

Abstract—During the last century, the population of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem has exhibited large fluctuations in abundance and migration behavior. From approximately 1900 to 1940, the abundance of sardine reached 3.6 million metric tons and the “northern stock” migrated from offshore of California in the spring to the coastal areas near Oregon, Washington, and Vancouver Island in the summer. In the 1940s, the sardine stock collapsed and the few remaining sardine schools concentrated in the coastal region off southern California, year-round, for the next 50 years. The stock gradually recovered in the late 1980s and resumed its seasonal migration between regions off southern California and Canada. Recently, a model was developed which predicts the potential habitat for the northern stock of Pacific sardine and its seasonal dynamics. The habitat predictions were successfully validated using data from sardine surveys using the daily egg production method; scientific trawl surveys off the Columbia River mouth; and commercial sardine landings off Oregon, Washington, and Vancouver Island. Here, the predictions of the potential habitat and seasonal migration of the northern stock of sardine are validated using data from “acoustic-trawl” surveys of the entire west coast of the United States during the spring and summer of 2008. The estimates of sardine biomass and lengths from the two surveys are not significantly different between spring and summer, indicating that they are representative of the entire stock. The results also confirm that the model of potential sardine habitat can be used to optimally apply survey effort and thus minimize random and systematic sampling error in the biomass estimates. Furthermore, the acoustic-trawl survey data are useful to estimate concurrently the distributions and abundances of other pelagic fishes.

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Prediction and confirmation of seasonal migration of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem

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Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem (CCE) vary greatly in terms of their abundance and migration behavior. For example, from approximately 1900 to 1940, sardine was the most abundant coastal pelagic fish species (CPS) in the CCE (Radovich, 1982), with its biomass estimated to be 3.6 million metric tons (Mt; MacCall, 1979). Tagging studies (Clark and Janssen, 1945) indicated that the “northern stock” resided largely off California in the spring, and off Oregon, Washington, and Vancouver Island in the summer. In the 1940s, the sardine stock, and thus the fishery, abruptly collapsed. During the subsequent 50 years of low abundance, the few remaining sardine schools concentrated in the coastal region off southern California (MacCall, 1976). With the gradual recovery of the stock in the late 1980s (Jacobson and MacCall, 1995; Wolf, 1992), perhaps due to the combination of conservation measures and favorable environmental conditions, sardine in the CCE expanded their biomass and distribution and resumed their seasonal migration between regions off southern California and Canada (McFarlane and Beamish, 2001). In the 1990s, Pacific mackerel (*Scomber japonicus*) had become scarce and the fishery shifted back to targeting sardine (Mason, 2004). The com-

bined landings of sardine off the west coasts of Mexico, the United States (U.S.), and Canada peaked at 0.12 Mt in 2007, driven mostly by the re-opening of the fishery in the northeast Pacific. The Pacific Fishery Management Council (PFMC) manages the sardine and Pacific mackerel fisheries using catch quotas based on annual stock assessments (Crone et al., 2009; Hill et al., 2010).

Sardine surveys and assessments

Since the mid-1980s, assessments of sardine in the CCE have been based on fisheries-independent estimates of their abundance from spring surveys off California conducted with the daily-egg-production method (DEPM; Lasker, 1985). Recent assessments of sardine biomass ranged from 1.3 Mt in 2006 to 0.6 Mt in 2010 (Hill et al., 2010). In 2009, the sardine catch was limited to 0.08 Mt (Hill et al., 2010). Concerned about assumptions in the DEPM and alarmed by the magnitudes and trend in catch quotas, the fishing industry resurrected the “optical-seine” method (Squire, 1972) [which combines information collected with cameras on aircraft and purse-seine nets deployed from fishing vessels] to survey sardine off Oregon and Washington during the summer

months of 2009 and 2010 (Hill et al., 2010). The results were included in the assessments for those years, but their influence was marginal because the random sampling errors were large and the portions of the stock surveyed were uncertain (Hill et al., 2010). Consequently, the PFMC sought a fisheries-independent survey method that could accurately and precisely quantify the entire northern stock of sardine.

Acoustic–trawl surveys

Combining information collected with sonars and nets, “acoustic–trawl” methods (those combining echosounder and trawl sampling) have been used to survey sardine off the west coast of the United States, within the CCE, for more than a half century. Beginning with “sonar mapping” in the 1950s (Smith, 1978), and single-frequency echo-sounding in the 1960s (Mais, 1977), the acoustic survey equipment and methods evolved to “broad bandwidth resonance scattering” in the 1970s (Holliday, 1972; 1977), and now to multiple-frequency and multibeam echo-sounding (e.g., Cutter Jr. and Demer, 2008). In all cases, interpretation of the acoustic backscatter data relies on information, including fish species and their distributions and sizes, from periodic net catches.

Sardine habitat and migration

Potential habitat To minimize uncertainties in estimates of sardine biomass, irrespective of the survey technique, the sampling effort must be optimally allocated to only the region containing the stock (Simmonds and MacLennan, 2005). On the basis of water temperatures associated with spawning activity and on evidence that sardine may be food limited above 16.5 °C, potential spawning-sardine habitat has been described as seawater with temperatures from 14° to 16°C (Jacobson et al.¹), 13.5° to 16.5°C (Agostini, 2005), and 12° to 15°C (Reiss et al., 2008). Notwithstanding these observed associations, accurate predictions of sardine distributions and densities have been elusive, until recently. Zwolinski et al. (2011) demonstrated accurate predictions of potential sardine habitat and the dynamics of its spatiotemporal distribution.

Based on a 12-year data set including samples of sardine eggs and concomitant remotely sensed oceanographic conditions, a probabilistic, generalized-additive model was developed which predicts the distributions of habitat for the northern stock of sardine. Significant relationships were identified between sardine eggs and sea-surface temperature, chlorophyll-a concentration, and the gradient of the sea-surface height. The model describes and accurately predicts the potential habitat and seasonal migration pattern of sardine, whether or not they are spawning (Fig. 1). The model predictions of

potential habitat were extensively validated by fishery-landing data from Oregon, Washington, and British Columbia, and trawl-survey data collected near the Columbia River mouth.

The predicted habitat can be used to optimize the locations for sardine surveys. For example, Zwolinski et al. (2011) showed that, averaged over twelve spring surveys, 92% of the sardine eggs were sampled by using 64% of the original survey effort. In other words, habitat predictions could have allowed approximately 36% of the survey effort to be reallocated to potential habitat—thus likely reducing the sampling error. The model of potential sardine habitat can also be used to optimize the survey timing.

Seasonal migration Traditionally, DEPM surveys of CPS have been performed in the spring, during the peak of the sardine spawning season (Lo et al., 2009). At that time, CPS mostly aggregate offshore of central and southern California, but some species, particularly Pacific herring (*Clupea pallasii*) and northern anchovy (*Engraulis mordax*), are located in a few coastal areas farther north. However, the model of potential sardine habitat indicates that acoustic–trawl surveys of sardine may be most efficiently conducted during the months of June and July, when the habitat is compressed along the coasts of Oregon and Washington (Fig. 1), the fish are located generally north of Point Conception and south of the Strait of Juan de Fuca, the days are longest and thus daytime sampling is maximized, and the survey can be augmented with fishery catch data from the same general time and place (Zwolinski et al., 2011).

In this study, model predictions of potential sardine habitat (Zwolinski et al., 2010) are compared to the results of two acoustic–trawl surveys of the entire west coast of the U.S., in spring and summer 2008. The principal objectives are 1) to estimate the geographic distributions and biomasses of the northern stock of sardine during the southern and northern portions of their migration; 2) to estimate random and systematic sampling errors in those estimates; 3) to further validate the model predictions of potential sardine habitat and its seasonal dynamics; and 4) to evaluate the feasibility of simultaneously surveying other CPS.

Materials and methods

Survey design

The west coast of the United States (U.S.) was surveyed twice in 2008, during spring (25 March to 30 April) and summer (6 July to 18 August). Sampling during the spring survey was conducted from the NOAA research vessels (RV) *David Starr Jordan* and *Miller Freeman*. Sampling during the summer survey was conducted from RV *David Starr Jordan*. During both seasons, the survey tracks (Fig. 2) mostly spanned and often extended well beyond the potential habitat of sardine (Fig. 1). A large amount of survey effort was expended outside of the

¹ Jacobson, L. D., N. C. H. Lo, S. F. Herrick Jr., and T. Bishop. 1995. Spawning biomass of the northern anchovy in 1995 and status of the coastal pelagic species fishery during 1994. NOAA Admin. Rep. LJ-95-11, La Jolla, 49 p.

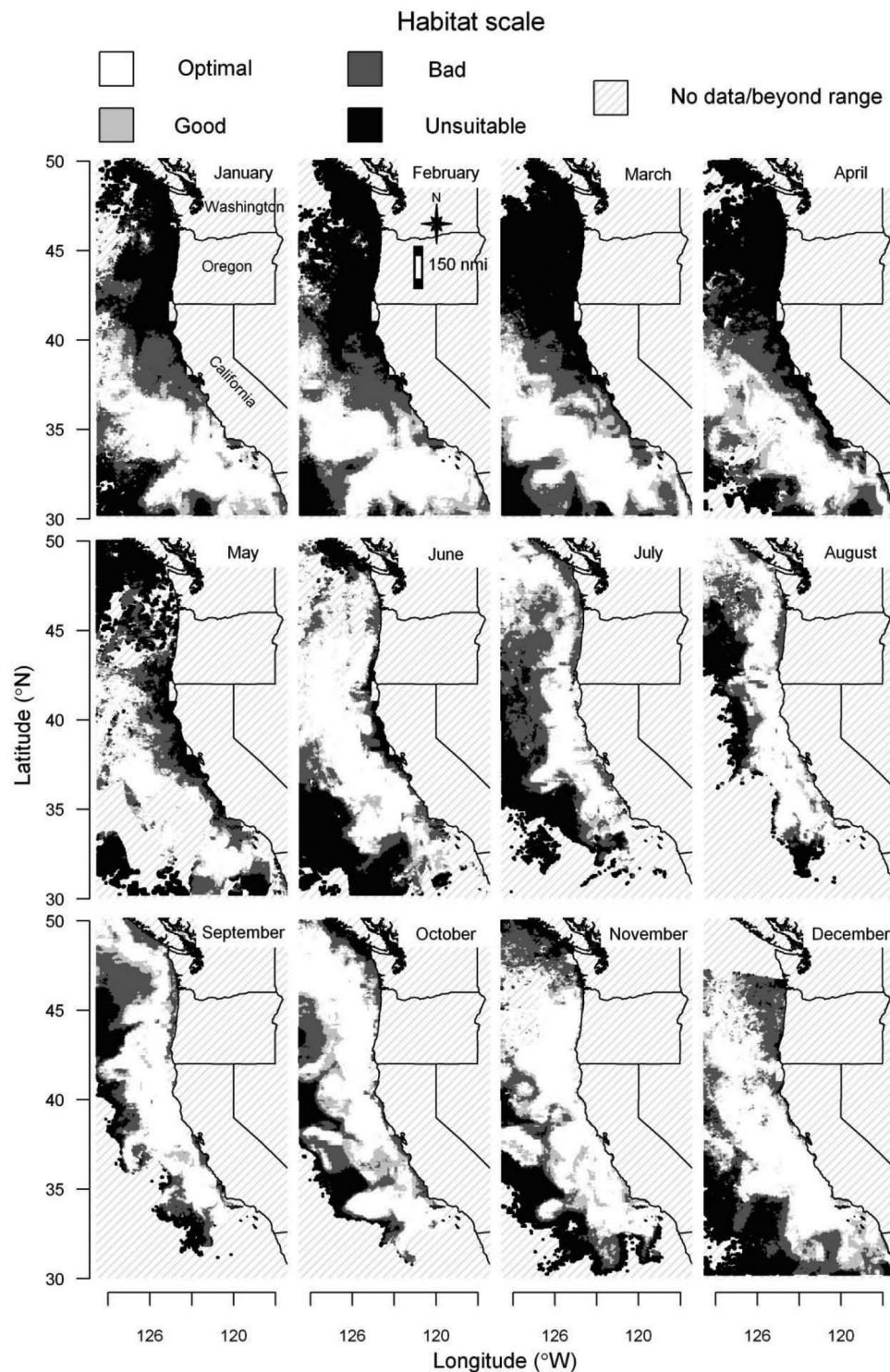
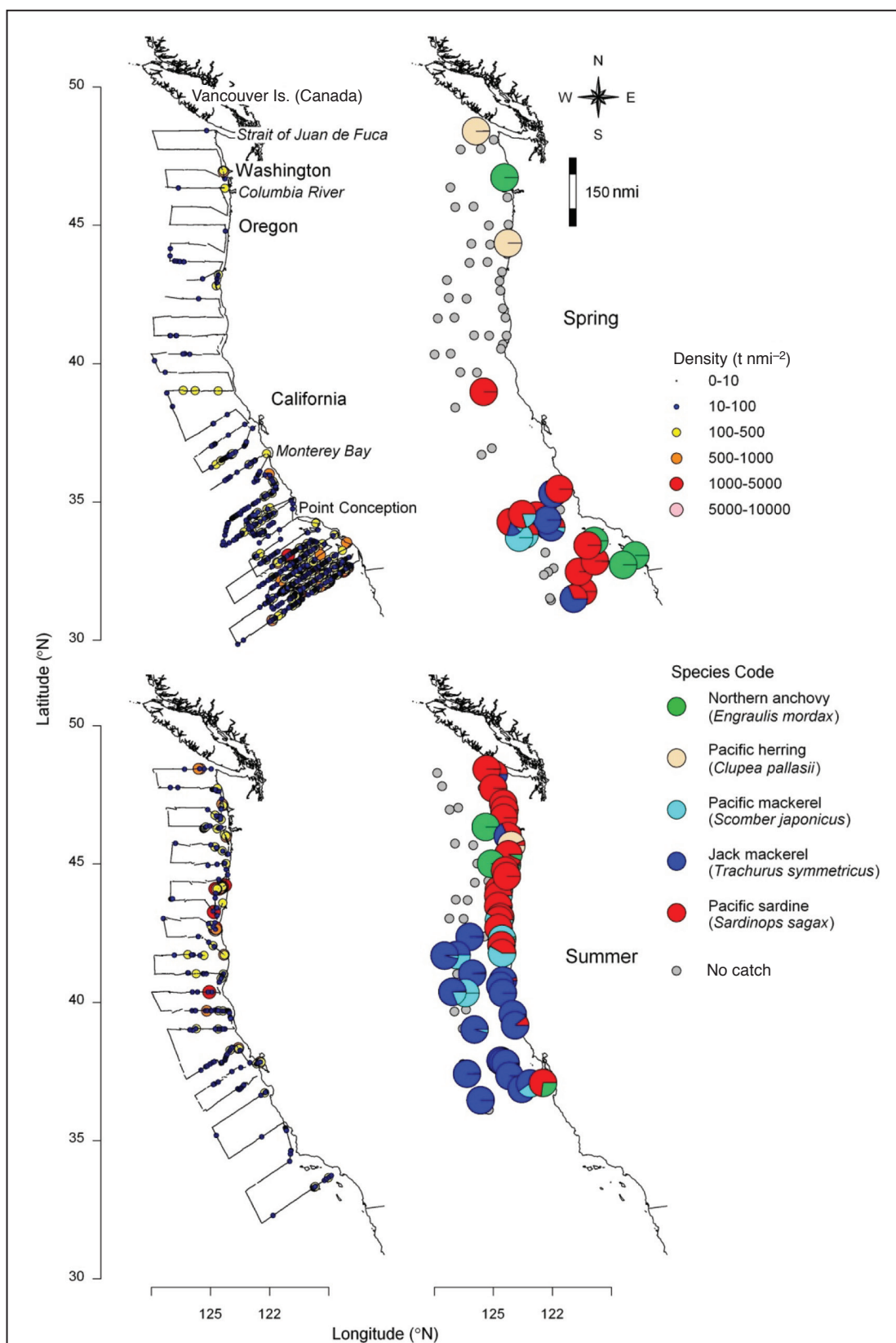


Figure 1

Average monthly distribution of the potential habitat of adult Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem (Zwolinski et al., 2011) during 2008. The model accurately predicts the habitat of sardine, irrespective of their spawning condition. "Optimal" habitat should include 80% of the sardine, "good" plus "optimal" habitat should include 90%; "bad" plus "good" plus "optimal" habitat should include 99%; and "unsuitable" habitat should include <1% of the total sardine. In the spring, the potential sardine habitat is located offshore of southern California. In the summer, the potential sardine habitat is compressed along the coasts of Oregon, Washington, and Vancouver Island.

**Figure 2**

Acoustically detected biomass densities of coastal pelagic fish species (CPS) [t nmi⁻²; sampling unit=0–70 m depth by 2-km trackline distance; left plots], and trawl catches including at least one CPS specimen (CPS catch) and no CPS catch (right plots) for the 2008 spring (upper plots) and summer (lower plots) surveys. For each catch including CPS, the proportion of each CPS is represented by the proportion of the circle with its color code.

potential habitat, to the north in the spring and to the south in the summer. This coverage served to assure that most of the sardine were indeed located within the predicted potential habitat.

Within their habitat, the dominant CPS in the CCE may be broadly and patchily distributed (Table 1), but are mostly aggregated in clusters of dense schools (Cutter Jr. and Demer, 2008; McClatchie, 2009). Because sampling of such skewed distributions is often the largest source of variance in acoustic-trawl surveys (Pennington, 1983; Demer, 2004), echosounder sampling was conducted continuously, and trawl sampling was conducted periodically, along parallel-line transects (Fig. 2). A large intertransect distance allowed independence of the mean acoustic backscatter between transects, permitting statistically unbiased estimations of mean biomass densities and sampling variances for target species (Jolly and Hampton, 1990). Transect independence was tested by applying the auto-correlation function to values of integrated echo energy for each species and stratum for all intertransect lags (distances).

Trawl sampling

CPS generally aggregate into schools during day and disperse, mix, and rise to the sea-surface at night (Holliday and Larsen, 1979; Cutter Jr. and Demer, 2008). Therefore, trawl sampling for identifying species and their sizes was performed at night, either at uniformly or randomly distributed, pre-assigned, or *ad hoc* stations along the transects. The trawl used was a Nordic 264 rope trawl with an opening of 600 m² (NET Systems, Bainbridge Island, WA). To minimize fish-size selectivity, the codend was fitted with an 8-mm-square mesh liner. The headrope was rigged with floats for towing at the surface at a speed of nominally 3.5 kn for 30 min. Up to four trawls were performed each night, beginning 30 to 60 min after sunset. The catch was sorted by species and weighed. From the catches with CPS, up to 75 fish from each target species were randomly selected. Those were weighed (g), and measured (mm), either in standard length (SL) for sardine, anchovy, and herring, or fork length (FL) for jack mackerel (*Trachurus symmetricus*) and Pacific mackerel. The length distributions of the sampled populations were estimated by using weighted averages of the length distributions from the trawls. The length data were first combined by transect, weighted by the acoustically estimated mean densities closest to each trawl. Then, the transect-weighted lengths were combined, weighted by the acoustically estimated mean densities for each transect.

Echosounder sampling

Echosounder sampling was conducted by using multi-frequency (18, 38, 70, 120, and 200 kHz) transceivers (Simrad EK60; Kongsberg, Norway) configured with split-beam transducers (typically Simrad ES18-11, ES38B, ES70-7C, ES120-7C, and ES200-7C, respectively). The echosounder systems were calibrated before

each survey by using the standard sphere technique (Foote et al., 1987) and a 38.1-mm diameter sphere made from tungsten carbide with 6% cobalt binder material. Throughout the surveys, conducted at a nominal ship speed of 10 kn, the echosounders synchronously transmitted 1024- μ s pulses every 0.5 s with powers equal to 2000, 2000, 1000, 500, and 100 W at 18, 38, 70, 120, and 200 kHz, respectively. Following each transmission, received-echo power (p_r ; W) data, indexed by time and geographic position, were recorded for periods corresponding to an observational depth of 250 m. The survey-depth range accommodated the maximum depth (70 m) of the expected sardine distribution, and that of other CPS (Table 1). With postprocessing software (Myriax Echoview; Hobart, Tasmania), the p_r values were converted to estimates of volume backscattering coefficient (s_v ; m⁻¹), and volume backscattering strength (S_v ; 10 log (s_v); dB re 1 m⁻¹).

Data analysis

Target identification Echoes may originate from sardine or other CPS such as jack mackerel, Pacific mackerel, northern anchovy, Pacific herring, and Pacific saury (*Cololabis saira*); semidemersal fish such as Pacific hake (also called Pacific whiting [*Merluccius productus*]) and rockfishes (*Sebastes* spp.); and krill (principally *Euphausia pacifica* and *Thysanoessa spinifera*). When analyzing the echosounder data, it was therefore necessary to objectively filter “acoustic bycatch,” i.e., backscatter not from the target species. Table 1 summarizes some relevant features of bycatch candidates. More detail regarding the principal target, sardine, is provided in the Appendix.

Identification of echoes from CPS, i.e., epipelagic fishes with swimbladders, was performed with a semi-automated data processing algorithm. First, background noise was estimated for each echosounder frequency and incoherently subtracted from the respective echograms of S_v . Portions of the “noise-reduced” echograms were designated “bad data” if the associated vessel speed was below a 5-kn threshold, indicating it was “on station,” or otherwise “off effort.”

Next, the S_v values in these “speed-filtered” echograms were preliminarily identified as echoes from fish with swim bladders if their sample-wise variance-to-mean ratio (VMR; Demer et al., 2009a) were within the -60 dB to -16 dB range. The S_v values outside this VMR range were set to -999 dB (practically zero). The “VMR-filtered” echograms were gridded into ten-sample-deep by three-transmission-long bins. The analysis bins were smaller than those used in studies of deeper dwelling fishes to accommodate the typical dimensions and shallower depths of CPS schools. The S_v values within each depth-distance window were replaced by the median value of the S_v ensemble. This procedure reduced the variance of the data and allowed comparisons of the median S_v values with predictions of backscattering spectra, backscatter versus frequency, for CPS. The echograms were ultimately apportioned to CPS,

Table 1

Geographic and depth distributions, maximum standard length (SL) (Miller and Lea, 1972)], and food preferences for coastal pelagic fish species in the California Current Ecosystem. All species, except Pacific hake (*Merluccius productus*), exhibit strong diel vertical migrations, often forming dense schools during daylight and dispersing near the sea surface at night. In contrast, Pacific hake aggregate more diffusely, generally deeper than the other species.

Species	South-north distribution	East-west distribution	Depth distribution	Max. SL	Prey	References
Jack mackerel (<i>Trachurus symmetricus</i>)	Baja California to the Gulf of Alaska	Coastal and oceanic; larger fish to 1000 nmi offshore	0–300 m (commonly 0–50 m)	81 cm	Large zooplankton, small fish, and squid	(Mais, 1974; MacCall and Stauffer, 1983)
Northern anchovy (<i>Engraulis mordax</i>)	Baja California to Canada (discrete locations)	Coastal	0–200 m	23 cm	Phyto- and zooplankton (typically larger than sardine prey)	(Miller and Lea, 1972; Mais, 1974)
Pacific hake (<i>Merluccius productus</i>)	Baja California to the Gulf of Alaska	Coastal and oceanic; larger fish further offshore	0–600 m	91 cm	Large zooplankton and small fish	(Alverson and Larkins, 1969; Mais, 1974; Quirolo, 1992)
Pacific herring (<i>Clupea pallasii</i>)	Northern Baja California to Alaska (discrete locations)	Neritic and coastal	0–200 m	46 cm	Zooplankton	(Lassuy ¹)
Pacific mackerel (<i>Scomber japonicus</i>)	Baja California to the Gulf of Alaska	Coastal and oceanic	0–300 m (commonly 0–50 m)	64 cm	Large zooplankton and small fish	(Fitch, 1958; Gluyas-Millán and Quiñonez-Velázquez, 1997)
Pacific sardine (<i>Sardinops sagax</i>)	Gulf of California to the Gulf of Alaska	Coastal and oceanic; larger fish to 300 nmi offshore	0–100 m (commonly 0–50 m)	41 cm	Phytoplankton and zooplankton	(Mais, 1974; Blaxter and Hunter, 1982)
Pacific saury (<i>Cololabis saira</i>)	Central and Northern California	Oceanic	0–250m	36 cm	Zooplankton	(Mais, 1974)

¹ Lassuy, D. R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)—Pacific herring. U.S. Fish. Wildl. Serv. Biol. Rep. 82(11.126), U.S. Army Corps Engineers TR-EL-82-4, 18 p.

Table 2

Species prevalence, the fraction of coastal pelagic fish species (CPS) catches that included the species; the total catch of the species; the fraction of the total CPS catch attributed to the species; and the ranges, means, and standard deviation (SD) values of fork (FL) or standard length (SL) values for the 2008 spring and summer surveys.

Species	Pacific sardine (<i>Sardinops sagax</i>)	Jack mackerel (<i>Trachurus symmetricus</i>)	Pacific mackerel (<i>Scomber japonicus</i>)	Northern anchovy (<i>Engraulis mordax</i>)	Pacific herring (<i>Clupea pallasii</i>)
Spring					
Prevalence (%)	59	23	23	18	9
Total catch (kg)	103.4	61	3	532	6
Catch fraction (%)	15	9	0.4	75	0.9
Length range (cm)	16.3 ≤ SL ≤ 25.9	28.0 ≤ FL ≤ 58.0	27.5 ≤ FL ≤ 34.7	10.7 ≤ SL ≤ 14.8	16.0 ≤ SL ≤ 18.0
Length mean (SD) (cm)	21.2 (1.5)	39.6 (4.7)	31.9 (2.3)	12.5 (0.9)	17.0 (1.4)
Summer					
Prevalence (%)	60	58	38	22	11
Total catch (kg)	2587	507	42	364	82
Catch fraction (%)	72	14	1	10	2
Length range (cm)	8.5 ≤ SL ≤ 25.7	6.0 ≤ FL ≤ 61.0	20.0 ≤ FL ≤ 37.0	8.6 ≤ SL ≤ 16.1	15.0 ≤ SL ≤ 18.0
Length mean (SD) (cm)	20.5 (2.2)	44.4 (8.0)	30.8 (3.5)	12.6 (1.2)	16.8 (0.7)

and non-CPS, with the following empirically derived ranges of S_v differences:

$$\begin{aligned}
 -12 &\leq S_{v18 \text{ kHz}} - S_{v38 \text{ kHz}} \leq 20.5; \\
 -17 &\leq S_{v70 \text{ kHz}} - S_{v38 \text{ kHz}} \leq 10; \\
 -17 &\leq S_{v120 \text{ kHz}} - S_{v38 \text{ kHz}} \leq 14; \text{ and} \\
 -14 &\leq S_{v200 \text{ kHz}} - S_{v38 \text{ kHz}} \leq 5 \text{ dB},
 \end{aligned}$$

and a requirement that the maximum S_v and the VMR at 38 kHz in the 5-m depth by 100-m distance cells exceeded -43 dB and -44.3 dB, respectively. For grid cells that did not meet all these criteria, their corresponding S_v values in the noise-free echograms were set to -999 dB. The resulting "CPS echograms" were given thresholds below $S_v = -60$ dB, which corresponds to a density of approximately 2 fish per 100 m³ in the case of 20-cm SL sardine (~0.1 kg per 20-cm sardine). The s_v values were then integrated within each 5-m depth by 100-m distance cell between an observational range of 10 and 70 m depth, or, if the seabed was shallower, to 3 m above the estimated dead zone (Demer et al., 2009b):

$$s_A = 4\pi(1852)^2 \int_{10}^{70} s_v dz. \quad (1)$$

The resulting s_A values (m² nmi⁻²), attributed to CPS, were then apportioned to the epipelagic-fish species by using trawl data. Because most CPS schools reside at depth during day and ascend to the surface and disperse to feed during night (Mais, 1974; Table 1), only the s_A values from the daytime portions of the surveys, the period between nautical twilights, were used to estimate the distributions and abundances of sardine and other CPS.

Target strength estimation The daytime- s_A values corresponding to CPS (S_{A_CPS}) were apportioned to the j species present by using the catch mixtures (Table 2) in the nearest (space and time) trawl samples (Nakken and Dommasnes²):

$$s_{A_i} = \frac{w_i \times 10^{(\langle TS_i \rangle / 10)}}{\sum_j w_j \times 10^{(\langle TS_j \rangle / 10)}} s_{A_CPS}, \quad (2)$$

where w_i = the proportion of the mass of the catch (kg) for the i -th species; and

$\langle TS_i \rangle$ = its length-weighted mean target strength (TS; dB re 1 m² kg⁻¹).

In other words, each $\langle TS_i \rangle$ is a mean TS weighted by the distribution of total length (TL) values for the sampled fish of that species. The 38 kHz-TS relationships employed were

² Nakken O., and A. Dommasnes. 1975. The application of an echo integration system in investigation of the stock strength of the Barents Sea capelin 1971–1974. ICES Council Meeting (C.M.) 1975/B:25, 20 p.

$$TS = -14.90 \times \log(TL) - 13.21, \text{ for sardine;} \quad (3)$$

$$TS = -12.15 \times \log(TL) - 21.12, \text{ for anchovy; and} \quad (4)$$

$$TS = -15.44 \times \log(TL) - 7.75, \text{ for jack and Pacific mackerel.} \quad (5)$$

where TL is in cm. These relationships were originally estimated for anchovy (*Engraulis capensis*), sardine (*Sardinops ocellatus*=*Sardinops sagax*), and horse mackerel (*Trachurus trachurus*), on the basis of a combination of backscatter-versus-length and mass-versus-length measurements of *in situ* fish (Barange et al., 1996). Because jack mackerel and Pacific mackerel have similar TS values (Peña, 2008), Equation 5 was used for both of these species. TL values of fish are derived from their measured SL or FL values by using linear relationships derived from measurements of CCE specimens: sardine, $TL = 0.3574 + 1.149SL$; anchovy, $TL = 0.2056 + 1.1646SL$; Pacific mackerel, $TL = 0.2994 + 1.092FL$; and jack mackerel $TL = 0.7295 + 1.078FL$.

Biomass and uncertainty estimation The s_A values were converted to fish biomass density for the i species (ρ_i ; kg nmi⁻²) by using the following equation:

$$\rho_i = \frac{s_{A_i}}{4\pi 10^{((TS_i)/10)}}. \quad (6)$$

Total biomass was calculated, by species, for strata having similar biomass densities and transect spacing. The mean biomass density of each stratum was calculated by a transect-length weighted average of the transect mean densities (Jolly and Hampton, 1990).

During the summer 2008 survey, there was evidence of increasing biomass densities toward the coast, suggesting that the mean sardine biomass density calculated for each transect did not account for the biomass in small coastal region between the end of the transects and the coastline. Therefore, a coastal stratum was created, and its mean biomass density was estimated as that measured in the transects from their inshore ends to 10 nmi offshore.

The sampling variances and confidence intervals were estimated by using bootstrapping because it provides better statistical inference than do traditional methods for data with unknown statistical distributions and small sample sizes (Efron, 1981). The 95% confidence intervals for the mean biomass densities were estimated as the 0.025 and 0.975 quantiles of the distribution of 1000 bootstrap survey-mean biomass densities. Coefficient of variation (CV) values were obtained by dividing the bootstrapped standard errors by the bootstrapped arithmetic means (Efron, 1981). Provided that statistical independence exists between the transects, bootstrap resampling of the transect means provides unbiased estimates of the variance for the survey mean, even for several levels of random variability nested (e.g., small-scale spatial sampling correlation or sparse

trawl-derived TS estimation) at the intra-transect level (Williams, 2000).

To evaluate the proportion of the sampling variance pertaining to species classification and TS estimation, the trawl samples with CPS were subjected to jackknife resampling. The jackknife procedure was performed by omitting one trawl sample per iteration. The variance was estimated by calculating the variance of the jackknife means, corrected by the number of trawls in each stratum as per Efron and Tibshirani (1993). Each time a trawl was removed from the set, the biomass densities of each target species in 100-m distance cells were recalculated, taking into consideration the new nearest-neighbor configuration (Fig. 2).

Results

During both the spring and summer surveys, the distributions of echosounder- and trawl-sampled CPS were reasonably well matched (Fig. 2). Also, sardine were the most common species, in terms of their occurrences in catches with CPS (Table 2). Excluding two large catches of anchovy, sardine were also the most abundant species in terms of total-catch mass. The next most abundant species in both surveys was jack mackerel. Anchovy and Pacific mackerel were caught in roughly the same proportions. The species-apportioned biomass densities (Fig. 3) reflect the distributions of sardine, and jack and Pacific mackerel in the trawl catches (Fig. 2). Too few trawl catches included anchovy and herring to allow evaluation of their distributions and abundances.

During the spring survey, most of the sardine biomass was located off southern California (Fig. 3). The total biomass of sardine from San Diego to the Strait of Juan de Fuca, 0.751 Mt with a CV of 9.2%, compared to 0.778 Mt from the 2010 assessment (Hill et al., 2010), was estimated by summing the biomasses within each stratum (Fig. 3). The stock of jack mackerel was estimated to be 0.147 Mt with a CV of 28.4%. The stock of Pacific mackerel was estimated to be 0.018 Mt with a CV of 51.8%, compared to 0.275 Mt from the 2009 assessment (Crone et al., 2009).

During the summer survey, most of the sardine biomass was located in the northern portion of the study area, off Oregon and Washington, whereas jack mackerel biomass was found mainly off central California. The biomass of Pacific mackerel was more scattered than sardine and jack mackerel (Fig. 3). The total biomass of sardine from San Diego to the Strait of Juan de Fuca, 0.801 Mt with a CV of 30.9%, compared to 0.778 Mt from the 2010 assessment (Hill et al., 2010), was estimated by summing the biomasses within each stratum (Fig. 3). The stock of jack mackerel was estimated to be 0.448 Mt with a CV of 33.9%. The stock of Pacific mackerel was estimated to be 0.055 Mt with a CV of 38.9%, compared to 0.275 Mt estimated from an assessment of the entire stock extending south to Cabo San Lucas, Mexico (Crone et al., 2009).

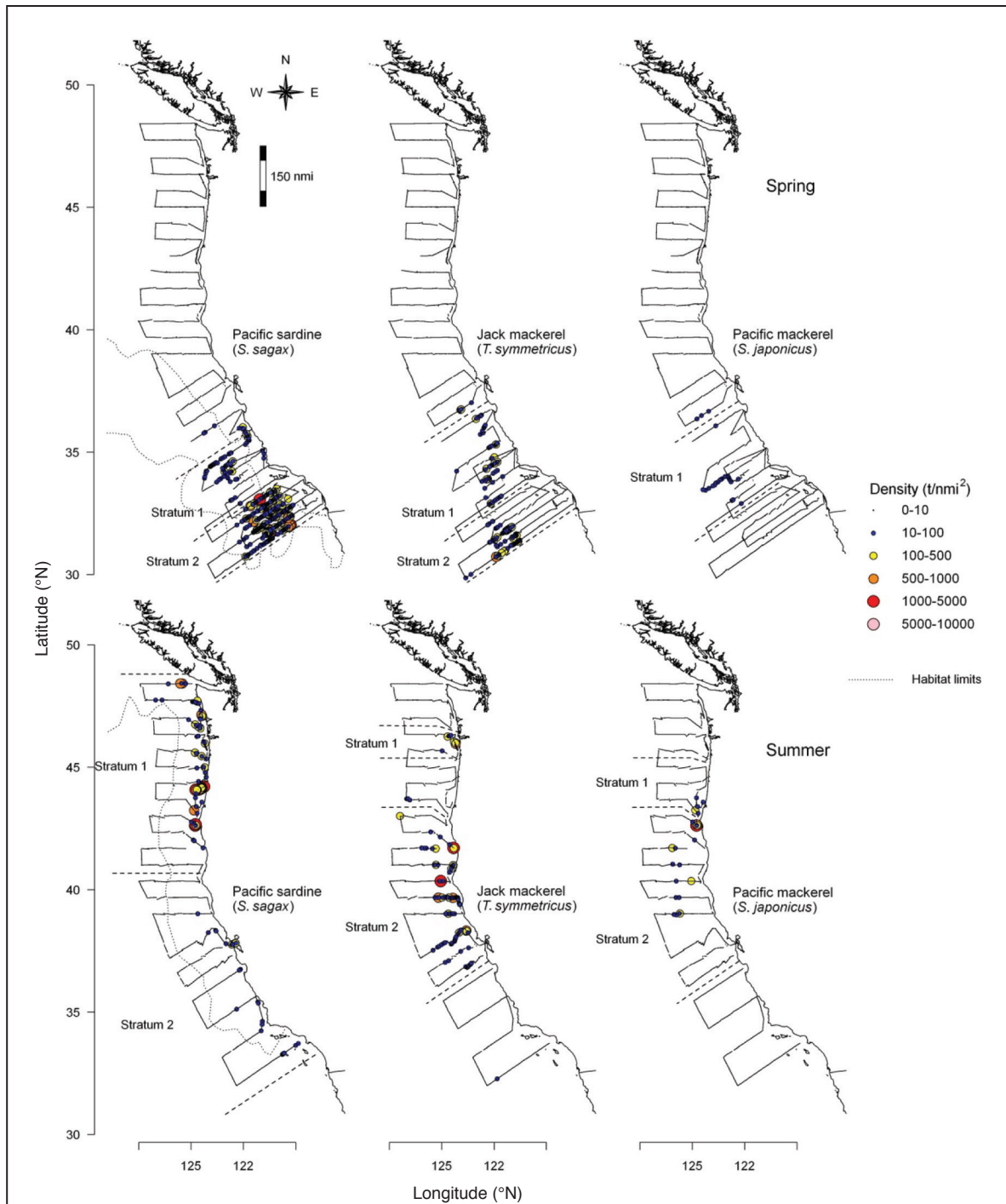


Figure 3

Spatial distribution of biomass densities estimated for Pacific sardine (*Sardinops sagax*) [left], jack mackerel (*Trachurus symmetricus*) [middle], and Pacific mackerel (*Scomber japonicus*) [right] for the 2008 spring (top) and summer (bottom) surveys. The estimates are based on the acoustic volume backscattering coefficients (s_v ; $m^2 m^{-3}$) integrated from 10–70 m depth; the acoustic composition of the nearest trawl; and the average target strength of each species. Strata (dashed lines) were created after each cruise. The predicted “optimal” plus “good” sardine habitat (Zwolinski et al., 2011) is circumscribed (left plots, dotted lines). Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), and other coastal pelagic fish species are not included owing to their low biomasses and the high sampling uncertainties for these species.

Table 3

Estimates of biomass in million metric tons (Mt) of Pacific sardine (*Sardinops sagax*), Jack mackerel (*Trachurus symmetricus*), and Pacific mackerel (*Scomber japonicus*) in the California Current Ecosystem during the 2008 spring and summer surveys, their coefficients of variation (CV) values (%), and 95% confidence interval (CI₉₅) values (Mt). Catches of other coastal pelagic fish species were too few to enable estimations of their biomasses. The total biomass values are apportioned to strata with areas (nmi²) defined in Figure 3. For the summer survey, the coastal stratum accounts for extrapolated sardine biomass in the unsampled nearshore region. Where the trawl CV is larger than the total CV, there were too few trawls to classify species and estimate target strength independently between transects. In those cases, the total CV values probably under-estimate the total random sampling error.

Season	Stratum	Area (nmi ²)	Trawls	Biomass (Mt)	Trawl CV (%)	Total CV (%)	CI ₉₅ (Mt)
<i>Pacific sardine (Sardinops sagax)</i>							
Spring	1	11,469	7	0.047	59.2	45.8	0.017–0.104
	2	22,771	7	0.704	33.2	9.3	0.579–0.823
	sum	34,240	14	0.751	31.4	9.2	0.611–0.870
	coast	2848	0	0.169	29.7	43.6	0.042–0.325
	1	25,971	29	0.573	22.7	31.3	0.266–0.952
	2	45,477	13	0.059	82.0	81.9	0.003–0.165
Summer	sum	74,296	42	0.801	18.9	30.9	0.371–1.299
<i>Jack mackerel (Trachurus symmetricus)</i>							
Spring	1	19,524	8	0.078	30.5	32.1	0.032–0.129
	2	22,771	7	0.069	139.6	47.5	0.019–0.140
	sum	42,295	15	0.147	67.6	28.4	0.075–0.232
Summer	1	9823	6	0.027	83.4	31.9	0.014–0.037
	2	78,532	26	0.421	13.9	36.0	0.136–0.724
	sum	88,355	32	0.448	14.0	33.9	0.159–0.749
<i>Pacific mackerel (Scomber japonicus)</i>							
Spring	1	19,524	8	0.014	88.7	51.8	0.005–0.037
Summer	1	49,453	22	0.055	129.1	38.3	0.019–0.103

Because the estimated sardine biomasses from the two surveys were not significantly different (Table 3), most or all of the stock appears to have migrated from the south and offshore in the spring to the north and inshore in the summer (Fig. 3). Of course, there is the possibility that nearly identical proportions of the stock could have been missed during the two surveys, e.g., not sampled off Mexico during the spring survey, and off Canada during the summer survey, or they resided too deep or offshore or both during spring and too shallow or inshore or both during summer.

The distributions of jack and Pacific mackerel also suggest seasonal migrations toward the north during the summer. However, relative to sardine, jack mackerel were located closer to shore in the spring and farther offshore in the summer (Fig. 3). Also, landings data (Crone et al., 2009) provide evidence that Pacific mackerel were distributed well beyond the sampling area, and most of their biomass was located to the south. Jack mackerel is not the target of a fishery; therefore no assessment or other form of abundance estimation is available for comparison.

The biomass densities of each evaluated species (Table 4) were not statistically correlated for any relevant lag (intertransect distance) in any of the defined strata,

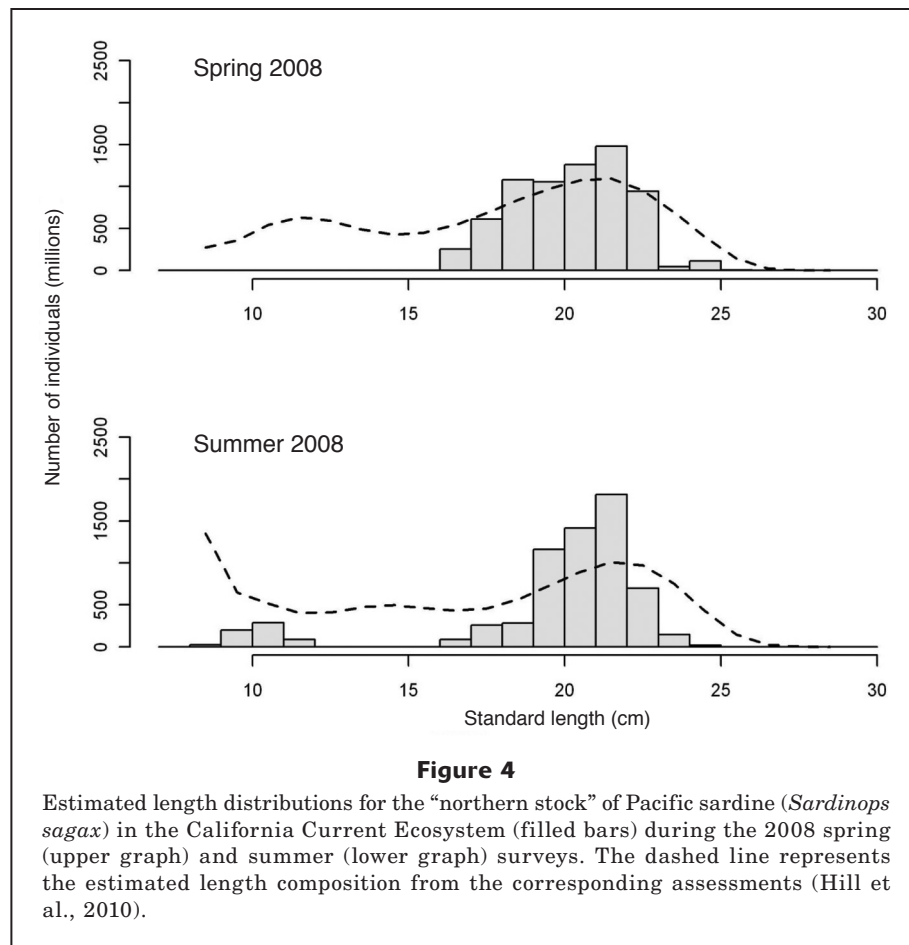
thereby enabling the bootstrap procedure to estimate the random sampling error. Thus, the CV values reflect the combined random sampling error of the echosounder and trawl sampling. For sardine and jack mackerel, these values may be sufficiently small to allow the results to be used in assessments, and their populations were apparently sampled in entirety. The much larger CV values for Pacific mackerel were the result of a lower biomass, patchy distribution, and too few trawl catches (Table 3).

The length distributions of sardine sampled during the 2008 spring (mean SL=21.2; standard deviation [SD]=1.5 cm) and summer (mean SL=20.5; SD=2.2 cm) had very similar modes which matched the major TL mode (Table 2, Fig. 4) in the assessment model (Hill et al., 2010). The major mode in the SL values was slightly larger in the summer versus spring survey data, as might be expected from growth. The secondary mode in the summer survey data is the result of one catch of small sardine off Monterey Bay. Because additional trawls were not conducted off central and southern California due to problems with the RV *David Starr Jordan*, the small acoustically-mapped CPS biomass in the central and southern California regions (Fig. 2) were ascribed to these sardine (Fig. 3).

Table 4

Mean daytime biomass density (kg nmi⁻²) and transect length (km) for each transect used to estimate the mean biomass densities and variances of fish for each stratum and survey. The respective stratum areas are defined in Table 3.

Survey	Stratum	Sardine (<i>Sardinops sagax</i>)		Jack mackerel (<i>Trachurus symmetricus</i>)		Pacific mackerel (<i>Scomber japonicus</i>)	
		Mean density	Length	Mean density	Length	Mean density	Length
Spring 2008	1	2911.2	162.2	3855.7	128.6	288.0	128.6
		14,315.0	37.3	843.9	71.7	0	71.7
		18,371.2	73.5	5090.5	162.2	214.3	162.2
		2097.2	68.4	0	37.3	0	37.3
		86.0	127.9	5583.7	72.8	754.8	72.8
		2782.1	87.5	7291.0	68.4	1669.3	68.4
		1520.6	186.6	692.1	196.9	47.0	196.9
		—	—	2311.8	87.5	3510.1	87.5
	2	—	—	7572.2	186.6	807.8	186.6
		42,629.8	184.4	1.0	184.4	—	—
		21,369.0	306.1	1563.4	306.1	—	—
		23,365.2	289.8	1119.3	289.8	—	—
		30,472.1	270.6	3943.9	270.6	—	—
		37,045.3	367.9	785.5	367.9	—	—
		33,815.6	286.9	10,408.3	286.9	—	—
		—	—	—	—	—	—
Summer 2008	Coastal	194,144.9	19.1	—	—	—	—
		26.0	27.7	—	—	—	—
		47,810.3	27.0	—	—	—	—
		429.3	20.9	—	—	—	—
		190.9	22.9	—	—	—	—
		5514.3	20.4	—	—	—	—
		3399.4	26.1	—	—	—	—
		64,819.1	30.0	—	—	—	—
		232,487.8	24.0	—	—	—	—
		31,404.8	26.7	—	—	—	—
		17.7	21.5	—	—	—	—
	1	76,099.4	57.1	3814.7	183.2	2277.4	175.7
		401.0	32.2	1430.7	136.3	19.9	168.5
		31,959.5	107.1	—	—	3192.2	190.8
		4689.2	51.2	—	—	2783.3	162.3
		23,070.9	82.9	—	—	0	251.5
		2684.6	76.6	—	—	1600.7	231.3
		1973.8	81.8	—	—	19.0	235.6
		20,620.5	112.9	—	—	71.4	238.1
		65,051.0	104.7	—	—	—	—
		12692.6	116.3	—	—	—	—
		8850.0	20.5	—	—	—	—
		43.4	112.1	—	—	—	—
	2	440.1	178.5	708.1	168.5	—	—
		27.6	144.8	96.9	190.8	—	—
		5.8	88.1	1835.5	162.3	—	—
		31.7	155.6	2553.8	251.5	—	—
		212.6	161.1	12,713.7	231.3	—	—
		35.6	80.6	21,192.0	235.6	—	—
		8742.8	122.8	8583.3	238.1	—	—
		—	—	4944.7	274.4	—	—
		—	—	1262.4	191.4	—	—
		—	—	457.4	249.3	—	—
		—	—	31.3	189.5	—	—



Discussion

Target detection

The depth range of the echosounder sampling for CPS (10–70 m) encompassed the daytime vertical extent of the CPS in the CCE, particularly for sardine, jack mackerel, and Pacific mackerel (Squire, 1972; Hill et al., 2010) and it was shallow enough to exclude the majority of hake (Dorn et al., 1994) and rockfishes (Butler et al., 2003). Most of the CPS backscatter sampled during these surveys (not shown) occurred in the upper 40 m, deeper during the day and rising near the sea surface at night—a finding that is consistent with early sonar observations of CPS in the Southern California Bight (Holliday and Larsen, 1979). Therefore, it is likely that the stocks of sardine, jack mackerel, and Pacific mackerel were effectively sampled at depths shallower than 70 m.

Fish may react to an approaching vessel (Ona et al., 2007), or not (Fernandes et al., 2000), and they may react more to larger “quiet” vessels (Ona et al., 2007), although not always (De Robertis et al., 2010). In other words, fish behavior in response to research vessels is poorly understood, and it likely varies among species and with many other factors (Vabø et al., 2002), such as

ontogeny, time of day, season, region, depth, sampling platform, and stimuli. In the CCE, a significant proportion of CPS schools reside near the sea surface (Mais, 1974; Holliday and Larsen, 1979). However, although schools of epipelagic fish may dive in response to a survey vessel, perhaps altering their TS and inducing some measurement error (Holliday and Larsen, 1979; Vabø et al., 2002; Patel and Ona, 2009), this behavior may position them deeper and allow their detection with down-looking echosounders. For example, schools of Spanish sardine (*Sardinella aurita*) located in the path of the vessel, initially in the upper 20 m, invariably descended a few meters before the passage of the survey vessel; the effect diminished with school depth, and the lateral movements were negligible (Gerlotto and Fréon, 1992). If this behavior is consistent for CPS in the CCE surveyed with down-looking echosounders from NOAA ships, the sampling bias due to this factor may be negligible.

To investigate this hypothesis, measurements were made of CPS schools during a 2006 survey of CPS by using a side-looking multibeam echosounder, pole-mounted on the RV *David Starr Jordan* (Cutter Jr. and Demer, 2008). Results supported earlier observations that near-surface fish dove beneath the vessel, well in

advance of its arrival (Ona et al., 2007). Also, the spatial distributions of acoustically detected CPS matched well those of the trawl catches in areas of high biomass. Furthermore, despite the sardine residing offshore during spring and shallower near the coast in the summer, the two 2008 acoustic-trawl survey estimates of sardine biomass were not statistically different from each other or from the assessment estimates. In other words, if sardine avoid a vessel significantly, it is likely that the associated bias would increase when the fish naturally reside in shallower water; however, there is no evidence of this effect.

Species identification and TS estimation

The echo energy was apportioned to species by using a numerical algorithm that incorporates the following assumptions: 1) echoes from fish schooling in the upper 70 m during the day can be identified as CPS by their backscattering spectra; 2) a representative portion of those CPS are sampled with the surface trawl at night; and 3) the TS-weighted proportions of the various CPS in the catches can be used to apportion the nearby CPS echoes to species. Because the distributions of the CPS echoes matched those of the CPS caught in the trawl, these assumptions appear to be valid. Where CPS were acoustically mapped, they were caught in the trawls; where CPS were not acoustically observed, they were absent from the catches (Fig. 2), in general. Furthermore, the distributions of catches showed some degree of segregation among the various species, which supports the method of ascribing CPS backscatter to species based on their proportions in the nearest catches.

Fish behaviour can affect trawl sampling. If certain species or sizes avoid capture, “net selectivity” causes a variable sampling bias. With the acoustic-trawl method, it is currently assumed that the net sampling is unbiased and therefore the proportions of CPS in the catch, and their length distributions, are representative of their respective stocks. However, there may be some net selectivity which will affect the species identifications and TS estimations, and cause variable sampling biases in the biomass estimates.

In the absence of TS models for the target species in the populations and conditions under study, the biomass estimates were computed by using TS-to-biomass relationships derived for related species in similar systems (Barange et al., 1996). The TS of fish with swim bladders are intrinsically variable, depending mainly on the acoustic frequency and the swim bladder size and orientation relative to the incident sound wave (Foote, 1980). The swim bladder size and orientation are related to fish anatomy, physiology, behavior, and ontogeny (Ona, 1990). Consequently, the TS-to-biomass relationships should ultimately be derived from measurements of target fish in the conditions under which they are sampled (Fässler et al., 2008). Future studies should evaluate uncertainty in the TS models; and new functions should be tailored for the populations in the CCE, accounting for acoustic frequency, fish length and

depth, and season. For example, high-resolution images from X-rays (e.g., Conti and Demer, 2003; Renfree et al., 2009) or magnetic resonance (e.g., Peña and Foote, 2008) can be used to parameterize scattering models and better predict TS as a function of acoustic frequency, and fish morphometrics, depth, and orientation (e.g., Horne, 2003; Cutter Jr. and Demer, 2007; Cutter Jr. et al., 2009). The frequency response of single- and mixed-species aggregations can then be simulated by summing the responses of fish varying in number, depth, and orientation.

Seasonal migration

Sardine were distributed in the south and offshore of southern and central California in the spring and were compressed along the coast, mainly from northern California to Washington, in the summer (Fig. 3). These findings are consistent with the predictions of seasonal changes in potential sardine habitat in the CCE (Fig. 1; Zwolinski et al., 2011). Small discrepancies, particularly in the dynamic nearshore upwelling areas, can be attributed to the density-dependent nature of sardine habitat use and temporal mismatches between the oceanographic conditions during the shipboard sampling and the multiweek averages used to map the habitat.

The potential sardine habitat annually oscillates between north and south as a consequence of seasonal oceanographic changes. On the basis of the similarities of the spring and summer estimates of sardine biomass, seasonal migration appears to have involved the entire population. During the summer, few sardine were mapped off central and southern California, south of 40°N (Fig. 3), suggesting that the inflow of individuals from the southern stock (Félix-Uraga et al., 2005) was negligible in summer 2008, most likely because the CCE was colder than average owing to La Niña conditions (McClatchie et al., 2009).

Jack mackerel also appear to be affected by the same mesoscale forcing to which sardine are subject. They are recurrently mapped in the warmer margins of the potential sardine habitat (Fig. 3). However, the northward migration of jack mackerel during the summer was not as marked as that of sardine. Pacific mackerel were scattered in offshore and coastal waters—usually among the more abundant jack mackerel and sardine, probably schooling with them.

In contrast to the predicted and observed migrations described above, northern anchovy exhibit a stronger geographic fidelity and were found in expected discrete locations in the southern California Bight (Smith and Hewitt, 1985), and off Oregon and Washington (Laroche and Richardson, 1980).

Future surveys

Although the acoustic-trawl method can be further refined, the results appear to be precise and accurate. The CV values are low, and the spring and summer

estimates of sardine biomass are not significantly different from each other or from the assessment-model estimates. Also, the spring and summer estimates of sardine distribution agree with the model predictions of potential sardine habitat (Fig. 3).

To further minimize the random sampling error in these surveys, sampling effort could be increased, or modeled predictions of potential sardine habitat could be used to optimally plan both DEPM and acoustic-trawl surveys, and thus save valuable time to increase sampling effort in areas of expected sardine presence. These strategies could potentially lower the variance and increase the accuracy of the estimates, or allow better sampling of the distribution of the less abundant species, such as anchovy and Pacific mackerel. Furthermore, as indicated by the CV values (Table 3), the sampling variance could be improved with more trawl sampling in the areas with higher acoustically observed fish densities (Petitgas et al., 2003).

Zwolinski et al. (2011) include a quantitative analysis of the potential benefits (i.e., reduced effort or decreased estimation variance) of using model predictions of potential sardine habitat to optimize sampling. In this study, the model from Zwolinski et al. (2011) indicated that the potential sardine habitat during spring 2008 was in a region offshore of southern California; and during summer of the same year, it was confined close to the coast and extended north to Canada. During both seasons, virtually all of the sardine biomass estimated by the acoustic-trawl method was inside the “optimal” and “good” habitat. Furthermore, the tiny fractions that were mapped outside of the potential sardine habitat, to the north in spring and to the south in summer, may not have been sardine because the closest trawl catches with sardine were at least one hundred miles away.

The results of the acoustic-trawl surveys conducted during these two seasons clearly show that the sardine were in these predicted habitat regions and therefore migrated north between spring and summer. Therefore, the benefits described in Zwolinski et al. (2011) should be attainable for sardine sampling, irrespective of the survey method. If this had been a single-species survey, about half of the transects (i.e., north of 38°N) could have been reallocated in the spring survey. In summer, about one-third of the offshore sampling could have been reallocated. Without making many assumptions (i.e., where daytime transects might have been reallocated and what the sardine densities may have been in those locations), it is not possible to quantify the likely reduction in sampling variance when the predicted sardine habitat is used to optimize sampling.

When acoustic-trawl surveys of Pacific sardine are performed during spring, the sampling should extend to the southern limit of the potential sardine habitat, perhaps south of the U.S.-Mexican border (Félix-Uraga et al., 2004). When acoustic-trawl surveys of Pacific sardine are performed during summer, attention should be paid to the northern limit of the potential sardine habitat, perhaps north of the U.S.-Canadian border

(Ware, 1999). Also, because sardine reside closer to the shore during summer, the eastern ends of the transects should be extended as close to shore as practical.

Sampling optimization can involve considerations of many resource factors and scientific objectives, e.g., availability of ship time and single-species assessments versus ecosystem-based assessments of multiple species. Nevertheless, optimization of surveys of single or multiple species, or ecosystems will benefit from *a priori* characterization of the probable population boundaries. Unless a survey region is defined as larger than any possible extent of the target population(s), which may be cost prohibitive or increase sampling variance, predictions of the population habitat(s) can be useful for optimally applying survey resources. On the other hand, if the survey region is defined somewhat arbitrarily and held constant, the proportion of the target stock(s) residing inside the survey area may vary between surveys, causing insidious variable bias(es). Although the accuracy of the habitat-model predictions may vary over time, they can be re-evaluated with the results from each survey, e.g., by quantifying the proportion of the target-species biomass residing near the edges of the modeled habitat.

Conclusion

Acoustic-trawl surveys can provide high-resolution, accurate and precise information about the biomasses, and geographic and vertical distributions of multiple species and trophic levels. Acoustic-trawl methods can be employed concurrently with other survey methods, perhaps enabling investigations of animal interactions with each other and their environments.

The principal challenges of acoustic-trawl surveys of sardine are to estimate and survey the potential sardine habitat (habitat estimation); to identify the contribution of sardine backscatter to the total acoustic backscatter (species identification); and to estimate the mean acoustic backscatter per average-individual sardine (TS estimation). Reduced uncertainty in the survey results will likely result from a more optimal allocation of sampling effort in space and time, increased net sampling, and refinements to acoustic-target identification and TS estimation.

Observed variations in time series of estimated abundance and distribution can result from population dynamics or from random and temporally and spatially varying systematic errors. Therefore, to optimally apply survey effort and minimize both random and systematic errors in survey results, it is important to identify *a priori* the area likely to contain the stock, the potential sardine habitat, and allocate the available sampling effort to the area. This study shows that the model by Zwolinski et al. (2011) can be used for this purpose. Generally, the model indicates that spring surveys of the northern stock of sardine may be focused offshore of central and southern California and perhaps northern Baja California, and summer surveys may be focused

nearshore, off northern California, Oregon, Washington, and perhaps Vancouver Island.

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Appendix

The following is a primer on Pacific sardine in the California Current Ecosystem (CCE), relevant to acoustic-trawl surveys.

Distribution

There are two sardine stocks in the CCE, a “northern” and “southern” stock, distinguishable with the use of serological techniques (Vrooman, 1964), water temperature (Félix-Uraga et al., 2004; 2005), population dynamics, and spawning grounds (Smith, 2005). These two stocks do not overlap substantially and are managed separately. The northern stock is the principal target of U.S. and Canadian fisheries and is therefore the focus of the U.S. stock assessment and the surveys described here.

During late winter through early spring, the northern stock aggregates to spawn in the coastal region between Ensenada, Baja California, and San Francisco, California (Smith, 2005)—typically off the continental shelf where micro- and mesozooplankton abundance are at maximum abundance (Lynn, 2003). During late spring and summer, the stock migrates north to the coastal feeding grounds, older fish migrate farther north (Emmett et al., 2005), and returns south offshore in the late fall (Zwolinski et al., 2011). Age-one sardine may not migrate and instead reside year-round in coastal waters where they were recruited (Emmett et al., 2005).

As in other eastern-boundary currents (Barange et al., 2009), sardine in the CCE are highly mobile and adapted to the large ranges of temperatures and salinities associated with variable coastal upwelling. They are most prominent in the neritic and coastal regions, but seasonally exhibit excursions to 300 nmi offshore (Macewicz and Abramenkoff³). Larger sardine tend to reside farther offshore. Sardine and other clupeoids re-

spond to oceanographic conditions, and, in the absence of predators and competitors, tend to aggregate near their prey in monospecific, epipelagic (ca. 0–70 m depth) schools (Robinson et al., 1995), comprising similar-size fish. Nevertheless, mixed-species schools are not uncommon (Fréon and Misund, 1999; Gerlotto, 1993).

Feeding

Sardine can filter-feed on phytoplankton and small zooplankton (van der Lingen, 1994) ranging in size from tens of μm (Garrido et al., 2007) to a few mm (Emmett et al., 2005). Although lacking teeth, they can also particulate-feed on larger prey, depending on their densities and types (Garrido et al., 2007; van der Lingen, 1994). However, because their gill rakers are not completely developed until they reach total lengths of approximately 100 mm (Scofield, 1932), small and large sardine generally feed on different prey.

Spawning

Sardine, like most CPS, are batch spawners and their eggs are fertilized in the water column (Blaxter and Hunter, 1982). Their fecundity is high, e.g., they spawn more than 300 eggs per gram of female mass (Lo et al., 2009), and each individual produces several egg batches throughout a usually extensive spawning season.

Sardine spawning appears to coincide with times and locations with low upwelling, and associated seawater temperatures ranging from 13.5° to 16.5 °C (Zwolinski et al., 2011). These areas and conditions provide adequate food supplies for adult sardine (Aceves-Medina et al., 2009) and their larvae (Lynn, 2003) and are conducive to nearshore retention of their eggs and larvae (Parrish et al., 1981). The peak spawning occurs in spring, April and May, off southern California, but can occur from January until August, and in higher water temperatures. The extent of the spawning season appears to be related to the food available to the adults, both before and during the spawning season (Somarakis et al., 2006; Aceves-Medina et al., 2009).

Sardine spawning aggregations persist for a few hours and comprise actively spawning females and a larger proportion of actively spawning males in advanced spawning conditions (Zwolinski et al., 2006; Ganas, 2008). Sardine eggs are positively buoyant and planktonic, but can take several hours to ascend to near the sea-surface. Sardine eggs hatch within 2–5 days, depending on the seawater temperature (Lo et al., 1986), and the larvae become juvenile sardine within two to three months (Lo et al., 1995).

The success of a reproductive season appears to be related to the joint contribution of three physical processes: enrichment, concentration, and retention (Bakun, 1996). Enrichment refers to high primary productivity. Concentration of these phytoplankton and microzooplankton allows efficient consumption by the larvae. Retention by eddies and low currents keeps

³ Macewicz, B. J., and D. N. Abramenkoff. 1993. Collection of jack mackerel, *Trachurus symmetricus*, off southern California during 1991 cooperative U.S.-U.S.S.R. cruise. SWFSC-NMFS Admin Rep. LJ 93-07, La Jolla, CA, 13 p.

the larvae from being advected to open ocean where the food supply, and thus the probability of surviving, is low. Intense upwelling, although nurturing primary productivity, can result in suboptimal feeding conditions (Uehara et al., 2005). A moderately stable water column is thus needed for concentration of the food and successful development of larvae (Lasker, 1981). Sardine recruitment improves during warm periods, characterized by an expansion of their habitat (; Lluch-Belda et al., 1991; Jacobson et al.¹), low-intensity coastal upwelling, and increased wind-stress-curl upwelling (Rykaczewski and Checkley, 2008).

Sizes

Sardine exhibit rapid growth and early maturation (Blaxter and Hunter, 1982), becoming mature during their first or second year of life. Increased length at

maturity is associated with lower water temperature and higher latitude and population size. Sardine grow to standard lengths of 41 cm (Miller and Lea, 1972) and normally live for as many as 8 years (Butler et al., 1996).

Physiology

Sardine and anchovy are physostomous, possessing a swim bladder with a pneumatic duct to the stomach and an anal duct to the cloaca (Whitehead and Blaxter, 1989). Like other clupeoids, sardine inflate their swim bladders by swallowing air at the surface and by forcing it from the stomach through the pneumatic duct into the swim bladder. These swim bladder features allow them to perform rapid vertical migrations, typically to the sea-surface to feed at night (Cutter Jr. and Demer, 2008), and predominantly contribute to their high acoustic backscatter (Foote, 1980).