for July 2003 and July 2004 was 39,184 t (0.57) and 84,120 t (0.93), respectively. The average active female sardine in the PNW spawned every 20–40 days compared to every 6–8 days off California. The spawning habitat was located in the southeastern area off the PNW coast, a shift from the northwest area off the PNW coast in the 1990s. Egg production in off the PNW for 2003–04 was lower than that off California and that in the 1990s. Because the biomass of Pacific sardine off the PNW appears to be supported heavily by migratory fish from California, the sustainability of the local PNW population relies on the stability of the population off California, and on local oceanographic conditions for local residence.

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Biomass and reproduction of Pacific sardine (*Sardinops sagax*) off the Pacific northwestern United States, 2003–2005

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Pacific sardine (*Sardinops sagax*; hereafter “sardine”) are distributed widely off the west coast of North America from Baja California, Mexico, to British Columbia, Canada; the majority of the population is located off California (Felin, 1954; Murphy, 1966; Emmett et al., 2005; McFarlane et al., 2005; Smith, 2005). Tagging studies have shown that sardine migrate along the west coast (Janssen, 1938; Clark and Janssen, 1945). The sardine population reached a peak in the early 1930s at 3.5 million metric tons (t) and declined rapidly in the mid-1950s (Marr, 1950). The sardine fishery off California and British Columbia dates from 1916 (Fig. 1). Pacific sardine was one of the economically important species off California and British Columbia in the 1930s when a fishery began off Oregon and Washington (the Pacific Northwest: PNW). The PNW catch peaked at nearly 50,000 t in 1938 (Marr, 1950; Mosher and Eckles, 1954; Murphy, 1966). In the 1960s, however, a moratorium on sardine fishing was established in U.S. waters because of low catches (Murphy, 1966; MacCall, 1976). In the mid 1980s, sardine became common as bycatch in fisheries off Baja California and California state (Wolf, 1992; Deriso et al., 1996) and reappeared from Oregon to British Columbia in 1992 (Emmett et al., 2005; McFarlane et al., 2005), apparently in response to the 1992–93 El Niño event. The sardine population now supports a relatively large fishery with annual catches over 50,000 t in recent years (Fig. 1). Sardine

also serve as important food for tuna, salmon, marlin, mackerel, sharks, and some groundfish species, as well as many seabirds, seals, sea lions, dolphins, and whales (Snodgrass and Lowry, personal commun.¹) (Preti et al., 2001, 2004; Emmett et al., 2005). The reappearance of sardine populations in the north California Current ecosystem adds another forage base for predators and an emerging resource of consumer interest to the ecosystem.

Pacific sardine off the PNW are considered to be a part of the northern subpopulation, the majority of which is distributed off the western United States and Canada (Smith, 2005), as determined from historical tagging studies (Clark and Janssen, 1945), size at age, and other biological characters. Historical tagging studies indicated that some large sardine migrate from California to the PNW in late spring and early summer to feed, and that the majority of the large sardine off the PNW move south to California in the winter to spawn in the spring (Clark and Janssen, 1945). The major spawning area of this northern subpopulation was believed to be located off southern California before the 1960s (Ahlstrom, 1948; Marr, 1960; Smith, 2005). Spawning also may have occurred in the PNW because young fish were caught by commercial boats in Canadian waters in 1940 (Hart, 1943). However,

¹ Snodgrass, Owyn. 2009. Southwest Fisheries Science Center, La Jolla, CA.
Lowry, Mark. 2009. Southwest Fisheries Science Center, La Jolla, CA.

the importance of the PNW as a spawning area has not been studied. After the resurgence of Pacific sardine off California, ichthyoplankton and fishery-independent trawl surveys have been conducted off California to assess the biological characteristics of the sardine population since the mid 1980s, when the estimated sardine biomass approached 20,000 t (Wolf, 1992; Lo et al., 2005). Beginning in the mid 1990s, sardine abundance, distribution, and ecological relationships off the PNW and Canada were analyzed with data from salmon surface-rope trawl surveys off the PNW and trawl surveys off Vancouver Island, Canada (Bentley et al., 1996; Emmett et al., 2005; McFarlane et al., 2005); however, very few of those surveys were designed specifically to assess the biological characteristics of Pacific sardine.

Four trawl surveys off the PNW were conducted in July 2003, March and July 2004, and March 2005 to provide fishery-independent measures of biological characteristics of sardine in this area, and to answer the following questions: 1) Do sardine migrate between the PNW and California? 2) To what extent does Pacific sardine spawning in the PNW depend on the sardine population off California? and 3) How much does the Pacific sardine egg production in the PNW contribute to that of the whole population? To answer these questions, we estimated spring and summer biomasses with length distributions to serve as signals of migration; the location and spatial extent of spawning habitat to examine the following: the effect of the reduction of the spawning area in the PNW to the local population; daily egg production and its contribution to the total egg production; adult reproductive parameters to estimate rates of spawning, fecundity and maturity; and spawning biomass. These measurements were compared with available PNW measurements from the mid-1990s and those off California in the same time period, to facilitate our understanding of the population dynamics of the Pacific sardine off the northern west coast of the North American continent, and to better manage the entire population.

Materials and methods

Survey

In order to obtain unbiased estimates of the biological characteristics of Pacific sardine off the PNW, the Fisheries Resources Division of the Southwest Fisheries Science Center, conducted four surveys in July 2003, March and July 2004, and March 2005 aboard the FV *Frosti*. Multiple gear types were used: a surface trawl to collect adult samples, the CalVET plankton net (California Cooperative Oceanic Fisheries Investigation vertical-egg-tow net; Smith et al., 1985), and the continuous underway fish egg sampler (CUFES; Checkley et al., 1997) to collect ichthyoplankton samples and record hydroacoustics. The survey region encompassed the area

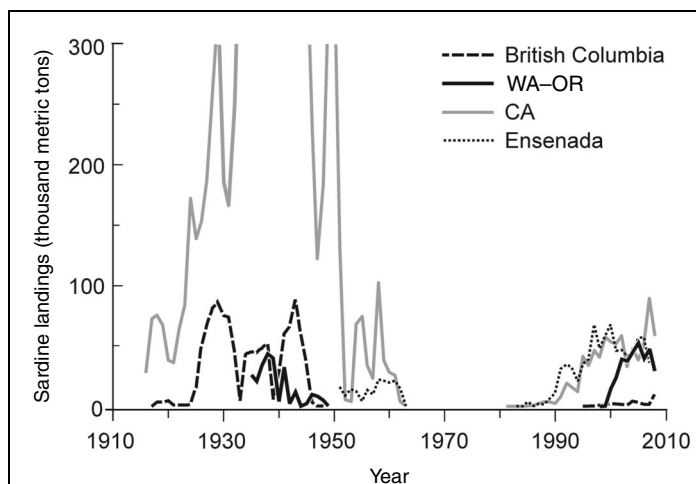


Figure 1

Commercial landings of Pacific sardine (*Sardinops sagax*) in British Columbia, Canada, Washington, and Oregon, and California; and Ensenada, Mexico, from 1916 through 2008. Y-axis is truncated because during 1933–45 and 1950–51 California landings exceeded 300,000 t with a peak in 1936 of 791,334 t.

of the northeast Pacific Ocean from 42° to 48°N latitude and from inshore out to 128°W longitude.

The basic survey pattern comprised seven transect lines oriented on the parallels at a spacing of 60 nautical miles (111 km). Stations were spaced at 30 nautical miles (55.5 km) along each transect measured from the offshore station. Forty-two predetermined stations were sampled by trawl and CalVET tow during each survey. For the July 2003 survey, the primary goal was to estimate the spawning biomass of Pacific sardine. In the offshore area, few trawls were undertaken because both acoustics and CUFES samples showed little sign of sardine schools and eggs. The inshore sampling was discontinued close to the 100-m isobath during July 2003 to avoid net damage in shallow water. All fishing was conducted at night, when Pacific sardine are distributed in the upper 50 m of the water column and oceanographic conditions at depths greater than 50 m would have little influence on the spatial and vertical distributions of sardine schools. Moreover, within 60 km from the shore, the densities of fish were not related to the distance from shore (Emmett et al., 2005). Therefore we expected little bias introduced from sampling along the 100-m isobath. With more experience, we found that we could tow the net at a shallower depth than initially expected, and during subsequent surveys we occasionally fished inshore at shallower depths (see below, Figs. 2–5). For the remaining three surveys, most trawls were evenly distributed along the transect line and between transect lines in the inshore area. Occasionally, trawls were made during transit between transect lines.

Both trawl and CalVET samples were collected during all four surveys and CUFES samples were collected during July surveys only (Figs. 2–5). Trawl-related

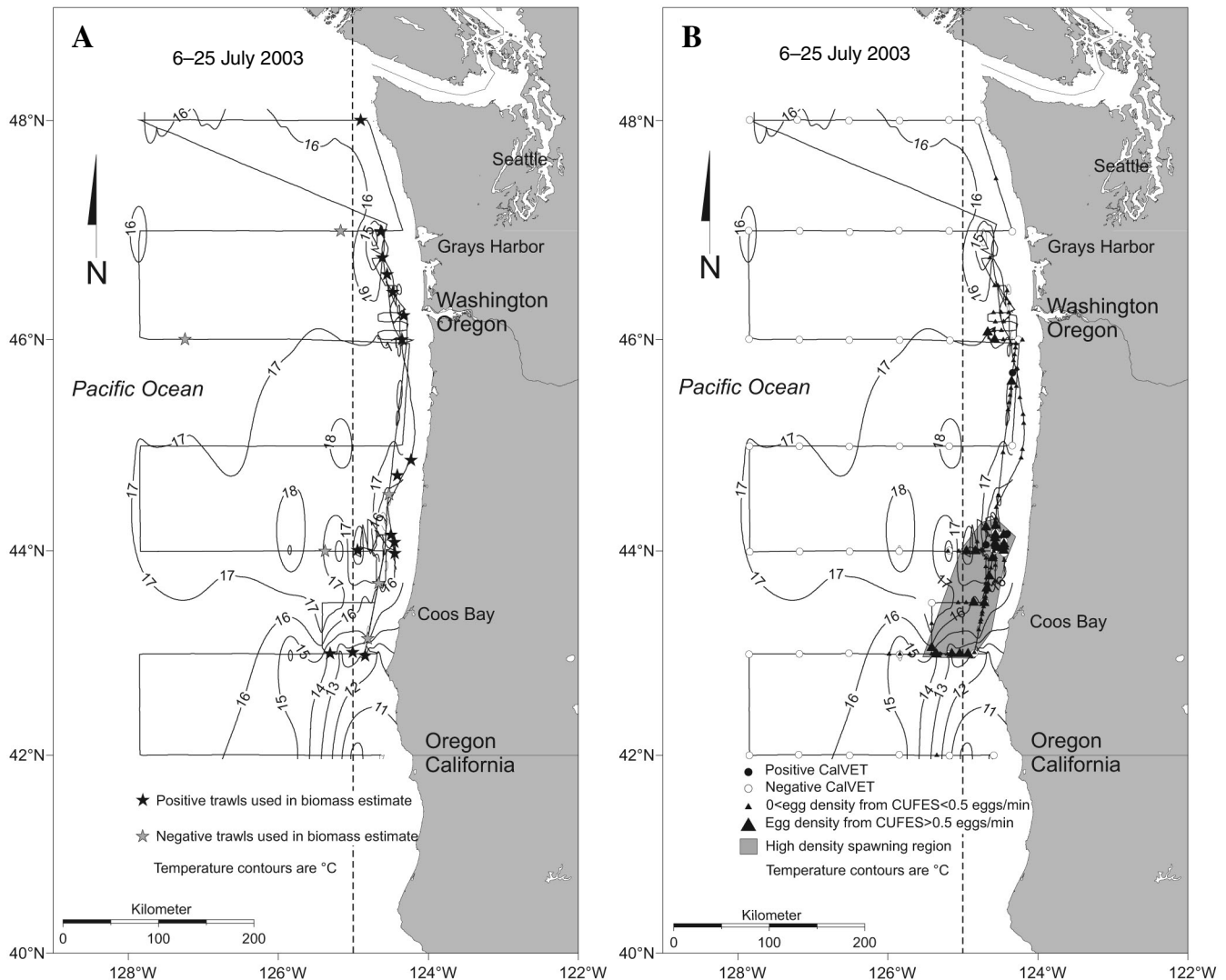


Figure 2

(A) Locations of trawls (stars) used for the estimation of biomass of Pacific sardine (*Sardinops sagax*), excluding added trawls in the inshore area (Table 1), and (B) locations of California vertical egg tows (CalVET: circles) and where continuous underway egg samples were taken (measured in eggs per minute (CUFES: triangles). Contours are sea surface temperatures ($^{\circ}\text{C}$). The dashed vertical line is the 125°W longitude divider of the two sampling strata. The offshore shaded area in (B) is the major spawning habitat. Positive tows were those tows during which sardine were caught. Negative tows were tows when sardine were not caught.

station activities were performed between twilight and dawn, whereas CalVET and CUFES samples were collected throughout all 24 hours. At each station, a CalVET sample was collected and sea surface temperature (SST) was recorded, whereas between stations, CUFES samples and water temperature were taken at a fixed 3-m depth (Figs. 2 and 4). The CUFES data were used primarily to map the spawning area based on the density of sardine eggs.

A Nordic 264 trawl (NET Systems, Bainbridge Island, WA), with a vertical opening of 20 m, a mouth area of approximately 360 m^2 , and a 7-mm codend mesh (Emmett et al., 2005), was towed to sample the

upper 18–20 m of the water column. The distance traveled by each trawl was recorded and was later converted to the volume sampled. The swept area (m^2) is the volume (m^3) divided by 20 m. During the July 2003 survey, few trawls were taken in the offshore area. Additional trawls were taken inshore to collect extra samples to determine reproductive parameters in areas of sardine spawning activity identified by sardine egg densities in CUFES samples or the presence of schools as indicated by acoustic signals (Fig. 2). Similarly, during July 2004, trawls were taken in the southern spawning area off Port Orford, OR (Fig. 4), in addition to the repositioned and between-transect

trawls. Data from the added trawls were excluded in estimating the total biomass to avoid bias. For the two March surveys, all locations (fixed stations and between-transects) were trawled regardless of spawning or acoustic signals (Figs. 3 and 5). The total number of trawls for each survey was close to 50 (Table 1).

For each trawl, the total weight (kg) of the Pacific sardine catch was recorded and up to 50 Pacific sardine were randomly sampled from each trawl where sardine were caught (hereafter referred to as a “positive trawl”). Sex was determined for each fish, and standard length (SL) and weight were measured. For the female fish, the ovaries were first examined for torpedo shape and or development of visible oocytes (yolking or hydrating). When oocytes were not visible and the ovary was small, clear, and torpedo shaped, the ovary was recorded as code 1 (clearly immature). Otherwise, the additional ovarian codes 2 (intermediate), 3 (active), or 4 (hydrated) (Table 2) were used to identify *potentially* mature females—because only histological analysis can verify sardine maturity with certainty (Macewicz et al., 1996). All ovaries were removed and preserved in 10% neutral buffered formalin. If a 50-fish subsample did not have 25 potentially mature females (ovary codes 2–4), more females were sampled to attain 25 per trawl for estimation of reproductive parameters used for computing spawning biomass. Additional females were also processed to estimate batch fecundity, but were not included in the original random subsample for length distributions. We also obtained length distributions based on data from commercial purse seine catches off the PNW in the summer seasons and from a test purse seine set in March 2005.

Seasonal biomass

A swept-area method was used to estimate the total biomass of Pacific sardine in summer and spring based on July and March trawl data, respectively. Because the efficiency of the trawl catch has not been evaluated, the biomass estimates must be considered as relative and minimum

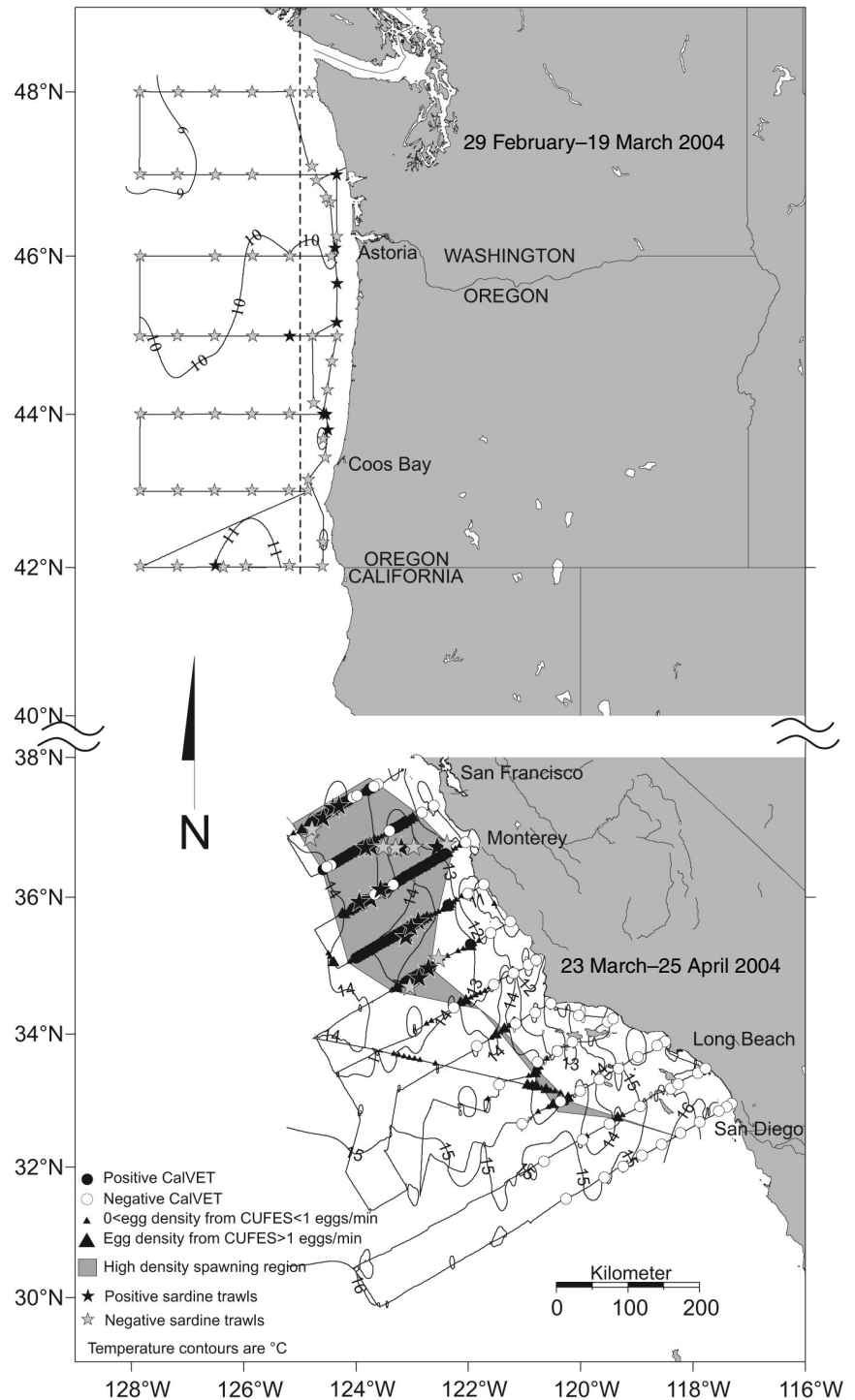


Figure 3

Locations of trawl (stars) and California vertical egg tows (CalVET: circles), for 2004 March ichthyoplankton-trawl survey off the Pacific Northwest (top map), and locations of trawls, CalVET tows (circles), and continuous underway egg sampling (CUFES: triangles) for the March–April 2004 California Cooperative Oceanic Fisheries Investigations (CalCOFI) daily egg production survey (bottom map). Solid symbols indicate that Pacific sardine (*Sardinops sagax*) were captured in the sample at that site. Contours are sea surface temperatures (°C). The dashed vertical line at 125°W longitude (seen in top map) is the divider of the two sampling strata. The shaded area on the bottom is the identified spawning habitat.

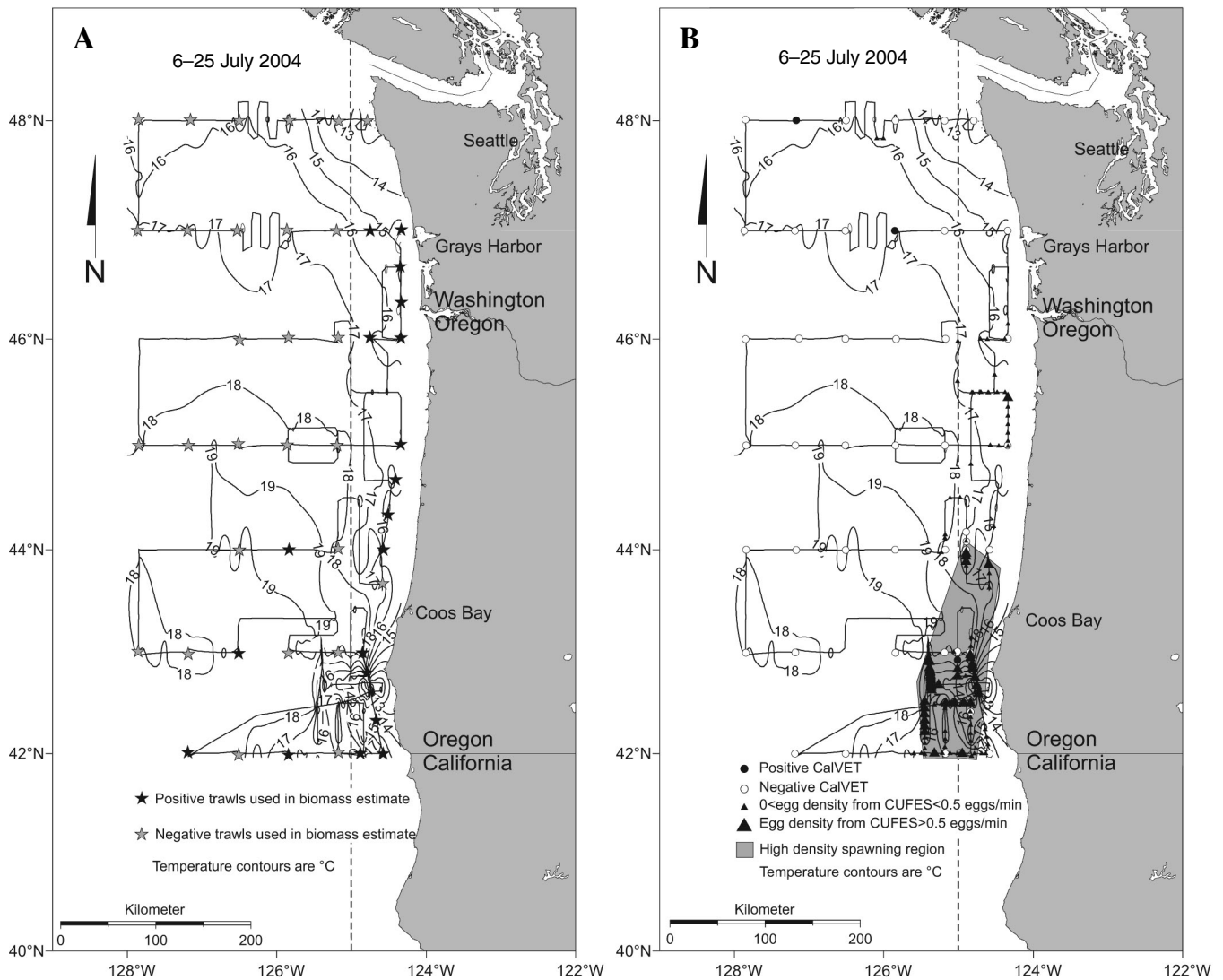


Figure 4

(A) Locations of trawls (stars) used for biomass estimation of Pacific sardine (*Sardinops sagax*), excluding added trawls in the inshore area (Table 1), and (B) California vertical egg tows (CalVET: circles) and continuous underway egg sampling in eggs/minute (CUFES: triangles) for 2004 July trawl-ichthyoplankton survey off the Pacific Northwest. Contours are sea surface temperatures ($^{\circ}\text{C}$). The dashed vertical line is the 125°W longitude divider of the two sampling strata. The shaded area is the major spawning habitat. Positive tows were those tows during which sardine were caught. Negative tows were tows when sardine were not caught.

abundances. A stratified sampling design was used to estimate biomass and spawning biomass, because more stations were assigned close to the shore than offshore. Otherwise, estimates would be biased toward the inshore area (Holt and Smith, 1979). The survey area was divided into an inshore area (stratum 1) and an offshore area (stratum 2) with 125°W longitude as the dividing line. For the July 2003 survey, we excluded the nonpredetermined trawls (i.e., those trawls locations of which were not determined before the survey) taken in the vicinity of positive trawls to prevent an overestimate of the total biomass. The catch for each tow was expressed as kg/m^2 ($=\text{catch} [\text{kg}]/\text{swept area} [\text{m}^2]=\text{catch} [\text{kg}]/\text{volume of water} [\text{m}^3]/\text{depth } 20 \text{ m}$), where the volume

of water filtered was computed as the distance covered by each tow multiplied by the area of the vertical trawl mouth opening of approximately 360 m^2 (with 20 m as diameter). We estimated relative total biomass (B) and its standard error (SE) for each survey as follows:

$$\hat{B} = \sum_i \bar{X}_i (A_i 10^6) / 1000, \quad (1)$$

$$SE(\hat{B}) = \left(\sum_i (\text{var}(\bar{X}_i) (A_i 10^6)^2) \right)^{1/2} / 1000 \quad (2)$$

where \hat{B} = the estimate of the total biomass (t); \bar{X}_i = the mean catch (kg/m^2); and

A_i = the area (km²) in stratum i , $i=1$ (inshore) and 2 (off-shore).

Note: the coefficient of variance (CV) of the estimate is $CV(\hat{B}) = SE(\hat{B})/\hat{B}$. Bootstrap simulation was used to estimate the bias of the estimate (Eq. 1), and the bias-corrected estimate (\hat{B}_c) as $\hat{B}_c = \hat{B} - (\hat{B}_b - \hat{B})$, where \hat{B} is computed from Equation 1, \hat{B}_b is the estimate from the bootstrap simulation, and the mean square error ($MSE = variance + bias^2$) of the biomass estimates (Eq. 2).

We also computed a crude estimate of the recruit biomass (age-zero year or incoming year class) as ancillary information for comparative purposes for spring in 2004 and 2005, based on the biomass of fish ≤ 120 mm SL because 120 mm was the break point for the length-frequency distribution in March surveys from this study (Fig. 6) and it was reported that age-0 sardine in the PNW were ≤ 110 mm (measured by fork length) (Emmett et al., 2005). Recruit biomass (B_R) was estimated by using Equations 1 and 2, where \bar{X}_i = the mean catch (kg/m²) of fish ≤ 120 mm SL in the i th stratum ($\bar{X}_{R,i}$). The catch of recruits for each trawl would be obtained as

$X_{R,ij} = X_{ij} * U_{ij, length \leq 120mm}$, where X_{ij} = the total catch from the j th trawl, and $U_{length \leq 120 mm}$ = the weight of fish ≤ 120 mm SL divided by the total fish weight based on our random samples with a maximum of 50 fish from each tow.

Spawning habitat

The spawning habitat was defined as the area of relatively high egg densities during early summer, because June–July was the peak spawning time for Pacific sardine off the PNW as determined from egg and larval data collected in the mid-1990s (Bentley et al., 1996). Because the number of positive CalVET tows was low (four of 54 tows during July 2003 and 3 of 48 tows during July 2004), we chose to use data from CUFES sampling. The spawning habitat area was defined as the area where the majority of egg densities exceeded a threshold of 0.5 eggs/min because the egg densities were generally low. Off California,

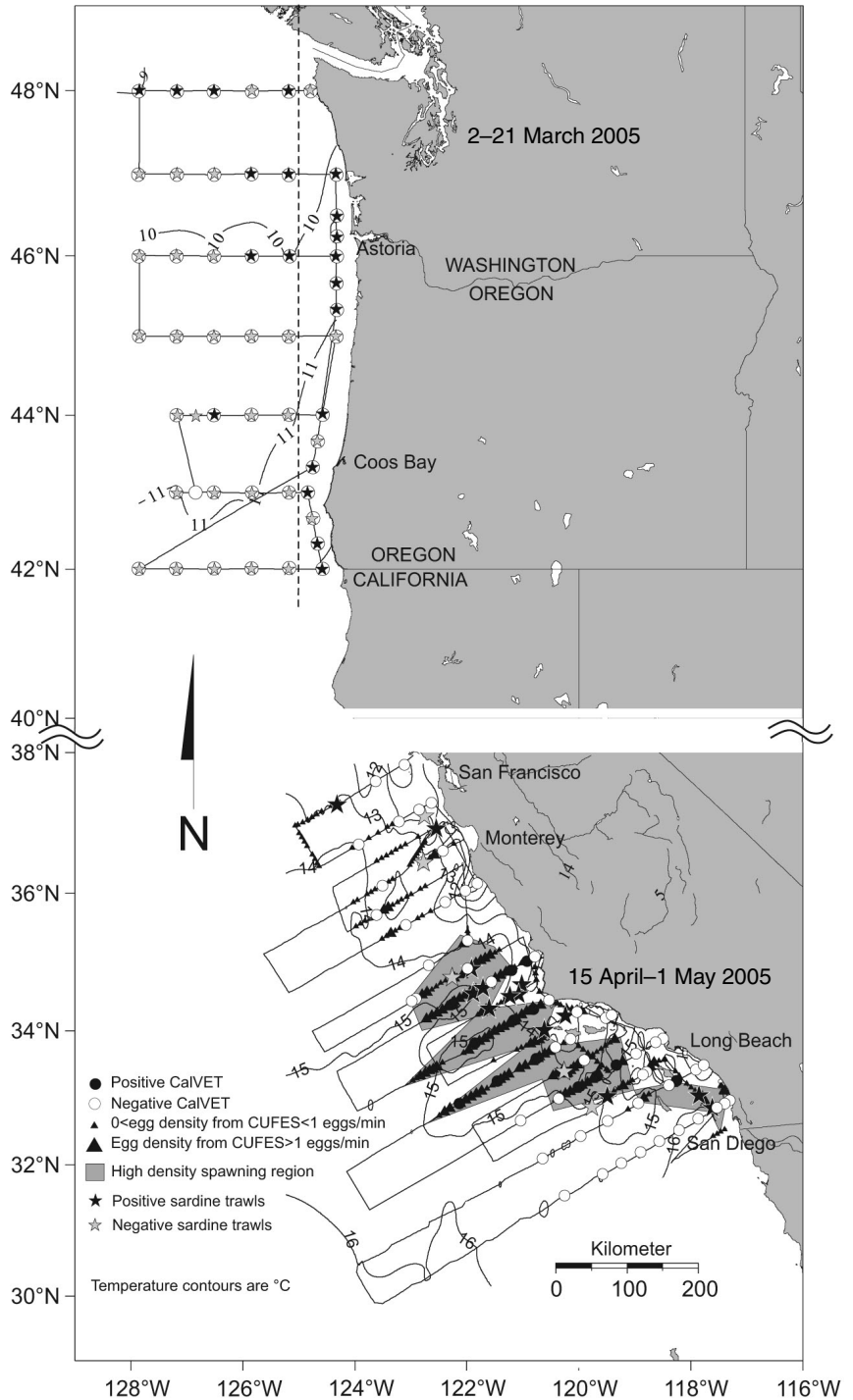


Figure 5

Locations of trawl (stars) and California vertical egg tows (CalVET: circles) for the 2005 March ichthyoplankton-trawl survey off the Pacific Northwest (top) and trawls, CalVET tows (circles), and continuous underway egg samples (CUFES: triangles) for the April–May 2005 California Cooperative Oceanic Fisheries Investigations (CalCOFI) daily egg production survey (bottom). Solid symbols indicate that Pacific sardine (*Sardinops sagax*) were captured in the sample at that site. Contours are sea surface temperatures (°C). The dashed vertical line is the 125°W longitude divider of the two sampling strata. The shaded area is the spawning habitat.

Table 1

Estimates of biomass of Pacific sardine (*Sardinops sagax*), biomass-related parameters for each survey (stratum 1, stratum 2 [with latitude 125°W as the dividing line between them], and the entire survey area), and confidence intervals for biomass and recruits: incoming year class (fish ≤ 120 mm standard length) in tons (t). Either the coefficient of variation (CV) or number of positive (pos) trawls is in parentheses.

	Stratum 1	Stratum 2	Entire survey area
July 2003			
Mean density (kg/m ³)	2.41e ⁻⁰⁰⁴	2.2e ⁻⁰⁰⁶	4.85e ⁻⁰⁰⁵
Biomass (t) (CV)	192,801(0.57)	7207(0.85)	200,008(0.56)
No of trawls ¹ (pos)	38(34)	10(2)	48(36)
No of trawls used for biomass (positive)	17(14)	5(2)	22(16)
Survey area (km ²) (% of entire survey area)	40,043(19)	166,333(81)	206,377(100)
Bootstrap results			
Biomass (t) (CV)	193,946(0.53)	7406(0.82)	201,360(0.51)
Mean square error (MSE) ^{1/2}	102,174	6094	102,378
Bias-corrected	191,656	7009	198,656
Confidence interval (t)			44,286–421,321
March 2004			
Mean density(kg/m ³)	2.6e ⁻⁰⁰⁵	4.6e ⁻⁰⁰⁸	5.2e ⁻⁰⁰⁶
Biomass (t) (CV)	21,243(0.83)	155(0.7)	21,398(0.82)
Recruits (t)(CV)	21,030(0.83)	69(1.0)	21,099(0.83)
No of trawls (pos)	25(7)	34(2)	59(9)
Survey area (km ²) (%)	40,043(19)	166,334(81)	206,377(100)
Bootstrap results			
Biomass (t) (CV)	22,494(0.81)	155(0.69)	22,650(0.8)
MSE ^{1/2}	18,260	106	18260
Bias-corrected	19,992	155	20,147
Confidence interval (t)			0–63,017
Recruits (t)(CV)	21,629(0.81)	69(1.02)	21,698(0.81)
MSE ^{1/2}	17,576	70	17,578
Bias-corrected	20,432	69	20,501
Confidence interval (t)			4749–45,808
July 2004			
Mean density (kg/m ³)	9.0e ⁻⁰⁰⁵	2.3e ⁻⁰⁰⁶	2.1e ⁻⁰⁰⁵
Biomass (t) (CV)	72,206(0.405)	6989(0.992)	79,194(0.379)
No of trawls ¹ (pos)	20(16)	38(11)	58(27)
No of trawls used for biomass (pos)	17(15)	30(14)	47(19)
Survey area (km ²) (%)	40,043(21)	150,932(79)	190,975(100)
Bootstrap results			
Biomass(t) (CV)	73,186(0.41)	7299(0.95)	80,485(0.38)
MSE ^{1/2}	29,723	6928	30,605
Bias-corrected	71,226	6678	77,903
Confidence interval (t)			30,474–146,176
March 2005			
Mean density (kg/m ³)	3.7e ⁻⁰⁰⁵	2.3e ⁻⁰⁰⁷	7.9e ⁻⁰⁰⁶
Biomass (t)(CV)	29,488(0.69)	700(0.57)	30,188(0.68)
Recruits (t) (CV)	55(1.0)	0(0)	54.80(1.0)
No of trawls (pos)	15(11)	34(9)	49(20)
Survey area (km ²) (%)	40,043(21)	150,932(79)	190,976(100)
Bootstrap results			
Biomass (t)(CV)	29,573(0.73)	705(0.57)	30,278(0.72)
MSE ^{1/2}	21,713	402	21,714
Bias-corrected	29,403	695	30,098
Confidence interval (t)			1800–86,035
Recruits (t) (CV)	56.6(0.98)	0(0)	57(0.98)
MSE ^{1/2}	56	0	56
Bias-corrected	53	0	53
Confidence interval (t)			70–1640

¹ During the July 2003 cruise, data from 22 out of 48 trawls were used for biomass computation. The total 48 trawls included 38 (34 with sardine) in stratum 1 and 10 (2 with sardine) in stratum 2. During the July 2004 cruise, only data from the first 47 trawls out of 58 trawls were used. The total 58 trawls included 20 trawls (16 with sardine) in stratum 1 and 38 trawls (11 with sardine) in stratum 2.

Table 2
Gross anatomical classification of female and male Pacific sardine (*Sardinops sagax*) gonads.

Gonad code	
Female: Ovary description	
1	<i>Clearly immature</i> : Oocytes are not visible. Ovary is very small, translucent or clear, and thin, but with rounded edges (torpedo shaped).
2	<i>Intermediate</i> : Individual oocytes are not visible to the unaided eye (no visible yolk or hydrate oocytes in the ovaries), but ovary is not clearly immature. Includes possible maturing and regressed ovaries.
3	<i>Active</i> : Yolked oocytes in ovaries visible to the unaided eye in any size or amount, including the smaller opaque oocytes (around 0.4–0.5 mm) to the large yellowish oocytes (about 0.6–0.8mm).
4	<i>Hydrated</i> : Hydrated oocytes are present, yolked oocytes may also be seen. Hydrated oocytes (large and transparent), from few to many, or even if loose or “oozing” or “running” from ovary, qualify for this class
Male: Testis description	
1	<i>Clearly immature</i> : Testis is very small, knife shaped, translucent or clear, and thin with a flat ventral edge.
2	<i>Intermediate</i> : No milt is evident and testis is not clearly immature (includes maturing or regressed testes).
3	<i>Active</i> : Milt is present either oozing from the gonopore, in the duct, or in the testis (observed when the testis was cut).

the threshold was one egg/min. We obtained the SST for CUFES samples with ≥ 0.5 eggs/min as a proxy for the oceanographic conditions. No biological variables such as zooplankton volume (Lynn, 2003) were collected during these surveys.

Daily egg production

The daily egg production (P_0) is defined as the newly spawned eggs produced per 0.05 m² per day, where 0.05 m² was the surface area covered by the CalVET net tow. The daily rate of egg production and the daily specific fecundity rate from adult parameters (Lasker, 1985) are needed to compute spawning biomass. In California waters, sardine egg data from CalVET tows and yolksac larval data from both CalVET tows and bongo nets, and sardine ages were used to model the embryonic mortality curve, a negative exponential curve (Lo et al., 1996, 2005):

$$P_t = P_0 e^{(-zt)}, \quad (3)$$

where P_t = the daily production rate at age t (days);
 z = the daily instantaneous embryonic mortality rate; and
 P_0 = the intercept, is the daily egg production at age zero.

Because few eggs were caught during CalVET net tows in July surveys and no eggs were caught in March surveys (Fig. 2–5, Table 3), no attempt was made to estimate egg production for the March surveys. For July surveys, it was impossible to model the egg mortality curve because the mortality curve requires sufficient

data on egg abundance for each egg stage and age. Instead, we used an alternative algorithm to estimate P_0 , an integral method ($P_{0,I}$) based on the standing stock of eggs from CalVET tows.

The estimate of P_0 ($P_{0,I}$) was based on the relationship between the mean catch of eggs from CalVET tows (\bar{Y}) and egg production (P_0) through the integral of P_t over the period from spawning to hatching (t_h). The mean catch of eggs from CalVET tows was a weighted average with the area in each stratum as weight. This method requires prior knowledge of the egg mortality rate and the temperature-dependent hatching time:

$$\bar{Y} = \int_0^{t_h} P_t dt = \int_0^{t_h} P_0 e^{-zt} dt. \quad (4)$$

Integrating the above equation yields the estimate of P_0 as a function of the mean egg density, \bar{Y} , incubation time, t_h , and the daily instantaneous mortality rate, z :

$$P_{0,I} = \frac{z\bar{Y}}{1 - e^{(-zt_h)}} \quad (5)$$

with variance calculated by using the delta method:

$$\begin{aligned} \text{var}(P_{0,I}) &= \left(\frac{\partial P_{0,I}}{\partial z}\right)^2 \text{var}(z) + \left(\frac{\partial P_{0,I}}{\partial \bar{Y}}\right)^2 \text{var}(\bar{Y}), \\ &= \left(\frac{\bar{Y}[1 - \exp(-zt_h)(1 + zt_h)]}{[1 - \exp(-zt_h)]^2}\right)^2 \text{var}(z) \\ &\quad + \left(\frac{z}{1 - \exp(-zt_h)}\right)^2 \text{var}(\bar{Y}). \end{aligned} \quad (6)$$

The z value was the estimate from the daily egg production method (DEPM) surveys off California in 2003 (0.48 [CV=0.08]) and 2004 (0.25 [CV=0.04]) (Lo et al., 2005) because of the lack of sufficient data to estimate z off the PNW. Age at hatching (in days) was 2.5 days computed from the temperature-dependent sardine egg development model for stage XII given in Lo et al. (1996): $t_h = 30.65 * \exp(-0.145 * \text{temp} - 0.037 * 12) * 12^{1.41} / 24$, where temp is the average temperature from positive CUFES collections during the July surveys, and equals

16.4°C and 16.3°C for 2003 and 2004, respectively. This integral estimate is biased upward on the basis of a comparison of $P_{0,I}$ and the P_0 from the nonlinear regression from four California daily egg production surveys and a simple theoretical population. Both cases indicated that the relative bias ($rb = (P_{0,I} - P_0) / P_{0,I}$) was close to 20% of $P_{0,I}$. Thus the bias-corrected egg production ($P_{0,c}$) would be $P_{0,c} = P_{0,I} (1 - rb) = P_{0,I} (0.8)$.

The mean density of eggs (\bar{Y}_i) (eggs/0.05 m²) was estimated for each of two strata ($i=1,2$), with 125°W latitude as the dividing line. The overall mean density (\bar{Y}) for the whole survey area was a weighted average with the area in each stratum as the weight and was used to estimate the daily egg production. No estimate of egg production for each stratum was obtained because of the small sample sizes.

To understand the relative contribution of egg production from the PNW area, we computed a ratio of the total egg production in the PNW to the total egg production in the whole area (PNW and California) as $P_{0,I} A_I / \sum P_{0,j} A_j$, where $P_{0,j}$ is the daily egg production during the peak spawning time in the survey area A_j ; $j=1$ refers to the PNW area in July and $j=2$ refers to California in April.

Adult reproductive state and parameters

For all four surveys, we used histological analysis of all ovarian tissues, along with trawl and female data, to provide accurate assessment of adult parameters and reproductive state such as maturity, spawning period, recent spawning activity, post-spawning condition, or identification of advanced oocyte development for a selection of females for batch fecundity estimation. In the laboratory, each preserved ovary was blotted and weighed to the nearest mg. A piece of each ovary was removed, a histological slide was prepared, and the tissue sections were stained with hematoxylin and eosin. We analyzed oocyte development, atresia, and post-ovulatory follicle age to assign

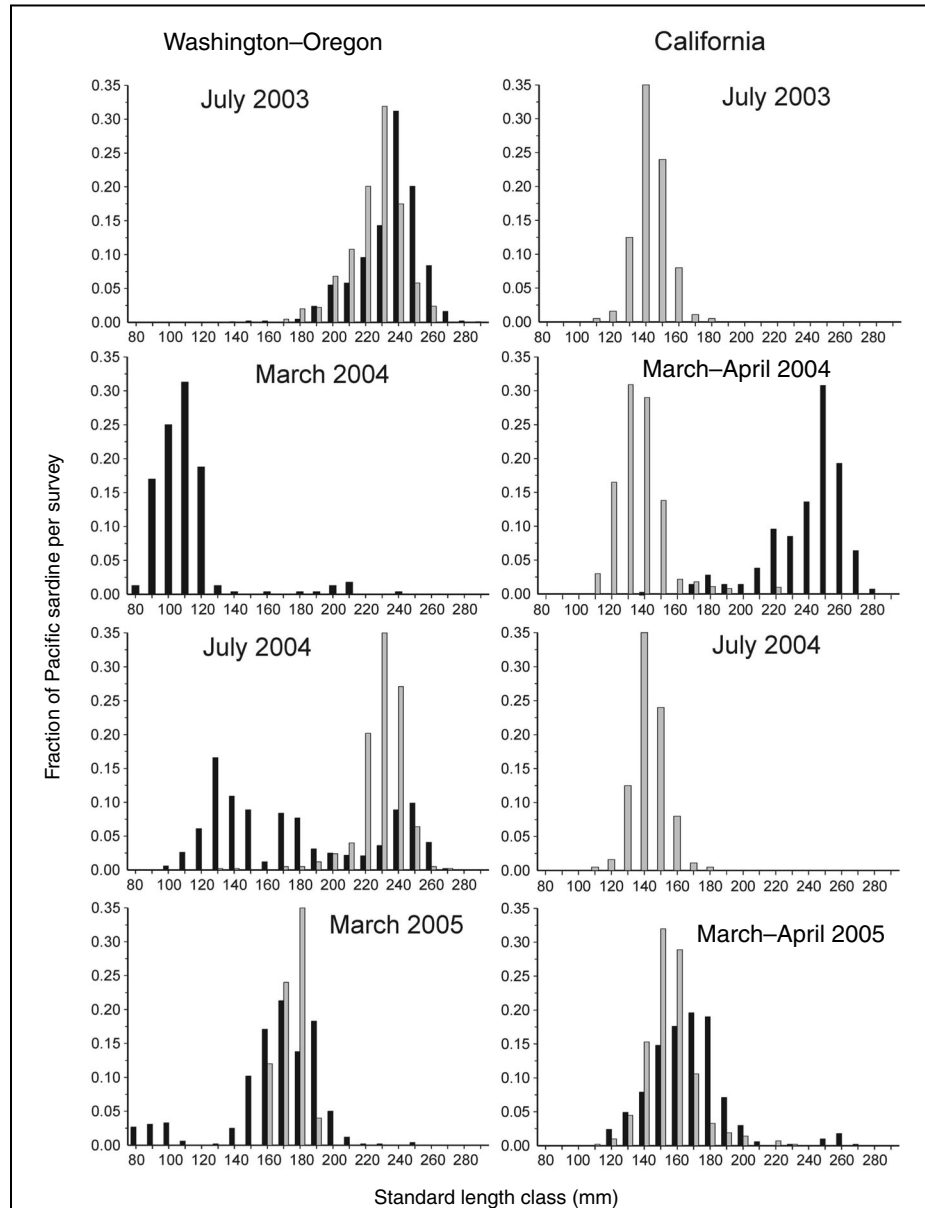


Figure 6

Length frequency distribution of Pacific sardine (*Sardinops sagax*) off Washington and Oregon, and California during 2003, 2004, and 2005 from fishery independent trawl surveys (black bars) and port sampling of commercial purse seine catches (gray bars). Catch data were provided by California Dept. of Fish and Game, Oregon Dept. of Fish and Wildlife, and Washington Dept. of Fish and Wildlife.

Table 3

Estimated Pacific sardine (*Sardinops sagax*) egg densities, egg production ($P_{0,c}$, Eq. 5) with coefficient of variation (CV) in parentheses, and number of collections with positive collections in parentheses from California Cooperative Oceanic Fisheries Investigation vertical egg tow net (CalVET) and continuous underway fish egg sampler (CUFES) samples in two strata with dividing latitude of 125°W and the entire survey area for the July 2003 and July 2004 surveys. Dashes indicate where statistics were not computed because of small or zero catches.

	Stratum 1	Stratum 2	Entire survey area
July 2003			
CalVET			
Egg density (eggs/0.05 m ²)(CV)	0.388(0.51)	0	0.073(0.51)
$P_{0,c}$ (Egg production /0.05 m ² /day)(CV)	—	—	0.04(0.51)
No. of CalVET tows (positive)	18(4)	36(0)	54(4)
CUFES			
Eggs/min (CV)	0.148(0.61)	0.05(0.74)	0.069(0.49)
No of CUFES samples (positive)	316(102)	166(15)	482(117)
Survey area (km ²)(%)	40,043(19)	166,334(81)	206,377(100)
July 2004			
CalVET			
Egg density (eggs/0.05 m ²)(CV)	0.0(—)	0.088(0.56)	0.070(0.56)
$P_{0,c}$ (Egg production /0.05 m ² /day)(CV)	—	—	0.037(0.58)
No. of CalVET tows (positive)	14(0)	34(3)	48(3)
CUFES			
Eggs/min (CV)	0.11(0.42)	0.097(0.67)	0.1(0.53)
No of CUFES samples (positive)	197(65)	450(64)	647(129)
Survey area (km ²)(%)	40,043(21)	150,932(79)	190,975(100)

Table 4

Percentage and average size in each maturity class of Pacific sardine (*Sardinops sagax*) females in the random samples from trawls conducted during four research surveys in 2003–05 off Oregon and Washington. Maturity was based on histological analysis of ovaries.

Survey dates (n females)	Maturity class	Percentage of females	Mean standard length (mm)	Mean whole body weight (g)
6–25 July 2003 (690)	Immature	0.7	204	124
	Mature	98.3	238	194
29 February–19 March 2004 (108)	Immature	97.2	108	14
	Mature	2.8	207	105
6–25 July 2004 (410)	Immature	62.2	147	43
	Mature	37.8	240	200
2–21 March 2005 (241)	Immature	89.2	161	51
	Mature	10.8	195	87

female maturity and reproductive state (Macewicz et al., 1996; Lo et al., 2005).

Sufficient numbers of immature and mature females in the random 50-fish subsample of a positive trawl for estimation of the length at which 50% were mature were collected during July 2004 and March 2005 (Table=4). Females were grouped into 10-mm length classes and the length at which 50% were mature was estimated by logistic regression: $y=1/(1 + e^{-(a+bL)})$, where y = the proportion of mature female sardine and L = the

standard length in mm. The length-specific maturation relationships were compared to those off California in April 1994, 2004, and 2005 (Macewicz et al., 1996; Lo et al., 2005).

Because the spawning season occurs in early summer, we used the two sets of July survey data to estimate the following adult reproductive parameters, which were used in the spawning biomass computation based on the daily egg production method (Lasker, 1985; Parker, 1985; Lo et al., 2005): the daily spawning fraction (S)

or the fraction of mature females spawning per day; the average batch fecundity (number of eggs per spawning per mature female: F); the fraction of mature fish that were female by weight (sex ratio: R); and the average weight of mature females (g) (W_f). The reproductive parameters were estimated from the data on the first 25 mature females per trawl or all mature females if there were <25 by following the methods in Macewicz et al. (1996). Females with ovaries histologically identified as containing hydrated oocytes (hydrated ovary) have temporarily inflated ovary weights. For each July survey, the relation between wet weight (y) and ovary-free wet weight (x) from mature females lacking hydrated oocytes was determined as $y = -9.0998 + 1.0758x$ in 2003 and $y = -6.316 + 1.05608x$ in 2004. Thus, the observed female weight was adjusted downward for females with hydrated ovaries when calculating average mature female weight (W_f) for each collection by year. During March of 2004 and 2005, adjustments were not necessary and fecundity was not estimated from mature females caught because none of them had ovaries with oocytes in the migratory-nucleus or hydrated stages. Mean batch fecundity was estimated by the gravimetric method for 54 females from 21 trawls from the July surveys. The relationship of batch fecundity to female weight (without ovary) was then determined.

Reproductive adult parameters were summarized for each trawl. Population values were estimated by methods in Picquelle and Stauffer (1985), where estimation of each adult parameter (S , F , W , R) was based on a ratio estimator (Picquelle and Stauffer, 1985; Lo et al., 1996) and used to calculate spawning biomass and its covariance for the July 2003 and July 2004 surveys.

Spawning biomass

The DEPM is a well-accepted method used for estimating spawning biomass for fish with indeterminate fecundity, i.e. multiple spawners (Hunter and Lo, 1993; Stratoudakis et al., 2006) and was used to estimate the spawning biomass of Pacific sardine in this area in 1994 (Bentley et al., 1996). The spawning biomass was computed with the following equation:

$$B_s = \frac{P_0 AC}{RSF / W_f}, \quad (7)$$

where P_0 = the daily egg production/0.05 m² at hatching;

A = the survey area in units of 0.05 m²;

C = the conversion factor from grams (g) to metric tons (t);

R = the fraction of mature fish that is female, by weight (sex ratio);

S = the daily spawning fraction: fraction of mature females spawning per day;

F = the average batch fecundity (number of eggs per spawn per mature female); and

W_f = the average weight of mature females (g).

The denominator (RSF/W_f) is referred to as the daily specific fecundity (number of eggs/population weight [g]/day).

The variance of the spawning biomass estimate (\hat{B}_s) was computed from the Taylor expansion in terms of the coefficient of variation (CV) for each parameter estimate and covariance for adult parameter estimates (Parker, 1985; Picquelle and Stauffer, 1985; Lo et al., 1996; 2005):

$$VAR(\hat{B}_s) = \hat{B}_s^2 \left[\frac{CV(\hat{P}_0)^2 + CV(\hat{W}_f)^2 + CV(\hat{S})^2}{CV(\hat{R})^2 + CV(\hat{F})^2 + 2COVS} \right] \quad (8)$$

The last term, involving the covariance term, on the right-hand side is

$$COVS = \sum_i \sum_{i < j} \text{sign} \frac{COV(x_i, x_j)}{x_i x_j}, \quad (9)$$

where x_i = the i th adult parameter estimate, e.g., $x_i = F$ and $x_j = W_f$. The sign of any two terms is positive if they are both in the numerator of B_s or denominator of B_s (Eq. 7); otherwise, the sign is negative. The covariance term is

$$\text{cov}(x_i, x_j) = \frac{[n/(n-1)] \sum_k m_k (x_{i,k} - x_i) g_k (x_{j,k} - x_j)}{\left(\sum_k m_k \right) \left(\sum_k g_k \right)}, \quad (10)$$

where $k = k^{\text{th}}$ tow, and $k=1, \dots, n$;

m_k and g_k = sample sizes; and

$x_{i,k}$ and $x_{j,k}$ = sample means from the k^{th} tow for x_i and x_j , respectively.

Results

Seasonal biomass

The relative abundance of Pacific sardine was higher in summer than in the following spring off the PNW. The bias-corrected seasonal biomass estimates were 198,600 t (CV=0.51) for July 2003, 20,100 t (CV=0.80) for March 2004, 77,900 t (CV=0.38) for July 2004, and 30,100 t (CV=0.72) for March 2005 over an area close to 200,000 km² (Table 1). The inshore stratum 1 made up 20% of the survey area. Yet, for all years stratum 1 had over 80% of the biomass. The recruit biomasses (fish ≤ 120 mm SL) in spring of 2004 and 2005 were quite different: 20,500 t (CV=0.81) for the 2003 year class and 53 t (CV=0.72) for the 2004 year class, respectively. The 2004 point estimate of the recruit biomass, 20,500 t, was greater than that of the total biomass of 20,100 t

but this was primarily due to the bias correction based on the bootstrap simulation and the difference was not statistically significant.

The relatively large 2003 year class constituted a major proportion of the total biomass in March 2004, whereas the 2004 year class constituted a very small proportion of the fish in 2005 (Fig. 6). Therefore, the relative abundance of Pacific sardine in the spring of 2004 and 2005 was primarily supported by the strong year class of 2003.

Spawning habitat

The spawning habitat was located east of 125.5°W longitude in July 2003 and 2004 (Figs. 2 and 4), and between 43° and 44.5°N latitude in July 2003, and between 42° and 44.5°N latitude in July 2004. The location of the spawning center, computed as the weighted latitude and longitude with the eggs/min (≥ 0.5) as the weight, was 124.7°W and 43.7°N in 2003 and 125.13°W and 42.9°N for 2004. Therefore, the spawning habitat shifted southwestward from 2003 to 2004. Because the eggs from the CUFES samples were distributed more to the west, the size of the spawning habitat was 10,716 km² for 2003 and 14,260 km² for 2004. The spawning habitat, determined from CUFES data, crossed the dividing line of 125°W between two strata based on trawl allocation. For both July cruises, the range of SST in the spawning habitat was 13.4–18.5°C with a mean close to 16°C (15.7°C and 16.0°C for 2003 and 2004). Note that the overall mean SST for July 2003 was 16.2°C (range 9.4–25.3°C) and the mean temperature was 16.8°C (range 9.7–19.9°C) in July 2004. The number of positive CUFES samples was 117 out of 482 in July 2003 and 129 out of 647 in July 2004. Therefore, the proportion of positive samples (24% in 2003, 19% in 2004) was similar during these two years.

Daily egg production

The mean density of eggs was 0.388 eggs/0.05 m² (CV=0.51) in stratum 1 and no eggs were caught by CalVET net tows in stratum 2 during the July 2003 survey. The opposite was true for the July 2004 survey: no eggs were caught in stratum 1 and the mean density in stratum 2 was 0.088 eggs/0.05 m² (CV=0.56) (Table 3). The overall mean densities were 0.073 eggs/0.05 m² (0.51) and 0.07eggs/0.05 m² (0.49) for 2003 and 2004, respectively. The bias-corrected estimates of the daily egg production from the integral method ($P_{0,c}$) (Eqs. 5 and 6) in July were 0.04 eggs produced/0.05 m²/day (CV=0.51) for 2003 and 0.037 eggs produced/0.05 m²/day (CV=0.58) for 2004. The mean egg capture rates from CUFES samples for 2003 and 2004 were 0.069 eggs/min (CV=0.49) and 0.1 eggs/min (CV=0.53) (Table 3).

The ratio of the total egg production in the PNW to the total egg production off the U.S. west coast (PNW and California) was 1.46% and 2.2% for 2003 and 2004 and therefore Pacific sardine off the PNW contrib-

uted approximately to 1.8% of the total egg production (Table 5).

Adult sardine reproductive parameters and spawning biomass

During the four surveys, 92 of the 214 trawls (Figs. 2–5, Table 1) captured adults or subadults. In the random subsamples from these trawls, 2862 sardine were measured (Fig. 6); standard length ranged from 99–289 mm for females, 106–281 mm for males, and 75–146 mm for individuals of indeterminate sex (where it was difficult to accurately determine sex without microscopic examination). Nearly all females were mature in July 2003 and nearly all were immature in March 2004 (Table 4). Using logistic regression we computed the standard length at which 50% were mature as 195.1 mm and 199.8 mm for July 2004 and March 2005, respectively (Fig. 7).

Mean batch fecundity was estimated for 35 females caught in July 2003 and 19 from July 2004 (Fig. 8). Analysis of covariance showed no differences in the relationship between female weight (without ovary, W_{of}) and batch fecundity (F_b) among years ($P=0.531$). Combining the data from July 2003 and 2004, we found that the relationship between female weight and batch fecundity, as determined by simple linear regression, was $F_b = -16755 + 372.1W_{of}$ with the $r^2=0.47$. Because the intercept did not differ from zero ($P=0.165$), we chose the regression without the intercept, which yielded the relationship $F_b = 295.83W_{of}$, where W_{of} ranged from 111–322 g (Fig. 8). The latter equation was used to calculate batch fecundity for each mature Pacific sardine female in the July trawl samples.

The population sex ratio (R) for mature fish was 0.534 female (CV=0.04) in July 2003 and 0.568 female (CV=0.05) in July 2004 (Table 5). The 657 mature female Pacific sardine analyzed from July 2003 and 196 from July 2004 were considered a random sample of the population in the area trawled. Population-level estimates of the other adult reproductive parameters were as follows: average batch fecundity (F)=55,986 eggs/spawning event (CV=0.04) in July 2003 and 55,883 eggs/spawning (CV=0.06) in July 2004; daily spawning fraction (S)=0.027 (CV=0.31) in 2003 and $S=0.010$ (CV=0.74) in 2004; and mean mature female fish weight (W_f)=194.36 g (CV=0.02) in 2003, and 193.16 g (CV=0.03) in 2004 (Table 5). The daily specific fecundity was calculated as 4.21 and 1.68 eggs/gm/day in 2003 and 2004, respectively (Table 5). The proportion of active females spawning was 0.05 and 0.025 for July 2003 and 2004, respectively, which meant that the average female was spawning roughly once every 20 to 40 days. None of the three mature females caught in March 2004 or the 37 mature females caught in March 2005 had histological evidence of imminent or recent spawning (hydrating oocytes or postovulatory follicles), and thus $S=0$; hence, spawning biomass was not estimated for either March (Table 5).

The estimated spawning biomass based on biased corrected egg production from the integral method ($P_{0,c}$)

and the adult reproductive parameters for July 2003 and July 2004 (Eq. 7, Table 5) was 39,184 t (CV=0.57) and 84,120 t (CV=0.93), respectively, for an area close to 200,000 km² from 42°N to 48°N off Oregon and Washington.

Discussion

Dynamics of biomass

Off the PNW, the seasonal relative abundances of Pacific sardine based on the swept area method are nonstationary (i.e., not static): high in summer and low in spring. Fish residing in the PNW in spring are those

over-wintering, and in the summer the majority of fish ≥ 190 mm SL are likely those migrating from California. The spatial distribution of the Pacific sardine was similar between summer and spring: high in the inshore area and low in the offshore area, except during March 2005 when small numbers of sardine were caught in the northern offshore area (Fig. 5). This distribution is quite different from that off California where the spatial distribution varied among years (Lo et al., 2005). The PNW biomass estimates, high in July and low in March, together with the differential length distributions are consistent with the conceptual migration schedule of Pacific sardine (a migration route that appears to be similar to that of Pacific hake, *Merluccius productus*), namely of movement to the PNW from California before

Table 5

Trawl information, estimated female adult parameters, egg production, and spawning biomass (estimated by the daily egg production method (DEPM)) for Pacific sardine (*Sardinops sagax*) from July and March surveys conducted from 2003 through 2005 off Washington and Oregon (Pacific Northwest) and from April surveys conducted from 2003 through 2005 off California and in 1994 off California and Mexico. Either the coefficient of variation (CV) or number of positive trawls is in parentheses. na=not available.

		Pacific Northwest				California			
		2003 July	2004 March	2004 July	2005 March	1994 April	2003 April	2004 April	2005 April
No. trawls (positive)		48(36)	59(9)	58(27)	49(20)	79(43)	0	25(17)	19(14)
Ave. surface temperature (°C) at sardine locations		15.4	10.4	15.6	10.4	14.36		13.59	14.18
Fraction of females by weight	R	0.534		0.568		0.538		0.618	0.469
Ave. mature female weight (g) with ovary	W_f	194.36	105	193.16	102.5	82.53		166.99	65.34
(g) without ovary	W_{of}	189.25	102.7	188.90	100.2	79.33		156.29	63.11
Average batch fecundity ^a	F	55,986		55,883		24,283		55,711	17,662
Relative batch fecundity (oocytes/g)		288		289		294		334	270
No. mature females analyzed		657	3	196	37	583		290	175
No. active mature females		374	1	81	11	327		290	148
Fraction of mature females ^b spawning per day (CV)	S	0.027 (0.31)	0	0.010 (0.74)	0	0.074 (0.23)		0.131 (0.17)	0.124 (0.31)
Fraction of active females ^c spawning per day	S_a	0.050	0	0.025	0	0.131		0.131	0.155
Daily specific fecundity	RSF W	4.21	na	1.68	na	11.7		27.04	15.67
Egg production/0.05 m ² /day (CV) (Eq. 5)	P_o	0.04 ^d (0.51)		0.037 ^d (0.58)		0.193 (0.21)	1.520 (0.18)	0.960 (0.24)	1.916 (0.42)
Survey area (km ²)	A	206,037		190,975		380,175	365,906	320,620	253,620
Spawning biomass (t) (CV)	B_s	39,184 (0.57)	na	84,120 (0.93)	na	127,102 (0.32)	485,121 (0.36)	281,639 (0.30)	621,657 0.54
Eggs/min from CUFES sample (CV)		0.069 (0.49)		0.1 (0.53)		na	1.57 (0.27)	0.78 (0.11)	0.62 (0.15)

^a Mature females: 1994 estimate was calculated with $F_b = -10858 + 439.53 W_{of}$ (Macewicz et al., 1996), in 2004 with $F_b = 356.46 W_{of}$ (Lo et al., 2005), in 2005 with $F_b = -6085 + 376.28 W_{of}$, and for Pacific Northwest in 2003 and 2004 with $F_b = 295.83 W_{of}$.

^b Mature females included females that were active and those that were postbreeding (incapable of further spawning during the season).

^c Active mature females were capable of spawning and had oocytes with yolk or postovulatory follicles less than 60 hours old.

^d Calculated by the integral method and corrected for bias ($P_{0,c}$).

summer to feed, and a return to the south before spring to spawn (Clark and Janssen, 1945; Dorn, 1995; Emmett et al., 2005; Smith, 2005).

The U.S. stock biomass of age 1+ Pacific sardine increased from 1981 to a peak of one million tons in 2000 and, according to the stock assessment, began to decline in 2003 (Hill et al., 2007). The high biomass off the PNW in 2003 was most likely due to the accumulation of migrant survivors from 1999 through 2002, when the stock assessment reported that biomasses were high. The PNW sardine biomass, estimated from surface rope-trawl surveys for salmon off the Columbia River, has been decreasing since 2003 (R. Emmett, personal commun.²). This decrease is likely due to 1) the decline of migratory fish as a result of the decreasing biomass since 2003 off California, 2) a decline in successful spawning off the PNW, or 3) the continued sardine movement northward into Canadian waters, or a combination of the three events.

The July 2003 survey indicated that the majority of fish were large (≥ 190 mm SL), whereas the July 2004 survey showed the opposite because most of the small fish were from the strong 2003 year class. The presence of large sardine off Oregon in July 2003 and California in March–April 2004 is consistent with the concept of the migration of large fish from the PNW to California before spawning. However, the large sardine off Oregon in July 2004 did not show up off either California or the PNW during March–April 2005 (Fig. 6). This finding may have been due to a lower total biomass and a smaller proportion of large fish off the PNW in July 2004 (Table 1, Fig. 6), or because during the 2005 California survey, few trawls were taken north of 34°N latitude where most migrants had resided according to the 2004 DEPM survey off California, or it could have been due to a combination of both factors (Fig. 5).

Although the summer PNW biomass estimates were different between years, the spring biomass estimates were stable. March surveys clearly revealed the relative magnitude of the migratory and the local PNW stocks during the survey years. The change in biomass off the PNW among years can be due to multiple reasons: a change in the biomass of the resident PNW fish, or a change in the biomass off California, or a change in the migration pattern due to food availability and oceanographic conditions, or both (MacFarlane et al., 2005). To better understand the dynamics of the Pacific sardine off the west coast of North America, spring and summer synoptic surveys from Baja California, Mexico, to British Columbia, Canada, and from tagging studies are necessary.

² Emmett, Robert. 2009. Northwest Fisheries Science Center, Newport, OR.

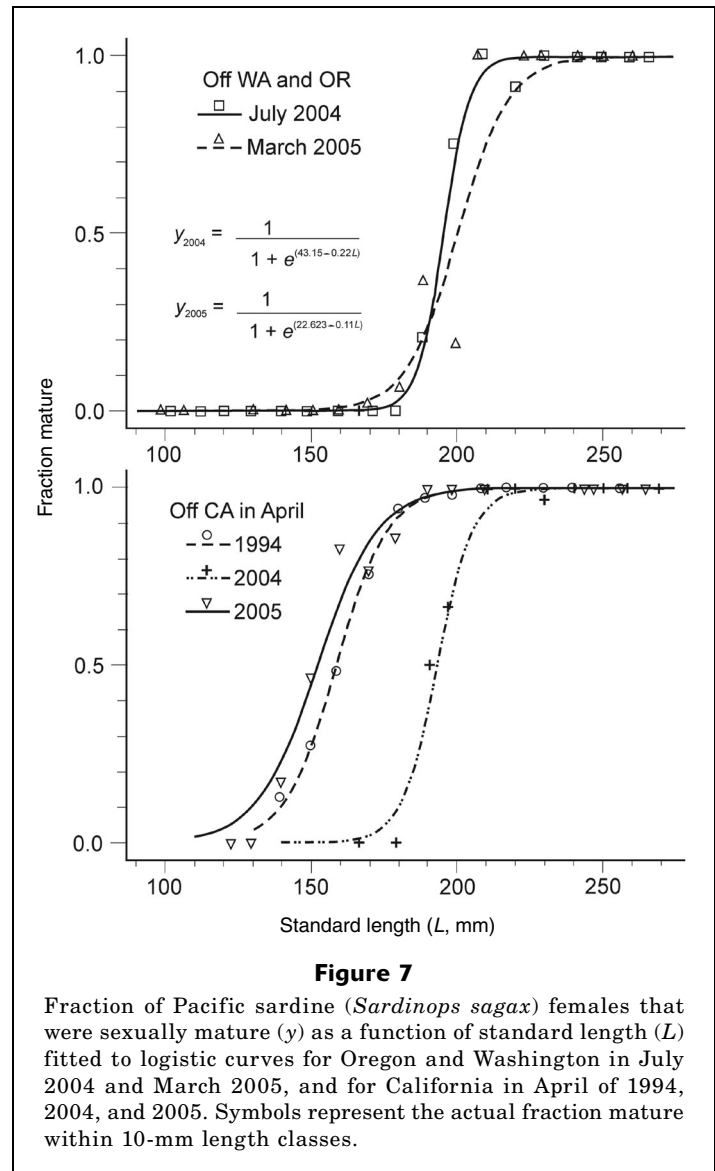
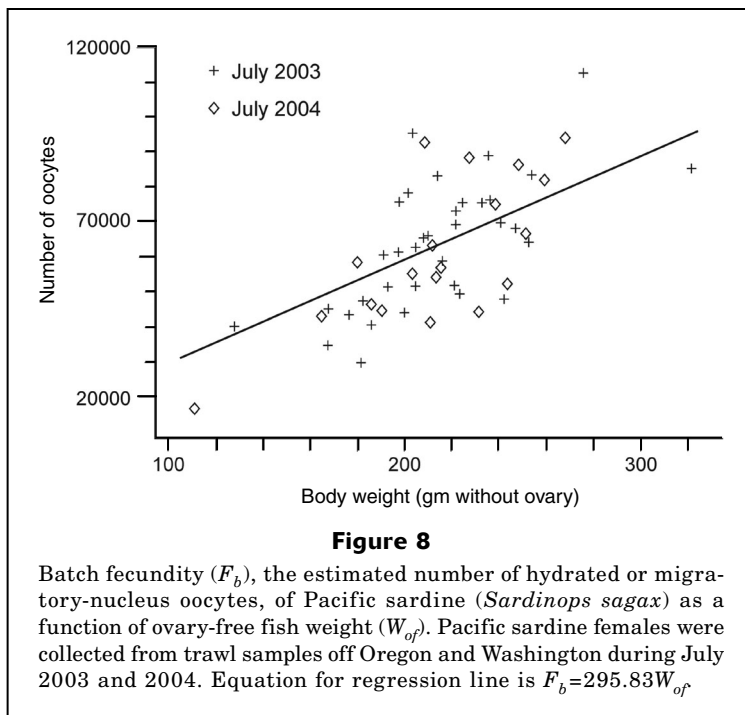


Figure 7
Fraction of Pacific sardine (*Sardinops sagax*) females that were sexually mature (y) as a function of standard length (L) fitted to logistic curves for Oregon and Washington in July 2004 and March 2005, and for California in April of 1994, 2004, and 2005. Symbols represent the actual fraction mature within 10-mm length classes.

Spawning habitat and daily egg production

The spawning habitats off the PNW in the summer of 2003 and 2004 were similar in size between 42–44.5°N and east of 125.4°W. The spawning area occupied 5–7% of the survey area, much smaller than that off California (20–25% of the survey area in 2003–04). The spawning habitat in the mid-2000s (2003 through 2005) seemed to contract southward and shoreward compared to the mid-1990s (1994 through 1998) when it extended to 46°N and close to 126°W (Emmett et al., 2005). The temperature range in the offshore spawning habitat in the 1990s (14–16°C) was similar to that in the 2003–04 inshore area (13–18°C); therefore, the change of oceanographic conditions may have caused the apparent contraction of spawning habitat between the mid-1990s and mid-2000s off the PNW. Because no adult samples were taken in the mid-1990s, we were unable to compare the adult



spawning characteristics during these two periods. The spawning habitats of sardine off the PNW in 2003 and 2004 were similar, whereas the spawning habitats off California were quite different: concentrated off central California in 2004 and distributed through the whole survey area in 2005. Note, no eggs were caught during the July California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys off California in either CalVET or bongo net tows.

The daily egg production off the PNW was low in both 2003 and 2004 (0.04 and 0.037 eggs produced/0.05 m²/day, respectively), lower than that in 1994 (0.50 eggs produced/0.05 m²/day) (Bentley et al., 1996), and lower than those off California (1.52 and 0.96 eggs produced/0.05 m²/day) in 2003, 2004, and other years. This low egg production in the PNW contributed only 1.8% of the total U.S. west coast egg production in 2003–04. The low PNW egg production estimates could be the result of the July surveys occurring after the spawning peak, possibly in June, as the SST was high (Emmett et al., 2005), or the result of the egg mortality of Pacific sardine off the PNW being different from that off California, or both. Future ichthyoplankton surveys with large sample sizes are needed to obtain direct estimates of the daily egg production and egg mortality off the PNW.

The egg production estimates from July 2003 and 2004 were very similar even though the relative abundances were quite different. With similar egg production in two years, one might expect that the biomass of recruits would be similar. However, the 2003 year class was much stronger than that of 2004. This difference would be most likely due to the more

favorable environmental conditions in 2003 than in 2004.

One interesting question to ask is what effect a reduction of the spawning habitat or egg production would have on the PNW Pacific sardine population. The sustainability of the Pacific sardine population off the PNW depends greatly on the Pacific sardine population off California, oceanographic conditions, and food availability (MacFarlane et al., 2005) because most of the spawners (>190 mm SL) off the PNW in the summer are migrants from California. As long as the Pacific sardine population off California is large enough to allow adequate migration to the PNW in the summer to spawn, the population off the PNW will be sustained. Of course, if environmental conditions are unfavorable, the proportion of spawners may be reduced, affecting both the recruits to the local population and the size of the population in the following spring. If the population off California decreases to the level of collapse, the population off the PNW may have been diminished well before the collapse off California. This status of the PNW population was evident from the history of landings in the last Pacific sardine collapse (Fig. 1). During the waning years of sardine population, the PNW commercial landings ended in 1949, 16 years before the California catch ended in 1965. The sardine population began recovering in the late 1970s–early 1980s off California. Incidental landings off California began in 1981, 11 years before an incidental catch of sardine off the PNW in 1992 due to the favorable El Niño conditions, and 17 years before directed landings in 1998.

Application of proper management strategies to preserve the population off California, and thus the mi-

grants, is essential because most of the migrants are mature fish and the leaders of migration imprints: older fish lead younger fish to migrate. This recent entrainment hypothesis (Petitgas et al., 2006) is a step forward from the theory that fish population life cycles are controlled only by physical conditions (Sinclair, 1988). The entrainment hypothesis implies that the older fish are essential to ensure the sustainability of population and fisheries of Pacific sardine off the PNW and thus along the entire west coast of the North American continent.

Adult reproductive parameters and spawning biomass

Pacific sardine spawn off the PNW, contrary to beliefs in the 1930s and 1940s that they spawn only off California. Although sardine eggs, larvae, and adults have been caught in surveys off the PNW since 1994 (Bentley et al., 1996; Emmett et al., 2005), only with the four surveys during 2003–05 were the reproductive parameters for female Pacific sardine off the PNW examined in detail.

The spawning season of Pacific sardine off the PNW apparently occurs primarily in the early summer, although a few fish possibly spawn in spring. If July is the spawning peak off the PNW, then spawning is less intense than during the peak off California in April. The daily spawning fraction of mature females ($S=0.027$ and 0.01) was much lower than that off California (0.07 – 0.17). Previous work has indicated that active mature females of *Sardinops* spp. worldwide spawn once every eight days (Macewicz et al., 1996). Recent results off California are similar (once every 6–8 days), where as active mature Pacific sardine females off the PNW spawned much less frequently (only once every 20–40 days). In addition, females in July produced about 288 eggs per gram of female weight (relative batch fecundity) off the PNW—few eggs than similar females off California that spawned 334 eggs per gram of female weight in April 2004 (Table 5). According to the April 2004 DEPM sardine survey off California, the large mature females, in particular those ≥ 200 mm SL, were spawning very vigorously ($S=0.131$) and these migratory females may not have recovered sufficiently to spawn at higher rates off the PNW during July 2004, a phenomenon similar to that which occurred with Pacific sardine off Chile, which were less active during a second annual spawning period (Tascheri and Claramunt, 1996). The presence of a high percentage of inactive mature females off the PNW in July (43% in 2003 and 59% in 2004) indicates two other possible explanations for the low level of spawning: July is not the peak spawning time for sardine off the PNW because they may be similar to northern anchovy where ovaries with high levels of atresia (indicating cessation of reproductive activity) are common at the end of the spawning season (Hunter and Macewicz, 1985); or, Pacific sardine in the PNW may behave like chub mackerel (*Scomber japonicus*) whose individuals spawn only for a short period and inactive mature females are

common throughout the spawning season (Dickerson et al., 1992). If so, it may be necessary in future surveys to analyze reproductive samples collected over a longer time to better define the peak spawning period, and to determine whether the peak spawning fraction is similar to the rate off California (about 0.13 spawning per day) or whether it remains low (<0.03).

Few mature Pacific sardine females were caught off the PNW during March and it seems that they may have followed warmer water south. The majority of the 40 mature females were inactive (postbreeding or resting) and none had spawned. It was surprising that we caught 12 females of 202–260 mm SL that were active (their ovaries contained some oocytes with yolk) and were potentially capable of spawning in the near future (3–30 days). We examined the locations where females were caught and their associated water temperatures. The average SST of trawls during March was 10.4°C . During March 2004, the three mature females (one active) were caught farthest south (42°N) in 11.1°C water. One inactive mature female was caught near Astoria, OR, in 11.1°C water during March 2005, and the other 36 (11 active) mature females were caught inshore, south of 44.5°N in 11.5°C (10.7 – 12.5°C) water. Immature female Pacific sardine were generally found north of 44.5°N in cooler water; on average 10.2°C (9.6 – 10.7°C) in March 2004 and 10.3°C (9.0 – 12.5°C) in March 2005. Thus, in the winter, the older fish were able to move south following the warmer water, while the younger fish, due to a lack of stored energy for long distance swimming, remained in the cold water. Overwintering immature females seem to tolerate water as cold as 9.0°C . The PNW generally has warmer coastal SSTs in the winter (from downwelling) than in summer. However temperatures in the estuaries can be very cold and die offs of age-0 sardine in the Columbia River and other estuaries have been observed during the winter (E. Dorval, personal commun.³).

Female Pacific sardine in the PNW mature at lengths greater than those off California. Fifty percent of the females caught off the PNW matured at around 195 mm and $> 90\%$ off California were mature at the size of the smallest mature PNW female (182 mm). A majority of sardine > 200 mm off the PNW migrate during fall–winter (Clark and Janssen, 1945; Nottestad et al., 1999). During the April 2004 DEPM survey, Pacific sardine were collected off central California between 34.8°N and 37.3°N and a majority were the large, migratory size (those ≥ 200 mm), whereas in 2005, the majority of positive adult samples were collected in the inshore area of Southern California between 32°N and 36°N and most sardines were < 200 mm. The length of females at 50% maturity off the PNW was similar to the length estimate (193 mm) in April 2004 off California which indicated that the large Pacific sardines off central California likely were winter migratory fish. This conclusion is consistent with the historical tagging

³ Dorval, Emanis. 2008. Librairie La Lumiere, Rue Baussan, # 34, Turgeau, Port-au-Prince, Haiti, W.I.

results, which indicated that the majority of the tags released off the PNW were recovered off central California (Clark and Janssen, 1945).

The point estimates of spawning biomass of Pacific sardine off the PNW differed, but were not statistically different because of a large coefficient of variation: 39,184 t and 84,120 t for July 2003 and 2004, respectively. They were close to 50,000 t in 1994 (Bentley et al., 1996). Theoretically, the spawning biomass should constitute a good proportion of the total biomass, which was not so for July 2003. This could be due to an underestimate of P_0 , to an overestimate of the spawning fraction, or both. The overestimate of the spawning fraction could be due to the movement of the postspawners out of the spawning area. A DEPM study is needed to evaluate such effects and model the effects of fish movement on estimates of spawning rate. The effect of the timing of the survey in relation to spawning and movement cycles needs to be studied with new data and modeling.

The difference between the spawning biomass estimates in 2003 and 2004 was primarily due to the difference in the estimated spawning fractions (0.027 in contrast to 0.01), because the estimates of daily egg production (P_0) were similar. The large coefficients of variation of spawning biomass estimates were mainly a result of the uncertainty in estimates of P_0 and the daily spawning fraction (S) in July 2004. For low values of P_0 and S , the number of samples has to be substantially increased to obtain a more precise estimate (Picquelle and Stauffer, 1985). Estimated spawning biomass for off the PNW in July was much smaller than estimates for off California during April in recent years. The smaller fish length at 50% maturity off California means that the more numerous smaller resident Pacific sardine are able to participate in local spawning at the same time as the larger migratory sardine.

Future work

The Pacific sardine spawning habitat and season in the PNW are loosely defined in this study and the magnitude and scope of the coastal migration are not fully explored. To better characterize these, we need to conduct synoptic trawl-ichthyoplankton-acoustic surveys from Baja California, Mexico, to British Columbia, Canada, during spring and early summer at three to five year intervals. To better characterize the spawning habitats in this area, we need to obtain physical and biological oceanographic data (Lynn, 2003; Emmett et al., 2005; Reiss et al., 2008) and demographic data of Pacific sardine over a broader geographic range because the Pacific sardine is a migratory species.

For trawl swept-area-based biomass estimates, the efficiency of the trawl needs to be calibrated. Biomass estimates from acoustic surveys would be another fishery-independent source of relative abundance. Because the coefficients of variation of all estimates are large, the number of trawls needs to be increased or other statistical estimation procedures should be explored, or

both, to improve the precision of estimates. To obtain a representative length distribution of the population, fishery-independent surveys covering the whole west coast area are essential, and length data from commercial vessels should be used with caution for both the PNW and California. For spawning biomass, we need to understand the maturation schedules of females and the spawning season off Oregon and Washington. Numerous plankton net tows are needed to obtain direct estimates of the daily egg production and egg mortality rates in early summer. Currently, only the spawning biomass of Pacific sardine off California is estimated from the annual April DEPM survey. Because mature females were caught during two March surveys off the PNW, efforts should be made to obtain trawl data off the PNW in April. Data for mature females collected off the PNW could then be combined with the April data set off California to estimate reproductive parameters and the spawning biomass of Pacific sardine off the whole west coast of the United States. To better understand the relationship between the sardine populations off California and the PNW, we need to examine migration characteristics (i.e., migration range, pattern and schedule) and the effect of fishing pressure on the migratory fish because most of these fish are mature and leaders of migration imprints. We need a long time series of abundance for all regions together, along with oceanographic and biological data, to enhance our understanding of the dynamics of the entire Pacific sardine population to provide information for the development of future strategies to sustain the population.

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